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Brood-parasite interactions between great spotted cuckoos and magpies: a model system for studying coevolutionary relationships

Abstract Brood parasitism is one of the systems where coevolutionary processes have received the most research. Here, we review experiments that suggest a coevolutionary process between the great spotted cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host. We focus on different stages of establishment of the relationship, from cuckoos selecting individual hosts and hosts defending their nests from adult cuckoos, to the ability of magpies to detect cuckoo eggs in their nests. Novel coevolutionary insights emerge from our synthesis of the literature, including how the evolution of "Mafia" behaviour in cuckoos does not necessarily inhibit the evolution of host recognition and rejection of cuckoo offspring, and how different populations of black-billed magpies in Europe have evolved specific host traits (e.g. nest and clutch size) as a result of interactions with the great spotted cuckoo. Finally, the results of the synthesis reveal the importance of using a meta-population approach when studying coevolution. This is especially relevant in those cases where gene flow among populations with different degrees of brood parasitism explains patterns of coexistence between defensive and non-defensive host phenotypes. We propose the use of a meta-population approach to distinguish between the "evolutionary equilibrium" hypothesis and the "evolutionary lag" hypothesis.

Key words Brood parasitism · *Clamator glandarius* · Coevolution · Meta-population · *Pica pica*

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Introduction

Coevolution, the process by which species specialise in their interactions with one another and the way in which these specialised relationships result in reciprocal evolutionary changes (e.g. Thompson 1994), has become one of the most important research topics in evolutionary ecology. In addition to revealing much about the evolution of specific ecological relationships, studies of coevolution can inform us about the causes of biodiversity (e.g. Thompson 1999). Avian brood parasitism is a reproductive strategy by which parasites lay their eggs in the nest of other species, the hosts, which incubate and rear the parasitic offspring. The study of brood parasites and their hosts provides an ideal system for studying and detecting coevolution (Rothstein 1990) because (1) most hosts are parasitised by a single species, (2) parental care in birds is elicited by vocal and visual cues which are easily detected and studied, (3) the spatial domain of the studies is well focused, because nearly all of the expected adaptations and counter-adaptations of hosts and parasites are manifested in or near the nest, and (4) the costs and benefits of any coevolutionary responses are clear since the brood parasite's fitness is maximised when the host loses its entire brood (Rothstein 1990). In this article we will review studies on the relationship between the great spotted cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host, trying to synthesise past findings into a pattern of past and present coevolutionary process.

Study areas

Most of the field-work described in this review has been carried out since 1982 in the Hoya de Guadix (37°18′N, 3°11′W). The study area is located in southeastern Spain, at approximately 1000 m above see level, and comprises 11 study plots that vary in area (0.57–4.15 km²) and ecological characteristics (for more detailed information see M. Soler et al. 1998a, 1998b). Distances between neigh-

bouring study plots are 0.5–8 km, and the two most widely separated study plots are 25 km apart. To test some of the experimental predictions at the population level we have also performed experiments in 14–15 magpie populations across Europe (see J.J. Soler et al. 1999a for locations and information on the different populations that were studied).

Species studied

The great spotted cuckoo

The great spotted cuckoo (38–40 cm, 138–169 g) is an obligate avian brood parasite of the family Cuculidae (subfamily: Cuculinae), and is phylogenetically close to other species of the same genus (*C. jacobinus*), where the evolution of brood parasitism has occurred independently of that in the genus *Cuculus* (Aragón et al. 1998). Palaearctic populations are migratory and those breeding in Europe are believed to winter in Africa, south of the Sahara (Cramp 1985). They arrive at our study area in late February or early March (Soler 1990). Adults leave the study area in mid-June, disappearing over a few days, while fledglings leave later, usually during July or the beginning of August (Soler et al. 1994a).

In Europe, the great spotted cuckoo mainly parasitises the magpie, although other species of the corvid family are known to be occasionally used (e.g., the carrion crow *Corvus corone* is often used as a secondary host species; Soler 1990). The African breeding population also focuses its parasitism on corvids, but also utilises starlings and hoopoes (Payne 1997a). Although social structure is unknown, genetic polygamy is frequent in this species (30%, Martínez et al. 1998a). A female cuckoo can lay more than 15 eggs (von Frisch 1969; Payne 1974, 1977a, 1977b; Arias de Reyna and Hidalgo 1982) over 10 weeks (Payne 1973, 1974), or 44 days in our study area (Martínez et al. 1998b). This brood parasite lays only one type of egg (Baker 1923; Friedman 1948; Alvarez et al. 1976; Soler 1990), which is elliptical to sub-elliptical, with blunt ends, smooth and fairly glossy, pale green-blue, thickly spotted, light brown or red brown colour (Cramp 1985). As with other brood parasitic species (e.g. Spaw and Rohwer 1987; Rahn et al. 1988; Brooker and Brooker 1989, 1991; Briskie and Sealy 1990; Moksnes et al. 1993), the eggs have a thick shell and the incubation period is short relative to adult body size (Soler 1990). Nestlings grow at a very high rate, mainly during the first 8 days, and leave the nest after 17–20 days on average (Soler and Soler 1991). Adult great spotted cuckoos sporadically visit parasitised nests at the end of the nestling period and, when parasitic chicks leave the nest, adult cuckoos may maintain contact with fledglings (Soler and Soler 1999). These contacts, as well as those between fledgling cuckoos from different nests, have been interpreted as necessary for the recognition of conspecific cues (Soler and Soler 1999). After leaving the nest, the parasitic chicks receive paren-

tal care from their foster parents for more than a month (Soler et al. 1994a), and usually form groups with fledglings from other parasitised nests (M. Soler et al. 1995a).

The magpie

The magpie is a medium size omnivorous single-brood corvid (43–50 cm, 220–236 g) that occurs throughout large parts of the Holarctic region. Magpies 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, and clutch size ranges from three to ten eggs (Birkhead 1991). Magpies normally build a domed, almost spherical nest with a stick framework in bushes or trees. After the framework is finished, a bowl of mud is built inside and lined with fibrous roots, hair and grass (referred to as the nest cup) (Birkhead 1991). It has been suggested that the size of the nest is a reliable indicator of territory and/or pair quality (J.J. Soler et al. 1995). Moreover, nest volume in magpies is a post-mating, sexually selected trait, because an experimental increase in nest size results in an increase in clutch size (J.J. Soler et al., in press, a). Magpies will lay a replacement clutch if the nest fails early during the reproductive cycle, with the frequency of replacement clutches decreasing as the season progresses (Birkhead 1991). Nestling magpies leave the nest after approximately 27 days (Buitron 1988; Soler and Soler 1991), and continue to receive parental care for several weeks (Birkhead 1991).

Peculiarities of the great spotted cuckoo-magpie system

An average of 2.4 cuckoo eggs are laid per magpie nest (M. Soler et al. 1998b), and one or more cuckoos may parasitise magpie nests with one or more eggs (Martínez et al. 1998a, 1998b). Moreover, the same cuckoo female may parasitise two different species of hosts (i.e. carrion crows and magpies; Martínez et al. 1998a).

