



Original Article

# Great spotted cuckoos disregard information on conspecific breeding success while parasitizing magpie hosts

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The study of mechanisms underlying host selection by brood parasites usually lays on selection by parasites of host traits that inform on host parental abilities or location. However, brood parasites might use information extracted from past reproductive performance of either their hosts or themselves, a possibility almost neglected. In this study, we use a long-term data set to analyze whether the probability of parasitism by great spotted cuckoos (*Clamator glandarius*) of a magpie (*Pica pica*) nest in a given year is related with the reproductive outcome of any of the 2 species in the surroundings of that nest the previous year. We found that probability of parasitism for a nest in a year was explained by previous year cuckoo reproductive outcome and parasitism rate in the area surrounding the focal nest, but not by host reproductive outcome. To discern between the effect of parasitism rate and that of parasite reproductive success on parasite choices, we carried out an experiment modifying the natural correlation found between parasitism status and host and parasite success in the patches. The results showed that neither host nor cuckoo reproductive outcome in a patch after the experiment explained probability of parasitism in the following year. Only parasitism rate in the surroundings of a nest before the experiment explained probability of parasitism for this nest in the following year. Hence, these results indicate that great spotted cuckoos disregard social information related to past parasitism outcome, probably because parasitism outcome is tightly correlated with parasitism itself.

**Key words:** cuckoo, breeding success, magpie, nest choice.

## INTRODUCTION

Obligate brood parasites lay their eggs in the nests of host species that carry out all the parental care, from egg incubation to chicks' feeding. Brood parasitism reduces dramatically the reproductive success of the hosts favoring the evolution of host defenses, which in turn can select for counter-defenses in the parasite, giving rise to a coevolutionary “arms race” (Davies 2000; Payne 2005). Because brood parasites entirely depend on their hosts to breed, their fitness is closely related to their efficiency in finding and/or selecting the best possible hosts (Rothstein 1990), and hence, determining the mechanistic basis of brood parasite host choices is a major

challenge in the understanding of the eco-evolutionary dynamics between brood parasites and their hosts.

Traditionally, within population parasitism patterns have been proposed to result from strategic host choices by parasites based on host traits enhancing parasite fitness (Soler et al. 1995; Parejo and Avilés 2007). Hence, for instance, brood parasites may select those hosts with larger nests within a population because the size of the nest may inform on parental ability, such as in magpie *Pica pica* hosts parasitized by great spotted cuckoos *Clamator glandarius* (Soler et al. 1995; de Neve et al. 2004), or may choose to lay in nests with a high degree of matching between eggs of hosts and parasites, so that the parasite eggs are less likely to be rejected (Avilés, Stokke, Moksnes, et al. 2006; Honza et al. 2014). Nonetheless, recent findings suggest that strategic host choices within a population are context-dependent, and will be more frequent when parasites have

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larger availability of host nests to choose (Molina-Morales et al. 2016). Alternatively, parasitism patterns may result from spatiotemporal availability and or detectability of host nests within host populations, so that, for instance, more likely parasitized nests are those close to vantage points where parasites can perch (Martinez et al. 1996; Strausberger 1998; Moskat and Honza 2000; Hauber 2001; Antonov et al. 2007; Fiorini et al. 2009; Begum et al. 2011; Patten et al. 2011; Hovik and Miller 2013; Jélinek et al. 2014). Despite this, the prevalent view is that brood parasites strongly rely on host traits when selecting where to lay their eggs.

Choosing a suitable nest to parasitize may be a challenging cognitive task, involving acquiring and evaluating many different types of information that could determine breeding success. These cues informing on host quality may be related either to parental (see above, Soler et al. 1995; Parejo and Avilés 2007) or to territory quality as, for example, risk of predation (Avilés, Stokke, and Parejo 2006; Pöysä and Paasivaara 2015), synchrony between hosts and parasites' laying dates (Moskat et al. 2006; Avilés et al. 2014) and risk of parasitism (Expósito-Granados et al. 2017). Alternatively, individuals may evaluate potential hosts' nests via indirect integrative cues revealing its suitability (Boulinier and Danchin 1997; Danchin et al. 2004). In predictable environments, local reproductive output one season is, among integrative indexes (Danchin et al. 2004), the most reliable source of information for the next season because it summarizes the effect of a number of environmental factors as food availability, predation risk, and other factors affecting fitness (Boulinier and Danchin 1997). Indeed, the use of conspecific breeding success as a cue for breeding habitat choice has been documented for many bird species, including some intraspecific brood parasites (Doligez et al. 2002, 2004; Pöysä 2003, 2006; Parejo et al. 2005, 2007; Seppänen et al. 2007; Ward 2005). In contrast, the possibility that interspecific brood parasites may rely on information provided by parasite's traits to choose their nests, even when those are traits likely to provide reliable information on parasite's reproductive success has been seldom considered. However, Louder et al. (2015) showed that probability of cowbird (*Molothrus ater*) parasitism of protonotary warbler (*Protonotaria citrea*) nests was influenced by cowbird but not host success in the previous year. Moreover, experimental manipulation of cowbird success at the nest 1 year influenced future cowbird laying decisions, corroborating that cowbirds rely on previously acquired information on cowbird success when choosing their nests (Louder et al. 2015). Whether this is a peculiarity of cowbirds, or a more widespread, but so far neglected, searching strategy of other interspecific brood parasites remains to be determined.

