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Juan José Soler · Manuel Soler · Anders Pape Møller
Juan Gabriel Martínez

Does the great spotted cuckoo choose magpie hosts according to their parenting ability?

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Abstract When brood parasites are about to lay an egg, they have to decide which nest to parasitize. The best nest in which to lay will depend on the parenting ability of the host. We have studied selection of magpie (*Pica pica*) hosts by great spotted cuckoos (*Clamator glandarius*). Great spotted cuckoos preferentially parasitize large host nests. Nest volume in magpies is a good indicator of territory quality, since there is a negative relationship between magpie nest size and breeding date, and timing of breeding in magpies is known to be positively related to territory quality. Moreover, magpies occupying high-quality territories have high breeding success. Therefore, nest size is positively related to the quality of magpies. Parasitized magpie nests were of greater volume than the nearest neighbouring nest not parasitized by the great spotted cuckoo. In order to test whether the great spotted cuckoos might select high-quality magpie hosts, we manipulated pairs of parasitized and non-parasitized nests with identical laying dates and habitats, introducing into each of the nests the same number of parasitic and non-parasitic eggs. The number of fledglings reared (magpie plus great spotted cuckoo chicks) in naturally parasitized nests was higher than in experimentally parasitized nests. Thus, the probability of survival of the parasite chicks increased if cuckoo eggs were laid in the nests of high-quality hosts originally chosen by the parasite.

Key words Brood parasitism · Host selection · Parenting ability · Nest building

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J.J. Soler (✉) · A.P. Møller
Department of Population Biology, Zoological Institute,
University of Copenhagen, Universitetparken 15,
DK-2100 Copenhagen Ø, Denmark

M. Soler · J.G. Martínez
Departamento de Biología Animal y Ecología, Facultad de
Ciencias, Universidad de Granada, E-18071 Granada, Spain

Introduction

Avian brood parasites lay their eggs in the nests of other bird species which incubate the parasite eggs and rear the young (Payne 1977; Rothstein 1990). When brood parasites are about to lay an egg, they have to decide where to lay (Krebs and Kacelnik 1991; Maynard Smith 1978). The best nest in which to lay the egg will be the one which provides the highest probability of hatching and producing a fledgling. If the probability of hatching and fledging successfully is increased by parasitizing certain host individuals, it would be of great value for the parasite to be able to recognize these good hosts from their behaviour, nest characteristics or other conspicuous features. Thus, the choice by parasites of hosts with high parenting ability would be favoured by natural selection because, as is commonly believed, parents of high-quality provide their young with a greater quantity/quality of food, and have higher fledging success than parents of low quality (Clutton-Brock 1991).

However, factors other than parental ability may also affect a parasitic female's decision of where to lay an egg. For example, defence against parasitism by the owner of the nest may also be important. For example, Davies and Brooke (1988) considered the possibility that the acceptance of non-mimetic eggs by a cuckoo host occurs mainly among naive breeders, and Lotem et al. (1992) found that great reed warblers (*Acrocephalus arundinaceus*) with juvenile plumage more frequently accepted cuckoo eggs than birds in fully adult plumage. By contrast, although brood parasites are known to select hosts in relation to the parental feeding ability of the host species (e.g. type of food, size of host) (Rothstein 1990), the importance of intraspecific individual differences in the potential capacity of hosts to raise parasitic offspring has not been investigated for any host species.

The great spotted cuckoo (*Clamator glandarius*) is an obligate brood parasite which, in Europe, mainly parasitizes the magpie (*Pica pica*), a corvid that normally builds a domed nest with a stick framework; if the nest is roofed, the overall shape is almost spherical. The magpies build a bowl of mud within the stick framework, and this is lined with fibrous roots, hair and grass (Birkhead 1991). The aims of this study were to answer the following questions, using this host-parasite system:

1. Is nest size of the host a good indicator of territory quality? The size of the magpie nest is highly variable. If it is costly to build nests, only individuals in good condition will be able to build large nests (Zahavi 1987). Thus nest building behaviour could provide information to pair members about the quality of the partner, and this assessment of mate quality may allow individuals to decide how much to invest in reproduction, as sexual selection theory predicts for monogamous species (Burley 1986; Moreno et al. 1994). If this is the case, we should expect a positive correlation between nest size and parental quality. Magpie breeding territories differ in quality, and there is a negative relationship between territory quality and laying date (Birkhead 1991; Goodburn 1991; Högstedt 1981). The prediction is that there will be a negative relationship between nest size and laying date.
2. Do great spotted cuckoos preferentially parasitize host nests of a specific size? There are two different possibilities:
   A. Cuckoos may prefer small nests, since a small nest may be more accessible. It will have fewer sticks in the roof (and sometimes be undomed), and the cup may be accessible through several entrances, while large nests only have one available entrance. Thus parasitism could be quicker than in large nests.
   B. Cuckoos may prefer large host nests, if large nests reflect higher quality territories.
3. Does the great spotted cuckoo selectively parasitize high-quality magpie pairs? As it should be advantageous for a cuckoo to lay its eggs in the nests of magpies of superior parenting ability, a larger number of chicks should be reared in parasitized magpie nests compared with unparasitized nests, if nest size reliably reflects host parenting ability.

Materials and methods

Study area

The study was carried out in Hoya de Guadix, southern Spain (37° 18′N, 3°11′W), a high-altitude plateau approximately 1000 m above sea level. The vegetation is sparse, including cultivated cereals (especially barley) and many groves of almond trees (*Prunus dulcis*), the habitat in which magpies are most abundant (Soler 1990). The distribution of trees is patchy and the distance between patches (study plots) varies from 4 to 15 km. (See Soler et al. (1994) for a more detailed description of the study area.)

Measurement of nest size

The preference of magpie nests by the great spotted cuckoo was studied in 85 magpie nests during 1992 and 1993 (52 and 33, respectively). We measured the size of nests using a ruler (precision ± 1 cm, as shown in Fig. 1). Nest volume was calculated as 4/3 $(\pi \times a \times b^2)/1000$ (in litres), where a is the largest radius of the ellipsoid nest and b is half the nest width. We measured only nests of first clutches placed in almond trees; nests of replacement clutches or nests built on top of older nests were not considered.

Experimental design

To test whether the great spotted cuckoo selectively parasitized high quality magpie pairs, we carried out an experiment during the breeding seasons of 1992 and 1993. In the first days of the laying period, pairs of parasitized and unparasitized nests with identical laying dates and habitats were located. We manipulated the clutches by introducing into both parasitized and unparasitized nests exactly the same number of parasitic and non-parasitic eggs. These nests were checked at least three times per week during the incubation period. We exchanged any crushed eggs in each nest (in the previously parasitized nests), because parasitism often leads to egg breakage. If an egg had not hatched at the normal time of hatching, it was replaced by a chick of the same age as the rest of the nestlings. We checked the number of parasite and host chicks in every nest (cuckoo chicks can leave the nest when 15 days old) 12–14 days after hatching. We checked the nests again 10 days later. Consequently, we matched nests with respect to area, number of eggs and, later, number of chicks. Thus, the only difference between two matched nests was that half of them had been previously parasitized by the great spotted cuckoo and the other half had not. Following the prediction, the number of chicks reared in naturally parasitized nests should be higher than in their matched experimentally parasitized ones.

Cuckoo eggs require a short incubation period and usually hatch before magpie eggs, thus enabling them to outcompete magpie chicks (Soler and Soler 1991). However, in order to control this natural cuckoo advantage, we forced hatching synchrony, and thus in all pairs of experimental nests the eggs hatched within 24 h; we created this situation because we were looking for differences in parental ability only.