Great spotted cuckoo females do not remove host eggs when laying, but damage to magpie eggs often occurs (on average, 2.4 broken eggs occur per parasitized nest; Soler et al. 1997), mainly because they lay from the rim of the nest (Arias de Reyna et al. 1982). The primary cost of the parasitism for magpies occurs during the egg incubation stage (Soler 1990; Soler et al. 1996, 1997; M. Soler et al. 1998b), not only because of egg damage, but also because early hatching of the cuckoo eggs (Alvarez and Arias de Reyna 1974; Soler 1990; Soler and Soler 1991) may provoke magpies to stop incubation prior to emergence of the last hatchling (Soler et al. 1997). Significantly more magpie eggs hatch in unparasitised (5.0) than in parasitised (1.3) nests (Soler et al. 1996).

After hatching, the cuckoo chick does not evict the magpie eggs and, although both parasitic and host chicks

hatch with a very similar size and weight (Soler and Soler 1991), the growth rate of the cuckoo chick is much higher than that of the host chicks (Soler and Soler 1991). This confers on the cuckoo a great competitive advantage (M. Soler et al. 1995b). Magpie nestlings will often starve due to the intense competition for food in the nest (Cramp 1985; Soler 1990; Soler and Soler 1991; Soler et al. 1996).

Magpies do not recognise the alien nature of cuckoo chicks (Rothstein 1990; M. Soler et al. 1995c). Rather, magpies feed cuckoo nestlings more often, not only because of their larger size but also because the cuckoo nestling has a gape with well-developed palatal papillae that acts as a super-stimulus (M. Soler et al. 1995b). Most parasitised nests produce no magpie chicks; on average there are only 0.6 (sample size=206, SE=0.09) magpie fledglings per parasitised nest, while the success of unparasitised nests is 3.5 (sample size=106, SE=0.14) magpie fledglings (Soler et al. 1996).

Adult cuckoos may act as nest predators of magpies that reject parasitic eggs from their nests. This peculiar cuckoo behaviour, which is known as "Mafia" behaviour, has been experimentally demonstrated (M. Soler

et al. 1995d), and it has been suggested that it is a counter-adaptation to the host's ability to recognise and reject cuckoo eggs and/or chicks (Zahavi 1979). In this review we shall pay special attention to this behaviour and its implications in the ongoing coevolutionary process in which magpies and great spotted cuckoos are engaged.

Evidence for coevolution between great spotted cuckoos and their magpie hosts

Here we review adaptations and counteradaptations of both host and parasites at two different stages of the reproductive cycle (before laying and during egg stage). These coevolutionary interactions are summarised in Figs. 1, 2.
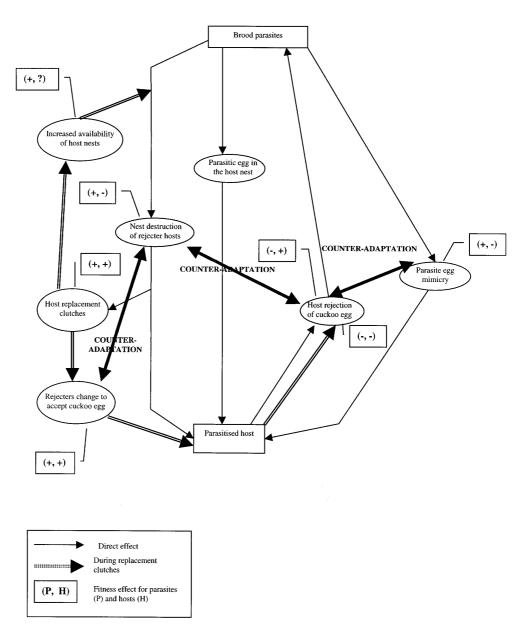
Before laying

Cuckoo host choice

Parasitism can occur at random if more than one magpie nest is available. However, if the fitness of brood

Fig. 1 Diagram showing interactions between the great spotted cuckoo and its magpie host including nest selection by cuckoos, nest defence by magpies, and parasite laying behaviour. Fitness effects for parasites and hosts are shown for each of the strategies adopted by cuckoos and hosts

Fig. 2 Diagram showing inter-
actions between the great spot-
ted cuckoo and its magpie hosts
including host rejection of
cuckoo eggs, cuckoo egg mim-
icry, cuckoo Mafia behaviour,
and adaptive change of rejecter
magpies to accept parasitic
eggs during replacement
clutches. Fitness effects for
parasites and hosts are shown
for each of the strategies adopt-
ed by cuckoos and hosts

parasites increases when using hosts of a given pheno-
type, natural selection will favour parasitism of this phe-
notype (Price 1980). This would be especially relevant if
cuckoos select hosts with high parental ability because
these foster parents will provide their young with a
greater quantity/quality of food than hosts of low paren-
tal ability (Fig. 1). In a test of this hypothesis, we
demonstrated that selected (i.e. parasitised) magpies
were able to successfully rear more nestlings than non-
selected (i.e. non-parasitised) magpies (J.J. Soler et al.
1995), even though selected and non-selected nests had
the same number of parasitic and non-parasitic eggs.

How do cuckoos estimate parental quality of poten-
tial hosts before or during laying? One possibility is to
use sexually selected traits that signal host parental
quality (Heywood 1989; Hoelzer 1989; Grafen 1990;
Price et al. 1993) such as nest size (J.J. Soler et al.
1998). In agreement with this hypothesis, great spotted

cuckoos prefer to parasitise larger nests (J.J. Soler et al.
1995).

Additional evidence of cuckoos selecting magpies
with large nests comes from a study of 14 European
magpie populations that vary in levels of parasitism (J.J.
Soler et al. 1999b). As nest size in magpies is a sexually
selected character (J.J. Soler et al., in press, a), parasitic
and sexual selection pressures should represent antago-
nistic forces working on the same character – the tenden-
cy to produce a nest of a certain size (Fig. 1). A reduc-
tion in nest size is predicted to be caused by an increase
in parasitic selection pressure. In accordance with the
hypothesis, nest volume was on average reduced by
33.2% in areas of sympatry between parasite and host, as
compared to areas of allopatry (J.J. Soler et al. 1999b).
Additionally, differences in the volume of magpie nests
within different populations were correlated in a signifi-
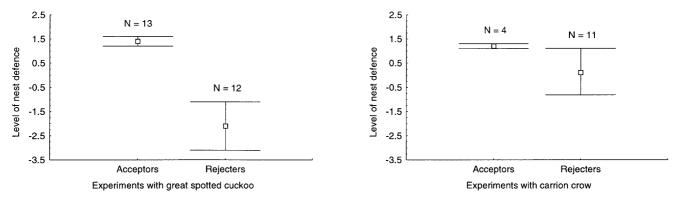cant and negative manner with levels of parasitic selec-

Fig. 3 Level of nest-defence of acceptor and rejecter magpies when exposed to a great spotted cuckoo or a carrion crow. See J.J. Soler et al. (1999c) for methodology to estimate level of nest defence. *Values* are from J.J. Soler et al. (1999c), and are means±SE

tion pressure (e.g. prevalence of parasitism and ability of magpies to recognise foreign eggs) (J.J. Soler et al. 1999b). (The latter analysis included a control for genetic distance between populations). Thus, there is strong evidence for the effect of great spotted cuckoos on the evolution of nest size in magpies.

