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Evolution, Vol. 49, No. 4 (Aug., 1995), 770-775.

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MAGPIE HOST MANIPULATION BY GREAT SPOTTED CUCKOOS: EVIDENCE FOR AN AVIAN MAFIA?

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Abstract.—Why should the hosts of brood parasites accept and raise parasitic offspring that differ dramatically in appearance from their own? There are two solutions to this evolutionary enigma. (1) Hosts may not yet have evolved the capability to discriminate against the parasite, or (2) parasite-host systems have reached an evolutionary equilibrium. Avian brood parasites may either gain re-nesting opportunities or force their hosts to raise parasitic offspring by destroying or preying upon host eggs or nestlings following host ejection of parasite offspring. These hypotheses may explain why hosts do not remove parasite offspring because only then will hosts avoid clutch destruction by the cuckoo. Here we show experimentally that if the egg of the parasitic great spotted cuckoo *Clamator glandarius* is removed from nests of its magpie *Pica pica* host, nests suffer significantly higher predation rates than control nests in which parasite eggs have not been removed. Using plasticine model eggs resembling those of magpies and observations of parasites, we also confirm that great spotted cuckoos that have laid an ejected egg are indeed responsible for destruction of magpie nests with experimentally ejected parasite eggs. Cuckoos benefit from destroying host offspring because they thereby induce some magpies to re-nest and subsequently accept a cuckoo egg.

Key words.—Brood parasitism, *Clamator glandarius*, coevolution, evolutionary equilibrium hypothesis, evolutionary-lag hypothesis, Mafia hypothesis, *Pica pica*.

Received March 30, 1993. Accepted June 21, 1994.

Parasite manipulation of host behavior is a common way of increasing parasite fitness in many kinds of host-parasite systems (Holmes and Bethel 1972; Ewald 1980). Manipulation of hosts by brood parasites also appears relatively common (reviews in Payne 1977; Rothstein 1990). Host acceptance of the offspring of brood parasites is at first glance maladaptive, because parasitism reduces host reproductive success (Rothstein 1990). Because nestlings of most avian brood parasites are dramatically different in appearance from those of their hosts (Rothstein 1990), it is an evolutionary enigma why hosts accept and care for such manifestly deviant juveniles.

Several solutions to this problem have been proposed. First, the hosts of brood parasites may not yet have evolved the capability of correct discrimination against the parasite, the evolutionary-lag hypothesis (Brooke and Davies 1988; Rothstein 1990). Second, the host-parasite relationship may evolve toward an evolutionary equilibrium in which parasites are accepted by hosts. Such an equilibrium may result from several behavioral mechanisms: (1) recognition and/or ejection costs incurred by the host removing eggs may be sufficient to allow parasitism to occur (Marchetti 1992); (2) if hosts need to learn or distinguish any egg or offspring types, brood parasites may exploit those hosts that have not yet learned to discriminate between their own eggs (e.g., young individuals) and those of the parasite (Lotem et al. 1992); or (3) the predatory habits of a brood parasite may ultimately result in very low reproductive success for discriminating hosts and therefore prevent the evolution of discrimination in the host population (Zahavi 1979).

An elaboration of this hypothesis highlights the potential for host manipulation by adult parasite behavior. There are two explanations for destruction of host offspring by parasites. The simplest explanation is that, if the host clutch is

destroyed following ejection of the parasite offspring from the host nest, the host may lay a second clutch that can be exploited by the parasite. The parasite can induce this behavior by depredating the host clutch. In turn, such a response dilutes the value of ejection for the host. Alternatively, host-offspring destruction can be viewed as retaliation, the threat of which modulates the host behavior in the first place. In effect, the parasite is like the Mafia, enforcing compliance with situations maladaptive for the host by imposing heavy costs if there is no compliance. For this enforcement hypothesis to work, parasitic cuckoos must revisit parasitized nests and, if they find that their offspring are not in the nest, destroy or prey upon host eggs or nestlings. This “Mafia” hypothesis may explain why hosts, which rear their own offspring together with those of the parasite, do not always eject parasite nestlings, because parasite-nestling ejection would result in host reproductive success higher than that following ejection or abandonment of a parasite egg. These two hypotheses are not mutually exclusive because the laying of a second clutch as a result of nest predation may initially increase the frequency of host acceptance of parasitic offspring. Once depredation is present in the parasite, the host can respond over behavioral time by learning, or over evolutionary time through selection, by reducing its tendency to eject parasite eggs. This indirectly enhances selective pressures favoring aggressive parasite behavior that may result in positive feedback between Mafia-like parasite and compliant host behaviors. Here we present the first experimental test of components of this Mafia hypothesis.

