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Research article

Multiparasitism and repeated parasitism by the great spotted cuckoo *Clamator glandarius* on its main host, the magpie *Pica pica*: effects on reproductive success, nest desertion and nest predation

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Brood parasites are expected to lay only one egg per parasitized nest, as the existence of several parasitic nestlings in a brood increases competition and can lead the starvation of some of them. However, multiparasitism (laying of two or more eggs by one or more parasitic females in a single host nest) is surprisingly frequent. Here, we study multiparasitism by different females or by the same female (repeated parasitism) in the great spotted cuckoo *Clamator glandarius*, a non-evictor brood parasite that mainly parasitizes the magpie *Pica pica*, and whose chicks may be raised together with host nestlings in the same nest. We used a total of 262 magpie nests found during four breeding seasons. Multiparasitism and repeated parasitism are very frequent because this brood parasite is less virulent than other cuckoo species and magpie hosts can successfully raise more than one parasitic nestling per nest. The total number of cuckoo chicks fledged was higher in multiparasitized nests than in single- or double-parasitized magpie nests. Magpie breeding success (i.e. the proportion of eggs that produce young that leave the nest) did not differ between single-, double-, and multiparasitized magpie nests. These results suggest that multiparasitism is an adaptation in the great spotted cuckoo. The intensity of parasitism (number of cuckoo eggs per nest), after controlling for the potential effect of year, did not affect nest desertion or nest predation rate, neither during the incubation nor the nestling periods. This implies that nest concealment does not affect the susceptibility of one nest being parasitized and predated, as nest predation rate was similar regardless of the intensity of parasitism. Predation rate during the nestling phase did not vary according to intensity of parasitism, which does not support either the 'mutualism' hypothesis or the 'predation cost of begging' hypothesis.

Keywords: breeding success, *Clamator glandarius*, multiparasitism, nest predation, *Pica pica*, repeated parasitism

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Introduction

Obligate brood parasitism is a breeding strategy in which animals evade parental care duties (Roldán and Soler 2011). Obligate brood parasites lay their eggs in the nest of other species, the hosts, which provide all the necessary parental care to the parasitic offspring (Davies 2000, Soler 2017a).

Avian brood parasites, mainly evictor and nestmate-killer brood parasite species, impose high fitness costs on their hosts, as parasitic nestlings evict or kill all hosts' eggs or nestlings (i.e. only one parasitic nestling per nest will survive), thus reducing host reproductive success to zero. But non-evictor brood parasitic species usually provoke high fitness costs too, mainly because their nestlings outcompete some or most of the host chicks in competition for food (Moskát et al. 2017, Soler 2017b). Thus, it is usually assumed that parasitic females should avoid laying in nests containing a previous parasitic egg (Moskát et al. 2006, Goguen et al. 2011), mainly in evictor and nestmate-killer brood parasites and those non-evictor–hosts systems in which usually only one brood parasite nestling survives. This may explain why in most brood parasitic species females defend territories from conspecific females (Wyllie 1981, Øien et al. 1996, Hauber and Dearborn 2003), lay only one egg per host nest (Ellison et al. 2006, Gloag et al. 2014a, Ursino et al. 2020), and avoid laying in nests previously parasitized by other females (Hann et al. 1999, McLaren et al. 2003).

However, selection against multiparasitism (or multiple parasitism: laying of two or more eggs by one or more parasitic females in a single host nest) is expected to be weaker in some cases. These are when the brood parasite is less virulent, when hosts can successfully raise more than one parasitic nestling in the same brood, and when appropriate host nests in the laying stage are scarce. Indeed, multiparasitism is surprisingly frequent, not only in non-evictor (Soler 1990, Martínez et al. 1998a, Gloag et al. 2012, Rivers et al. 2012), but also in evictor and nestmate-killer brood parasites (Moskát et al. 2009, Spottiswoode 2013, Stevens et al. 2013), though parasitism by the same female laying repeatedly in the same host nest (i.e. repeated parasitism) is much more rare. As far as we know, repeated parasitism only has been reported in three parasitic species: the shiny cowbird (*Molothrus bonariensis*; de la Colina et al. 2016), the brown-headed cowbird (*M. ater*; Rivers et al. 2012), and the cuckoo finch *Anomalospiza imberbis* (Stevens et al. 2013).

The great spotted cuckoo *Clamator glandarius* is a non-evictor brood parasite that mainly parasitizes the magpie *Pica pica*, and whose chicks may be raised together with host nestlings in the same nest (Soler 1990). However, adult magpies preferentially feed on cuckoo chicks, which hatch earlier, gain a size advantage, and beg at a higher rate than magpie chicks, causing the latter to starve (Soler et al. 1996, 1998a). The parasitism rate of the great spotted cuckoo in magpie nests may be relatively high in some populations (e.g. ~ 50% in our study site; Soler et al. 1998b, Soler et al. 2013), but it can also show remarkable temporal and spatial (between study plots) variability (0–100%; Soler et al. unpubl.). A highly variable parasitism rate also occurs when it is parasitizing its secondary host, the carrion crow *Corvus corone* (7–55.6%; Soler et al. 2001, Roldán et al. 2013).

Eggs of both species, magpies and great spotted cuckoos, are of similar size (Soler 1990). Great spotted cuckoo females, during each egg laying event, very often damage one or more magpie eggs, which are either pecked, crushed or cracked, and are removed later by magpies (Soler et al. 1997). As a consequence, magpie clutch size, which in non-parasitized nests is usually between five and seven eggs, in parasitized nests is significantly smaller than in non-parasitized nests (Soler 1990). In doubly (two cuckoo eggs per nest) or multiparasitized (more than two cuckoo eggs per nest) nests, magpie eggs are very scarce or even absent (this study). The existence of more than one parasitic nestling per nest increases competition and can lead to starvation in some of them (Soler et al. 1998a).