Nest defence by hosts

The first opportunity for hosts to avoid parasitism is to defend their nests against brood parasites (Fig. 1) (Payne 1997b). It is possible that the same behavioural adaptations that defend a nest against parasitism evolved from behavioural patterns that defend the occupants of a nest from predation. In an experiment using three great spotted cuckoos and one carrion crow (the primary predator of magpies), we found that magpies defended their nests against cuckoos at a level similar to that used against carrion crows (J.J. Soler et al. 1999c). Evidence as to whether specific behaviours evolved in response to predation or parasitism can be obtained through analysis of coevolutionary patterns. For example, if magpie nest defence evolved in direct response to parasitism, then we should be able to observe coevolved mechanisms in cuckoos that overcome the nest defence mechanisms of magpies. In fact, great spotted cuckoos have a special laying behaviour called "distraction strategy" (Fig. 1; Arias de Reyna 1998). When a female cuckoo is about to lay, the cuckoo's mate provokes an attack by both male and female magpies. As soon as the hosts leave the nest, the female cuckoo will lay her egg in 2–3 s (Alvarez and Arias de Reyna 1974; Arias de Reyna et al. 1982). In areas of high predation, one might predict the evolution of magpie behaviour at two levels that would mitigate susceptibility to the cuckoo's distraction strategy. Magpies could evolve an ability to recognise the approach of a parasitic cuckoo, and take action to prevent the approach, or magpies could redress the consequences of cuckoo parasitism after the distraction strategy has been employed by evoving an ability to recognise parasitic

eggs and reject them from the nest. In fact, one might predict trade-offs in the evolution of these two patterns – i.e. magpies that can recognise and remove parasitic eggs may be less effective at defending the nest against the approach of a cuckoo, compared to magpies that cannot recognise and remove parasitic eggs. Additionally, if these behavioural differences were due to the direct response to parasitism, it can be predicted that "recogniser" magpies and "non-recogniser" magpies would not differ in their patterns of predator response.

To test these predictions, we (J.J. Soler et al. 1999c) performed an egg recognition experiment with the same magpies that were tested for their ability to defend the nest against a carrion crow or a great spotted cuckoo. We found that magpies with the ability to recognise and reject cuckoo eggs defended their nests against the great spotted cuckoo with less intensity than non-recogniser magpies. Moreover, the level of nest defence did not vary between recogniser and non-recogniser magpies when they were exposed to the predator (crow; Fig. 3, data from J.J. Soler et al. 1999c). These results imply that the tendency for lower nest-defence behaviour of non-recogniser magpies is a coevolutionary trait that has developed as a direct consequence of selection pressures from the "distraction strategy", and not as a secondary consequence of evolved anti-predator defences.

Magpies have a second possible mechanism to reduce the probability of being parasitised: female magpies could concentrate egg laying within a short interval, thus diluting the effects of the parasitism. Cuckoos must then synchronise their egg-laying date to that of the magpies because the success of cuckoo offspring depends on precise coordination with the magpie laying sequence (Soler 1990; Soler et al. 1997; M. Soler et al. 1998b). Cuckoo females have a long period of egg laying (i.e., more than 1 month), but the magpie egg laying period is only 1 week (Birkhead 1991). Dilution of parasitism would be maximised if magpies started to lay synchronously with the rest of the population (Martínez et al. 1996). This possible magpie adaptation does not rely on group-selection arguments – it only requires selection to favour behaviour in individuals that causes them to start laying in response to common environmental cues. Moreover, since laying date has a genetic component (Stearns 1992) and is related to magpie quality (Birkhead 1991), by selecting specific host phenotypes (i.e., high-quality mag-

pie parents), great spotted cuckoos would provoke a synchronisation of magpie egg laying, thereby, indirectly causing a negative feedback for cuckoo fitness (Fig. 1). In accordance with this scenario, Martínez et al. (1996) found that magpies breeding in plots with synchronised laying dates, and with a high density of nests, experienced a lower probability of being parasitised than magpies breeding with asynchronous laying dates and lower nest densities.

During egg stage

Cuckoos destroying magpie eggs when laying

Magpies often stop incubating eggs about 5–8 days after the first chick has hatched (Soler et al. 1997). Late-laid cuckoo eggs will experience a lower probability of successful hatching than early-laid eggs. However, cuckoos, by destroying magpie eggs when laying late or after the magpie clutch is finished, would reduce the number of magpie nestlings that otherwise could hatch before cuckoo offspring. By artificially parasitising magpie nests at different times during the magpie laying sequence, we (Soler et al. 1997) demonstrated that this cuckoo behaviour is an adaptation because:

1. Cuckoo breeding success in experimentally parasitised nests was lower than in naturally parasitised nests (with some magpie eggs destroyed by the adult cuckoo).
2. The proportions of both cuckoo eggs hatched and chicks fledged were significantly lower in artificially paratised nests than in naturally parasitised nests.
3. When the laying of a parasite egg early in the breeding cycle of the host was simulated, the reproductive success of the cuckoo was similar in naturally and artificially parasitised nests. In another experiment, Soler and Martínez (in press) found that the number of magpie eggs broken in artificially parasitised nests did not depend on the number of magpie eggs in the nest, and that it was significantly lower than in cases of natural parasitism. Moreover, the cuckoo "decision" to damage more eggs than expected depends on the number of eggs already present in the nest when parasitism occurs, as predicted from the hypothesis that the egg damage behaviour of cuckoos is an adaptation to reduce the costs of late laying (Soler and Martínez, in press).

Adaptive responses by magpies to egg destruction by cuckoos

One possible way for magpies to reduce the effect of parasitism, or counteract the advantage of egg-damage by cuckoos, could be to use damaged eggs as a cue to perform a careful inspection of all eggs in the nest, thereby increasing the probability of detection and rejection
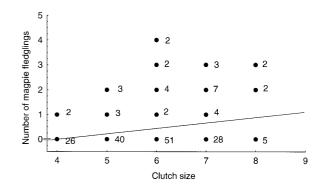

Fig. 4 Relationship between clutch size and fledgling success of parasitised magpie nests where some cuckoo chicks fledged. Data are from 1982–1996. *Numbers* refer to the number of points with the same value. *Line* is regression line ($y=0.22-0.89x$); partial correlation coefficient controlling for laying date, $r=0.29$, $P=0.01$)

of parasitic eggs (M. Soler et al. 1999). To date, this hypothesis has not been supported. Magpie responses to artificial parasitism did not differ between nests where eggs were and in nests where no eggs were damaged. This implies that magpies do not use damaged host eggs to assess parasitism.

