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# Cuckoo–host coevolution: from snapshots of an arms race to the documentation of microevolution

It is not often that a notable study in evolutionary biology published in *Nature* has nearly all of its assumptions and conclusions challenged by a second paper. But that is precisely what happened when Zuniga and Redondo[1] questioned Soler and Møller's[2] work on coevolution between the brood parasitic great spotted cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host. These authors reported that varying degrees of egg discrimination shown by three magpie populations correlate with the duration of sympatry between the host and its parasite. They found that magpies never reject even strongly nonmimetic eggs in Uppsala, Sweden, where cuckoos are absent. But most importantly, they argued that significant differences in behavior between two magpie populations only 60 km apart in Spain exist because magpies at one site, Guadix, have been sympatric with cuckoos only since the 1960s, while those at Santa Fe have experienced cuckoos for much longer. Thus, the data obtained from the two sites appeared to reflect different stages in a continuing evolutionary arms race between the cuckoo and its host. Soler and Møller also argued that cuckoos at Guadix area show other characteristics expected of a new parasite–host association, for example, many cuckoo eggs per magpie nest, cuckoo parasitism of additional host species, and an overall high reproductive success in the parasite owing to weak host defenses.

Zuniga and Redondo's doubts about these findings have recently been rebutted by Soler *et al.*[3], who also present new evidence for coevolutionary changes in the past 10–15 years. So, what started as a controversy over the correct facts and the sorts of evolutionary inferences one can make from them may lead the research on avian brood parasitism into a new phase in which microevolutionary change is observed during the course of a long-term study, rather than simply inferred during a short-term comparative study.

The relationships between parasitic cuckoos and their hosts are thought to represent clear cases of coevolution[4]. The cost of being parasitized selects for the evolution of host defenses against the parasite, which in turn, select for counter-adaptations in the parasite. Several experimental and comparative studies strongly support this coevolutionary scenario[5–8]. For example, actual and potential cuckoo hosts exhibit higher rejection rates of nonmimetic eggs than do species unsuitable as hosts[5,6]. Although convincing, such evidence does not involve a direct observation of evolutionary change because inferences regarding evolutionary change in the past are based only upon patterns and selective pressures observed in the present. But now, depending on which side of the great spotted cuckoo controversy one chooses to believe, the study of avian brood parasitism may finally have its own case of 'industrial melanism' in which microevolutionary changes have actually been observed. One thing that is clear is that the great spotted cuckoo is potentially a very strong selective pressure on magpies. Although other corvids are occasionally parasitized at <5% of their nests, European populations of this cuckoo specialize on the magpie, with local parasitism rates sometimes exceeding 50% and parasitized magpies often failing to raise any of their own young[3,9].

Zuniga and Redondo's[1] challenge of Soler and Møller's original paper made three fundamental assertions. (1) There is no reliable evidence for differences in the duration of sympatry between Guadix and Santa Fe. (2) The characteristics of a new parasite–host association that Soler and Møller claimed for Guadix apply just as well to Santa Fe. (3) Any differences between magpie responses to foreign eggs at these two sites could be due to a conditional response, with higher cuckoo populations at one site stimulating magpies to inspect their eggs more thoroughly or more often, thereby leading to higher rejection rates.

Only the third criticism is of general importance and also totally testable; thus, it should be the target of future efforts. While the duration of sympatry at Guadix is an essential point, no clear resolution of this particular argument seems possible. Soler and Møller's evidence for recent sympatry at Guadix is based on local hunters who shot a great spotted cuckoo there in 1962 and claimed never to have seen such a bird before. While this cuckoo is a large, and at times, noisy bird, this whole issue depends on how much faith one places in the observational skills of nonbiologists. We have both known nonbiologists who were remarkably attentive observers of natural history and others who were unaware of common birds they have lived among all their lives. So this issue is simply not resolvable, especially since cuckoo presence may be episodic as they have died out in much of North Africa during this century[10]. Also, cuckoos could have been at Guadix long ago because they were wide- spread in Spain over 120 years ago. Saunders (in Ref. 11) noted that this primarily African species was very common at Aranjuez, 300 km north of the Guadix area before 1870 and that multiple parasitized magpie nests occurred frequently. Although Soler and Møller[2] supported their claim of recent sympatry at Guadix by suggesting that cuckoos rarely occur in such mountainous areas, Wadley[12] found them to be 'well distributed' parasites of magpies throughout Anatolia, Turkey, at high elevations (900–1050 m versus 900–1100 m at Guadix).

In arguing that Guadix does not show the characteristics putatively associated with the recent arrival of a parasite, Zuniga and Redondo pointed out that the claim for an expanded host niche at Guadix is weak because of the simple fact that several corvid species breed there but only the magpie occurs at Santa Fe. However, their argument that Santa Fe and not Guadix shows such characteristics as frequent multiple parasitism, and high overall cuckoo breeding success is weakened by Soler and Møller's new analyses. The latter demonstrate that various breeding parameters show temporal variation that could have confounded

Zuniga and Redondo's comparisons between Santa Fe and Guadix. So this issue is still unresolved, and it may not be of central importance because Soler and Møller[3] argue that habitat differences alone could affect features of parasitism. Furthermore, it is not necessarily clear what one should predict in an area recently occupied by a brood parasite. While high reproductive success and an expanding population of parasites resulting from a low level of host defenses is a reasonable prediction, one could argue that a parasite that stays at a low population level is also evidence for recent colonization because a recently settled area may represent marginal habitat for a newly arrived species. This appears to be the case for the parasitic brown-headed cowbird (*Molothrus ater*) in the Sierra Nevada Mountains of California, USA[13].