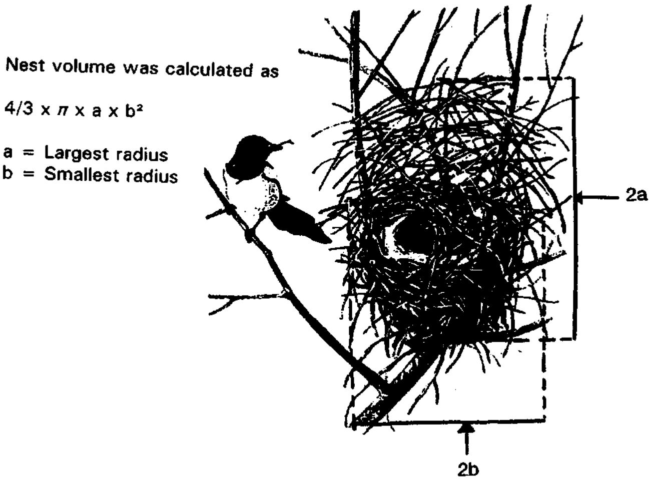

Fig. 1 Magpie nest and the formula used to calculate nest volume

We manipulated 20 nests (10 matched pairs, 7 in 1992 and 3 in 1993) and the number of eggs in each nest were 4+2 (magpie and cuckoo eggs, respectively) in seven matched pairs, 4+3 in two matched pairs and 4+1 in one matched pair.

Statistical procedures

Both nest volume and laying date were normally distributed and we have therefore used parametric tests (Sokal and Rohlf 1981). We used paired *t*-tests to analyse the difference in volume between parasitized and unparasitized nests, and parasitized and unparasitized nests were matched with respect to study plot and breeding date. That is, we selected one parasitized nest and its matched nest was the nearest unparasitized nest. We have not considered pairs of nests from different patches or different years, and remote nests were excluded because we were unable to match these with other nests in the same study plot. We used each nest only once. In order to control for the date effect on nest size (there is a negative relationship), we used residual values of nest size from the regression of nest size (dependent variable), on laying date (independent variable) (Sokal and Rohlf 1981). These residuals are the positive or negative differences between the expected and the observed values, and control for the effects of laying date. The number of fledglings in naturally and experimentally parasitized magpie nests were compared in a Wilcoxon matched-pairs signed-ranks test (Siegel and Castellan 1988). All tests are two-tailed.

Results

Is nest size a good predictor of breeding date?

Our data show a significant negative correlation between magpie nest size and laying date ($r=-0.35$, $n=85$, $P<0.001$; Fig. 2). Thus, large nests are associated with early breeding in accordance with our prediction. Therefore, we can establish a direct relationship between nest size and breeding date.

Does the great spotted cuckoo preferentially parasitize nests of a specific size?

Larger magpie nests were preferentially used by the great spotted cuckoo. Parasitized magpie nests had a significantly larger volume (positive residual, see Materials and methods) than its nearest matched unparasitized nest (pairs *t*-test, $t=2.20$, $df=22$, $P=0.04$; Fig. 3). This result is consistent with the second possibility of prediction number two.

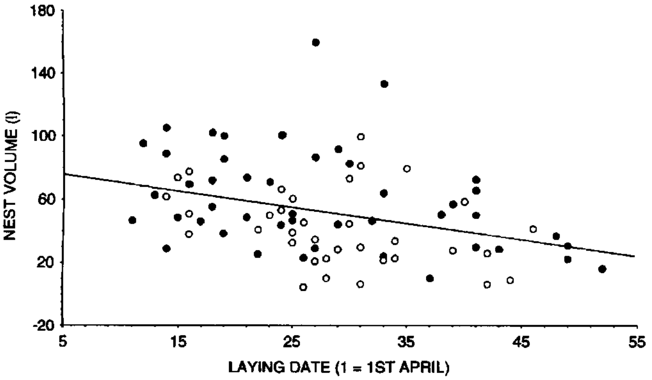

Fig. 2 Relationship between laying date and nest volume (l) of magpie nests (*solid circles* parasitized nests, *open circles* unparasitized nests). $r=-0.35$, $n=85$, $P<0.001$

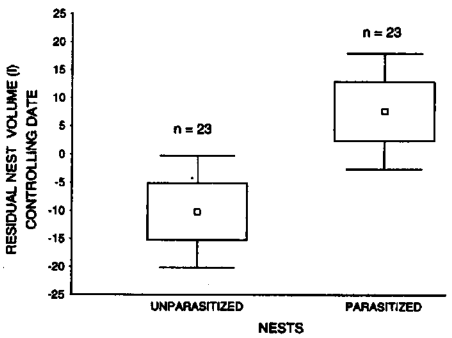

Fig. 3 Residual size of parasitized and unparasitized magpie nests after controlling for laying date. Values are means (*small squares*), standard error (SE) (*boxes*) and 95% confidence intervals (*bars*); $t=2.20$, $df=22$, $P=0.04$