In this study, by using a long-term data set (11 years), we aim to investigate whether the interspecific parasite great spotted cuckoo (hereafter cuckoo) relies on previously available information about parasite's traits to choose hosts' (magpies) nests to parasitize. Previous work in this system have shown that cuckoos can cue on magpie nest size indicating host parental quality to select hosts nests (Soler et al. 1995; Molina-Morales et al. 2016), and that a proportion of magpie females are always parasitized whereas others are not (Molina-Morales et al. 2014). All these patterns have been explained in terms of host characteristics (either nest availability or habitat features used by hosts). However, several sources of evidence have shown that great spotted cuckoo females visit the host breeding area before, during (Martinez et al. 1998; Bolopo et al. 2016) and after laying (Soler et al. 1995b). Additionally, cuckoo females have been shown to revisit the nests where they have laid their eggs supposedly to feed or defend their chicks (Soler et al. 1999). Also, during our long-term monitoring study, we have

2 anecdotal records of adult great spotted cuckoos contacting (even feeding) cuckoo fledglings after they had left the nests, which altogether indicate that great spotted cuckoo would have the potential to assess their own and/or conspecific reproductive success. Thus, adult great spotted cuckoos might potentially gather information on both hosts and conspecifics' traits and breeding performance, making this a suitable system to test if cuckoos could use information about conspecific success to choose particular hosts' nests or areas in future reproductive attempts. Concretely, we will analyze here whether the status of parasitism of a nest in a given year  $t$  depends on (host or parasite) fledgling production or patch parasitism rate in the surroundings of that nest in the previous year  $t-1$ . If cuckoos use cuckoo fledglings as an estimate of habitat quality, we predict that probability of parasitism in year  $t$  would be higher in those patches where more cuckoo chicks fledged in year  $t-1$ . If cuckoos use host fledglings instead, we predict that cuckoo will parasitize those areas where more host chicks fledged in year  $t-1$ . Finally, if cuckoos are selecting particular areas to lay their eggs as a function of cuckoo nest choice in  $t-1$  (i.e., conspecific presence), we predict that cuckoos will parasitize in year  $t$  those nests located in patches with high parasitism rate in year  $t-1$ . Correlations cannot unambiguously provide support for the use of host or parasite's breeding success as cues for choosing nests because these and other factors, such as patch parasitism rate, are likely intercorrelated in nature (see Methods for this specific study system). Therefore, to qualify the relative importance of predictors of the probability of parasitism, we manipulated patch parasitism rate to artificially change host and parasite success, hence breaking up the natural correlations (see Methods). We predict that if cuckoo presence is the most important factor determining nest choice, the probability of parasitism in year  $t$  would be higher in areas more parasitized in year  $t-1$ . However, if cuckoo reproductive outcome is the most important factor, we predict higher probability of parasitism in year  $t$  for those nests whose surroundings had been modified to be more productive in terms of cuckoo reproductive outcome in year  $t-1$ .

## METHODS

### Study area and system

The study was conducted in La Calahorra (37° 10' N, 3° 03' W, Hoya de Guadix, Granada, Southern Spain) during the years 2007–2017. We used data obtained between 2007 and 2015 for the correlational study, whereas the experiment was carried out in the period 2015–2017. Study area is a patchy area of about 12 km<sup>2</sup> where groves of almond trees (*Prunus dulcis*), in which magpies preferentially build their nests, are very common. Magpies are territorial, sedentary, and socially monogamous long-lived passerines (Birkhead 1991). In our study area, magpies lay 1 clutch during April to May, and are the only host of the great spotted cuckoo. Great spotted cuckoos arrive to the study area after wintering in Africa around the middle of February and depart from the beginning of June (adults) till the beginning of August (juveniles; Soler 2016).

In our population, cuckoo reproductive success is highly and positively related to parasitism rate at the patch scale (see Methods) because most parasitized nests in the area fledged cuckoo chicks (in 133 out of the 177 parasitized nests (75.14%) across the study period at least 1 cuckoo chick fledged). Moreover, patch cuckoo reproductive success is inversely related to magpie reproductive success because cuckoos' success leads usually to magpie breeding failure (in 149 out of 177 parasitized nests [84.2%], no magpie chicks fledged).

The percentage of parasitized nests in our population (i.e., parasitism rate) varied between years (15.9% in 2007, 25.4% in 2008, 65.6% in 2009, 50.7% in 2010, 55.8% in 2011, 35.6% in 2012, 19.4% in 2013, 28.6% in 2014, 23.2% in 2015, 24.52% in 2016, and 24.35% in 2017).

