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Location of suitable nests by great spotted cuckoos: an empirical and experimental study

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Abstract Brood parasites depend entirely on their host species to raise their nestlings until independence. Thus, brood-parasite females must discover and select nests that are at a suitable stage for parasitism, and thus, the location of each parasitic egg is crucial in determining the brood-parasite female's fitness. In relation to host behaviour, one of the main hypotheses proposed to explain how brood-parasite females find and select a suitable nest posits that the most active hosts during nest building should undergo a higher risk of being parasitised (the "host-activity hypothesis"). Here, using the great spotted cuckoo, *Clamator glandarius*–magpie, *Pica pica* system, we found that not only cuckoo females parasitise magpie nests regardless of the location and characteristics of nests, but also that the parasite's observation of host activity near the nest determines a cuckoo female's decision of laying in a nest. Only one experimental nest (without host activity) was parasitised before the magpie started laying, while 34.14 % of natural active nests were parasitised before the magpie started laying. These observations support the host-activity hypothesis for nest location in great spotted cuckoos.

Keywords Brood parasites · *Clamator glandarius* · Host-activity hypothesis · Location of nests · *Pica pica*

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Brood parasitism is a type of parental-care parasitism (Roldán and Soler 2011) in which females lay their eggs in the nests of other species (hosts), which, by caring for the unrelated parasites, suffer important costs and select for the evolution of host defences. Such host defences, in turn, triggers the development of parasitic counter-defences, giving rise to a coevolutionary arms race (Rothstein 1990; Davies 2000; Soler and Soler 2000). The best host strategy would be to avoid being parasitised, and hosts have developed several adaptations to thwart brood-parasite females in their search for appropriate nests (Moskát and Honza 2000; Saunders et al. 2003; Fiorini et al. 2009). Brood parasites, in turn, have developed counter-adaptations that improve their abilities to locate suitable host nests (Øien et al. 1996; Banks and Martin 2001; Honza et al. 2002; Fiorini and Reboreda 2006).

Numerous hypotheses have been proposed to explain how brood-parasite females find and select suitable host nests. Most hypotheses address a variety of environmental features related to nest placement, but some are also related to host behaviour (reviewed in Patten et al. 2011). With respect to nest placement, several parameters have been suggested to affect brood parasitism, including the proximity of trees or other suitable lookouts for host nests (the "perch-proximity hypothesis"; Álvarez 1993; Øien et al. 1996; Clotfelter 1998), nest visibility (Clotfelter 1998; Clarke et al. 2001), nest size (Moskát and Honza 2000; McLaren and Sealy 2003) and nest height (Briskie et al. 1990; Budnik et al. 2002). With respect to host behaviour, two features have been hypothesised to affect nest parasitism: nest-defence behaviour of hosts against brood parasites, which could be used as a cue to find the nest (Smith et al. 1984; Gill et al. 1997), and host activities during nest building (the "host-activity hypothesis"), according to which the most active hosts would undergo higher parasitism risks (Banks and Martin 2001; Svagelj et al. 2009). These proposals are not mutually exclusive and have received different levels of support, depending mainly on the brood parasite, host species and habitat type.

The great spotted cuckoo (*Clamator glandarius*) is a specialist brood-parasite cuckoo species that uses the magpie (*Pica pica*) as its main host (Soler 1990). Magpies defend their nests against great spotted cuckoos (Soler et al. 1999a), and, as a counter-adaptation, great spotted cuckoos have evolved a specialized laying behaviour in which the male cooperates by provoking an attack by both male and female magpies and then the female cuckoo takes advantage of the host absence in order to quickly lay her egg (Álvarez and Arias de Reyna 1974; Soler and Soler 2000). In this brood parasite–host system, it has been experimentally demonstrated that great spotted cuckoos choose potential host pairs with larger nests because nest size indicates host parental quality (Soler et al. 1995a).

Many studies have sought to determine the cues and search methods used by brood-parasite females to find nests, reporting that parasitic females locate host nests by observing host activity from suitable lookouts. This general scheme, which has been frequently argued (Chance 1940; Norman and Robertson 1975; Wyllie 1981; Wiley 1988; Banks and Martin 2001), is really composed of two separate hypotheses. First, brood-parasite females observe host behaviour near their nests from nearby perch sites. This perch-proximity hypothesis has been convincingly supported for several brood-parasite species of Cuculidae as well as Icteridae families (Álvarez 1993; Øien et al. 1996; Clotfelter 1998; Moskát and Honza 2000; Antonov et al. 2007; Begum et al. 2011). However, brood-parasite females also select nests based on host activity (the host-activity hypothesis), which is not so clear. This hypothesis has been experimentally tested several times in some parasitic cowbirds (Grieef and Sealy 2000; Robinson and Robinson 2001; Fiorini and Reboreda 2006; Svagelj et al. 2009), but never in parasitic cuckoos.

