Evidence for Avian mafia!

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An unwritten rule in evolutionary biology is that anything that *can* evolve *will* evolve. Birds are remarkable for their extraordinary effort at nest building and brood care. Given that so many species of birds spend so much time and effort at these activities, there is plenty of room for some species to take it easy, lay their eggs in the nests of other species and hitch-hike on their hosts. The cuckoo that lays its eggs in the nests of a variety of host species is well known. Indeed, over 80 species, i.e. over 1% of bird species are known to be such obligate inter-specific *brood parasites.* These include two-sub-families of cuckoos, two types of finches, the honey-guides, the cowbirds and the black-headed duck[1]. Because parasite species often use more than one host species, many more than 1% of bird species act as hosts to brood parasites. Interspecific brood parasitism has evolved independently at least seven times in birds and can have a significant effect on the populations of the host species and even lead to their extinction. Although hosts sometimes detect and eject alien eggs, their success in ridding their nests of parasite eggs is often very limited and that is why brood parasitism has survived as a way of life. One reason for such limited success of the hosts is the often exquisite mimicry on the part of the parasites whose eggs are virtually indistinguishable from those of the host[1]. What is perplexing, however, is that many parasite species lay eggs that look nothing like their host's eggs and yet get away with it. Obviously hosts have not perfected the art of removing all or most of the alien eggs. But why should this be so?

There are two philosophically different approaches to this question. One is that the process of adaptation of the hosts to the onslaught of the parasites is ongoing and there has not been enough time for it to be perfected. A standard way of expressing this is to say that we are in the middle of an evolutionary arms race and what we are seeing today is no more than an evolutionary snap-shot; given enough time, host species will perfect the art of removing all parasite eggs. This may well be the truth but unfortunately we have no way of telling. It is a hypothesis that can neither be proved nor disproved. The other, rather different approach is to assume that this is the best that hosts can do and we are already in an evolutionary equilibrium. In other words it does not pay the hosts to get better and remove all the parasite eggs. This equilibrium hypothesis may be as wrong or as right as the evolutionary snap-shot hypothesis but it has one major advantage over the former. It compels us to try and discover what the reasons might be for the equilibrium level of perfection on the part of the hosts; why is it that hosts cannot get any better than they already are? This is a more satisfying situation because it gives you something to do. If you find the nature and magnitude of the costs and benefits of alien egg removal to be such that they correctly predict the observed equilibrium level of egg removal then we have much more confidence in our hypothesis. Not that we are anywhere close to achieving this goal, but some exciting leads have been found.

One obvious cost of assiduously removing parasite eggs is the danger of mistakenly discarding one's own eggs. Even when the host and parasite eggs look rather different from each other to our eyes, it is not obvious that they do so to the birds. It is not even obvious that a naive bird knows which is its own egg and which is the parasite's. One way to solve this problem is to be rather