The great spotted cuckoo *Clamator glandarius* is an obligate brood parasite that in Europe mainly parasitizes the magpie *Pica pica* (Cramp 1985). As a rule, the great spotted cuckoo's egg hatches several days before magpie host eggs. The parasite chick does not eject host eggs or nestlings

(Cramp 1985), but host reproductive success is reduced by intense competition for food between the large, fast-growing cuckoo young and the smaller magpie nestlings (Cramp 1985; Soler 1990; Soler and Soler 1991). Data reported here suggest that the great spotted cuckoo repeatedly visits nests it has parasitized, a precondition for the Mafia hypothesis.

The Mafia hypothesis predicts that a great spotted cuckoo, after discovering that a parasitized nest no longer contains its egg or nestling, will depredate the host nest. The hypothesis also predicts that this behavior causes hosts to benefit from accepting parasite eggs, because a host that accepts a parasite egg will raise more of its own offspring than a host that ejects the cuckoo egg (and thereby loses its own clutch later). The work reported here tests these predictions.

MATERIALS AND METHODS

Study Area

We studied magpie-cuckoo interactions from April to July, 1990–1992, in study plots in the high-altitude plateau Hoya de Guadix (37°18'N, 3°11'W), Spain, approximately 1000 m in elevation. This area has recently been colonized by the great spotted cuckoo, as evidenced by a recent dramatic increase in the incidence of ejection of cuckoo eggs by the magpie host (Soler 1990; Soler and Møller 1990; Soler et al. 1994). A detailed description of the study site and the incidence of great spotted cuckoo parasitism of its magpie host appears elsewhere (Soler 1990).

General Field Procedures

We examined the effects of natural removal of cuckoo eggs on reproductive success of magpie hosts. Parasitized magpie nests were located during 1991 and 1992. A nest was defined as "parasitized" if it contained great spotted cuckoo eggs. The response of magpies to parasitized nests was classified as (1) acceptance (the cuckoo egg remained in the nest between consecutive nest visits), (2) ejection (the cuckoo egg disappeared between two nest visits), or (3) abandonment (the nest was found containing cold eggs). The fate of magpie nests was classified as depredated if nest contents disappeared between consecutive nest visits.

Magpies defend large, all-purpose territories up to several hectares in size containing food and nest sites (Birkhead 1991). Nests were usually built near territory centers. Magpie clutches were considered replacement clutches if a new nest was constructed following failure of a previous nest in any given season. The distance between the first nest and a replacement nest was usually less than 100 m, considerably less than the distance to the territory boundary. Studies of color-banded magpies in the Guadix and other populations demonstrate that replacement nests are built in the territory near the previous nest (Birkhead 1991; D. Parrott pers. comm. 1993).

Magpie reproductive success was estimated as the number of nestlings present during the last visit to a nest, just before the presumed date of fledging. Annual reproductive success of magpie pairs was the total number of fledglings produced in first and replacement clutches.

Experimental Procedures

Parasitized magpie nests found during the egg-laying stage in 1990–1992 were used to test predictions of the Mafia hypothesis. Nests were randomly assigned to two groups: (1) experimental nests ($N = 29$), from which the cuckoo egg was artificially removed 0–3 d after laying; and (2) control nests ($N = 28$), visited in the same manner as experimental nests. The magpie nests were matched with respect to laying date and study plot following the random assignment of nests to treatments.

All experimental and control nests were revisited every 3 d, and the fate of the clutch recorded, as follows: (1) completely destroyed (all eggs or nestlings missing), (2) completely destroyed by carrion crows *Corvus corone* (the nest lining was torn out in a characteristic fashion), or (3) partially destroyed (some of the eggs or nestlings were missing).

Statistical Procedures

Differences in predation rate between magpie nests varying in response to cuckoo eggs or receiving different experimental treatments were tested by Fisher exact probability tests or log-likelihood ratio tests, depending on expected values (Bishop et al. 1975; Siegel and Castellan 1988). Differences in the laying dates of different groups of magpies were tested with Mann-Whitney *U*-tests because of skewed frequency distributions of dates (Siegel and Castellan 1988).