There is also one alternative possibility; that is, the size of the nest is positively related to clutch size. The fact that both nest size and clutch size in the magpie decline over the season (see references in Birkhead 1991; our data, clutch size and laying date: $r=-0.27$, $n=104$, $P=0.005$) could explain the negative relationship between nest size and laying date. However, our data reveal no relationship between clutch size and nest size ($r=0.01$, $n=104$, $P=0.91$).

Does the great spotted cuckoo preferentially parasitize high-quality magpie pairs?

The number of fledglings reared (magpie plus great spotted cuckoo chicks) in naturally parasitized nests was higher than in experimentally parasitized nests (Wilcoxon matched-pairs signed-ranks test, $T=0$, $P=0.04$, n(with differences)=5, n(experiments)=10; Fig. 4, Table 1). In no case did magpies with an experimentally parasitized nest rear more chicks than the matched parasitized nest, and in five naturally parasitized nests the number of fledglings was higher than in experimentally parasitized nests ($n=10$). In seven pairs of nests the number of parasitic fledglings was identical while in the other three, it was higher in naturally parasitized than in experimentally parasitized nests (Wilcoxon matched-pairs signed-ranks test, $T=0$, $P=0.11$, n(with differences)=3, n(experiments)=10; Fig. 4, Table 1). The number of host fledglings was higher in two experimentally parasitized nests than in their matched nest, while in four pairs of nests the opposite was the case; and in the other four nests there were no fledglings. However, there was no significant difference in the number of host fledglings between experimental groups (Wilcoxon matched-pairs

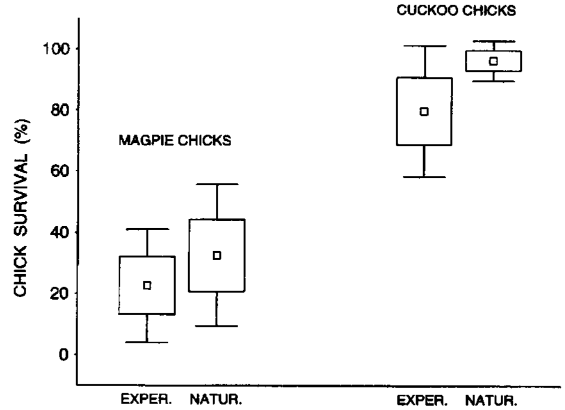

Fig. 4 Survival of magpie and cuckoo chicks in experimentally and naturally parasitized nests. Values are means of percentages (*small squares*) standard error (SE) (*boxes*) and 95% confidence intervals (*bars*)

signed-ranks test, T=5, P=0.25, n(with differences)=6, n(experiments)=10; Fig. 4, Table 1).

The naturally parasitized nests were also larger than the experimentally parasitized nests, although the difference was not significant (using only the pairs in the same tree species, mean (naturally parasitized) =84.5 l, SE=25.7; mean (experimentally parasitized) =47.3 l, SE=8.7; one-tailed paired t-test, t=1.35, df=6, P=0.11).

Since the great spotted cuckoo and magpie fledglings leave the nest at similar body weights (Soler and Soler 1991), we can estimate the energy spent by the magpie pairs as the total number of chicks reared in the nest. Therefore, since naturally parasitized pairs rear more chicks than the experimentally parasitized ones, our experimental results provide evidence that great spotted cuckoos preferentially parasitize magpies of high parental ability.

Discussion

Is host nest size a good indicator of territory quality?

We found a negative relationship between magpie nest volume and breeding date. Timing of breeding by magpies is directly related to the availability of food in their territory (Högstedt 1981), or territory quality (Birkhead 1991; Goodburn 1991), which positively affects the breeding success of magpies (Baeyens 1981; Birkhead 1991; Goodburn 1991; Møller 1982). Therefore, we can establish a direct relationship between nest size and the quality of magpie pairs, and nest size can be used as a reliable indicator of the rearing ability of magpie pairs. This hypothesis is also supported by the fact that nests of young magpie pairs (low quality) are more frequently undomed and therefore smaller than the nests of older magpies (Baeyens 1981; Birkhead 1991).