Here, we report the results of an experiment to test the host-activity hypothesis in the great spotted cuckoo–magpie system. Considering that magpies attack great spotted cuckoos near the host nests and that aggression could endanger the cuckoo female (Soler et al. 1999a), we made two predictions. First, magpie activity could be used as a cue by great spotted cuckoos to select nests in which to lay, and second, it would be adaptive for great spotted cuckoo females to avoid well-defended nests, which could provoke mistakes of parasitising unattended (abandoned or depredated) nests. Thus, given that brood-parasite females can also discover nests by directly searching the habitat (Davies 2000; Fiorini and Reboreda 2006; Svagelj et al. 2009), it is possible that great spotted cuckoo females would prefer to lay in unattended (experimental, without host activity) nests.

Methods

Study site

This study was conducted on the Hoya de Guadix (southern Spain), a high-altitude plateau (approximately 1,000 m.a.s.l.) with cereal crops (especially barley), almond (*Prunus dulcis*) orchards and some holm-oak trees (*Quercus rotundifolia*). More detailed information on this area can be found elsewhere (Soler 1990; Soler et al. 1998a).

The Guadix magpie population is distributed across several nearby plots differing significantly in ecological conditions including food availability, magpie density and brood-parasitism rates (Soler et al. 1994, 1998a,b, 1999b; Martín-Gálvez et al. 2007). This study was made in Charches (37°17′ N, 2°57′ W), one of the plots with the highest parasitism rate during recent years.

General field procedures

The fieldwork was conducted during the 2011 breeding season, although we also used data on parasitism timing from previous years for comparison. We started intensively searching for magpie nests on March 10th, about 2 weeks before magpies started laying. Most nests (91 out of 131; 69.5 %) were found during the building stage and some (21; 16.0 %) before egg laying. After a nest was located, it was visited at least three times each week to record egg laying by both the female magpie as well as any instances of parasitism.

At each nest, we recorded the following: (1) nest visibility was recorded dichotomously as visible or not; we considered a nest not visible when it was not possible to see it from the tree surroundings; (2) nest height, i.e. the perpendicular distance from the nest to the ground; and (3) nest volume (measured after the fledglings left the nest) was calculated as: $4/3\ (\pi \times a \times b^2)/1{,}000$, where “$a$” is the axial radius of the ellipsoid and “b” is the equatorial radius (Soler et al. 1995a).

Experimental design

We designed an experiment to test the hypothesis that great spotted cuckoo females use host activity to locate and parasitise magpie nests. Magpies build very strong nests with a stick framework holding a cup of mud lined mainly with fibrous roots (Birkhead 1991). Frequently, these nests remain stable and intact from 1 year to the next (especially when they are well concealed in dense oak bush). To conduct our experiment, we looked for stable and intact old nests from the previous year that were <200 m from the new nest, and we cleaned and repaired them when the female

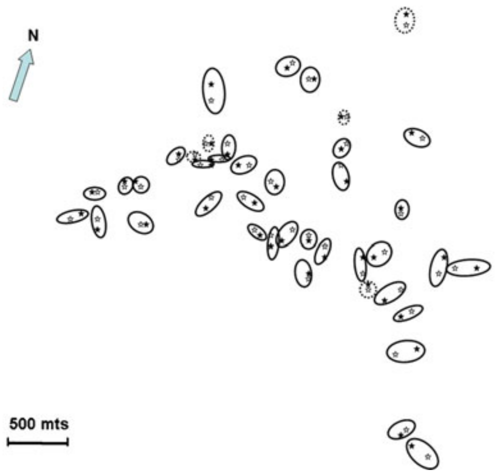

Fig. 1 Distribution of pairs of nests (black start experimental, empty start natural) in the study area. Pairs of nests surrounded by a dashed line are those in which both starts would be superposed because the two nests were too close together

magpies were preparing the nest cup (with the fibrous roots) of their new nest. Well-conserved magpie nests from the previous year are almost indistinguishable from new ones. In fact, we frequently have to climb to the nest to determine whether it is an old or a new one. The state of the roots and the presence or not of remains inside the cup differentiates them, so that, after we cleaned and tidied the roots inside the cup, the experimental nests looked new. In this way, we had 41 pairs of nests (with and without host activity) that were approximately 75 m one from another (mean±SE=75.8±7.6 m; see Fig. 1).