### Magpie nests and individual monitoring

Magpie nests were monitored from the beginning of March to the beginning of July each breeding season. Nests were found by careful inspection of all trees in the area, GPS positioned and then visited at 5 days intervals. In order to determine whether nests were parasitized, during egg laying and hatching, they were visited every 2–3 days. We considered that nests were parasitized when at least 1 cuckoo egg was found in the nest. Magpies in our study area only reject about 5% of real cuckoo eggs (see Soler et al. 1995), and so the risk of not detecting parasitized nests (because magpies rejected the cuckoo eggs quickly) is very low. The information on each nesting attempt recorded included laying date (estimated as the number of days from 1 April), cuckoo and magpie eggs and number of cuckoo and magpie nestlings that fledged.

### Great spotted cuckoo and magpie reproductive success

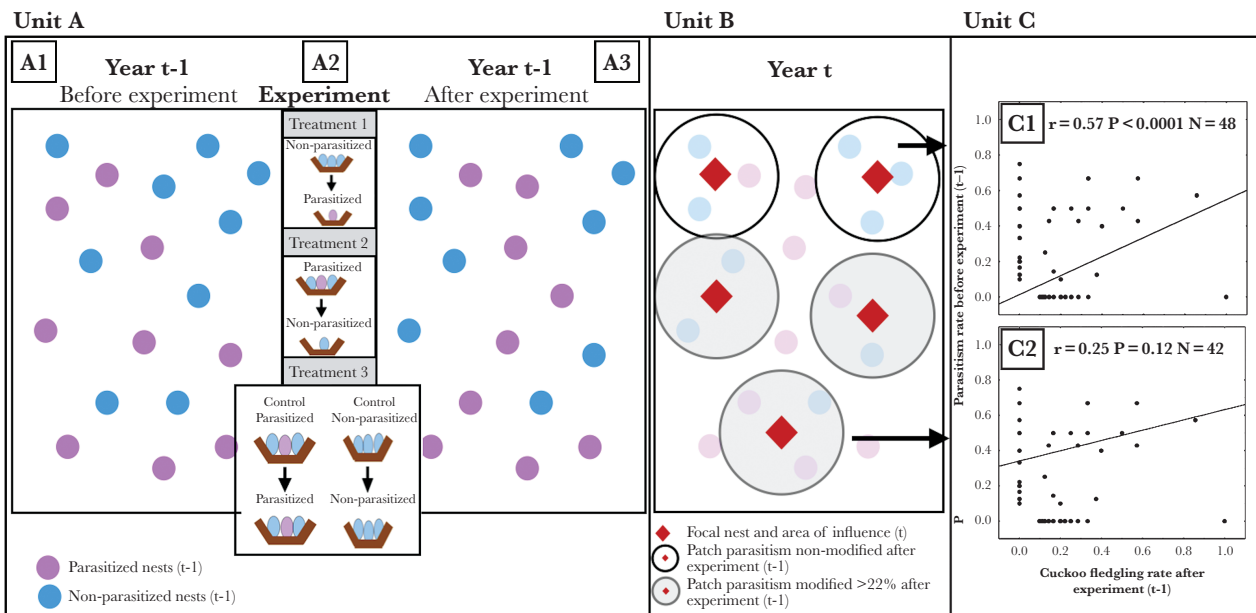
We sampled a total of 559 magpie nests during years 2007–2015. We discarded 124 nests because we lacked information about some variables.

In a first step, we evaluated the effect of cuckoo reproductive success in a given year (t-1) on the following year (t) probability of parasitism. Because magpies build a new nest every year, we

cannot evaluate this effect in the same nests (as studies using nest-boxes do, e.g., Louder et al. 2015). Instead, we considered a focal nest in year t and delimited a circle of 300 m of radius around that nest using R software (*package FNN, R4NM*). This is the minimum area in which all the focal nests in the population had at least one magpie neighboring nest within the area (mean = 4.33, SD = 2.33, range = 1–10, N = 435). Using circles of 100 m and 200 m of radius, the 80.3% and 32.7% of the focal nests, respectively, had no magpie nests surrounding them. We, then, identified all the nests in that area around each focal nest in both years: t and t-1 (see Figure 1 for a similar approach used in the experiment), and determined whether they were parasitized or not and the fate of magpie and great spotted cuckoo reproduction. In a first step we performed the analyses with all the data (n = 435 nests; 58 nest in 2008, 53 in 2009, 69 in 2010, 41 in 2011, 56 in 2012, 60 in 2013, 53 in 2014, and 45 in 2015). However, we failed to determine the status of parasitism in 94 nests due to nest predation before clutch completion or logistic problems, which may affect calculation of host and parasite productivities at the patch level. Therefore, we repeated the same analyses with the subset of nests in which we know the status of parasitism for all nests surrounding the focal nest in year t-1 (n = 341 nests) (see Supplementary Material).

For each focal nest in year t, we calculated the following variables in the surrounding area:

- Parasitism rate in t-1 as the number of parasitized nests divided by the total number of nests in the area.
- Cuckoo fledglings rate in t-1 as the number of cuckoo chicks that fledged divided by the total number of nests in the area.