Annual reproductive success (measured as the total number of fledglings produced per breeding season) had a nonnormal frequency distribution; thus, the difference in reproductive success between magpie abandoners, ejectors, and acceptors was tested by Kruskal-Wallis one-way ANOVA (Siegel and Castellan 1988). Both fully and partially destroyed magpie clutches were used in the calculations of host reproductive success. All magpie nests used in other field experiments were excluded from calculations of reproductive success. All statistical tests are two-tailed. Values reported are means (\pm SE).

RESULTS

Natural Parasitism

We found a total of 277 magpie nests, of which 176 (63.5%) were parasitized by the great spotted cuckoo. We excluded 42 parasitized nests and 12 nonparasitized nests to be used in other experiments (not reported here), leaving 134 parasitized magpie nests available for analyses from 1991 and 1992. A total of 5.2% of the cuckoo eggs were ejected, whereas 7.5% of the nests were abandoned. All other cuckoo eggs were accepted. Most magpie nests with ejected cuckoo eggs were depredated (86% of 7 nests), whereas only 12% of nests with accepted cuckoo eggs were depredated. This difference in predation rate between magpie nests with accepted and ejected cuckoo eggs is statistically highly significant (6 of 7 nests vs. 14 of 117 nests, Fisher exact probability test, $P = 2.2 \times 10^{-6}$), suggesting that nest predation was directly associated with ejection of parasite eggs by magpies. These rates of nest predation should be compared with predation on unparasitized magpie nests, which was only 22.5% ($N = 89$). Eight of the ten magpies that abandoned a parasitized

TABLE 1. The fate of experimental magpie nests parasitized by the great spotted cuckoo in which the parasite eggs were removed and control magpie nests that were visited, but from which the parasite eggs were not removed.

| Nest category | Percent | Sample size |
|---------------------------|---------|-------------|
| Experimental nests | | |
| Complete nest predation | 55 | 16* |
| Partial nest predation | 10 | 3† |
| Carrion crow predation | 3 | 1 |
| Successful nests | 31 | 9† |
| Total | 100 | 29 |
| Control nests | | |
| Complete nest predation | 11 | 3 |
| Successful nests | 89 | 25 |
| Total | 100 | 28 |

* Two of these nests previously suffered partial predation.

† Includes one nest that was parasitized twice and from which we did not remove the second parasite egg.

nest laid a replacement clutch; five of these replacement clutches were parasitized again by the great spotted cuckoo. Only two of the seven magpies that ejected the cuckoo egg laid a replacement clutch; both of these were parasitized again by the cuckoo. Magpies accepted the parasite egg in all seven replacement nests that were parasitized.

Experimental Parasitism

Laying date did not vary significantly between experimental and control nests (experimental nests—mean May 1: 2.7 d, $N = 29$; median April 26; control nests—mean April 29: 3.0 d, $N = 28$; median April 24; Mann-Whitney U -test, $z = 1.35$, NS).

Although 16 of the 29 experimental nests were completely destroyed, only 3 of the 28 control nests suffered this fate (table 1). One experimental magpie nest was preyed upon by carrion crows and was therefore excluded from analyses. Two other nests that were parasitized twice were also excluded, because we did not remove the second parasite egg (one of these doubly parasitized nests was partially depredated). Two experimental nests suffered partial predation but were not deserted by the host. Thus, 73% of 26 experimental nests were completely or partially depredated (table 1) whereas only 11% of the 28 control nests suffered from predation. This is a highly significant difference in predation rate between treatments (log-likelihood ratio test, $G^2 = 23.66$, $df = 1$, $P < 0.001$). Magpie nests from which great spotted cuckoo eggs were experimentally removed suffered a higher nest-predation rate than did control nests retaining parasite eggs.

The simplest explanation for destruction of host offspring by great spotted cuckoos is that it induces repeat laying in the host, whereas in the retaliation scenario, the threat of parasite aggressive behavior modulates host behavior. For host re-laying, one would predict that nest predation would occur only as long as the magpie is likely to lay a replacement clutch. The retaliation scenario predicts destruction of host nests whenever parasite eggs are ejected, even late in the season. Because the probability of re-laying by magpies after nest failure decreases rapidly toward the end of the breeding season (Birkhead 1991), we can use our data to discriminate

between the two alternatives. There was a slight, but non-significant indication that late nests suffered a higher probability of destruction than early nests, contrary to the predictions of the re-laying hypothesis, since depredated experimental magpie nests were initiated on average 12 d later than nests not suffering from predation (depredated nests: mean May 9, $SE = 5.5$; median May 11, $N = 11$; successful nests: mean April 21, $SE = 2.3$; median April 22, $N = 3$, Mann-Whitney U -test, $z = 1.48$, NS; [data from 1990]).