With this experimental approach, one nest having host activity (easier to detect but defended by magpie owners) and one nest lacking host activity (more difficult to detect but undefended and thus easier to parasitise) were simultaneously available to the cuckoos. This avoided potential problems encountered by previous studies concerning the use of artificial nests (Grieef and Sealy 2000). Another potential problem of experimental tests of the host-activity hypothesis is the use of artificial or other species' eggs to bait the experimental nests (Grieef and Sealy 2000; Fiorini and Reboreda 2006; Svagelj et al. 2009) because of morphological differences and predator attraction. However, the introduction of eggs in experimental nests would allow testing what cue the brood parasitic female is preferentially using when deciding which host nest to parasitise: presence and activity of parents or presence of eggs. We tried to test the differences between these two cues by initially considering in our experimental design two additional experimental groups in which two quail (*Coturnix coturnix*) or two real magpie eggs were introduced in experimental old nests. However, unfortunately, these experimental nests baited with real eggs ($N=8$) were depredated in <48 h. For these reasons, we did not bait the experimental old nests with eggs, so that our experimental nests lacking host activity were compared with natural magpie nests prior to laying (i.e. empty nests), which are frequent in our study area (see below).

Statistical analyses

To normalize distributions, we log transformed some variables before analysis, i.e. nest volume and host egg-laying date. After these transformations, none of the distributions differed significantly from normal distributions ($P>0.20$ in both cases), and parametric tests were used (Sokal and Rohlf 1995). However, we were unable to normalize the distribution of nest-finished date or exposure time (i.e. time that the nest remains empty, from the nest-finished date until the day the first magpie egg is laid), and we therefore employed non-parametric tests when using these variables in the analyses (Siegel and Castellan 1988).

A generalized linear model with a binomial distribution and logistics link was performed using the probability of being parasitised (yes or no) as the dependent variable, the

Table 1 Different breeding variables in relation to parasitised and unparasitised nests of magpies by the great spotted cuckoo (sample sizes differ because complete data set were not collected for all variables)

Variables	Parasitised				Unparasitised				*P* value
	Mean	SE	Percent	*n*	Mean	SE	Percent	*n*	
Heigh above ground (m)	3.07	0.13		106	3.04	0.19		25	0.92
Nest volume (l)	28.81	1.07		106	29.22	1.85		25	0.78
Host egg laying date (days)	22 April	1.68		95	16 April	1.85		21	0.20
Nest finished date (days)	12 April	2.01		101	7 April	2.82		22	0.53
Exposure time (days)	10.69	0.90		95	7.61	1.34		21	0.20
Nest visibility			40.5	106			48.0	25	0.49

For laying date, 1=1 April. Differences between means were estimated using a *t*-test (heigh above ground, nest volume and host egg laying date) and a Mann–Whitney *U* test (nest finished date and exposure time) and a χ^2 test (nest visibility) for comparison of percentages

Table 2 Results from logistic regression of likelihood of parasitism against various nest use variables

Variables	Estimate	SE	Wald	*df*	*P* value
Height above ground (m)	0.08	0.21	0.15	1	0.69
Nest volume (l)	−0.02	0.82	0.00	1	0.97
Host egg laying date	−1.86	1.26	2.17	1	0.14
Nest finished date	0.16	0.08	3.83	1	0.05
Exposure time (days)	0.27	0.10	6.29	1	0.01
Nest visibility	0.06	0.25	0.05	1	0.81

nest visibility as categorical factor, and nest volume, height above ground, nest-finished date, exposure time and host egg laying date as continuous predictors.

In addition, using a generalised linear model with multinomial distribution, we investigated the host-nest traits that affected parasitism intensity. We used the parasitism intensity (null, 0 cuckoo eggs; light, 1–2 cuckoo eggs; medium, 3–4 cuckoo eggs; and extreme, >5 cuckoo eggs) as the dependent variable. The same variables described above were used as the categorical factor and continuous predictors.

Possible models explaining both the probability of being parasitised and the parasitism intensity were evaluated using the Akaike information criterion (Burnham and Anderson 2002).

All analyses were performed using Statistica version 7.1 (Statsoft, Inc. 2004).

Results

We found 131 magpie nests in which the female magpie laid eggs. The parasitism rate was 80.9 %, and the intensity of parasitism was 3.03±0.21 (*n*=106 nests) great spotted cuckoo eggs per parasitised nest.

Location of suitable nests

Most of the variables we examined were very similar and not significantly different in parasitised and unparasitised nests (Table 1).

The best model that best described the variation in parasitism risk included date when the nest was finished, exposure time and host egg laying date ($\text{chi}^2=11.52$, $df=3$, $P=0.009$), but only exposure time reached statistical significance (Table 2). We also used a generalised linear model with multinomial distribution considering the same independent variables but with intensity of parasitism as dependent variable. However, in the resulting model ($\text{chi}^2=13.40$, $df=6$, $P=0.037$), none of the potential explanatory variables significantly predicted the probability of parasitism.

