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Article

Brood parasitism, provisioning rates and breeding phenology of male and female magpie hosts

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Parental care is a costly behaviour that raises the prospects of offspring survival. In species with biparental care these costs are shared by both parents, although there may be a conflict regarding the relative investment of each sex. Avian brood parasites leave all the costs of rearing offspring to their hosts. The magnitude of these costs and their consequences on the relative role of both sexes in parental care and future reproduction remain mostly unknown. Here, we investigate whether provisioning rate of nestlings by magpie hosts *Pica pica* differs between broods parasitized by the great spotted cuckoo *Clamator glandarius* and non-parasitized broods, and whether the relative contribution of each sex to provisioning is affected by parasitism. Furthermore, we explore the effect of parasitism on magpie's future reproduction. We found that provisioning rate was similar in parasitized and non-parasitized broods, and that the relative contribution of males and females was also similar, irrespectively of the parasitism status. However, rearing parasitic offspring seems to have a negative long-term effect on magpie's breeding phenology in the following breeding season. Our results suggest that, although brood parasitism by great spotted cuckoos does not seem to influence the relative contribution of both sexes to parental care, it may entail long-term extra costs in terms of breeding delay for magpies.

Keywords: brood parasitism, costs of reproduction, great spotted cuckoo, laying date, magpie, provisioning rate

Introduction

Parental care comprises any investment made by parents that increases the prospects of survival of their progeny (Clutton-Brock 1991). Because parental investment has associated costs in terms of fecundity and/or survival for the caring parents (Trivers 1972, Stearns 1992), different species have evolved distinct strategies to optimize the trade-off between benefits and costs of parental care (Clutton-Brock 1991). In species with biparental care, such as most bird species, the offspring survival relies on the effort of both parents (Schroeder et al. 2013); however, the relative investment of each parent might differ. How much effort to invest can be influenced by many factors, such as



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adult sex-specific longevity (Bonduriansky et al. 2009), food availability (Eldegard and Sonnerud 2009), extra-pair paternity (Møller and Cuervo 2000) and brood size (Komdeur et al. 2002). Furthermore, each member of the pair can adjust its parental effort to that of its mate by either matching it (Johnstone and Hinde 2006) or exploiting it (Houston et al. 2005, Harrison et al. 2009), although there may be a continuum of possibilities between matching and exploiting a mate's effort (Johnstone and Hinde 2006).

Avian brood parasites lay their eggs in the nests of hosts, and hosts assume all the parental duties of rearing the parasitic offspring (Payne and Sorensen 2005, Davies 2010). Brood parasitism entails short-term costs for the hosts, being the reduction in current reproductive success the main one. Some brood parasites (e.g. Cuculidae) reduce their host's breeding success to zero through, for example, the eviction of host eggs performed by parasitic cuckoo nestlings; whereas in other species (e.g. *Molothrus* sp.), the negative effect of brood parasitism can be less drastic, and parasitic nestlings are regularly raised together with host nestlings (Rothstein 1990). In any case, brood parasitism imposes a strong selective pressure on hosts that has driven the evolution of defences against brood parasites, which, as a consequence, has favoured the evolution of counter-adaptations in brood parasites which facilitate host exploitation, leading in some instances to coevolutionary arms races (Rothstein 1990, Soler 2014).