**Figure 1**

Unit A. Representative scheme of great spotted cuckoo parasitism in magpie nests before and after the experimental manipulation. A1. Panel represents naturally parasitized (purple dots) and nonparasitized (blue dots) magpie nests in experimental years (t-1). A2. Scheme of experimental treatments. A3. Panel shows the change in the parasitism status of the nests after the manipulation in experimental years. Unit B. Effect of the experiment in year t-1 on focal nests in year t. Red diamonds represent magpie nests in a given year (t). Black circles represent for each focal nest in year (t) the influence area (a circle of 300 m radius) in t-1 that might affect the probability of parasitism in the following year. We used this area to calculate parasitism rate in (t-1) and magpie and cuckoo fledglings rate in year (t-1) density of magpie nests in year (t). Gray filled circles represent those patches in which the experiment was effective and the natural correlation between parasitism rate and cuckoo fledgling rate was broken up (N = 42). Unfilled circles represent those patches in which the natural correlation was not broken up. Unit C. Pearson correlation coefficients between parasitism rate before the experiment and cuckoo fledgling rate in patches in which the manipulation was not (panel C1) or was (panel C2) efficient.

- Magpie fledglings rate in  $t-1$  as the number of magpie chicks that fledged divided by the total number of nests in the area.
- Magpie density in  $t$  as the number of magpie nests surrounding the focal nest in  $t$ . This variable was included in analyses to take into account the possibility that cuckoos could rely on host presence in an area just before laying.
- Magpie density in  $t-1$  as the number of magpie nests surrounding the focal nest in  $t-1$ .

### Experimental manipulation of host and parasite success in the patches

In years 2015 and 2016, we manipulated parasitism status of some nests to change host and parasite fledgling outcome. For that purpose, magpie nests were randomly assigned to one of the following 3 treatments (Figure 1): 1) “Experimentally parasitized nests”: we introduced one great spotted cuckoo egg or chick (2–3 days old) from naturally parasitized nests in a naturally nonparasitized nest ( $n = 29$ ) and removed all the previous content of the nest (i.e., magpie chicks), 2) “Experimentally nonparasitized nests”: we introduced one magpie chick (2–3 days old) in every nest and removed great spotted cuckoo eggs or chicks from parasitized nests or magpie chicks from nonparasitized nests ( $n = 26$ ). Finally, 3) “Control nests”: those nests either parasitized or nonparasitized that did not suffer any manipulation ( $n = 121$ ).

Nests receiving cuckoo or magpie eggs or chicks from experimental nests had, as far as possible, the same phenology than donor nests. In that way, all the chicks (cuckoos and magpies) sharing the nests had the same age (days). In those nests where we introduced only 1 chick (treatments 1 and 2), we removed the other chicks that were relocated to nonexperimental nests, with chicks of the same age. We always tried to introduce removed chicks from experimental nests in nests with small clutch size, so that parents could assume the costs of rearing all the chicks. During the chicks transfer from one nest to another, none of the chicks suffered any harm or damage.

Effects of this manipulation on probability of parasitism of magpie nests were measured in 2016 and 2017. In these 2 years, 176 nests were sampled. For all these nests, we calculated for the previous year ( $t-1$ ) the difference between the rate of parasitism before and after the experimental performance in the surrounding area (following the same method described above for the correlational study). This allowed us to identify those patches where the manipulation effectively modified both parasitism rate and parasite and host outcome. In whole, for 90 focal nests in year  $t$ , the patches or influence area in year  $t-1$ , were affected (i.e., parasitism rate in the area surrounding the nest was modified) by the manipulation. However, the correlation between parasitism rate and cuckoo and magpie outcome in the patches (year  $t-1$ ) was effectively broken only for their associated 42 focal nests in year  $t$ , in which patch parasitism rate before and after the experiment changed in at least a 22% (Pearson correlations: parasitism rate vs. great spotted cuckoo outcome ( $r_p = 0.25$ ,  $t = 1.59$ ,  $P = 0.11$ ,  $N = 42$  nests); parasitism rate versus magpie outcome ( $r_p = 0.18$ ,  $t = 1.21$ ,  $P = 0.23$ ,  $N = 42$  nests) (Figure 1). To find the level of change in parasitism rate that was relevant to remove the natural correlation between parasitism rate and cuckoo outcome, we tested the correlation in samples of nests where we gradually included nests in which the change varied in more than 2 points each time. That is, we first tested the correlation in all nests in which the change in patch parasitism rate was higher than 2%, the following analysis was done including nests

with a change in patch parasitism rate higher than 4%, and so on. The 42 nests are, hence, the target of our experimental analyses.

### Statistical analyses

#### Correlations between variables

A general linear mixed model in which variation in parasitism rate  $t-1$  (dependent variable) was modeled in relation to  $t-1$  patch cuckoo fledglings rate while accounting for year as a random intercept and the interaction between year and  $t-1$  cuckoo fledglings rate revealed that parasitism rate and cuckoo success were significantly and positively related within patches ( $F_{1,418} = 562.74$ ,  $P < 0.001$ ,  $N = 434$ ) (see Supplementary Table S1).