Multiparasitism – parasite eggs laid either by different females or by the same female laying several eggs in the same nest (repeated parasitism) (Soler 1990, Martínez et al. 1998b, Soler et al. 1998a) – is very frequent in parasitized magpie nests. This is a well-known fact that was emphasized by the pioneering researchers working on the great spotted cuckoo (Mountfort and Ferguson-Lees 1958, Mestré-Raventós 1968, Valverde 1971). Nests with two parasitic eggs are very common in the great spotted cuckoo–magpie system, and the same parasitic female can frequently lay two eggs in the same nest (Soler et al. 1998a, Martínez et al. 1998b). This suggests that laying two eggs in the same host nest can be adaptive (because magpies are able to successfully rear several parasite nestlings: 1.8, 2.6, 2.6, 2.0, and 3.8 in multiparasitized nests with 3, 4, 5, 6, and 7–12 cuckoo eggs, respectively; Soler et al. 1998a), whereas it is generally assumed that multiparasitism is not. Thus, while brood parasitism literature usually considers multiparasitism to occur when there are two or more parasite eggs in a single host nest, separate study of host nests containing two eggs, and nests containing three or more parasitic eggs, may shed light on the adaptive value of each of these strategies in the spotted cuckoo–magpie system. Accordingly, in this study, multiparasitized nests were defined as those magpie nests containing three or more parasitic eggs; see General procedures).

Aims and hypotheses

The main objectives of this study are: first, to determine a) the proportion of magpie nests that remain unparasitized and those that are parasitized with a different number of great spotted cuckoo eggs, and b) the number of great spotted cuckoo females laying in the same magpie nest.

Second, we aim to assess the effect of the intensity of parasitism (the number of great spotted cuckoo eggs per parasitized nest) on the reproductive success of both great spotted cuckoo and magpie hosts. We expect that the number of cuckoo eggs hatched and number of cuckoo chicks fledged in multiparasitized nests will be higher than in singly- or doubly-parasitized nests (Predictions 1 and 2, respectively). On the other hand, considering the high costs imposed by great spotted cuckoo parasitism on magpie hosts (Soler et al. 1996), we predict that the number of magpie eggs hatched and number of magpie chicks fledged will be negatively related to the intensity of parasitism (Predictions 3 and 4, respectively).

Third, we aim to evaluate the effect of brood parasitism, as well as the effect of parasitism intensity, on the probability of nest desertion by magpies. Our predictions are based on two alternative and mutually exclusive hypotheses. Given that nest desertion is often assumed to be a defensive response against brood parasitism (Martín-Vivaldi et al. 2002, Servedio and Hauber 2006, Hale and Briskie 2007, Peer and Rothstein 2010, Begum et al. 2012), it can be predicted that nest desertion will be more frequent in parasitized than in unparasitized nests, and in multiparasitized than in single- or double-parasitized nests (Prediction 5). Alternatively, considering that desertion is not an unambiguously specific response against brood parasitism, especially in medium- and larger-size hosts (Soler et al. 2015a), and that it has been demonstrated that nest desertion rates do not differ between experimentally parasitized and control nests in some host species (Hill and Sealy 1994, Kosciuch et al. 2006, Vikan et al. 2010, Soler et al. 2015a), it can be predicted that nest desertion will not be more frequent in multiparasitized than in parasitized and non-parasitized nests (Prediction 6).

Fourth, we intend to determine the effect of parasitism and its intensity on nest predation probabilities. Given that, in our study area, partial predations only rarely occur and always eventually result in the complete depredation of the nest (Roldán et al. 2013, personal observation in the present study), a nest was considered to have been depredated when it was found empty before the predicted date of fledging. Here, we have predictions based on two mutually exclusive hypotheses. Considering that it has been shown that predation rate in parasitized carrion crow nests during the nestling phase is lower than in non-parasitized nests, presumably because the fetid cloacal secretion produced by cuckoo nestlings deters predators (Canestrari et al. 2014, but see Soler et al. 2017), it can be predicted that predation rate during the nestling phase would be lower in parasitized than in non-parasitized nests (Prediction 7), and lower as the intensity of parasitism increases (Prediction 8). Alternatively, given that begging of brood parasitic nestlings, including great spotted cuckoos, is of higher intensity and loudness than that of host nestlings (Dearborn 1999, Soler et al. 1999, 2012, Hannon et al. 2009), and that begging can directly attract predators (Haskell 1999, Ibáñez-Álamo et al. 2012), we predict that parasitized nests will be predated at a higher rate than non-parasitized nests (Prediction 9), and higher as the intensity of parasitism increases (Prediction 10).

Material and methods

Study area

This study was conducted in Hoya de Guadix, southern Spain. This area is a high-altitude plateau (approximately 1000 m a.s.l.) with extensive non-cultivated areas, cereal crops (especially barley), and some other areas with dispersed trees in which magpies build their nests (Soler 1990). These areas include abundant groves of almond *Prunus dulcis*, some plantations of pine *Pinus halepensis* and *P. pinaster*, and some dispersed holm-oak *Quercus rotundifolia*. Brood parasitism by the great spotted cuckoo is very common in magpie nests within the study area (54.8%, n = 778; Soler et al. 2013). Potential nest predators in the area are stone martens *Martes foina*, genets *Genetta genetta*, jackdaws *Corvus monedula*, common ravens *Corvus corax*, magpies and carrion crows. The Guadix magpie population is composed of several nearby plots differing significantly in ecological conditions including food availability, magpie density or brood-parasitism rates (Soler et al. 1994, 1998b, 2013, Martín-Gálvez et al. 2007). Our study site was located in Charches (37°17′N, 2°57′W), one of the plots with the highest parasitism rate during recent years (Soler et al. 2015b).

General procedures

We used a total of n = 262 magpie nests (161 parasitized and 101 non-parasitized) found during four breeding seasons (2011–2014), which did not suffer any type of experimental manipulation except for egg recognition trials, which do not affect the reproductive success of the host or the parasite. We assessed the effect of brood parasitism intensity on nest desertion (n = 262 nests), nest predation during the egg stage (n = 252), and nest predation during the nestling stage (n = 198). The effect of the intensity of parasitism was studied in a total of 146 nests (deserted and predated nests excluded; n = 10 and n = 106, respectively). Once a nest was found it was visited at least twice per week, which allowed determination of hatching, fledging, and breeding success.