Brood parasitism might also influence host parental care (Krüger 2007). For instance, studies on brood parasite–host systems where parasitic and host nestlings do not share the nest have either failed to find statistically significant differences in provisioning rate between parasitized and non-parasitized nests (Kilner et al. 1999, Mark and Rubenstein 2013, Samaš et al. 2019), or found lower provisioning rates in parasitized nests (Soler et al. 1995a, Požgayová et al. 2015, Samaš et al. 2018). In contrast, studies on brood parasite–host systems in which parasitic and host nestlings share the nest (e.g. some species of *Molothrus* and their hosts) have shown that provisioning rate tends to be higher in parasitized than non-parasitized nests (Dearborn et al. 1998, Hoover and Reetz 2006, Grayson et al. 2013, but see Canestrari et al. 2014 for a non-cowbird brood parasite where provisioning rates are lower in parasitized nests). Furthermore, brood parasitism could also affect the relative parental contribution of males and females, for example, by affecting brood size (Komdeur et al. 2002), a possibility seldom explored. For example, Požgayová et al. (2015) found that males work less in great reed warbler *Acrocephalus arundinaceus* nests parasitized by the common cuckoo *Cuculus canorus* than in non-parasitized nests, even in monogamous pairs, which constitute an important part of the population. Contrastingly, red-winged blackbird *Agelaius phoeniceus* nests parasitized by the brown-headed cowbird *Molothrus ater* were more likely to receive care from the male than non-parasitized nests (Grayson et al. 2013). Hence the potential effect of brood parasitism on the relative role of each sex might be species-specific, and overall, the potential effect of brood parasitism on parental care remains poorly understood.

Beyond detrimental effects on the parasitized breeding attempt, brood parasitism may also have long-term consequences and impact adult host survival and future reproduction. Life-history theory predicts that current reproductive effort compromises future reproductive output by increasing adult mortality and/or decreasing the capacity to invest in future reproduction (Stearns 1989, Wedell et al. 2006). So far the long-term consequences of raising brood parasites are not well understood and most studies have focused on host breeding dispersal, survival and return rates in response to previous brood parasitism. These studies have found that brood parasitism either has no clear effect on host survival and return rates (Brooker and Brooker 1996, Payne and Payne 1998, Hoover 2003a, Hauber 2006, Samaš et al. 2019), or that it can affect them negatively (Hoover and Reetz 2006, Mark and Rubenstein 2013, Koleček et al. 2015). By contrast, parasitism does not seem to affect breeding dispersal distances between years (Hoover 2003a, b, Sedgwick 2004, Hoover and Reetz 2006, Koleček et al. 2015) or may even reduce dispersal distances of some male hosts (Molina-Morales et al. 2012). However, brood parasitism, through the costs of parental care, may potentially mediate long-term changes in life-history traits such as clutch size or laying date, a possibility seldom considered. Up to date, only two studies have evaluated this scenario. Hauber (2006) found no statistically significant effect of parasitism on clutch size or laying date in second breeding attempts in eastern phoebes *Sayornis phoebe*, even though parasitic cowbird nestlings were capable of increasing host provisioning rates (Hauber and Montenegro 2002). In contrast, parasitism by the Central America striped cuckoo *Tapera naevia* negatively affects rufous-and-white wren *Thryophilus rufalbus* hosts' re-nesting phenology and the probability of breeding in the subsequent season (Mark and Rubenstein 2013). Altogether, these mixed results imply that the long-term consequences of brood parasitism on adult host survival or future reproduction remain poorly understood.

In this study we explore both short- and long-term effects of brood parasitism in magpies *Pica pica*, a common host of the great spotted cuckoo *Clamator glandarius*. Great spotted cuckoo parasitism often reduces magpie's current breeding success to zero, and in most parasitized nests cuckoo nestlings are reared alone or together with other cuckoo nestlings (i.e. multiparasitism; Martínez et al. 1998). Soler et al. (1995a) have previously reported that the total amount of food delivered in non-parasitized magpie nests is higher than that delivered in both natural and experimentally parasitized nests, suggesting that magpies could be working less when rearing parasitic cuckoos. Moreover, Buitron (1988) found that male' provisioning rates were significantly higher than those of females, but this study was carried out in a non-parasitized magpie population. Changes in host parental workload and in the relative role of each sex in response to parasitism, as above explained, may have long-term life-history effects worth investigating.