A similar model was used to test for the relationship between cuckoo and magpie fledglings rate in a patch and revealed that both variables were significantly and inversely related ( $F_{1,419} = 50.94$ ,  $P < 0.0001$ ,  $N = 435$ ) (see Supplementary Table S2).

#### Correlational study

All continuous variables were standardized prior to run analyses using SAS 9.0 (SAS 2002–2008 Institute, Cary, NC). We constructed Generalized Linear Mixed Models (GLMM, GLIMMIX procedure in SAS) in which probability of parasitism in year  $t$  was entered as a binary dependent variable (link function: logit). Following our predictions, both parasitism rate (as an estimate of cuckoo preference for a given area) and cuckoo fledglings rate (as an estimate of cuckoo success in a given area) in year  $t-1$  might influence the cuckoo decision to parasitize in the same area. However, as parasitism rate and cuckoo fledgling rate are highly correlated (see previous section above and Table 1 in Supplementary Appendix), we decided to introduce in the analyses only one of these 2 variables each time. Therefore, we performed, on the one hand, analyses in which the explanatory factor was the parasitism rate in  $t-1$  and, on the other hand, analyses with cuckoo and magpie fledgling rate in  $t-1$  as explanatory factors. These last 2 variables were introduced together in analyses because their correlation coefficient was lower than 0.75, which is the limit threshold for serious collinearity issues. In all analyses, the year was introduced as a random factor. Previous studies in this system have demonstrated that parasitism rate in the population may influence the probability of parasitism of particular nests (Molina-Morales et al. 2016). Therefore, we included this factor in year  $t$  in all the analyses as a categorical variable (higher and lower parasitism rate than the median population parasitism rate [34.9%]) and their interaction with the target variables as well. Because interactions were far from significance ( $P > 0.1$ ), they were removed from the analysis. In addition, we included in the analyses magpie density and laying date (estimated as the number of days from the first of April until the first host egg was laid) in year  $t$  because it has been shown that probability of parasitism is explained by these 2 variables (Martínez et al. 1996; Stokke et al. 2007; Grim et al. 2011; Molina-Morales et al. 2016). Finally, in all statistical models, the number of magpie nests per patch in year  $t-1$  (magpie density in  $t-1$ ) was introduced as a covariate to control for the fact that the number of magpie nests varied among patches and thus the quality of available information.

#### Experimental study

We analyzed by using a logistic regression (GENMOD procedure in SAS) whether the probability of parasitism of a nest in year  $t$  (as a binomial variable) was related to the status of parasitism of

**Table 1**  
**Relationship between the rate of parasitism in the influence area a year (t-1) and the probability of parasitism in the following year (t)**

Random effects					
Term	Covariance parameter	SE	$\zeta$	<i>P</i>	
Year	0.151	0.14	1.06	0.14	
Fixed effects					
Term	Estimate	SE	df	<i>F</i>	<i>P</i>
<b>Magpie Density (t)</b>	<b>-0.35</b>	<b>0.12</b>	<b>1,422</b>	<b>8.07</b>	<b>0.004</b>
<b>Magpie laying date (t)</b>	<b>0.31</b>	<b>0.11</b>	<b>1,422</b>	<b>7.25</b>	<b>0.007</b>
<b>Local parasitism rate (t-1)</b>	<b>0.35</b>	<b>0.11</b>	<b>1,422</b>	<b>8.93</b>	<b>0.003</b>
<b>Population parasitism rate (t)</b>	<b>-0.83</b>	<b>0.35</b>	<b>1,422</b>	<b>5.57</b>	<b>0.018</b>
Magpie Density (t-1)	0.085	0.10	1,422	0.65	0.421

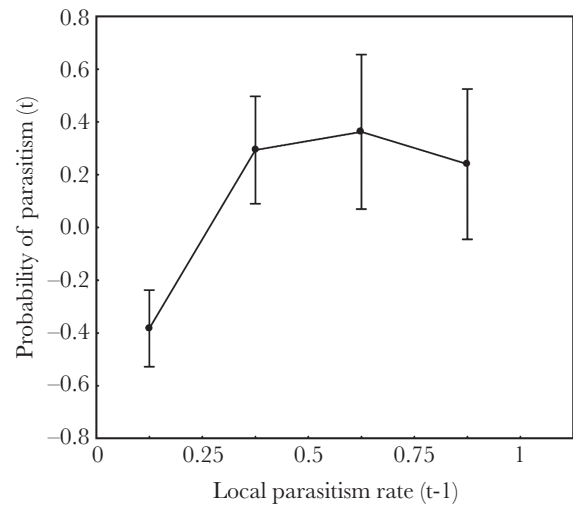
Results of GLMM ( $n = 435$  nests) correcting by magpie density, laying date and population parasitism rate in year t and magpie density in t-1. All variables were standardized. Significant terms are highlighted in bold.

nests in the patch before the experiment in year t-1, or to host and parasite fledging rate in the patch after the experiment in year t-1. Therefore, the explanatory variables considered for this analysis were parasitism rate in the area in year t-1 before the experiment on one hand, and magpie and cuckoo fledging rate in year t-1 after the experiment on the other hand. Also, we included number of magpie nests in the patch in t-1. We included magpie density and laying date in year t to control for the effect of these variables in the current year. We did not include parasitism population rate in t in the analyses because during the 3 years the parasitism rate was similar (see Study area and system, Methods).