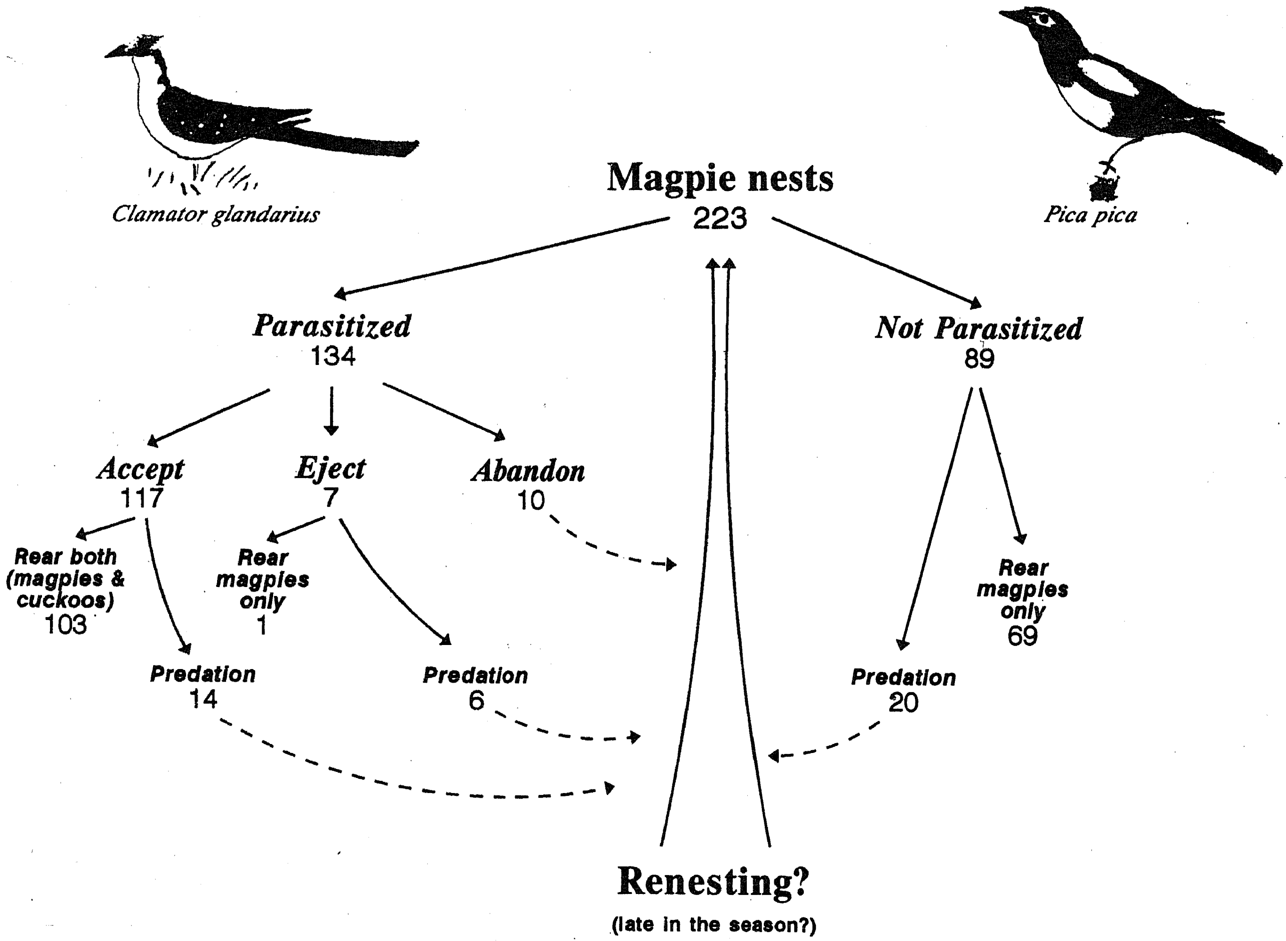

Figure 1. Rates of parasitization, acceptance, ejection and abandoning in the study population in Moya de Guadix in Spain during 1991–92. The host, black-billed magpie *Pica pica* and the parasite, the great spotted cuckoo *Clemator glandarius* are also shown. Data from Soler *et al.*[5].

conservative in one's first attempt at breeding, learn what one's eggs are supposed to look like and efficiently get rid of the parasite's eggs in subsequent breeding attempts. This will mean that in the population as a whole, there will be an equilibrium between nests that accept parasite eggs and those that do not, but if we look closely enough we will find that first year breeders will be more likely to accept parasite eggs while experienced breeders will be more likely to eject parasite eggs. Zahavi and his colleagues have found evidence for such a hypothesis in the case of cuckoos (parasite) and warblers (host) in Japan[2,3].

Amotz Zahavi has suggested yet another factor that might lead to an equilibrium point where host species do not get rid of all parasite eggs. This is the hypothesis that parasites such as cuckoos may repeatedly visit the parasitized nests and destroy the eggs of the host if it has ejected the parasite's eggs and not do so if the host has accepted and is taking good care of the parasite's eggs/chicks[4]. In the presence of such a parasite 'Mafia', hosts who are incapable of defending themselves against the attacks of the parasites may find it better to accept some parasite eggs and additionally rear at least some of their own eggs rather than lose all their eggs in the parasite attack. Soler *et al.*[5] have attempted to test this Mafia hypothesis using the great spotted cuckoo *Clamator glandarius* and its host the black-billed magpie, *Pica pica* in the high altitude plain, Hoya de Guadix in Spain. A magpie that finds cuckoo eggs in its nest appears to have three options – accept the parasite's egg/s and rear both magpie and cuckoo chicks, eject the cuckoo eggs and rear only its own offspring or abandon the nest altogether and start all over again. In addition to laying its eggs in black billed magpie nests, the great-spotted cuckoo also destroys magpie eggs in nests not containing cuckoo eggs, making the Mafia hypothesis plausible, in the first place. There is evidence, both circumstantial and direct, that cuckoos visit nests where they have laid eggs and peck at magpie eggs if their own eggs are missing. There is good reason to believe that cuckoos do not eat magpie eggs or nestlings; their diet consists mainly of lepidopteran caterpillars. This makes the Mafia hypothesis even more plausible by ruling out direct nutritional benefits to the cuckoos and suggesting retaliation as a possible motive for destroying the magpie eggs.