To address these issues here we first quantify provisioning rate (as a proxy to parental workload) in parasitized nests and compared it to that in non-parasitized nests. We predict

1) that provisioning rates should be smaller in parasitized nests due to the smaller number of nestlings in the nests. We explore the relative role of males and females in provisioning in a context of parasitism. As a consequence of the lower brood size in parasitized nests (Methods), 2) we expect that males should reduce their provisioning rates as it has been found in other hosts (Požgayová et al. 2015). Finally, to identify possible long-term consequences of raising parasitic nestlings for hosts, we investigate whether parasitism status and magpie provisioning rates in a breeding attempt can influence its presence in the breeding population and its breeding phenology in the subsequent breeding season. We predict 3) a negative effect of increased provisioning rates on the probability of host presence and egg laying dates in the following season. As we predict lower provisioning rates in parasitized nests and the time to fledge for cuckoo nestlings is shorter than that for magpies (Soler and Soler 1991), we expect that parasitized magpies would have higher probability of surviving to the next breeding season and would advance their breeding phenology.

Methods

Study area and system

This study was conducted in La Calahorra (37°10'N, 3°03'W, Granada, southern Spain) during the breeding seasons (March–July) of 2008–2012 and 2016–2017. The study area is characterized by cereal fields patched with groves of almond trees *Prunus dulcis* in which magpies preferentially build their nests. Magpies are territorial, sedentary and socially monogamous (Birkhead 1991, Molina-Morales et al. 2012) and pair bonds have been reported to be long-lasting (Birkhead 1991). In our study area, the percentage of nests parasitized by great spotted cuckoos (hereafter cuckoos) ranges from 15.9% to 65.6%, depending on the year (15.9% in 2007, 25.4% in 2008, 65.6% in 2009, 50.7% in 2010, 55.8% in 2011, 35.6% in 2012, 24.5% in 2016 and 24.4% in 2017; Molina-Morales et al. 2013, Martínez et al. 2020). Cuckoo eggs hatch earlier than magpie eggs (Soler et al. 1997), and so, by the time magpie eggs hatch, cuckoo nestlings are already 4–5 days old (Soler and Soler 1991) and monopolize feeds, leading in most cases to the starvation of magpie nestlings.

Individual marking and sex assignment

This magpie population is under long-term monitoring since 2005 (Molina-Morales et al. 2013, 2014, Avilés et al. 2014, Martínez et al. 2020) and a large number of individuals have been ringed either shortly before fledgling (15–18 days old) or captured and marked as adults with a unique combination of colour rings. At the time of ringing, a blood sample was collected from each individual by puncturing the brachial vein with a sterile needle. Since magpies are only slightly dimorphic in size, individual sex was assigned by extracting DNA

from each blood sample and using the sex-specific primers P2/P8 (Griffiths et al. 1998) and Z43B (Dawson et al. 2016).

Nest and pair monitoring

Magpie nests were monitored from the beginning of March each year, when the earliest pairs start building their nests, to the beginning of July, when the last fledglings leave the nest. Nests were found by careful examination of all trees in the study area and GPS positioned. To identify the individuals of each nest, we observed the nests during the nest building stage using a telescope. Observations were performed from a hide or a car, 70–100 meters away from the nest. Nests were visited every four to five days to record laying date, parasitism status, clutch size, hatching date, number of eggs hatched whenever possible, and number of chicks fledged (estimated as the number of chicks in the nest 15–18 days after hatching).

Laying and hatching dates were estimated as the number of days after the first of April. All dates were expressed as deviations from the annual average laying date of each year (mean-centered by year) to account for inter-annual variability in phenology. As nest size has been suggested to be a signal of parental ability in magpies (Soler et al. 1995b, de Neve et al. 2004b), after the clutch was completed, the nests were measured. Nests were assumed to be spheroidal and their volume was estimated from their height and width, which were measured using a measuring tape (precision within 1 cm), and calculated as $4/3(\pi \times a \times b^2)/1000$ (in litres), where a is the largest radius of the nest and b is the smallest radius of the nest (Soler et al. 1995b).

Provisioning rate

We estimated provisioning rate (Schroeder et al. 2013, Bowers et al. 2014) of males and females only in nests where at least one of the caring parents was ringed, so that we were able to distinguish between male and female. Unringed individuals involved in provisioning observations could have changed their partner during the study period, and thus there is a possibility that we observed the same unringed individual twice in two different years, although we think that it is unlikely because magpie pair bonds are long-lasting (Birkhead 1991).