Another possible way for magpies to reduce the negative effect of the cuckoo's egg-damaging behaviour is to increase clutch size, which will increase the probability of successful hatching of some magpie eggs (J.J. Soler et al., in press, b). In accordance, clutch size in a heavily parasitised area (Guadix) explained breeding success of parasitised magpies (Fig. 4). Moreover, by analysing the clutch size of 15 sympatric and allopatric magpie populations, we found significantly larger clutch sizes in magpie populations sympatric with cuckoos, even when controlling for the effect of latitude and laying date. The differences among populations were explained by variation in the level of selection imposed by cuckoos (e.g. prevalence of parasitism, and rejection of cuckoo model eggs; while controlling for latitude, or while controlling for genetic distances among populations) (J.J. Soler et al., in press, b). Because clutch size in magpies is not significantly influenced by experimental food provisioning (Högstedt 1981; Hochachka and Boag 1987; Knight 1988; Dhindsa and Boag 1990), we have concluded that the increased clutch size of magpie populations sympatric with cuckoos is due to selection caused by the egg damaging behaviour of cuckoos. These results are congruent with the hypothesis that parasites may influence the optimum values of life-history traits (Richner and Heeb 1995).

Laid cuckoo eggs and host rejection of parasitic eggs

Once the cuckoo female has successfully laid her egg in the host nest, selection should favour a host's ability to recognise and reject it (Fig. 2). To date, this is the best-studied host defence against brood parasitism (Payne 1977a, 1977b; Rothstein 1990; Johnsgard 1997), and
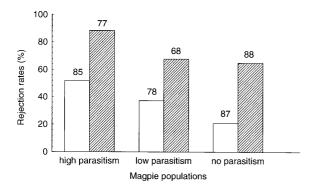
Fig. 5 Rejection rate of mimetic (*open bars*) and non-mimetic model eggs (*hatched bars*) in areas of *high parasitism*, in areas of sympatry between cuckoos and magpies but with *low* (or no) *parasitism*, and in areas of allopatry (*no parasitism*). *Numbers* are sample sizes. Data are from J.J. Soler et al. (1999a)
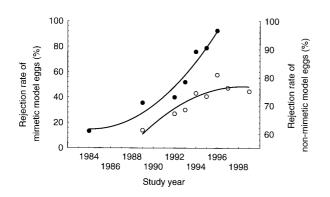

Fig. 6 Rejection rates of mimetic (*open circles*) and non-mimetic (*filled circles*) model eggs in the Guadix magpie population from 1984 to 1998. *Lines* are negative exponential curves fitted to the points

represents the case where coevolutionary relationships have been most clearly defined (e.g. Brooke and Davies 1988; Davies and Brooke 1989a, 1989b; Soler and Møller 1990; Briskie et al. 1992; Davies and Brooke 1998; Robert and Sorci 1999). In the great spotted cuckoo-magpie system, egg recognition and rejection by hosts are the result of a coevolutionary process. This conclusion comes from two different lines of experimentation. First, the highest rejection rate of model eggs occurs in sympatric areas with a high frequency of parasitism, the lowest rejection rate occurs in allopatric populations, and intermediate rejection rates occur in sympatric populations with low parasitism rates (Fig. 5) (Soler and Møller 1990; J.J. Soler et al. 1999a). Moreover, differences in the frequency of parasitism among European magpie populations explained differences in parasitic egg rejection rates (J.J. Soler, J.G. Martínez, M. Soler and A.P. Møller, unpublished work). Second, within a sympatric area, rejection rates of both mimetic and non-mimetic model eggs have increased since 1984 (Fig. 6) (Soler et al. 1994b; M. Soler et al. 1998a).

Adaptive responses of cuckoos to host recognition and rejection of eggs

The best-studied brood parasite response to egg recognition and rejection by the hosts is the evolution of egg mimicry (Fig. 2). Mimicry of parasitic-eggs is a classic example of coevolution (Rothstein 1990; Davies and Brooke 1998), which has been studied primarily in the European cuckoo (e.g. Brooke and Davies 1988; Davies and Brooke 1989a, 1989b; Moksnes et al. 1991; Øien et al. 1995; Soler and Møller 1996). In morphology and size, great spotted cuckoo eggs are similar to those of the magpie, its main host in Europe (Cramp 1985). Baker (1923, 1942) and Jourdain (1925), studied parasitism of magpies in Europe and claimed that the great spotted cuckoo is a perfect example of evolutionary mimicry. However, Friedman (1948) pointed out that great spotted cuckoos in Africa parasitise hosts with eggs that are different in colour and pattern from those of the European corvids. (The pied starling *Spreo bicolor*, the primary host of the great spotted cuckoo in South Africa, lays blue eggs, and the cape crow *Corvus capensis*, a secondary host, lays pink eggs.) Despite these differences in host characteristics, the eggs of the great spotted cuckoo are similar to those laid by European populations, both in size and colour (Friedman 1948). Thus, it is unlikely that the mimicry observed for European cuckoos evolved as a result of selection caused by the recognition and rejection of cuckoo eggs by magpies.

Another possible means for cuckoos to reduce the cost imposed by egg rejection is to inflict additional costs on those hosts that reject a parasitic egg from their nest. Zahavi (1979) first suggested that brood parasites could act as nest predators on hosts that reject parasitism (Mafia hypothesis), thereby reducing the advantages for rejecter hosts. There are anecdotal reports of cuckoos acting as nest predators (Vincent 1933; Wyllie 1981; Bibby and Thomas 1985; Davies and Brooke 1988; Alvarez 1994; Palomino et al. 1998), but this behaviour does not appear to be related to host rejection of parasitic eggs.

We (M. Soler et al. 1995d) tested the Mafia hypothesis in the Guadix magpie population by experimental removal of cuckoo eggs from magpie nests, while keeping other parasitised nests as controls. The analyses of predation rates revealed that those nests from which we experimentally removed cuckoo eggs suffered a significantly higher predation rate than parasitised control nests (M. Soler et al. 1995d). Magpie pairs that fail in their first reproductive attempt lay a replacement clutch. Predatory cuckoos could directly benefit from this behaviour because rejecter hosts which fail to breed due to Mafia behaviour from parasitising cuckoos would lay a replacement clutch and thus offer a second opportunity to the brood parasite (Fig. 2; Arcese et al. 1992). In addition, retaliatory behaviour by cuckoos would be advantageous if, during the first breeding attempt, rejecter hosts learn that it is not beneficial to remove cuckoo eggs from their nests, and they subsequently change their response

to cuckoo eggs in replacement clutches and become acceptors (Fig. 2; M. Soler et al. 1995d).