The intensity of brood parasitism is often considered to be the number of parasitic eggs laid per host nest. However, since great spotted cuckoo females lay a high percentage (~ 33.5%) of their eggs in non-appropriate stages of the breeding cycle (before the start of laying, incubation, or even nestling period), and these non-synchronized parasitic eggs are wasted (Soler et al. 2015b), we have defined the intensity of brood parasitism as the number of great spotted cuckoo eggs laid per magpie nest during the magpie laying period. This index reflects the 'effective intensity of brood parasitism' and provides a more realistic picture of the effect of brood parasitism on reproductive success.

The number of great spotted cuckoo females laying per magpie nest was calculated based on egg shape, color and spotting patterns, given that each individual female lays eggs of a very similar appearance, which has also been confirmed in other brood parasites (Moksnes et al. 2008, Spottiswoode and Stevens 2011, Gloag et al. 2014b). In the case of the great spotted cuckoo, it has been demonstrated that the number of females laying in a nest does not differ significantly when using egg morphology or genetic data, because estimations based on egg morphology are very accurate (Martínez et al. 1998b).

We considered four different groups of nests according to the number of great spotted cuckoo eggs per nest:

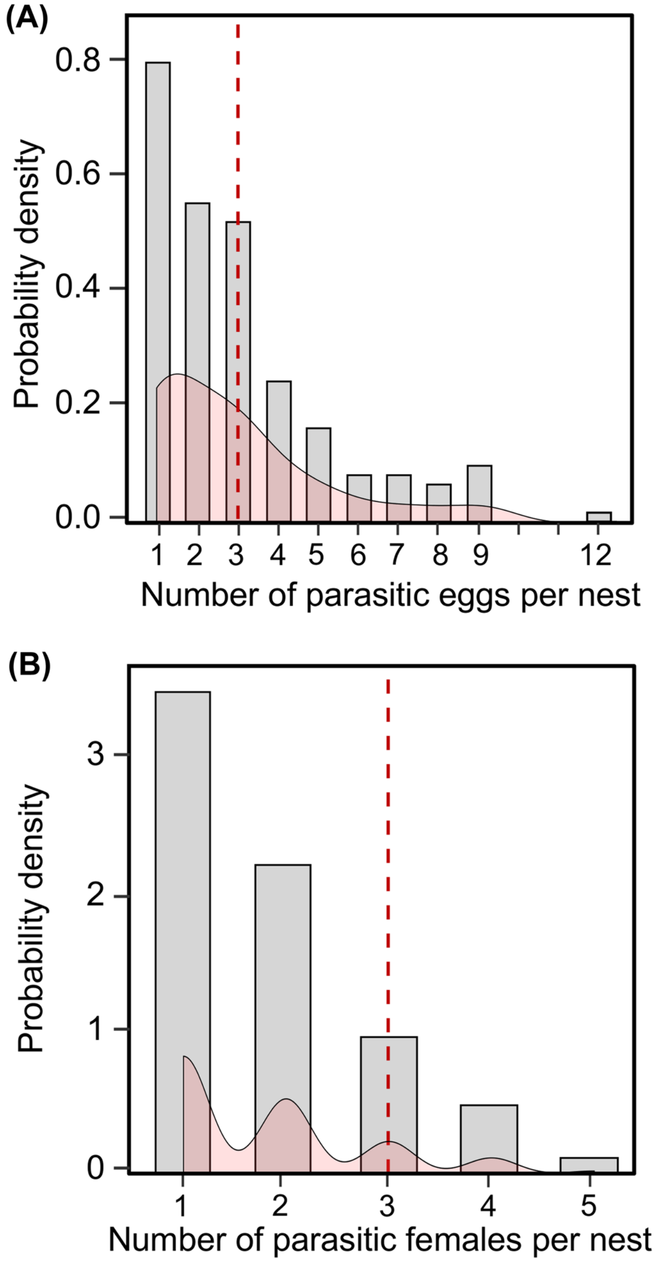

Figure 1. Density plot showing the distribution of parasitized magpie nests according to the total number of cuckoo eggs per nest (A) and the total number of cuckoo females laying in the same nest (B).

unparasitized, single-, double-, and multiparasitized (three or more parasitic eggs per nest) nests. Two parasitic eggs per nest (which is considered multiparasitism in the brood parasitism literature) in the great spotted cuckoo–magpie system is very common, and frequently both eggs may be laid by the same female. This suggests that there can be relevant biological differences between nests with two and nests with three or more eggs (above). This is supported by the fact that, in multiparasitized nests, more cuckoo nestlings survive than in doubly parasitized nests (see Reproductive success of great spotted cuckoos according to intensity of parasitism).

Breeding success was studied only in nests where at least one parasitic or host young fledged (i.e. deserted or predated nests were not considered in our analyses). Thus, for both the great spotted cuckoo and the magpie, the total number of hatched and unhatched eggs was computed, as well as the total number of fledged and dead nestlings. It should be noted that dead chicks are often a consequence of brood reduction due to starvation when they are the smallest/youngest chicks in the nest (Soler 2017b). We also assessed hatching success (the proportion of eggs that hatched in successful clutches), fledging success (the proportion of chicks that fledged from hatched eggs), and reproductive success (the proportion of eggs producing young that left the nest) for both the brood parasite and its host.

Statistical analyses

All analyses and graphs were performed using R ver. 4.2.1 (www.r-project.org). We use a randomization test to determine the statistical significance of the correlation between the number of great spotted cuckoo females laying in the same nest and the number of cuckoo eggs per nest, since these two variables may be coupled. Briefly, we compared our observed correlation coefficient to a null distribution of correlation coefficients generated from 10 000 simulations of our data, where the number of cuckoo eggs per nest was randomized across parasitism intensity.