Provisioning observations were carried out between 7 a.m. and 3 p.m., when nestlings were 8–18 days old (cuckoo nestlings ages ranged from 8 to 18 days, mean age = 11.9, median = 11, SD = 3.3; magpie nestlings ages ranged from 9 to 16 days, mean age = 11.9, median = 11.5, SD = 2.2), during the breeding seasons of 2008–2011 and 2016. We observed nests that allowed a clear identification of adults using a telescope from a hide or a car at a distance of 70–100 m. We registered the number of visits performed by each individual during 90–180 min from the first visit of an adult to the nest. This duration has been suggested to be adequate to quantify parental effort (Lendvai et al. 2015). Individual provisioning rate was estimated as the number of visits performed

per hour. The number of parasitized nests observed was 17, containing a mean of 1.88 nestlings (median = 2, SD = 0.86, ranging from 1 to 4 cuckoo nestlings), while the number of non-parasitized nests observed was 22, containing a mean of 4.54 nestlings (median = 4.5, SD = 1.59, ranging from 1 to 7 magpie nestlings). These mean brood sizes are similar to the mean brood sizes observed at the population level (parasitized nests: 1.65 (0.76) nestlings, median = 1, n = 100; non-parasitized nests: 4.33 (1.57) nestlings, median = 4, n = 164; data from years 2008 to 2014). A small percentage of nests in the population contains mixed broods (3%, 8 out of 272 nests, data from years 2008 to 2014), and due to the scarcity of this type of broods we did not perform observations on them and they were not included in average calculations of brood sizes. Mean brood size significantly differed between parasitized and non-parasitized nests in both cases (our dataset: Mann–Whitney test, $U = 33.5$, p -value < 0.001 ; population: Mann–Whitney test, $U = 1214$, p -value < 0.001). Most parasitized nests in the population contain 1 or 2 cuckoo nestlings (83% of the parasitized nests), while most non-parasitized nests contain 4 or more magpie nestlings (74% of the non-parasitized nests). Similarly, of the nests observed in this study, 83% of parasitized nests contained 1 or 2 cuckoo nestlings and 82% of non-parasitized nests contained 4 or more magpie nestlings.

Statistical analysis

All statistical analyses were performed in R ver. 3.6.1 (<www.r-project.org>), and all mixed models were constructed using the lme4 package (ver. 1.1.21, Bates et al. 2015). All continuous variables were z-standardized and categorical variables were mean-centered (Schielzeth 2010). Non-significant interactions were excluded from final models by backward stepwise selection, although results of full models (including those interactions) are shown in Supplementary information.

Provisioning behaviour

Aiming to analyse whether provisioning rates differed between individuals rearing parasitized or non-parasitized broods, we constructed a generalized linear mixed model (hereafter GLMM) with a Poisson distribution (log link function and log observation duration as an offset) in which the individual number of visits was the dependent variable, and parasitism status (non-parasitized = 0; parasitized = 1) and parental sex (male = 0; female = 1) were included as fixed effects. We also incorporated brood size and brood age as continuous fixed effects to the model because they may affect provisioning rates. Nest volume and laying date were also included as continuous fixed effects because they have been suggested as proxies of parental quality in magpies (Soler et al. 1995b, de Neve et al. 2004a, b). Moreover, we included two two-way interactions: one between parental sex and parasitism status to ascertain whether provisioning rate differed between sexes depending on the species being raised, and another one between parasitism status and brood size to separate the effect of both variables. Pair identity and year were firstly

included as random effects but the model could not handle two random effects (it did not converge), and so pair id was finally included as a random effect and year was included as a categorical fixed effect (levels: 2008, 2009, 2010, 2011 and 2016).