An explanation involving group selection can be offered to interpret the evolution of retaliatory behaviour in cuckoos. Predation on the nests of an entire host population would create a selective pressure that prevents increases in the rejection rate of the host magpie population over evolutionary time (Guilford and Read 1990; but see also Robert et al. 1999). As an alternative, it is possible that a learning component comes into play over behavioural time, and is involved in the magpie response to Mafia behaviour (M. Soler et al. 1995d). Because the magpie is a long-lived species, individuals may learn over a single lifetime that it is less costly to accept than reject a cuckoo egg from their nest. This latter possibility requires that rejection be a condition-dependent decision. That is, the decision of a recogniser-host concerning whether or not to reject a parasitic egg should depend on environmental factors, which is likely to be the case (e.g. Alvarez 1996; Davies et al. 1996; Brooke et al. 1998; Lindholm 1999; J.J. Soler et al.1999d). As the environment (e.g. food availability, predation intensity; Sorci et al. 1997) changes from one breeding period to the next, the cost of rejecting or not-rejecting a parasitic egg will also change. Cuckoos could exploit the possibility of magpies learning to change from rejecters to non-rejecters during the same breeding season (J.J. Soler et al. 1999d). The positive benefits received by an individual cuckoo who participates in retaliatory behaviour, and induces a magpie to change from a rejecter to a non-rejecter, can explain the evolution of retaliatory behaviour through selection operating at the level of individual phenotypes, removing the need to invoke group-selection arguments (M. Soler et al. 1995d).

Adaptive responses of magpies to Zahavian cuckoos

One can also take the perspective of the magpie in assessing coevolutionary responses to Mafia behaviour by parasitizing cuckoos. We (J.J. Soler et al. 1999d) experimentally tested whether the rejection behaviour of magpie hosts within a breeding season is dependent on nest predation by cuckoos. We performed mimetic-egg recognition tests in a magpie plot with a low parasitism rate (level of parasitism <10%) and in others that had suffered from intense parasitism (>50%) during the previous 5-year period. After having scored the magpies as acceptors or rejecters, we simulated cuckoo predation behaviour by breaking the eggs and leaving them in the nest (for further explanations of experimental design and sample sizes see J.J. Soler et al. 1999d). In accordance with the hypothesis, we found that the frequency of change from rejection to acceptance was significantly different from zero, when assessed for the period between the first and subsequent clutches. The change was more frequent in plots with higher rates of parasitism (J.J. Soler et al. 1999d). The results match the prediction from the hypothesis that parasitism pressure modulates host rejection behaviour during replacement clutches.

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 that is likely to converge on a narrow range of recognition abilities within a population. This hypothesis is driven by acceptance of the notion that it is beneficial for magpies to reject parasitic eggs during the first breeding attempt and change to acceptance for parasitism of subsequent clutches (M. Soler et al. 1995d). This scenario would yield a slow process of selection, favouring an equilibrium at some level of non-recognition. In Guadix, however, where we tested the Mafia hypothesis, the rate of parasitism changes from one year to the next (M. Soler et al. 1998a). In such an environment, an alternative scenario can be envisioned concerning the evolution of different egg-recognition phenotypes. Assuming that the probability of parasitism determines whether hosts should accept or reject cuckoo eggs (Davies et al. 1996; Brooke et al. 1998), selection must exist for fairly fine-tuned abilities to recognise parasitic eggs in magpies. Recognition abilities should be somewhat flexible (i.e., high levels of phenotypic plasticity) in an environment with variable rates of parasitism. During years of low parasitism, recogniser magpies that reject parasitic eggs during the first breeding attempt will have the advantage of laying a replacement clutch with a low probability of being parasitised (close to the population parasitism rate), even if their first clutch is depredated by retaliatory cuckoos. The probability of a parasitised magpie nest being revisited by predatory cuckoos depends on the number of cuckoos in the area (Soler 1990; Zuñiga and Redondo 1992; Soler et al. 1994a). In a year of high parasitism, non-rejecters may be at an advantage, since they would avoid retaliatory behaviour by cuckoos that could destroy the first clutch, and not be at a disadvantage to rejecters since second clutches are equally likely to be parasitised whether a bird is a rejecter or non-rejecter. It is clear that one can justify both the rejecter and non-rejecter phenotypes within a population depending on the levels of parasitism, predation and retaliatory behaviour by cuckoos. We conclude that cuckoo Mafia behaviour does not necessarily imply an evolutionary equilibrium in the level of recognition ability of magpies. Studies on differential lifetime fitness of recogniser and non-recogniser magpies across multiple years of variable parasitism frequency are needed to reach further conclusions.

In study plots with a high parasitism rate, the rejection rate of replacement clutches of pairs that had their first clutch experimentally depredated without presentation of a model egg, did not differ from the overall rejection rate in first clutches (J.J. Soler et al. 1999d). We believe that both nest depredation after rejection of a cuckoo egg, and a high probability of replacement clutches being revisited by cuckoos, are required to provoke a change in the behaviour of magpies from rejection to acceptance.

The importance of a meta-population dynamic approach

Most of the studies and models describing interactions between brood parasites and their hosts are based on single isolated host populations (e.g. Kelly 1987; Takasu et al. 1993; Davies et al. 1996; Pagel et al. 1998; Takasu 1998a, 1998b; Rodríguez-Gironés and Lotem 1999; Robert et al. 1999). During the past few years, it has become clear that use of the meta-population dynamic approach (Levins 1969) is important, not only for the study of the evolution of adaptive traits in general (e.g. Slatkin 1987; Avise 1994; Dias 1996; Holyoak and Lawler 1996), but also of those resulting from coevolutionary interactions (e.g. Thompson 1994; Gandon et al. 1996; Thrall and Burdon 1997; Lively 1999; Nuismer et al. 1999; Parker 1999). For instance, recent theory suggests that the dynamics and migration rates of hosts and parasites are important factors in the maintenance of genetic polymorphisms in resistance and virulence (see review by Thrall and Burdon 1997).

The meta-population approach can inform us about the primary causes of coevolutionary processes in host-parasite systems. Several hypotheses have been proposed to explain why rejection is not universal among hosts of brood parasites. The "evolutionary lag" hypothesis states that although it would be adaptive for hosts to reject parasitic eggs, there has not been sufficient time for them to evolve the ability to do so (e.g. Dawkins and Krebs 1979; Davies and Brooke 1988, 1989b; Rothstein 1990; Moksnes et al. 1991; Øien et al. 1995; Soler and Møller 1996). The "evolutionary equilibrium" hypothesis proposes that it is not necessarily adaptive for hosts to reject parasitic eggs because, for some individuals, the cost of rejection may outweigh the cost of acceptance (Lotem et al. 1992, 1995). Before proceeding to the possible contributions of the meta-population approach, we need to further consider the role of costs in driving coevolutionary dynamics in brood parasite-host systems, especially within the context of the evolutionary equilibrium hypothesis. Following Winfree (1999), equilibrium can be interpreted as the dividing line along which the net benefits of being a rejecter and an acceptor are equal; a given host will be on one side or the other of this line, and will be selected to reject or accept accordingly. Coevolution within populations of the host, infected with the brood parasite, would result in increasing or decreasing levels of defence, which would converge around the set equilibrium line when assessed over long periods. If, however, parasitic pressure varies within the lifetime of a host, and the host's response to parasitism is phenotypically plastic, then the equilibrium may be perennially unstable, moving back and forth across the equilibrium along shorter time scales.