Painstakingly gathered data over two years, on the rates of parasitism of magpie nests by the cuckoo, rates of acceptance of cuckoo eggs by the magpies, ejection of cuckoo eggs by the magpies, abandoning of their parasitized nests by the magpies and predation of magpie nests by the cuckoo, by Soler *et al.*[5] are shown in Figure 1. There is more evidence consistent with the Mafia hypothesis in Figure 1. When magpies ejected cuckoo eggs, 86% of their nests were depredated by the cuckoos, but when they accepted cuckoo eggs, only 12% of their nests were attacked, a difference that is statistically significant. Predation rates were of the order of 22% in non-parasitized nests. All magpies re-nesting after loss of eggs to cuckoo depredation accepted cuckoo eggs without ejecting them or abandoning their nests in the second breeding attempt. But did the cuckoos destroy magpie eggs just to get the magpies to re-nest and provide another opportunity for them to lay their own eggs? Although the predictions of this relaying hypothesis and the previously mentioned Mafia or retaliation hypothesis are not mutually exclusive, re-laying is unlikely to be the major factor inducing the cuckoo's depredatory behaviour. If inducing the magpies to re-lay was the main objective, magpie nests, early in the season (which have a higher probability of re-nesting) rather than those late in the season (which have a substantially lower probability of re-nesting), should suffer higher rates of attack by the cuckoos. The data show, if anything, the opposite; late nests suffered a slight, though non-significantly higher rate of predation compared to early nests.

Differential rates of predation can only suggest the plausibility of the Mafia hypothesis. Reproductive success of the different magpie strategies namely, acceptance, ejection and abandonment are essential for drawing any definitive conclusions. These data are also provided by the authors of the study under discussion. Magpies that accepted the cuckoo eggs produced 0.43 ± 0.10 (105) (mean $\pm$ SE, sample size in parenthesis) fledglings per nest, while those that ejected the cuckoo eggs produced 0.29 ± 0.29 (7) fledglings per nest and finally, those that abandoned their nest and started all over again produced 0.40 ± 0.31 (10) fledglings per nest. The measured reproductive success of the abandoners should at least be halved because the probability of recruitment of offspring into the breeding population decreases dramatically as the season progresses, thus giving us a figure of about 0.20 fledglings per nest for the abandoners. Not surprisingly, it is the ejectors that have the highest variance in their reproductive success; it must be that some of them lose all their eggs to cuckoo retaliation while others escape cuckoo attacks. But the acceptors do seem to have the highest reproductive success, higher compared to ejectors and abandoners. However these differences are not statistically significant.

A more powerful approach is to experimentally remove cuckoo eggs from some parasitized magpie nests and do no such thing in a group of control, parasitized nests. This too the authors have done to find that the nests from which cuckoo eggs were experimentally removed (equivalent to ejectors) produced 0.85 ± 0.28 (29) fledglings while the control nests (equivalent to acceptors) produced 0.54 ± 0.24 (28) fledglings per nest. These numbers are also not statistically significantly different. At first sight it may appear that lack of significant differences between the acceptors, abandoners and ejectors in the natural population and the experimental and control nests in manipulated sample weaken the case for Mafia hypothesis but a little reflection should show otherwise. It would be naive to expect the Mafia to be so powerful as to destroy every nest from which cuckoo eggs were ejected. Not only would this be biologically unreasonable to expect, but it would also then lead to acceptance behaviour on the part of all magpies and that has not happened (see Figure 1). The higher variance in reproductive success of the ejectors is consistent with this reasoning. It is therefore far more reasonable to expect that the Mafia would work with a certain level of less than perfect efficiency and that ejectors, acceptors and abandoners would coexist. Indeed one can postulate a frequency-dependent selection on different magpie strategists so that acceptance begins to pay better if everybody else is ejecting and ejection begins to pay off if everybody is accepting. With this more reasonable scenario, a realistic prediction of the Mafia hypothesis would be that acceptors should not have significantly lower reproductive success than the ejectors. This prediction is borne out by both the natural population data as well as the experimental manipulation data.

Have we then solved the paradox of why host birds accept and rear parasite eggs? Far from it. We have barely scratched the surface of the problem. But there is no denying that here is beginning of a promising theoretical framework and an empirically and experimentally tractable system that can be employed to demystify the host's behaviour of accepting strikingly different-looking parasite eggs. In addition to more data, observations on individually marked magpie nests, identified eggs and colour banded or radio-tracked cuckoos (the authors have already used one cuckoo fitted with a radio transmitter) will be necessary. So will careful modelling of the costs and benefits of different magpie strategies at different frequencies of the strategists prove essential. We dare not mention more studies on different host–parasite species for, that is bound to introduce more noise in the system. Another species may have a different 'truth' altogether; perhaps the inevitable slowness of the process of learning to discriminate parasite eggs may be the main factor causing equilibrium in another host–parasite pair – such is the charm of biological diversity!

1. Rothstein, S. I., *Annu. Rev. Ecol. Syst.*, 1990, **21**, 481–508.
2. Lotem, A. H., Nakamura, H. and Zahavi, A., *Behav. Ecol.*, 1992, **3**, 128–132.
3. Zahavi, A., *Am. Nat.*, 1979, **113**, 157–159.
4. Gadagkar, R., *Down To Earth*, 1993, **2**, 46–47.
5. Soler, M., Soler, J. J., Martinez, J. G. and Moller, A. P., *Evolution*, 1995, **49**, 770–775.

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