## RESULTS

### Correlational study: variables affecting probability of parasitism

Out of the 435 nests used in this study, 168 (38.6%) were parasitized in year t by great spotted cuckoos. The results of the first model showed that the probability of parasitism in year t was significantly explained by parasitism rate in the area surrounding the nest in year t-1 (Table 1). Parasitized nests in year t were mainly those whose neighborhood in the previous year showed a higher rate of parasitized nests (Figure 2). Also, we found that the probability of parasitism (in year t) of a magpie nest was significantly related to density of conspecifics in the same year (Table 1): non-parasitized nests were located in areas with higher density of magpie nests whereas the opposite was true for parasitized nests. Also, laying date explained probability of parasitism (in year t); the probability of parasitism increased with the advance of the breeding season, with those pairs breeding later having a larger probability of being parasitized (Table 1).



**Figure 2**

Relationship between patch parasitism rate in year t-1 and probability of parasitism for a focal magpie nests in t (mean and SE). Plot shows mean probability of parasitism (t) after taking into account additional significant explanatory variables (i.e., residuals from the statistical model in which those variables were the only explanatory variables of the probability of parasitism). Parasitism rate in year t-1 was treated as a continuous variable in the analysis, although for graphical purposes it was divided in 4 categories showing a parasitism gradient.

In the second model, we analyzed the effect of cuckoo and magpie fledging production in year t-1 on the probability of parasitism in year t. We found that cuckoo fledging rate in t-1 explained the probability of parasitism in year t (Table 2). Nests in year t were more likely parasitized when they were located in areas where more cuckoos fledged the previous year (Figure 3). Magpie fledging rate in t-1 did not have any effect on probability of parasitism in year t (Table 2). Magpie density and laying date in year t also were related with probability of parasitism in year t (Table 2). In addition, we found a marginal effect of parasitism rate in the population in year t in the probability of parasitism in the following year (Table 2).

After repeating the analyses for the subset of nests ( $n = 341$ ) for which we have more accurate data (see Methods), we found the same patterns explained before for all variables except for population parasitism rate (see Supplementary Tables S3 and S4).

### Experimental study

The analysis showed that only parasitism rate in the patch before the experiment in year t-1 (Table 3) explained the probability of parasitism of a nest in year t. Nests located in areas with higher number of naturally parasitized nests the previous year were more likely to be parasitized the following year (Figure 4). Neither host nor cuckoo fledging rate after the experiment in the patch explained parasitism status in the following year. In the same way, density of magpie nests and laying date in the current year did not explain the probability of parasitism (Table 3).

## DISCUSSION

Evidence that brood parasitism is determined by factors acting in the year of parasitism comes from studies with cuckoos (Polaciková et al. 2009; Honza et al. 2014; Stokke et al. 2018), cowbirds (Merrill et al. 2017; Scardamaglia et al. 2017), and great spotted cuckoos (Molina-Morales et al. 2016; Expósito-Granados et al. 2017).

**Table 2**

**Relationship between the cuckoo and magpie fledgling success in the influence area in a year t-1 and the probability of parasitism for all nests in the following year t**

Random effects					
Term	Covariance parameter	SE	$\zeta$	<i>P</i>	
Year	0.21	0.18	1.17	0.12	
Fixed factors					
Term	Estimate	SE	df	<i>F</i>	<i>P</i>
<b>Magpie Density (t)</b>	<b>-0.31</b>	<b>0.12</b>	<b>1,422</b>	<b>6.39</b>	<b>0.01</b>
<b>Magpie laying date (t)</b>	<b>0.30</b>	<b>0.12</b>	<b>1,422</b>	<b>6.47</b>	<b>0.01</b>
<b>Cuckoo fledgling rate (t-1)</b>	<b>0.46</b>	<b>0.14</b>	<b>1,422</b>	<b>10.83</b>	<b>0.001</b>
Magpie fledgling rate (t-1)	-0.13	0.12	1,422	1.07	0.30
Population parasitism rate (t)	-0.75	0.39	1,422	3.61	0.05
Magpie Density (t-1)	-0.08	0.10	1,422	0.69	0.40

Results of GLMM ( $n = 435$  nests) correcting by magpie density, laying date and population parasitism rate in year t and magpie density in t-1. All variables were standardized. Significant terms are highlighted in bold.