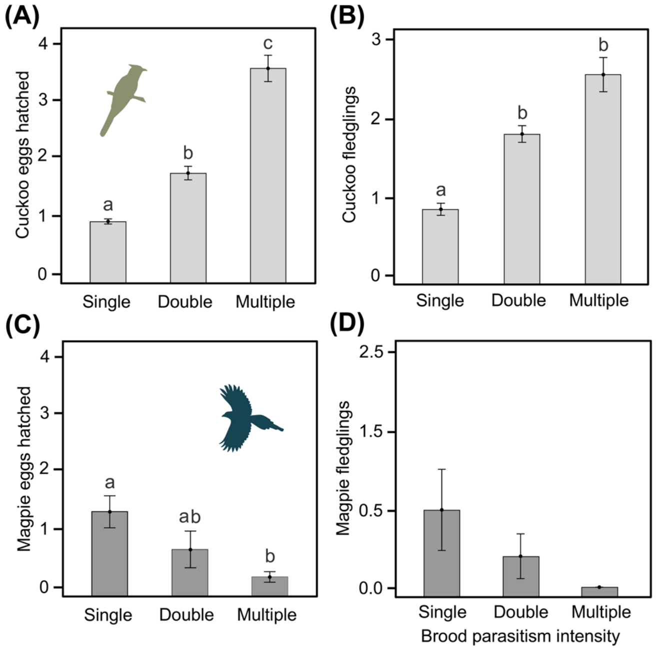

Figure 2. Total number of hatched cuckoo eggs and fledged cuckoo chicks according to brood parasitism intensity (A–B). Total number of hatched magpie eggs (laying date was centered to a mean of 0) and fledged magpie chicks according to brood parasitism intensity (C–D). Different letters show statistically significant differences in post hoc tests.

The effect of brood parasitism intensity on the total number of cuckoo and magpie eggs hatched, as well as on the total number of cuckoo and magpie chicks that fledged in host nests, was evaluated through linear models. To account for the presence of coupled variables and reduce the number of Type 1 errors, significance was assessed by permutation tests (10 000 permutations) using the 'permuco' package (Frossard and Renaud 2021). The effect of brood parasitism intensity on hatching success, fledgling success, and breeding success of cuckoos and magpies was assessed through generalized linear mixed models (GLMM) with quasi-binomial error distribution using the *glmmPQL* function from the 'mass' package (Ripley et al. 2013). These models included 'parasitism intensity (single, double, multiple)', 'magpie clutch size', 'laying date', and the two-way interactions between 'parasitism intensity' and 'clutch size' and 'laying date' as fixed effects. The models assessing the total number of cuckoo and magpie chicks fledged in host nests included the 'number of magpie chicks' rather than clutch size. We also used the 'lme4' package (Bates et al. 2015) to evaluate the effect of brood parasitism on nest desertion (yes|no), and predation rate during incubation and nestling stage (yes|no), through GLMM with a binomial distribution. These models included 'brood parasitism (non-parasitized, single, double, multiple)', 'magpie clutch size', 'laying date', and the two-way interactions between 'brood parasitism' and 'clutch size' and 'laying date' as fixed effects. All GLMM included 'year' as a random effect. Two-way interactions were dropped from models when non-significant (Engqvist 2005). We also quantified the proportion of variance explained for our GLMM (Nakagawa and Schielzeth 2013). Briefly, we calculated the marginal R2 (R^2_m) to describe the proportion of variance explained by the fixed factors alone, and the conditional R2 (R^2_c) to describe the proportion of variance explained by both fixed and random terms. Post hoc comparisons were performed using the 'lsmeans' package (Lenth 2016). All values are presented as mean ± SE.

Results

The parasitism rate in our study area during the four years of study was 59.5%. If only the subset of nests used in this study is considered, the average parasitism rate was 61.4% (n = 262).

Intensity of brood parasitism

The number of great spotted cuckoo eggs per nest was highly variable. We found that 30.1% of nests contained one great spotted cuckoo egg, which means that most parasitized nests hosted more than one parasitic egg (mean ± SE = 3.01 ± 0.17 cuckoo eggs per nest; n = 161 nests; Fig. 1A). Our data revealed that multiparasitism (as considered in this study: three or more cuckoo eggs per nest) was the most frequent situation in parasitized nests (48.4%). Nonetheless, if nests containing two parasitic eggs per nest are considered as multiparasitized, as it is usual in brood parasitism literature, then the multiparasitism rate reached 69.6%. The multiparasitism rate was directly related to parasitism rate (r = 0.95, $p < 0.0001$; data series of 11 years in our study area).

The number of great spotted cuckoo females laying in the same nest was also variable (Fig. 1B). The empirical correlation under the null hypothesis between the number of females laying in the same nest and the number of cuckoo eggs per nest under the null hypothesis was 0.92 (2.5 and 97.5 centiles; 0.91, 0.93), indicating that the observed correlation (0.92) was not different to that expected under a null expectation (p = 0.49, Supporting information). Repeated parasitism (i.e. parasitism by the same female) is frequent in great-spotted cuckoos; however, we did not record the number of eggs laid by each individual female in this study, since we focused on the number of eggs and parasitic females per nest. When considering only those nests parasitized by a single great spotted cuckoo female (n = 72), we found that 68.1% of nests received one parasitic egg, 29.2% received two parasitic eggs, 1.4% received three parasitic eggs, and 1.4% received four eggs from the same great spotted cuckoo female.

Reproductive success of great spotted cuckoos according to intensity of parasitism

As expected, the total number of cuckoo eggs hatched was positively related to the intensity of cuckoo parasitism (F = 45.25, df = 2, Resampled-p = 0.0001, Supporting information, Fig. 2A). The total number of cuckoo eggs hatched in multiparasitized nests was higher than in single- or double-parasitized nests (post hoc tests, $p < 0.0009$ in both cases, Fig. 2A), which supports Prediction 1. Nonetheless, when we considered the proportion of eggs that hatched in successful clutches, we found that cuckoo hatching success did not differ between single-, double-, and multiparasitized nests (GLMM, $\chi^2 = 1.59$, df = 2, p = 0.451, Supporting information, Fig. 3A).