A new dimension is added to the evolutionary equilibrium hypothesis when a meta-population perspective is considered. When, for instance, brood parasites migrate from one host population with high level of defence to another with a low level of defence, the population of hosts can be moved in one large jump to one side of the equilibrium line or the other (M. Soler et al. 1998a). In this simple scenario, where parasites can move from one host population to another, absolute measures of host defence should not necessarily reflect time of coevolutionary interactions with the brood parasite. Instead, host defences will reflect the frequency with which brood parasites invade, and subsequently leave, a population of hosts (Thompson 1998).

When the possibility that individual hosts may migrate from one population to another is taken into account, the scenario becomes even more complex. In magpies, it is known that long distance movements sometimes occur in response to adverse environmental conditions (Birkhead 1991). A differential migration rate for rejecter and acceptor individuals can be predicted in a parasitised host population (J.J. Soler et al. 1999a) since breeding success of rejecter and acceptor individuals is predicted to be different within and among host populations. Juvenile dispersal phenotypes of susceptible individuals (rejecter or acceptor) will vary among populations. For instance, if a host population is heavily exploited by brood parasites, juvenile recruitment would be very low. Then, this population is likely to function as a sink population where parasitic pressures would allow for some host juvenile recruitment and immigration (source population; e.g. Dias 1996). The differential migration rates of rejecter and non-rejecter hosts from parasitised and non-parasitised areas can explain not only the rapid increase in rejection rate of newly exploited host populations (Soler and Møller 1990; Lotem and Rothstein 1995; Robert and Sorci 1999), but also the fact that in host populations rejecter and non-rejecter phenotypes coexist. In accordance, Nuismer et al. (1999), by modelling coevolutionary interactions, demonstrated that gene flow alters the outcome of local interactions and allows the maintenance of allelic polymorphism across all communities under a range of selection intensities and rates of migration.

In magpies and great spotted cuckoos, gene flow seems to be extensive between nearby populations, higher for magpies than cuckoos, and especially high for magpie populations within the area of distribution of the great spotted cuckoo (Martínez et al. 1999). These results suggest that there is extensive genetic exchange between parasitised magpie populations, which might mitigate genetic differentiation. Gene flow in sympatric populations might be interpreted as being a consequence of the host-parasite interaction itself (Martínez et al. 1999). Magpie dispersal might be favoured in a heavily parasitised source population composed mainly of acceptors. If the recipient population is not parasitised, offspring of acceptors will have a higher probability of success by breeding after dispersal than by remaining in the parasitised natal population (Martínez et al. 1999). On the other hand, in a parasitised host population, the majority of dispersers to other populations would be the offspring of rejecters because most acceptors leave no offspring. In this scenario, we (J.J. Soler et al. 1999a)

investigated the influence of gene flow on the rejection ability of magpies from 15 European populations. We estimated genetic differences among the populations using three microsatellite loci as markers (Martínez et al. 1999). Results were in accordance with the rejecter-gene flow hypothesis because rejection rates of non-mimetic model eggs demonstrated a strong genetic component, whereas rejection rates of mimetic model eggs had a strong geographic component (J.J. Soler et al. 1999a). However, there was still a proportion of variance in rejection rates that was not explained by gene flow. One explanation of the residual variance is that an ongoing coevolutionary process is acting in the magpie metapopulation. Accordingly, current parasitism could explain variation in rejection ability after controlling for the effect of gene flow. By taking into account genetic and geographic distances among the magpie populations, we were able to control for the effect of gene flow. We (J.J. Soler, J.G. Martínez, M. Soler and A.P. Møller, unpublished work) found a significant relationship between rejection rates of non-mimetic model eggs, which have a strong genetic component, and parasitism prevalence after controlling for genetic or geographic distances. Correlation analyses cannot be used to make inferences about causation. However, since 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 that suggest that the great spotted cuckoo has been restricted to the Mediterranean basin during the Pleistocene and Holocene, while the European cuckoo *Cuculus canorus* (which may serve as an appropriate control species) occurs throughout Europe (Tyrberg 1998). Thus, the rejection rate of model cuckoo eggs in currently allopatric populations does not seem to be related to a more extensive distribution of the parasite in the past.

By taking into account genetic and geographic distances among the studied magpie populations, we were able to control for the effect of gene flow in the resulting rejection rate of each magpie population. These results allow us to conclude that a coevolutionary process is likely to be currently acting in the great spotted cuckoo-magpie meta-populations, and claim that the use of a meta-population approach is required to know whether hosts and parasites are involved in an ongoing coevolutionary process or whether they exist at an evolutionary equilibrium.

References

Alvarez F (1994) Cuckoo predation on nests of nearest neighbours of parasitized nests. Ardea 82:269–270

Alvarez F (1996) Model cuckoo *Cuculus canorus* eggs accepted by rufous bush chats *Cercotrichas galactotes* during the parasite's absence from the breeding area. Ibis 138:340–342

Alvarez F, Arias de Reyna L (1974) Mecanismos de parasitación por *Clamator glandarius* y defensa por *Pica pica*. Doñana Act Vert 1:43–66

Alvarez F, Arias de Reyna L, Segura M (1976) Experimental brood parasitism of the magpie *Pica pica*. Anim Behav 24:907–916

Aragón J, Møller AP, Soler JJ, Soler M (1998) Molecular phylogeny of cuckoos supports a polyphyletic origin of brood parasitism. J Evol Biol 12:495–506

Arcese P, Smith JNM, Hochachka WM, Rogers CM, Ludwig D (1992) Stability, regulation, and the determination of abundance in an insular song sparrow population. Ecology 73: 805–822

Arias de Reyna L (1998) Coevolution of the great spotted cuckoo and its hosts. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts. Oxford University Press, Oxford, pp 129–142

Arias de Reyna L, Hidalgo SJ (1982) An investigation in egg-acceptance by azure-winged magpie and host recognition by great spotted cuckoo chicks. Anim Behav 30:819–823

Arias de Reyna L, Recuerda P, Corvillo M, Aguilar I (1982) Reproducción del críalo (*Clamator glandarius*) en S. Morena Central. Doñana Acta Vert 9:177–193

Avise JC (1994) Molecular markers, natural history and evolution. Chapman and Hall, London

Baker ECS (1923) Cuckoo's eggs and evolution. Proc Zool Soc Lond 1923:277–294

Baker ECS (1942) Cuckoo problems. Witherby, London

Bibby CJ, Thomas DK (1985) Breeding and diets of reed warblers at a rich and a poor site. Bird Study 32:19–31

Birkhead TR (1991) The magpies. Poyser, London

Briskie JV, Sealy SG (1990) Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107:789–794

Briskie JV, Sealy SG, Hobson KA (1992) Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46:334–340

Brooke M de L, Davies NB (1988) Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. Nature 335:630–632

Brooke M de L, Davies NB, Noble DG (1998) Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. Proc R Soc Lond B 265:1277–1282

Brooker MG, Brooker LC (1989) The comparative breeding behaviour of two sympatric cuckoos, Horsfield's bronze-cuckoo *Chrysococcyx basalis* and the shining bronze-cuckoo *C. lucida*, in western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. Ibis 131:528–547

Brooker MG, Brooker LC (1991) Eggshell strength in cuckoos and cowbirds. Ibis 133:406–413