However, very few studies have explored how aspects related to parasitism in 1 year influence the probability of parasitism in the following year. To our knowledge, most of these studies have targeted cowbirds and their hosts. Female cowbirds use the same nests or nest-boxes repeatedly in different breeding seasons (Hauber 2001; Hoover et al. 2006), which suggest they may use the information obtained in previous breeding events in their decision-making. Recently, one study has shown that cowbird reproductive success in a year explained the probability of parasitism in the following year (Louder et al. 2015).

Here, we use a different parasite–host system, the great spotted cuckoos and magpies, to test the effect of past host and/or parasite cues on current probability of parasitism using a long-term data set of 11 years and combining a correlative and an experimental approach. We found that either patch cuckoo productivity or parasitism rate in 1 year, but not host productivity, explained the probability of parasitism for a focal nest in the same patch in the following year. These results suggest that great spotted cuckoo females may use the information about conspecific reproductive success or decisions and not that of their host, which is intriguing given that most host selection studies by avian brood parasites have focused on how host traits influence parasitism (e.g., Molina-Morales et al. 2016). The results of the experiment in which we broke up the natural correlation between parasitism status and magpie and cuckoo productivity in nests revealed that local parasitism rate before the experiment 1 year is the key variable determining probability of parasitism in the following year and that neither cuckoo nor magpie reproductive outcome in the patches after manipulation had an

**Table 3**

**Results of GLZ model on probability of parasitism in year t after the experimental modification of parasitism status and, hence, of cuckoo and magpie fledgling success ( $n = 42$ )**

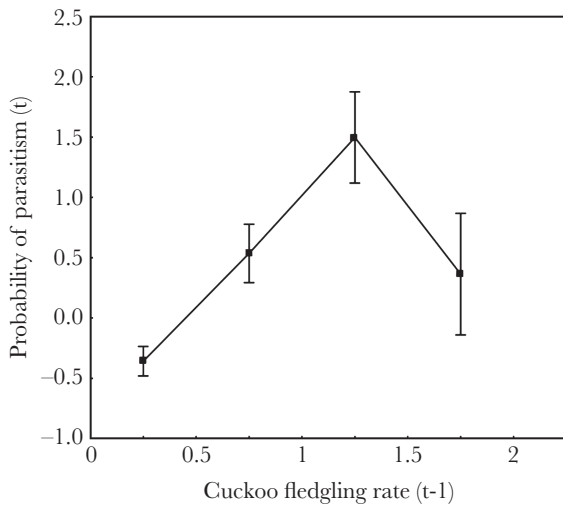
	Estimate	SE	df	X <sup>2</sup> Wald	<i>P</i>
Intercept	1.58	0.60	1	6.83	0.009
Magpie density (t)	0.57	0.68	1	0.79	0.37
Magpie laying date (t)	-0.39	0.51	1	0.60	0.44
<b>Local parasitism rate before experiment (t-1)</b>	<b>1.23</b>	<b>0.49</b>	<b>1</b>	<b>8.34</b>	<b>0.004</b>
Cuckoo fledgling rate after experiment (t-1)	0.14	0.39	1	0.13	0.73
Magpie fledgling rate after experiment (t-1)	-0.25	0.57	1	0.19	0.66
Magpie density (t-1)	-0.64	0.73	1	0.81	0.37

All variables were standardized. Significant terms are highlighted in bold.

effect. Therefore, our results show that cuckoo parasitism is more frequent in magpie nests from areas already used in previous years independently of magpie and cuckoo fledgling success.

The reproductive outcome in predictable habitats has been proposed to be the most reliable source of information to assess breeding habitat quality (Danchin et al. 2004; Schmidt et al. 2010). However, for the great spotted cuckoo, it seems that they prefer using the area where they have previously laid, maybe because cuckoo fledgling success is likely to be very high once a magpie nest is parasitized. Indeed, cuckoos fledged in most naturally parasitized nests (77%). Consequently, relying on past memories of successful laying could be a good strategy for cuckoos because this cue is likely to integrate information to cuckoos about host defenses before and during egg laying more than on host parental abilities, which, in view of the high cuckoo fledgling success, seems to be equally valuable. This is because most magpies that are unable to avoid the parasite egg are good parents for cuckoos, which is a completely different scenario from that found in cowbirds, where parasite success widely varies in parasitized nests (Louder et al. 2015). Moreover, local conspecific presence estimated through parasitism rate (i.e., based on eggs) is probably a less costly cue to gather than the reproductive output because intensity of nest defense increases with the reproductive value of the brood in magpies (Redondo and Carranza 1989). In the case of cowbirds, however, cowbird reproductive success acquired more importance (Louder et al. 2015). It might be explained because cowbirds in most of the cases lay more than 1 egg in the same host nest and parasite and host chicks are raised together (Hoover 2003). Therefore, if cowbirds would evaluate the quality of the foster parents and the success of the own cowbird chicks, they might gather that information during the fledgling stage. Finally, we cannot discard that differences in spatial scale between this study and the one performed by Louder et al. (2015) were behind contrasting results. Magpies build a new nest every year, and they do not nest in fixed places as do protonotary warblers breeding in nest-boxes. Hence, we cannot address questions related with success for the same nest as Louder et al. (2015) have done.