The total number of cuckoo chicks fledged was positively related to the intensity of cuckoo parasitism (F = 15.02, df = 2, Resampled-p = 0.0001, Supporting information, Fig. 2B), which supports Prediction 2. However, when we considered the proportion of chicks that fledged out of hatched eggs, we found that cuckoo fledgling success did not differ between single-, double-, and multiparasitized nests (GLMM, $\chi^2 = 3.27$, df = 2, p = 0.195, Supporting information, Fig. 3B). Cuckoo breeding success (i.e. the proportion of eggs that produce fledglings), however, differed significantly between nests according to the intensity of parasitism (GLMM, $\chi^2 = 5.76$, df = 2, p = 0.046, Supporting information, Fig. 3C), with multiparasitized nests showing reduced breeding success compared to single- (post hoc tests, p = 0.044) and double-parasitized nests (post hoc tests, p = 0.019).

Reproductive success of magpies according to intensity of parasitism

The total number of magpie eggs that hatched was negatively related to the intensity of cuckoo parasitism (F = 3.53, df = 2,

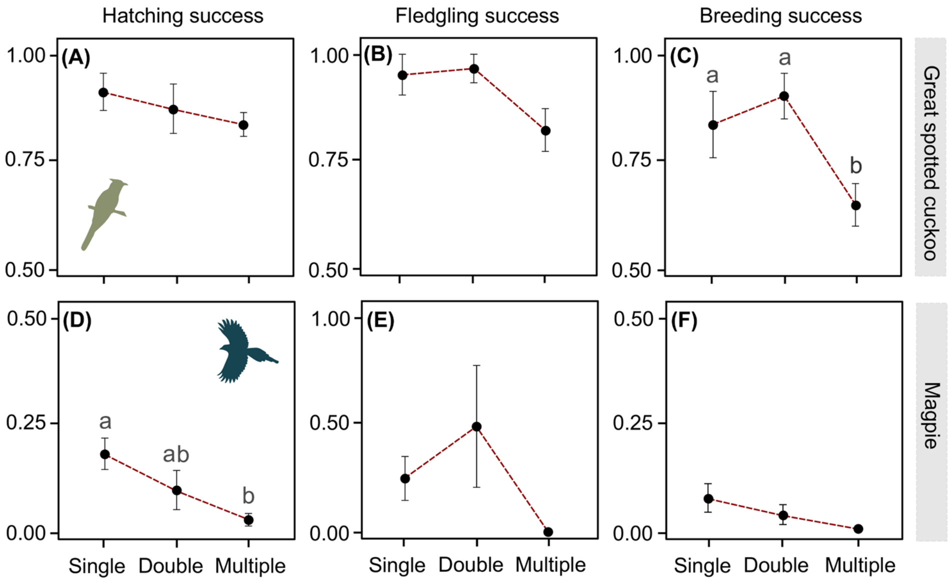

Figure 3. Hatching success, fledgling success, and breeding success of great spotted cuckoos (A–C) and magpies (D–F) according to brood parasitism intensity. Different letters show statistically significant differences in post hoc tests.

Resampled-p = 0.034, Supporting information, Fig. 2C), which is in agreement with Prediction 3. Similarly, when we considered the proportion of eggs that hatched in successful clutches, we found that parasitism intensity had a negative impact on magpie hatching success (GLMM, $\chi^2 = 7.02$, df = 2, p = 0.029, Supporting information, Fig. 3D). Post hoc tests revealed that magpie hatching success was lower in multiparasitized nests compared to single-parasitized nests (post hoc test, p = 0.015, Fig. 3D). Doubly parasitized nests also showed lower hatching success than singly parasitized nests, and higher than the multiparasitized ones, but these differences were not significant (post hoc test, $p > 0.207$ in both cases).

The total number of magpie chicks that fledged decreased as brood parasitism intensity increased, but these differences were not significant (F = 0.213, df = 2, Resampled-p = 0.820, Supporting information, Fig. 2D), which does not support Prediction 4. As expected, the total number of magpie chicks that fledged was positively related to the number of chicks in the nest (F = 43.36, df = 2, Resampled-p = 0.002). When we considered the proportion of chicks that fledged out of hatched eggs, we found that brood parasitism intensity did not affect magpie fledgling success (GLMM, $\chi^2 = 0.33$, df = 2, p = 0.846, Supporting information, Fig. 3E). Finally, magpie breeding success (i.e. the proportion of eggs that produce young that leave the nest) did not differ between single-, double-, and multiparasitized magpie nests (GLMM, $\chi^2 = 3.80$, df = 2, p = 0.149, Supporting information, Fig. 3F).

Nest desertion according to intensity of parasitism

Nest desertion rate in magpie nests was 1.25, 6.31, 1.85, and 6.06% in 2011, 2012, 2013, and 2014, respectively. After controlling for the potential effect of year, we found that desertion probabilities did not differ significantly among groups (GLMM, $\chi^2 = 3.89$, df = 3, p = 0.274, Supporting information; non-parasitized: 4.4%, n = 112; single-parasitized: 3.7%, n = 53: double-parasitized: 6.8%, n = 29; multiparasitized: 1.7%, n = 58). This result therefore supports Prediction 6 instead of Prediction 5. Nest desertion probabilities increased across the breeding season (GLMM, $\chi^2 = 5.78$, df = 1, p = 0.016).

Nest predation according to intensity of parasitism during the incubation period

During the incubation stage, predation rate in magpie nests was 29.11, 13.48, 22.64, and 22.58% in 2011, 2012, 2013, and 2014, respectively. Predation probabilities did not differ significantly among groups when considering intensity of parasitism (GLMM, $\chi^2 = 5.07$, df = 3, p = 0.167, Supporting information; non-parasitized: 17.7%, n = 107; single-parasitized: 25.0%, n = 52; double-parasitized: 22.2%, n = 27; multiparasitized: 20.2%, n = 69). These results do not change when all parasitized nests are considered together, as predation probabilities did not differ between non-parasitized and parasitized nests (GLMM, $\chi^2 = 1.38$, df = 3, p = 0.240). Finally, predation probabilities during the incubation stage increased across the breeding season (GLMM, $\chi^2 = 21.43$, df = 1, $p < 0.0001$) and were negatively related to magpie clutch size (GLMM, $\chi^2 = 6.93$, df = 3, p = 0.008).