The other possibility is that the size of the nest is positively related to clutch size. A decline in clutch size over the season could explain the negative relationship between nest size and laying date. However our results do not support this hypothesis.

It is known that males of many bird species (for example weavers) use their nest to attract females, who select a mate based on the quality of the nest (Lack 1968). Nest size in those species appears to be affected by sexual selection. In the magpie, both members of the pair participate in nest building, but the male makes significantly more trips to collect mud and large twigs, and generally collects more sticks than the female, who, in turn, spends more time at the nest placing material brought by the male (Birkhead 1991). The function of a big nest and particularly the big dome, (which explains the large nest volume since there is a correlation between nest volume and height of the dome: r=0.98, n=199, P<0.000001) has been explained as a deterrent to nest predators (see references in Birkhead 1991). However, we found no relationship between size of nest (independent variable) and predation (depen-

Table 1 Number of magpie and cuckoo eggs and fledglings in experimentally and naturally parasitized nests (more information about the experiment is given in Materials and methods)

		Naturally parasitized nests		Experimentally parasitized nests	
Host eggs	Parasite eggs	Magpie fledglings	Cuckoo fledglings	Magpie fledglings	Cuckoo fledglings
4	3	0	2	1	0
4	2	2	2	0	2
4	1	3	1	1	1
4	1	0	1	0	1
4	2	0	2	0	2
4	2	0	2	0	2
4	2	0	2	0	2
4	2	2	2	1	2
4	2	2	2	3	1
4	3	4	2	3	1

dent variable) (log-linear regression, r=0.004, n=114, χ^2=0.28, df=1, P=0.6). We suggest that the number of trips and/or the size of sticks brought by a male magpie could signal his quality and willingness to invest in reproduction. Similarly, the number of trips and the time spent by the female in arranging the nest material could signal her quality and willingness to invest. Thus, when both pair members are of good quality, the result will be a big nest. Recently, a similar sexual selection process has been demonstrated in the black wheatear (*Oenanthe leucura*) where mainly males, but also females, carry stones without any reproductive function to the nest (Moreno et al. 1994).

Do great spotted cuckoos preferentially parasitize nests of a specific volume?

It is very important for the great spotted cuckoo to lay its eggs as quickly as possible, because if it is caught inside the nest by the magpie (a stronger bird), it could suffer physical damage. Therefore, it might conceivably be advantageous for the cuckoo to lay in small host nests, where fewer sticks provide easier entry and faster egg laying. However, great spotted cuckoos significantly preferred to parasitize larger magpie nests. Thus, the cost for the great spotted cuckoo of being surprised by a magpie during parasitism may be lower than the benefit from parasitizing a large host nest. Nevertheless, the ability of great spotted cuckoos to lay eggs quickly may be an important advantage. In an area of presumably recent sympatry between the great spotted cuckoo and the magpie, such as the Guadix area (Soler 1990; Soler and Møller 1990; but see Zuñiga and Redondo 1992), where the host initially does not recognize the parasite, attacks by magpies against cuckoos are infrequent. It might be particularly advantageous for the parasite to lay its eggs in large host nests in this situation.

A non-adaptive hypothesis may explain why larger nests are parasitized more frequently: large nests are more conspicuous and take longer to construct. Both these factors could provide the cuckoo with a greater opportunity to detect large nests. However, in our study area, it is very easy to find magpie nests independent of their size, because at the beginning of the breeding season the almond trees do not have leaves.

We suggest that a preference for large host nests by great spotted cuckoos could oppose sexual selection promoting increased host nest size. While sexual selection might favour large nests (as suggested above), a parasite's preference for large nests, because it uses nest size to infer the quality of host, selects for a reduced nest size. This idea is supported by the fact that magpie nests are larger in areas of allopatry than in areas of sympatry (England, T.R. Birkhead, pers. comm.; Denmark, Sweden, personal observations).

Does the great spotted cuckoo selectively parasitize high-quality magpie hosts?