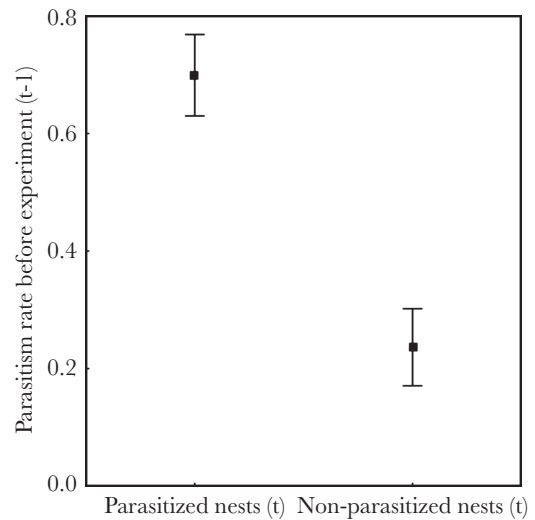
There are several alternatives to explain how previous parasitism rate in a patch might influence parasitism in the following season. First, if cuckoo females were philopatric, they could use their own experience (personal information) in a previous

**Figure 3**

Relationship between patch cuckoo fledgling rate in year  $t-1$  and probability of parasitism for a focal magpie nests in  $t$  (mean and SE). Plot shows mean probability of parasitism ( $t$ ) after taking into account additional significant explanatory variables (i.e., residuals from the statistical model in which those variables were the only explanatory variables of the probability of parasitism). Cuckoo fledgling rate in year  $t-1$  was treated as a continuous variable in the analysis, although for graphical purposes data it was divided in 4 categories showing a gradient of parasitism.

breeding season to select breeding patches. Indeed, there is anecdotal evidence suggesting that cuckoos come back to the same areas in consecutive breeding seasons (J.G.M., unpublished data). Another possibility could be that parasite fledglings returned as recruits to breed in the areas where they were raised or to habitats resembling their natal ones (“imprinting habitat” hypothesis sensu Teuschl et al. 1998). Other possible explanation is that every year different female cuckoos cued on the same host/habitat features indicating host or habitat quality, leading to some magpies to be more likely exposed to suffer parasitism. In accordance with that, it has been demonstrated that there are some magpie females that suffer repeated parasitism over their lives while others are never parasitized, which was explained in terms of habitat characteristics and phenotypic traits such as nest volume and laying date (Molina-Morales et al. 2014). To discern among those possibilities, further research involving individually ringed cuckoo females or genetic data to perform parentage analysis would be necessary, allowing us a better understanding of nest selection in this species.

Our results, from a long-term correlational study, show that probability of parasitism for a focal nest in a given year is determined by factors related to the probability of parasitism in the system such as magpie density or laying date in the year. Probability of parasitism was higher for those nests located in places with less magpie nests in the surrounding area and increased as the magpie’s breeding season progressed. These results are in agreement with previous studies in this and other brood parasite–host systems (Martinez et al. 1996; Clofelter and Yasukawa 1999; Massoni and Reboreda 2001; Fiorini et al. 2009; Molina-Morales et al. 2014, 2016; Dominguez et al. 2015). Magpie aggregation in space and time decreased the chance of parasitism, which may be explained due to an effect of dilution of parasitism risk, because there are more active nests available than the cuckoos are able to parasitize (Martinez et al. 1996). However, at the end of the breeding season there are less active

**Figure 4**

Patch parasitism rate (means and SE) before the experiment in year  $t-1$  for parasitized and nonparasitized nests in year  $t$ .

(and more isolated) nests and, therefore, the probability of parasitism increased at that time. In view of the results obtained, great spotted cuckoos could choose areas to parasitize each breeding season based on previous year cues and then inside these areas decide which nests to parasitize by cueing on information from magpies. For instance, female cuckoos synchronize their laying activity with that of their host by visiting the nests and laying most of their eggs during magpie laying period (Soler et al. 1997).

In conclusion, our results show that probability of parasitism for a focal nest was related both to past local great spotted cuckoo parasitism rate and current magpie reproductive traits, such as laying date and conspecific density. However, neither cuckoo nor magpie reproductive outcome in a previous breeding season predicted future breeding decisions for cuckoos. This pattern suggests that great spotted cuckoos may primarily select areas to lay based on previous conspecific information, and, that they subsequently may refine their choices based on host cues perceived during the current breeding season such as host laying dates and densities. Thus, the relative role of parasite and host cues in determining probability of parasitism appears to vary among different avian–brood parasitic–host systems. Future studies in different brood parasitic–host systems, and, in the same systems but combining different populations with variable levels of temporal and spatial autocorrelation in parasitism, may help to understand how the use of co- and heterospecific cues that brood parasites use to choose among suitable hosts have evolved.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Molina-Morales et al. (2018).

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