Buitron D (1988) Female and male specialization in parental care and its consequences in black-billed magpies. Condor 90:29–39

Cramp S (ed) (1985) The birds of the western Palaearctic, vol IV. Oxford University Press, Oxford

Davies NB, Brooke M de L (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284

Davies NB, Brooke M de L (1989a) An experimental study of coevolution between the cuckoo, *Cuculus canorus* and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224

Davies NB, Brooke M de L (1989b) An experimental study of coevolution between the cuckoo, *Cuculus canorus* and its hosts. II. Host egg marking, chick discrimination and general discussion. J Anim Ecol 58:225–236

Davies NB, Brooke M de L (1998) Cuckoos versus hosts: experimental evidence for coevolution. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts. Oxford University Press, Oxford, pp 59–79

Davies NB, Brooke M de L, Kacelnik A (1996) Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. Proc R Soc Lond B 263:925–931

Dawkins R, Krebs JR (1979) Arms race within and between species. Proc R Soc Lond B 205:489–511

Dhindsa M, Boag DA (1990) Influence of food supplementation on the reproductive success of black-billed magpies *Pica pica*. Ibis 132:595–602

Dias PC (1996) Sources and sinks in population biology. Trends Ecol Evol 11:326–330

Friedman H (1948) The parasitic cuckoo of Africa (Monograph 1). Washington Academy of Sciences, Washington, DC

Frisch O von (1969) Die Entwicklung des Häherkuckucks (*Clamator glandarius*) im Nest der Wirtsvögel und Nachzucht in Gefangenschaft. Z Tierpsychol 26:641–650

Gandon S, Capowiez Y, Dubois Y, Michalakis Y, Olivieri I (1996) Local adaptation and gene-for-gene coevolution in a metapopulation model. Proc R Soc Lond B 236:1003–1009

Grafen A (1990) Sexual selection unhandicapped by the Fisher process. J Theor Biol 144:475–516

Guilford T, Read AF (1990). Zahavian cuckoos and the evolution of nestling discrimination by hosts. Anim Behav 39:600–601

Heywood JS (1989) Sexual selection by the handicap mechanism. Evolution 43:1387–1397

Hochachka W, Boag D (1987) Food shortage for the black-billed magpie (*Pica pica*): an experiment using supplemental food. Can J Zool 65:1270–1274

Hoelzer GA (1989) The good parent process of sexual selection. Anim Behav 38:1067–1078

Högstedt G (1981) Effect of additional food on reproductive success in the magpie (*Pica pica*). J Anim Ecol 50:219–229

Holyoak M, Lawler S (1996) The role of dispersal in predator-prey metapopulation dynamics. J Anim Ecol 65:640–652

Johnsgard PA (1997) The avian brood parasites. Deception at the nest. Oxford University Press, Oxford

Jourdain FCR (1925) A study of parasitism in the cuckoos. Proc Zool Soc Lond 1925:639–667

Kelly C (1987) A model to explore the rate of spread of mimicry and rejection in hypothetical populations of cuckoos and their hosts. J Theor Biol 125:283–299

Knight RL (1988) Effects of supplemental food on the breeding biology of the black-billed magpie. Condor 90:956–958

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lindholm A (1999) Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. J Anim Ecol 68:293–309

Lively CM (1999) Migration, virulence, and geographic mosaic of adaptation by parasites. Am Nat 153:s34–s47

Lotem A, Rothstein SI (1995) Cuckoo-host coevolution: from snapshots of an arm race to the documentation of microevolution. Trends Ecol Evol 10:436–437

Lotem A, Nakamura H, Zahavi A (1992) Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav Ecol 3:128–132

Lotem A, Nakamura H, Zahavi A (1995) Constraint of egg discrimination and cuckoo host coevolution. Anim Behav 49:1185–1209

Martínez JG, Soler M, Soler JJ (1996) The effect of magpie breeding density and synchrony on brood parasitism by great spotted cuckoos. Condor 98:272–278

Martínez JG, Burke T, Dawson D, Soler JJ, Soler M, Møller AP (1998a) Microsatellite typing reveals mating patterns in the brood parasitic great spotted cuckoo (*Clamator glandarius*). Mol Ecol 7:289–297

Martínez JG, Soler JJ, Soler M, Burke T (1998b) Spatial patterns of egg laying and multiple parasitism in a brood parasite: a non-territorial system in the great spotted cuckoo (*Clamator glandarius*). Oecologia 117:286–294

Martínez JG, Soler JJ, Soler M, Møller AP, Burke T (1999) Comparative population structure and gene flow of a brood parasite the great spotted cuckoo (*Clamator glandarius*), and its primary host, the magpie (*Pica pica*). Evolution 53:269–278

Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behavior 116:64–89

Moksnes A, Røskaft E, Braa AT (1993) Rejection behavior by common cuckoo hosts towards artificial brood parasite eggs. Auk 108:348–354

Nuismer SL, Thompson LN, Gomulkiewicz R (1999) Gene flow and geographically structured coevolution. Proc R Soc Lond B 266:605–609

Øien IJ, Moknes A, Røskaft E (1995) Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo *Cuculus canorus*. Behav Ecol 6:166–174

Pagel M, Møller AP, Pomiankowski (1998) Retaliatory cuckoos select for hosts that rear cuckoo nestlings. Behav Ecol 9:566–572

Palomino JJ, Martin-Vivaldi M, Soler M (1998) Early arrival is not advantageous for bush robins in a population parasitized by common cuckoos. Auk 115:235–239

Parker MA (1999) Mutualism in metapopulations of legumes and rhizobia. Am Nat 153:s48-s60

Payne RB (1973) Individual laying histories and the clutch size and numbers of eggs of parasitic cuckoos. Condor 75:414–438

Payne RB (1974) The evolution of clutch size and reproductive success in parasitic cuckoos. Evolution 28:169–181

Payne RB (1977a) The ecology of brood parasitism in birds. Annu Rev Ecol Syst 8:1–28

Payne RB (1977b) Clutch size, egg size, and the consequence of single vs. multiple parasitism in parasitic finches. Ecology 58:500–513

Payne RB (1997a) Family Cuculidae. In: Hoyo J del, Elliot A, Sargatal L (eds) Handbook of the birds of the world, vol 4. Sandgrouses to cuckoos. Lynx, Barcelona, pp 508–607

Payne RB (1997b) Avian brood parasitism. In: Clayton DH, Moore J (eds) Host parasite coevolution. General principles and avian models. Oxford University Press, Oxford, pp 338–369

Price PW (1980) Evolutionary biology of parasites. Princeton University Press, Princeton

Price T, Schluter D, Heckman EN (1993) Sexual selection when the female directly benefits. Biol J Linn Soc 48:187–211

Rahn H, Curran-Everett L, Booth DT (1988) Eggshell differences between parasitic and non-parasitic Icteridae. Condor 90:962–964

Richner H, Heeb P (1995) Are clutch size and brood size patterns in birds shaped by ectoparasites? Oikos 73:435–441

Robert M, Sorci G (1999) Rapid increase of host defense against brood parasites in a recently parasitized area, the case of the village weaver in Hispaniola. Proc R Soc Lond B 266:941–946