The breeding success of magpies appears to be determined largely by phenotypic quality; high-quality parents have a better breeding territory, lay earlier in the breeding season, provide their young with a greater quantity or quality of food and have higher fledging success than parents of lower quality (Birkhead 1991; Goodburn 1991). Thus, parasite fitness could increase if their eggs were laid in the nests of high-quality host pairs, particularly if the great spotted cuckoo female lays more than one egg in the same magpie nest, as is the case in our study area (Soler 1990; Soler et al. in press a; Zuñiga and Redondo 1992). We have experimentally demonstrated that parasitized magpies are able to rear more chicks than non-parasitized ones, and so we can conclude that the great spotted cuckoo selects high-quality foster parents for their young. However, Lotem et al. (1992) found that older hosts are more likely to reject cuckoo eggs and, selection of a naive host should therefore be advantageous. The great spotted cuckoo and magpie system differs from that of the european cuckoo (*Cuculus canorus*) in two important ways: (1) great spotted cuckoos often lay more than one egg in the same nest, and (2) we have evidence of enforcement of parasitism on hosts by adult parasites (a "mafia mechanism" Zahavi 1979; Soler et al. in press b). Both characteristics of this host-parasite system could explain differences in the selection of host by great spotted cuckoos and european cuckoos.

Consequences of host selection by parasites

Brood parasites and their hosts are involved in an evolutionary arms race (Brooke and Davies 1988; Davies and Brooke 1989; Dawkins and Krebs 1979; Rothstein 1990), and their relationship is considered a model system for coevolution (Rothstein 1990). In this paper we have shown a preference in the parasite for high-quality hosts. We should therefore expect a decrease in the phenotypic quality of magpies and, if selection arising from the parasite was intense, it could reduce the host population to the level of extinction (May and Robinson 1985). However, if some individuals in the magpie population evolved counter-tactics against the parasite, such traits would quickly be favoured by natural selection because it would result in the avoidance of parasitism. We suggest that the territory quality of magpie pairs would be a very important factor for the evolution of such anti-parasite responses by hosts. High availability of food near the host nest would be a necessary condition for an efficient defence against parasitism. We do not expect this to be the case in the Guadix area, because magpies leave their breeding territory to search for food elsewhere (personal observations), and they are therefore rarely able to defend their nest successfully against great spotted cuckoos.

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References

Baeyens G (1981) Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. Ardea 69: 125–139

Birkhead TR (1991) The magpies. The ecology and behaviour of black-billed and yellow-billed magpies. Poyser, London

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

Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. Am Nat 127 : 415–445

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

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

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

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

Goodburn SF (1991) Territory quality or bird quality? Factors determining breeding success in the magpie *Pica pica*. Ibis 133 : 85–90

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

Krebs JR, Kacelnik A (1991) Decision-making. In: Krebs JR, Davies NB (eds) Evolutionary ecology. An evolutionary approach. Blackwell, Oxford, pp 105–168

Lack D (1968) Ecological adaptations for breeding birds. Chapman and Hall, London

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

May RM, Robinson SK (1985) Population dynamics of avian brood parasitism. Am Nat 126 : 475–494

Maynard Smith J (1978) Optimization theory in evolution. Annu Rev Ecol Syst 9 : 31–56

Møller AP (1982) Characteristics of magpie *Pica pica* territories of varying duration. Ornis Scand 13 : 94–100

Moreno J, Soler M, Møller AP, Lindén M (1994) The function of stone carrying in the black wheatear *Oenanthe leucura*. Anim Behav 47 : 1297–1309

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

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

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research. Freeman, New York

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

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 : 49–51

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

Soler M, Soler JJ, Martinez JG (in press a) Sympatry and coevolution between the great spotted cuckoo and its magpie host. In: Rothstein SI (ed) The ecology and evolution of brood parasitism.

Soler M, Soler JJ, Martínez JG, Møller AP (in press b) Magpie host manipulation by great spotted cuckoos: evidence for an avian mafia? Evolution

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

Zahavi A (1987) The theory of signal selection and some of its implications. In: Delfino VP (ed) International symposium on biological evolution. Adriatica, Bari, pp 305–327

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

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