Effect of parental activity

Experimental nests without host activity were parasitised less frequently (1 of 41; 2.4 %) than new natural nests with host activity (14 of 41; 34.14 %; Fig. 2; $\text{chi}^2=13.79$, $df=1$, $P=0.0002$). The only experimental nest parasitised was situated only 1 m from the new nest being built by the

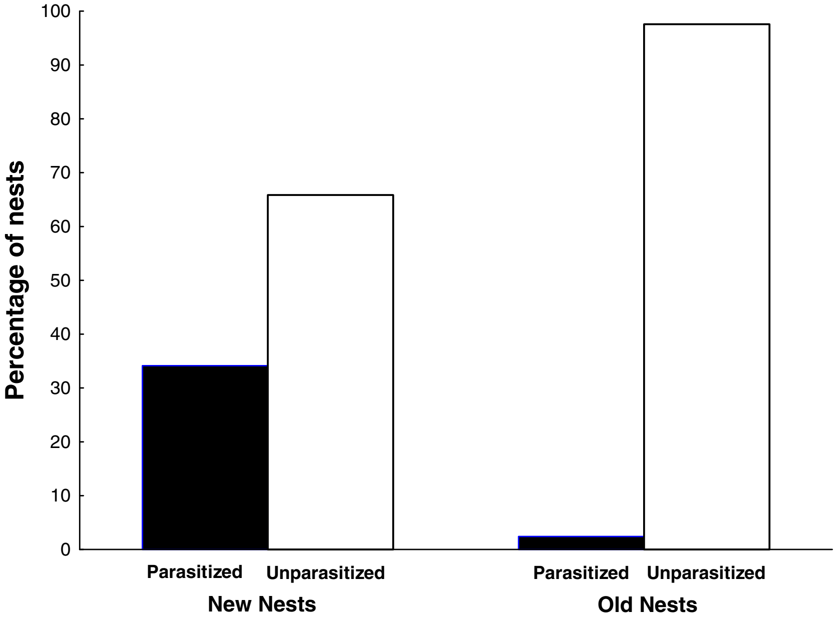

Fig. 2 Percentage of parasitised and unparasitised nests in natural (with host activity) and experimental (without host activity) nests before the female magpie laid her first egg

magpie pair, which was also parasitised. Natural nests that were parasitised before host egg laying tended to be more heavily parasitised later, during the egg-laying period (13 of 14; 92.8 %) than were the unparasitised nests (21 of 27; 77.8 %), but differences did not reach statistical significance ($\chi^2=1.48$, $df=1$, $P=0.228$).

Discussion

Location of suitable nests

Our results show that nest visibility, height above ground, nest volume and host egg laying date do not provide effective cues for great spotted cuckoos to parasitise host nests, but the probability of parasitism increased with exposure time. The fact that those variables did not significantly affect the probability of parasitism may simply be the consequence of a high parasitism rate (i.e. density of great spotted cuckoos). Although no information is available on the effects of these variables in hosts for any cuckoo species, in cowbirds, it has often been reported that frequency and intensity of brood parasitism are related to the density of brood parasites (Brittingham and Temple 1983; Goguen and Mathews 2000; Robinson and Smith 2000), and thus, a high parasitism rate may simply reduce the effect of potential factors that provide cues for brood parasites (Robinson et al. 1995; Burhans 1997; Robinson and Smith 2000; Svagelj et al. 2009).

Effect of parental activity

Our results showing that experimental nests without host activity do not provoke egg laying by great spotted cuckoos (Fig. 2) coincide with findings in previous studies on *Molothrus* cowbirds and their hosts (Grieef and Sealy 2000; Robinson and Robinson 2001; Fiorini and Reboreda 2006; Svagelj et al. 2009) and are supported by observations on the common cuckoo showing that abandoned or old empty nests were only rarely parasitised (Moskát and Honza 2002). Considering that brood-parasite females are able to discover experimental nests without host activity (Fiorini and Reboreda 2006; Svagelj et al. 2009), we conclude from our experimental study that great spotted cuckoos, as well as cowbirds, base their decision of parasitism on the observation of host activity near the nest.

With respect to which cue is used by the great spotted cuckoo female when deciding which host nest to parasitise (presence and activity of parents or presence of eggs), the fact that nests that were parasitised during the prelaying period tended to be more parasitised during the laying period implies that the presence and activity of magpie hosts are more important than the presence of eggs.

Our observation that great spotted cuckoos base their decision of parasitism on the observation of host activity, which has also been found in parasitic cowbirds, may also be the case with other cuckoo species and brood parasites in general. Host activity may be the critical cue for eliciting parasitism, which seems to be the most adaptive strategy, given that it would maximize the likelihood of brood parasites successfully producing offspring. Parasitising nests without host activity would waste some parasitic eggs when deposited in abandoned or depredated nests.

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Ethical standards Research has been conducted according to relevant Spanish national (Real Decreto 1201/2005, de 10 de Octubre) and regional (permissions provided yearly by la Consejería de Medio Ambiente de la Junta de Andalucía) guidelines.

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