Nest predation according to intensity of parasitism during the nestling period

During the nestling stage, predation rate was 37.5, 28.5, 14.6, and 12.5% in 2011, 2012, 2013, and 2014, respectively. After controlling for the potential effect of year, we found that predation rate during the nestling phase did not differ significantly among magpie nests with different intensity of cuckoo parasitism (GLMM, $\chi^2=6.02$, df=3, p=0.110, Supporting information; non-parasitized: 19.3%, n=88; single-parasitized: 39.14%, n=46; double-parasitized: 19.2%, n=26; multiparasitized: 32.4%, n=37). As in the incubation stage, these results do not change when all parasitized nests are considered together, as predation probabilities did not differ between non-parasitized and parasitized nests (GLMM, $\chi^2=2.46$, df=3, p=0.117). These results indicate that cuckoo parasitism does not reduce the probability of nestling predation (as stated by Predictions 7 and 8), but neither does it increase it (as stated by Predictions 9 and 10). Finally, predation probabilities during the nestling stage increased across the breeding season (GLMM, $\chi^2=15.01$, df=1, $p < 0.001$, Supporting information).

Discussion

The presence of multiparasitized nests was the most frequent situation in magpie nests in our study area, and some of these multiparasitized nests were hosting three or more cuckoo eggs per nest (48.4%). To compare with data provided in the literature, we should consider as multiparasitized those nests with two or more cuckoo eggs per nest, which reaches a higher multiparasitism rate (69.6%). This is one of the highest rate of multiparasitism reported in the literature for any brood parasite–host system. However, in the screaming cowbirds *Molothrus rufoaxillaris*–greyish baywing *Agelaioides badius* system, similar or even higher percentages can be reached as Ursino et al. (2020) reported, in a host population with an extremely high parasitism rate (96.5%), with a mean of parasitic eggs per nest of 5.7 ± 0.45, which is almost double than the value found in our study (3.01 ± 0.17).

As the number of great spotted cuckoo eggs per nest increases, the number of females laying in the same nest also increases. Thus, there exist a clear linear relationship between parasitism rate, multiparasitism, and the number of parasitic females laying in a single nest: as parasitism rate increases, multiparasitism rate increases and, as multiparasitism rate increases, the number of cuckoo females laying per nest also increases. This supports the view that multiparasitism is likely the consequence of the abundance of brood parasites, and the scarcity of host nests in the appropriate egg-laying stage, or both, as suggested for many brood parasite species (Martínez et al. 1998a, Moskát and Honza 2002, McLaren et al. 2003, Ellison et al. 2006, Rivers et al. 2012, Ursino et al. 2020). The importance of great spotted cuckoo abundance was evidenced by comparing parasitism rate of different host species in the same area and during the same period: the parasitism rate in the carrion crow rose from 7% in 2006 and 11% in 2007 to the very high rate of 54% in 2008. During these years, parasitism rate of magpie nests in the same area was 45.1, 33.7, and 58.5%, respectively. Considering that both hosts can be parasitized by the same cuckoo female laying in the nests of both species (Martínez et al. 1998b), it can be accepted that the higher parasitism rate found in both hosts during 2008 was the consequence of a greater abundance of great spotted cuckoos during that year. On the other hand, the effect of scarcity of appropriate host nests was demonstrated by analyzing the characteristics (i.e. breeding stage and parasitism status) of daily available host nests for brood parasitism. It was found that the number of cuckoo eggs laid in one nest increased with decreasing daily availability of host nests that were at a suitable breeding stage for parasitism (Soler et al. 2015b). When the parasitism rate is high, synchronization of egg laying with that of the host – which is crucial to the reproductive success of the brood parasite because non-synchronized parasitic eggs are usually wasted – is poorer during the years of high parasitism rate (Soler et al. 2015b). All this information, considered together, supports the above-mentioned relationship between parasitism rate, multiparasitism, and the number of cuckoo females laying per nest.

High levels of multiparasitism can be considered maladaptive because magpies usually cannot rear more than four cuckoo nestlings in the same nest (M. Soler and T. Pérez-Contreras), but laying in non-synchronized nests (before magpies start laying during the late incubation period) is also maladaptive, and it frequently occurs in years or plots with a high parasitism rate (Soler et al. 2015b). Thus, it seems that the most important parameter affecting multiparasitism is abundance of great spotted cuckoos, which provokes a high parasitism rate and a shortage of host nests during the laying stage. Another piece of evidence supporting this assertion is the discovery of one multiparasitized magpie nest with 18 great spotted cuckoo eggs (Fig. 4) near to Jódar (situated 65 km north of our Guadix study area), which was the only magpie nest in a zone visited by many great spotted cuckoos because in that area there were abundant plantations of pines infected by pine processionary *Thaumetopoea pityocampa*, one of the main components of the diet of the great spotted cuckoo (Cramp 1985). The abundance of parasites and a shortage of host nests have also been suggested as the factors responsible for a high percentage of multiparasitized nests in an evictor brood parasite, the common cuckoo *Cuculus canorus*. In this case, multiparasitism is clearly maladaptive because only one nestling can survive per parasitized nest; but, in a great reed warbler *Acrocephalus arundinaceus* population in central Hungary with a very high parasitism rate (64%), more than half of the cuckoo eggs were laid in multiparasitized nests (Moskát and Honza 2002).