Nevertheless, the cuckoos at Guadix do seem to be very successful, and the combined data of all of these workers suggest that the situation there is changing. In 1982–1984, 30.8–41.2% of magpie nests were parasitized and 20% of all magpie nests contained more than one cuckoo egg. In 1990–1992, 61% of the nests were parasitized and 36.2% contained more than one cuckoo egg[1,3,9]. Whether the cuckoos are newcomers in Guadix or whether they are old residents, it seems clear that they have become a more potent factor in magpie biology since the early 1980s. This sets the stage for a testable hypothesis of microevolution because a detectable increase in rejection among magpies, since Soler's early studies at Guadix, is likely. An increase might occur either because the increased rate of parasitism has accelerated the rate at which rejection was increasing or because the increased parasitism has shifted the selective value of rejection from negative or neutral to positive[4].

Soler *et al.* present two lines of evidence for increased rejection rates since the 1980s. First, they show that rejection of naturally deposited cuckoo eggs increased after 1990 but they caution that natural parasitism is not a reliable indicator of host defenses because eggs may be ejected before observers ever see them. More importantly, they report that the rate of rejection of experimentally placed nonmimetic eggs has increased significantly at Guadix. It was 61% in 1983–1984, 71% in 1989, 73% in 1992 and 89% in 1993, for an overall increase of 2.27% per year. There was also a marginally significant increase in the rejection rate of model eggs painted to resemble cuckoo eggs, which closely mimic magpie eggs. So these are the vital data that may be the first fully documented example of microevolution in interactions between parasitic birds and their hosts.

However, as Soler *et al.* acknowledge briefly toward the end of their paper[3], there still remains the problem of Zuniga and Redondo's third criticism. Namely, variation in rejection rates may reflect conditional responses to the presence of adult parasites and not evolutionary (genetic) changes. If the rate of parasitism has gone up, then cuckoos must be visiting magpie nests more often, which itself could explain the increase in rejection according to Zuniga and Redondo's arguments. Soler *et al.* thoroughly analyzed their data for any evidence that experience with cuckoos affects rejection behavior. They argue against such effects because cuckoos were more common at Guadix than at Santa Fe, yet rejection was more common at Santa Fe, and because there was no significant correlation among sites at Guadix between the site-specific rejection rate of naturally placed cuckoo eggs and the local abundance of cuckoos. But the latter correlation was positive and had a *P*-value of 0.07, which could be taken as evidence that adult cuckoos affect host responses.

Thus, it seems to us that there is still a glimmer of hope for Zuniga and Redondo's conditional effect hypothesis and that further analyses that use data on natural parasitism or on measures of cuckoo abundance are not the best way to proceed. It would be much more efficacious to experimentally test the hypothesis directly, as has been done for the common cuckoo[7,8]. Namely, experiments need to be done in which some magpies that are artificially parasitized are also exposed to a mounted or live cuckoo near their nest, while some are not given such exposure. Perhaps the conflicting parties might even consider doing such experiments jointly so as to head off any debate about the validity of the data and interpretations. Another possible explanation for the recent increase in rejection rate in Guadix is gene flow from an area of ancient sympatry. Soler *et al.* did not consider the possibility that the same factors responsible for changes in cuckoo distribution could also have increased gene flow between magpie populations.

It is clear from Soler *et al.*'s[3] latest contribution that something is indeed changing at Guadix, and it may not be long before the precise cause of that change is determined. But southern Spain is not the only place where cuckoos have recently begun to interact with new hosts. Nakamura[14] reported that the common cuckoo in central Japan has recently begun to parasitize the azure-winged magpie (*Cyanopica cyana*). Similar to the results of Soler *et al.*, Nakamura also found a recent increase in the host's rejection rate of cuckoo eggs, but the increase in Japan is so rapid that it seems fairly certain that it cannot be because of genetic changes alone (Ref. 15 and H. Nakamura, pers. commun.). In this case, the cuckoo seems also to be evolving a new egg type that matches the host eggs more closely.

The studies of Soler *et al.* in Spain and Nakamura in Japan suggest that evolutionary changes in parasite–host interactions may be common and rapid enough to be demonstrated by long-term studies. The recent expansion of cowbirds in North America is especially well documented[16,17] and may also yield some evolutionary changes. Extensive studies of cuckoo hosts in Europe and Japan and cowbird hosts in North and South America (summarized in Ref. 4, see also Ref. 18) will become even more valuable if researchers return to old study sites to check for possible evolutionary changes. Perhaps, some day, a lucky researcher will even be able to demonstrate that a host population has developed a defense since an earlier experimental study showed the absence of this host defense.

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