Robert M, Sorci G, Møller AP, Hochberg ME, Pomiankowski A, Pagel M (1999) Retaliatory cuckoos and the evolution of host resistance to brood parasites. Anim Behav 58:817–824

Rodríguez-Gironés MA, Lotem A (1999) How to detect a cuckoo egg: a signal-detection theory model for recognition and learning. Am Nat 153:633–648

Rothstein SI (1990) A model system for studying coevolution: avian brood parasitism. Annu Rev Ecol Syst 21:481–508

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236:787–792

Soler JJ, Møller AP (1996) A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. Behav Ecol 7:89–94

Soler JJ, Soler M, Møller AP, Martínez JG (1995) Does the great spotted cuckoo choose magpie hosts according to their parenting ability? Behav Ecol Sociobiol 36:201–206

Soler JJ, Møller AP, Soler M (1998) Nest building, sexual selection and parental investment. Evol Ecol 12:427–441

Soler JJ, Martínez JG, Soler M, Møller AP (1999a) Rejection behavior of European magpie populations in relation to genetic and geographic variation: an experimental test of rejecter-gene flow. Evolution 53:947–956

Soler JJ, Martínez JG, Soler M, Møller AP (1999b) Host sexual selection and cuckoo parasitism: an analysis of nest size in sympatric and allopatric magpie *Pica pica* populations parasitized by the great spotted cuckoo *Clamator glandarius*. Proc R Soc Lond B 266:1765–1771

Soler JJ, Soler M, Pérez-Contreras T, Aragón S, Møller AP (1999c) Antagonistic anti-parasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. Behav Ecol 10:707–713

Soler JJ, Sorci G, Soler M, Møller AP (1999d) Change in host rejection behavior mediated by the predatory behavior of its brood parasite. Behav Ecol 10:275–280

Soler JJ, Neve L de, Martínez JG, Soler M (in press, a) Nest size affects clutch size and the start of incubation in magpies: an experimental study. Behav Ecol

Soler JJ, Martínez JG, Soler M, Møller AP (in press, b) Host life-history and brood parasitism: an analysis of sympatric and allopatric magpie *Pica pica* populations parasitized by the great spotted cuckoo *Clamator glandarius*. Ecology

Soler M (1990) Relationship between the great spotted cuckoo, *Clamator glandarius*, and its corvid hosts in a recently colonized area. Ornis Scand 21:212–223

Soler M, Martínez JG (in press) Is egg-damaging behaviour by great spotted cuckoo an accident or an adaptation? Behav Ecol

Soler M, Møller AP (1990) Duration of sympatry and coevolution between great spotted cuckoo and its magpie host. Nature 343:748–750

Soler M, Soler JJ (1991) Growth and development of great spotted cuckoos and their magpie host. Condor 93:49–54

Soler M, Soler JJ (1999) Innate versus learned recognition of conspecifics in great spotted cuckoos *Clamator glandarius*. Anim Cogn 2:97–102

Soler M, Palomino JJ, Martínez JG, Soler JJ (1994a) Activity, survival, independence and migration of fledgling great spotted cuckoo. Condor 96:802–805

Soler M, Soler JJ, Martínez JG, Møller AP (1994b) Micro-evolutionary change in host response to a brood parasite. Behav Ecol Sociobiol 35:295–301

Soler M, Palomino JJ, Martínez JG, Soler JJ (1995a) Communal parental care by monogamous magpie hosts of fledgling great spotted cuckoos. Condor 97:804–810

Soler M, Martínez JG, Soler JJ, Møller AP (1995b) Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* chicks. Behav Ecol Sociobiol 37:7–13

Soler M, Soler JJ, Martínez JG, Møller AP (1995c) Chick recognition and acceptance: a weakness in magpies exploited by the parasitic great spotted cuckoo. Behav Ecol Sociobiol 37:243–248

Soler M, Soler JJ, Martínez JG, Møller AP (1995d) Magpie host manipulation by great spotted cuckoos: evidence for an avian mafia? Evolution 49:770–775

Soler M, Martínez JG, Soler JJ (1996) Effects of brood parasitism by the great spotted cuckoo on the breeding success of the magpie host: an experimental study. Ardeola 43:87–96

Soler M, Soler JJ, Martínez JG (1997) Great spotted cuckoos improve their reproductive success by damaging magpie host nests. Anim Behav 54:1227–1233

Soler M, Soler JJ, Martínez JG, Pérez-Contreras T, Møller AP (1998a) Micro-evolutionary change and population dynamics of a brood parasite and its primary host: the intermittent arms race hypothesis. Oecologia 117:381–390

Soler M, Soler JJ, Martínez JG (1998b) Duration of sympatry and coevolution between the great spotted cuckoo (*Clamator glandarius*) and its primary host the magpie (*Pica pica*) In: Rothstein SI, Robinson SK (eds). Oxford: Oxford University Press; 113–128

Soler M, Soler JJ, Pérez-Contreras T (1999) The cost of host egg damage caused by a brood parasite: experiments on great spotted cuckoos (*Clamator glandarius*) and magpies (*Pica pica*). Behav Ecol Sociobiol 46:381–386

Sorci G, Soler JJ, Møller AP (1997) Reduced immunocompetence of nestlings of replacement clutches in the European Magpie (Pica pica). Proc R Soc Lond B 264:1593–1598

Spaw CD, Rohwer S (1987) A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307–318

Stearns S (1992) The evolution of life histories. Oxford University Press. New York

Takasu F (1998a) Modelling the arms race in avian brood parasitism. Evol Ecol 12:969–987

Takasu F (1998b) Why do all host species not show defence against avian brood parasitism: evolutionary lag or equilibrium? Am Nat 151:193–295

Takasu F, Kawasaki K, Nakamura H, Cohen JE, Shigesada N (1993) Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses. Am Nat 142:819–839

Thompson JN (1994) The coevolutionary process. The University of Chicago Press, Chicago

Thompson JN (1998) The population biology of coevolution. Res Popul Ecol 40:159–166

Thompson JN (1999) Specific hypotheses on the geographic mosaic coevolution. Am Nat 153:S1–S14

Thrall PH, Burdon JJ (1997) Host pathogen dynamics in a meta-population context. The ecological and evolutionary consequences of being spatial. J Ecol 88:743–753

Tyrberg T (1998) Pleistocene birds of the Paleactic: a cataloge. Nuttall Ornithological Club, Museum of Comparative Zoology, Harvard University Press. Cambridge

Vincent J (1933) Cuckoo killing nestling meadow-pipits. Br Birds 27:51

Winfree R (1999) Cuckoos, cowbirds and the persistence of brood parasitism. Trend Ecol Evol 14:338–343

Wyllie I (1981) The cuckoo. Batsford. London

Zahavi A (1979) Parasitism and nest predation in parasitic cuckoos. Am Nat 113:157–159

Zuñiga JM, Redondo T (1992). No evidence for variable duration of sympatry between the great spotted cuckoo and its magpie host. Nature 359:410–411