Our egg phenotype analyses revealed that repeated parasitism by the same great spotted cuckoo female is frequent. These results are supported by previous parentage analyses of four females, which showed that all females laid more than one egg per nest in some nests: in two cases parasitic females laid in one-third of parasitized nests and, in another case, they laid in half of the nests (Martínez et al. 1998a). The frequent use of the same nest by the same female reported in the great spotted cuckoo is not common in other brood parasite species. As a rule, single females avoid laying twice in the same host nest, even when parasitizing hosts that

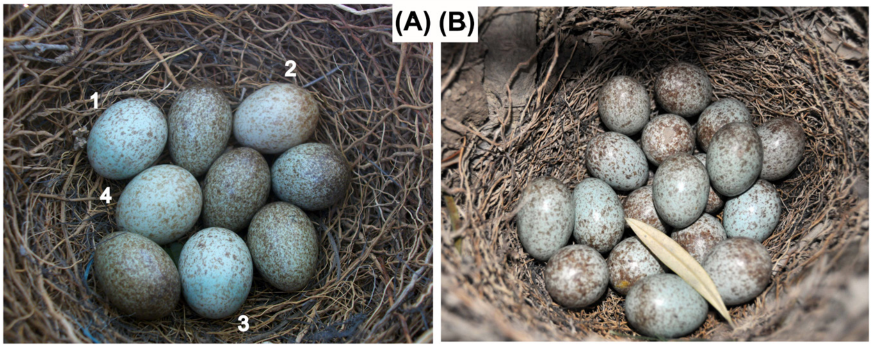

Figure 4. (A) Multiparasitized magpie nest with four great spotted cuckoo eggs (numbered) and five magpie eggs (photo: Francisco Ruiz-Raya). (B) Multiparasitized magpie nest with 18 great spotted cuckoo eggs located in Jódar (Jaén), 65 km north of our Guadix study area. Such high intensity of brood parasitism is rare and was because this was the only magpie nest in the area, which was visited by several great spotted cuckoos coming from pine plantations infected by pine processionary *Thaumetopoea pityocampa*, the main component of the diet of the spotted cuckoos (photo and information: Miguel Yanes).

can rear several nestlings (Ortega 1998, Ellison et al. 2006, Gloag et al. 2014a). Even in the screaming cowbird, the species with a very high multiparasitism rate, parasitic females typically lay one egg per nest (Ursino et al. 2020). Repeated parasitism has also been reported in the shiny cowbird and the brown-headed cowbird, but only in a few heavily parasitized host populations (Alderson et al. 1999, McLaren et al. 2003, Rivers et al. 2012, de la Colina et al. 2016). As far as we know, there is only one other brood parasite species that practices repeated parasitism as the general rule: the cuckoo finch (Stevens et al. 2013).

Why do females of these two species not avoid repeatedly parasitizing nests of their hosts? The high frequency of repeated parasitism in these two species raises the question of whether they should benefit from this strategy. This seems likely because, in both species, hosts can successfully rear broods of several parasitic nestlings and these do not actively kill their nestmates (Soler et al. 1990, Stevens et al. 2013). In the case of the cuckoo finch, it was experimentally demonstrated that, as the proportion of parasitic eggs increased, the African tawny-flanked prinia *Prinia subflava* hosts are less likely to reject them, suggesting that repeated parasitism is likely an adaptation because it increases the probability of host acceptance of parasitic eggs (Stevens et al. 2013). This possibility of a reduction of rejection rate when there are several parasite eggs in the nest has also been proposed in the common cuckoo (Moskát et al. 2009, Bán et al. 2013, Manna et al. 2019).

In the case of the great spotted cuckoo, though multiparasitism is more frequent when parasitism rate is higher, it cannot be accepted that multiparasitism is only the consequence of scarcity of unparasitized nests for two main reasons: first, about 30% of the total nests are multiparasitized despite the fact that 40% of the nests are unparasitized. Second, great spotted cuckoo females select for parasitism magpie nests at the laying stage, but preferably those previously harboring one or two cuckoo eggs (Soler et al. 2020). Thus, laying in a previously parasitized nest is likely an active decision of great spotted cuckoo females.

Effect of the intensity of parasitism on the breeding success of both great spotted cuckoos and magpies

Breeding success of the great spotted cuckoo was lower in multiple than in single or double parasitism (Fig. 3C). This is the general rule in non-evictor parasites because multiparasitism can provoke severe competition among parasite nestlings (Ortega 1998, Trine 2000, Goguen et al. 2011, de la Colina 2016). However, in cowbirds the survival of parasitic nestlings decreases in multiparasitized nests in host species of smaller size, but not in species of larger size that are very effective in raising several cowbird nestlings (Weatherhead 1989, Trine 2000, Hoover 2003, Goguen et al. 2011). Nevertheless, in the great spotted cuckoo, although in magpie nests cuckoo nestlings are able to outcompete their nestmates because magpies are only slightly larger than great spotted cuckoos (del Hoyo et al. 1992–2011) and cuckoo nestlings hatch earlier than magpie nestlings (14 versus 18 days, respectively; Álvarez and Arias de Reyna 1974), in nests of its secondary host the carrion crow (which is about double the size of the parasite) fledging and breeding success of the cuckoo is much lower than in magpie nests, because cuckoo nestlings are not able to outcompete their larger crow nestmates as they do with magpie nestlings (see "Effect of the intensity of parasitism on the breeding success of both great spotted cuckoos and magpies", Soler et al. 2001).

As predicted, the number of cuckoo eggs hatched, as well as the number of chicks fledged, were higher in multiple than in single- or double-parasitized magpie nests, which means that multiple eggs laid in magpie nests are not completely wasted as happens in evictor brood parasites (Moskát and Honza 2002), or in non-evictor brood parasites using as hosts species of small size that are not able to raise more than one parasitic nestling per brood (Smith and Arcese 1994, Goguen et al. 2011).

Multiparasitism by great spotted cuckoos imposes a strong impact on magpie reproductive success, as has been reported in most brood parasite–host systems in which multiparasitism occurs (Ortega 1998, Trine 2000, Tuero et al.