Magpie nests were depredated at both egg and chick stages. Of the 19 depredated experimental nests, 7 were depredated at the egg stage, 10 at the chick stage, and 2 suffered two cases of partial predation (1 at the egg stage, another at the chick stage). In both of the latter cases, the second predation incident eliminated all remaining host young. Destruction of magpie chicks always occurred before they were 7-d old.

During 1990, we obtained circumstantial information indicating that great spotted cuckoos were responsible for destroying experimental nests. Attacks on the experimental nests were recognizable because injured nestlings remained in the nest (and injured nestlings sometimes survived until fledging), which is not what one expects from ordinary predators. By contrast, corvid nest predators always remove and eat their victims. We have never found injuries among hundreds of magpie nestlings in Denmark (A.P.M.) and England (T. R. Birkhead pers. comm. 1993), where the great spotted cuckoo is absent, but five species of corvid nest predators are present. Moreover, we never recorded partial predation among several hundred magpie nests in 7 yr in the Guadix area, when host ejection behavior was much rarer (Soler 1990; Soler et al. 1994).

On three occasions when we were scolded by cuckoos (see below), we removed the parasite eggs and replaced all magpie eggs (one, three, and four, respectively) with plasticine model eggs matching magpie eggs in size, color, and spotting pattern. The cuckoo inspected the nest in each case, and when we rechecked the nests just after the cuckoo left, one, three, and two model eggs, respectively, had peck marks. In one case (in which the female cuckoo had a radio transmitter), the female that laid the egg was demonstrably the one that pecked the model eggs. We have never observed great spotted cuckoos consuming eggs or nestlings of the magpie, and the diet of cuckoos is mainly lepidopteran caterpillars (Cramp 1985).

These natural history observations thus strongly suggest that cuckoos "punish" hosts that remove cuckoo eggs.

Reproductive Success of Hosts in Relation to Their Response

The Mafia hypothesis assumes that the reproductive success is higher for magpie hosts that accept a parasite egg than for those that eject the cuckoo egg. We have two pertinent kinds of data.

First, we have information on the reproductive success of magpie acceptors that raised the cuckoo, ejectors that ejected the cuckoo egg, and abandoners that abandoned their nest after being parasitized. Acceptors raised as many of their own offspring as did abandoners or ejectors (table 2). The number of fledglings produced per season did not differ sig-

TABLE 2. Reproductive success of magpies with a first clutch parasitized by great spotted cuckoos if subsequently abandoning their nests, ejecting the cuckoo egg, or accepting the cuckoo egg. Data are from 1991 and 1992. Values are means (SE).

| No. of fledglings | Abandoners | Ejectors | Acceptors |
|-------------------------|-------------|-------------|-------------|
| Magpie offspring | | | |
| First clutch | 0.00 | 0.29 (0.29) | 0.43 (0.10) |
| Replacement clutch | 0.40 (0.31) | 0.00 | 0.00 |
| Total | 0.40 (0.31) | 0.29 (0.29) | 0.43 (0.10) |
| Cuckoo offspring | | | |
| First clutch | 0.00 | 0.00 | 1.18 (0.10) |
| Replacement clutch | 0.50 (0.27) | 0.00 | 0.18 (0.06) |
| Total | 0.50 (0.27) | 0.00 | 1.35 (0.11) |
| Sample size | 10 | 7 | 105 |

nificantly among magpie abandoners, ejectors, and acceptors (Kruskal-Wallis one-way ANOVA, $H = 0.09$, $df = 2$, NS). However, the probability of recruitment by magpie fledglings decreases dramatically as the breeding season progresses (Birkhead 1991), and magpies fledged from replacement clutches have a recruitment probability less than 50% of that of fledglings from first clutches (Birkhead 1991). If we conservatively assume that the recruitment probability of fledglings from replacement clutches is half that of first clutches, acceptors have higher annual reproductive success (0.43 fledglings, SE = 0.10) than do ejectors (0.29 fledglings, 0.29) and abandoners (0.20 fledglings, 0.31) (Kruskal-Wallis one-way ANOVA, $H = 3.43$, $df = 2$, NS). There were statistically significant differences in the number of cuckoos produced by the three categories of parasitized magpies (table 2; Kruskal-Wallis one-way ANOVA, $H = 18.70$, $df = 2$, $P < 0.001$). Acceptor magpies produced more great spotted cuckoo fledglings than the two other behavioral categories of parasitized magpies.

The second data set originates from the experiment. Reproductive success of magpies in the experimental group was higher than that of control magpies, although not significantly so (experimentals: 0.85 fledglings, SE = 0.28, $N = 29$; controls: 0.54 fledglings, 0.24, $N = 28$; Mann-Whitney U -test, $z = 0.95$, NS). The experimental group raised no cuckoo fledglings, but the control group raised 1.39 fledglings (SE = 0.27), a highly significant difference (Mann-Whitney U -test, $z = 3.83$, $P < 0.001$). This suggests that magpies that did not raise cuckoo nestlings produced slightly (but not significantly) more of their own offspring than did magpies that raised cuckoo nestlings.

DISCUSSION

Nest destruction by cuckoos could be due to (1) Mafia cuckoos, in which case, the female that laid the ejected egg destroys the nest, or (2) any cuckoo as part of a general strategy to increase the frequency of host laying. The second alternative is highly unlikely unless females in a particular area tend to be close kin. Female great spotted cuckoos have exclusive breeding territories where they account for most instances of brood parasitism (Arias de Reyna et al. 1987). Great spotted cuckoos irregularly guard and defend parasitized magpie nests during the entire nesting cycle of the host (M. Soler, J. J. Soler, and J. G. Martinez unpubl. data): During

the laying period and the first 10 d of incubation, we were scolded by cuckoos on 25% of 56 visits to 30 parasitized magpie nests, whereas we were scolded by magpies in only 5% of our visits. On 11 occasions, a great spotted cuckoo inspected a magpie nest directly after we had visited it. Clutch destruction following parasite egg ejection is probably caused by the territorial female that laid the egg, as shown by one observation of a female provided with a radio transmitter.

The simplest explanation for the destruction of host offspring by great spotted cuckoos is that it induces repeat laying in the host. Beyond this, destruction could be viewed as retaliation, the threat of which modulates the host behavior in the first place. In both cases, host re-laying and fresh opportunities for parasitism result. These two hypotheses are not mutually exclusive, because the induction of re-laying as a result of nest predation initially may increase the frequency of host acceptance of parasitic offspring. Once nest predation is present in the parasite, the host can respond by learning over behavioral time, or selection over evolutionary time, by reducing ejection of parasite eggs. Positive feedback between Mafia-like parasite and compliant host behaviors indirectly enhances selection on aggressive parasite behavior. Because the magpie and cuckoo are long-lived, individual magpies may learn that it is less costly to accept than reject a cuckoo egg; this host response will benefit a philopatric cuckoo by reducing its own egg mortality. These two scenarios predict different temporal patterning of nest predation by cuckoos. For host re-laying, one would predict that nest predation would occur only as long as the magpie is likely to lay a replacement clutch. The retaliation scenario predicts destruction of host nests whenever parasite eggs are ejected, even late in the season. The probability of re-laying by magpies after nest failure decreases rapidly toward the end of the breeding season (Birkhead 1991). In our tests, there was a slight, but nonsignificant indication that late nests suffered a higher probability of destruction than early nests, contrary to the prediction of the re-laying hypothesis. However, the power of this test is low because of the small sample size, and the result thus does not discriminate between the induced-re-laying scenario and the retaliation scenario.

The Hoya de Guadix population of magpies has only recently been parasitized by great spotted cuckoos, and natural ejection of cuckoo eggs has increased in frequency during the last few years (Soler 1990; Soler and Møller 1990; Soler et al. 1994). Compared with the rate in Guadix, the ejection rate of artificial cuckoo eggs was considerably higher in a presumed area of ancient sympatry near Santa Fe, (Soler 1990; Soler and Møller 1990). We suggest that the ejection rate in the Guadix area is low because it has only recently been colonized by great spotted cuckoos, but this does not preclude the destruction of host clutches by cuckoos.