2007). Magpie breeding success did not differ between single-, double- or multiparasitized nests (Fig. 3F). This is because the main effect of great-spotted cuckoo parasitism is not that provoked during the nestling period by parasitic nestlings outcompeting host nestlings, but the one occurring during the laying period, as female great spotted cuckoos frequently damage host eggs. Few undamaged magpie eggs remain in the nest even in singly parasitized nests, because the first great spotted cuckoo female that lay its egg destroys a higher number of magpie eggs as the number of previously laid magpie eggs increases (Soler et al. 1997). With the laying of subsequent cuckoo eggs, more magpie eggs become damaged or destroyed while cuckoo eggs remain unaffected (Soler and Martínez 2000), because their eggs have an eggshell that is thicker and with smaller and more randomly oriented calcite crystals, a microstructure that provides a higher resistance to breakage (Soler et al. 2019). Thus, in doubly and multiparasitized nests, undamaged magpie eggs are very scarce or even absent.

The number of magpie chicks fledged was lower as brood parasitism intensity increased, but these differences were not significant (Fig. 2D). This trend agrees with previously published information on brown-headed cowbird–host systems (Trine 2000, Hoover 2003, Tuero et al. 2007). However, it is worth mentioning that this negative effect on survival of host nestlings mainly affects host species of small size, with larger host species being less affected (Smith and Arcese 1994, Trine 2000). This is not surprising, because differences in size among nestlings in a brood is a crucial issue driving food acquisition by nestlings (Soler 2017b). In fact, in nests of its larger carrion crow host, the fledging success of host nestlings is very similar in parasitized and unparasitized nests (about 83%; Soler et al. 2001).

Is multiparasitism an adaptation in the great spotted cuckoo?

There is abundant evidence suggesting that the response to this question should be affirmative.

First, repeated parasitism is very frequent and seems to be a fixed characteristic in great spotted cuckoo females. Each tends to lay only 1–2 eggs per nest and prefer laying in already parasitized nests containing one or two cuckoo eggs (Soler et al. 2020).

Second, although breeding success of great spotted cuckoos (but not magpies) decreases according to intensity of parasitism (Fig. 3C), multiparasitized nests produce a higher number of cuckoo fledglings than single- or double- parasitized nests (Fig. 2B). Thus, nests with three or more cuckoo eggs are more successful.

Third, multiparasitism could provide relevant benefits by favoring imprinting on their own species given that the presence of two or more parasitic nestlings in the nest could provide appropriate imprinting stimuli to each other (Kruijt et al. 1983, Soler and Soler 1999, Soha and Marler 2000).

Fourth, multiparasitism could have also been selected because of benefits provided at the fledging stage, given that when more than one great spotted cuckoo chick leaves the nest together, they form a group, which is highly beneficial for them (Soler et al. 2004, 2005).

Fifth, multiparasitism usually prevents survival of any host young, which would avoid the possibility of comparison of the parasitic fledgling with host's own fledglings; an important cue for magpies that allows them to discriminate fledgling cuckoos as foreign (Soler et al. 2014).

Effect of the intensity of parasitism on nest desertion

Our results show that nest desertion is very similar in the four groups. This supports our Prediction 6 and agrees with the argument that large-sized hosts, as is the case of the magpie, do not use nest desertion as a mechanism to reject parasitic eggs (Soler et al. 2015a), which has been reported in a majority of medium- or large-size host species (Lorenzana and Sealy 2001, Underwood et al. 2004, Peer and Rothstein 2010, but see Begum et al. 2012).

Effect of the intensity of parasitism on nest predation

Predation rate of magpie nests during the incubation stage did not vary significantly among groups of different intensity of parasitism, being similar in non-parasitized and parasitized nests. Similarly, during the nestling period there were no significant differences among the four groups of different intensity of cuckoo parasitism, and predation probabilities did not differ either between non-parasitized and parasitized nests. These results allow us to discuss the possible relationship between brood parasitism and nest predation, considering two main points of view:

First, it has been suggested that concealment of the nest and parents' activity near the nest play an important role in the susceptibility of one nest being parasitized (Moskát and Honza 2000, McLaren and Sealy 2003, Fiorini and Reboreda 2006, Soler and Pérez-Contreras 2012) or predated (Martin et al. 2000, Ibáñez-Álamo et al. 2015). If both brood parasites and predators use the same cues to detect the nest of their victims, it could be expected that as nests are more easily detected by brood parasites, they should also be more easily detected by nest predators. However, this was not the case, at least in our study area. We have a clear gradient related to intensity of parasitism by a brood parasite (non-parasitized, singly, doubly, and multiparasitized) and this gradient does not coincide with difficulty of nest finding by predators, given that all groups were predated at a similar rate.

Second, contrary to what was stated by the 'mutualism hypothesis' (Canestrari et al. 2014), our results show that predation rate during the nestling phase does not vary according to intensity of parasitism, nor decrease as the intensity of parasitism increases. In fact, predation rate tends to be lower in non-parasitized than in parasitized nests. These results agree with previous findings showing that parasitized nests were not predated at a lower rate than non-parasitized nests, neither in magpie nor in carrion crow nests; and, in addition, the experimental parasitism of magpie nests that were not selected for parasitism by cuckoos did not reduce the probability of predation (Soler et al. 2017). The fact that predation rate tends to be higher in magpie nests with great spotted cuckoo chicks than in nests without cuckoo chicks (but not significantly: p = 0.117) partially supports the idea that the exaggerated loudness of begging calls of great spotted cuckoo chicks ('predation cost of begging hypothesis'; Soler et al. 1999, 2012) could attract predators, as evidenced by the study of Ibáñez-Álamo et al. (2012) in which experimental parasitism of blackbirds' nests with great spotted cuckoo nestlings doubled the probability of nest predation.

Summarizing, multiparasitism (and repeated parasitism) is an adaptation in the great spotted cuckoo because multiparasitized nests produce a higher number of cuckoo fledglings than single- or double-parasitized nests, which does not affect nest desertion nor nest predation.

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Author contributions

Manuel Soler: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Writing – original draft (lead); Writing – review and editing (lead). **Tomás Pérez-Contreras**: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Francisco Ruiz-Raya**: Data curation (equal); Formal analysis (equal); Writing – review and editing (equal).

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Data availability statement

The data are publicly accesible at Digibug Digital Repository: https://hdl.handle.net/10481/81780 (Soler et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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