Learning by individual hosts may play an important role in the Mafia mechanism, and the behavior of individual hosts may depend on individual circumstances and history of exposure to parasites. Individual magpie hosts differ in their intensity of defense of nests against potential great spotted cuckoo parasites. Some hosts behave aggressively, whereas others do not react to the presence of a parasite (pers. obs.). The best option for a host may depend on learning in relation to its physical condition, territory quality, age, and the be-

havior of the parasite. Some hosts may therefore behave adaptively by ejecting cuckoo eggs, whereas others maximize their reproductive success by accepting parasite eggs. A whole range of host responses is therefore possible in a single host population. The only necessary conditions for the Mafia mechanism to enter a population of great spotted cuckoo parasites is that (1) ejection of parasite eggs occurs at least at a low frequency, and (2) host-nest depredation by cuckoos induces re-laying. The costs and the benefits of different behavioral strategies by hosts (acceptance vs. ejection) and parasites (Mafia behavior vs. its absence) depend on the moves made by the two interacting players, and this will give rise to frequency-dependent selection. At the behavioral equilibrium of this evolutionary game, fitnesses among the host strategies available, given parasitism, are supposed to be equal. This outcome is supported in the case of the magpie (table 2).

The Mafia hypothesis assumes that the reproductive payoff to magpie hosts that accept the cuckoo egg is not lower than it would be to those that eject the parasite egg. Magpies that accepted the cuckoo egg did not raise fewer of their own offspring than did magpies that abandoned their first nest or ejected the cuckoo egg and subsequently suffered from nest predation (table 2, when the probability of recruitment by magpie fledglings is taken into account). The reproductive success of experimental magpies that had cuckoo eggs removed from their nests was higher than that of magpies in the control group, although not significantly so. Magpie nestlings raised together with cuckoos weighed, on average, only 3.5% less than magpie nestlings raised alone (Soler and Soler 1991), and this is unlikely to affect their probability of recruitment (Birkhead 1991). Acceptor magpies therefore did not appear to have lower current reproductive success than ejector or abandoner magpies.

Parasitized magpie hosts may still have increased their reproductive investment by accepting and producing a cuckoo as compared with a brood of magpies, and this is a precondition for the evolution of ejection behavior by hosts. The average cost of producing a single cuckoo nestling was not higher than that of producing a single magpie nestling because their body masses were approximately similar (Soler and Soler 1991). We have also demonstrated that magpies do not bring more food to parasitized as compared with unparasitized nests (Soler et al. 1995a). However, magpies provide care for cuckoo fledglings almost twice as long as they do for magpie fledglings (Soler et al. 1995b). Prolonged post-fledging care is likely to result in parasitized magpies delaying their annual molt compared with nonparasitized magpies. The production of more offspring (magpies as well as cuckoos) by acceptors as compared with abandoners and ejectors suggests that acceptors may have a higher reproductive investment. These observations clearly suggest that parasitized magpies incur an increased reproductive effort compared to nonparasitized magpies.

The Mafia hypothesis, as stated by Zahavi (1979), views the parasite-host interaction as the result of a host strategy (acceptance of parasitic offspring) maintained in a state of evolutionary equilibrium, rather than as an outcome of a continuing coevolutionary arms race between hosts and parasites. We suggest that the Mafia mechanism could be an

important process even when hosts adopt alternative strategies. If cuckoos kill host young or destroy host eggs in parasitized nests that do not contain a cuckoo egg or nestling, this should prevent evolution of host discrimination against both parasite eggs and young. We found a high predation rate in the nests from which cuckoo eggs had been removed, but not every experimental nest was destroyed by great spotted cuckoos. For example, if parasites do not kill all offspring in every host nest from which their eggs have been removed, then host ejection of parasite eggs could be successful, and a state of equilibrium with alternative strategies of host acceptors and rejectors could be reached.

In conclusion, magpies that respond to parasitism by great spotted cuckoos by accepting the parasite egg do not have lower reproductive success than ejectors or abandoners, because ejection frequently results in nest predation by the brood parasite. This provides support for the Mafia hypothesis, which suggests that the hosts of brood parasites are forced to accept parasitism.

ACKNOWLEDGMENTS

We thank T. Ortiz and C. Zamora for help in making the plasticine magpie model eggs. Constructive comments from T. Guilford, R. D. Holt, M. Lindén, J. Moreno, S. Rothstein, S. G. Sealy, M. Sorenson, S. Ulfstrand and A. Zahavi greatly improved the manuscript. Our research was supported by the Commission of the European Communities (SC* CT92-0772) to A. P. Møller and M. Soler and Junta de Andalucía (grupo 4104) to J. G. Martínez, J. J. Soler, and M. Soler.

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Corresponding Editor: R. Holt