Since brood size was smaller in parasitized nests (see section ‘Provisioning behaviour’), there was a strong correlation between parasitism status and brood size (correlation ratio $\eta = 0.72$). Collinearity between two fixed effects increases the standard error of the coefficients estimated for all the other fixed effects in the model, and can reduce the statistical significance of influential predictors (Dormann et al. 2013). We tested the possible effect of collinearity by performing an additional LMM with the same structure as described above, but in which we eliminated one of the correlated fixed effects (as suggested in Forstmeier and Schielzeth 2010): since brood size was a strong predictor in the model (Results, Table 1), we did not drop it, so parasitism status was dropped instead, and estimates from this additional model were compared with that of the former model. A variance inflation factor (VIF) was also calculated for both fixed effects, and never exceeded a threshold of five (Sheather 2009). As there were no important differences in the estimates of both models (Table 1 and Supplementary information), VIF were low, and parasitism status was one of the factors we were most interested in, we decided to keep both fixed effects in the final model. Moreover, these two predictors are not redundant, and the model may lose biological sense without one or the other, besides the fact that this model will be used to draw predictions in the system in which this study was conducted, where

Table 1. Factors affecting provisioning rate in magpies (n = 78 individuals, 39 nests).

Fixed effects	β	Lower CI	Upper CI	Z	p-value
Intercept	1.08	0.98	1.18	20.64	<0.001
Parasitism status	0.15	-0.17	0.48	0.92	0.356
Brood size	0.19	0.03	0.34	2.34	0.019
Brood age	0.14	0.02	0.26	2.40	0.016
Nest volume	-0.10	-0.22	-0.01	-1.80	0.072
Laying date	0.03	-0.08	0.15	0.57	0.565
Sex	-0.13	-0.32	0.06	-1.35	0.177
Year: 2009	-0.11	-0.54	0.32	-0.50	0.617
2010	0.07	-0.25	0.39	0.51	0.681
2011	0.15	-0.29	0.58	0.66	0.507
2016	0.21	-0.17	0.59	1.09	0.273
Random effect	σ			LRT	p-value
Pair identity	0.06			0.06	0.800

Results of a GLMM (Poisson distribution, log link function) testing the effect of parasitism status, brood size, brood age, nest volume, laying date, sex, year and pair identity on provisioning rates in magpies. 95% CI were calculated by the Wald approximation; parameter estimates were calculated by the Gauss–Hermite approximation to the log-likelihood with 25 quadrature points; p-values for fixed effects were calculated by a Wald Z test; p-value for the random effect was calculated by a likelihood ratio test. Marginal $R^2 = 0.20$; Conditional $R^2 = 0.21$ (calculated following Nakagawa and Schielzeth 2013; MuMIn package, ver. 1.43.15, Bartoń 2019). Significant estimates are highlighted in bold.

collinearity between these two fixed effects should remain constant (Dormann et al. 2013).

Additionally, we tested whether individual provisioning rates differed between non-parasitized nests that contained four or more magpie nestlings ($n = 18$ nests) and parasitized nests that contain one or two cuckoo nestlings ($n = 14$ nests), which are the most common situations in our population (see section Provisioning rate). We then constructed a GLMM (Poisson distribution, log link function and log observation duration as an offset) in which the individual number of visits to the nests was the dependent variable and parasitism status, brood age, nest volume, laying date, parental sex and a two-way interaction between parasitism status and sex were included as fixed effects and pair identity was included as a random effect. Year was not included in this model to avoid model over-fitting and because it had little effect on provisioning rates (Table 1).

Parents' presence and breeding phenology in the following season

We tested whether different variables related to magpies' current reproduction (such as provisioning rate or laying date) could affect adults' presence (the equivalent to return rate) in the population and/or their breeding phenology in the following season. Thus, we firstly constructed a GLMM (binomial distribution, logit link function) in which adults' presence in the breeding population in the subsequent breeding season (year $t + 1$; yes = 1, no = 0) was the dependent variable and the following variables related to the previous breeding season (year t) were included as fixed effects: parasitism status (non-parasitized = 0, parasitized = 1), brood size (continuous variable), provisioning rate (continuous variable), laying date (continuous variable), sex (male = 0, female = 1) and a two-way interaction between parasitism status and brood size. Pair identity was included as a random effect. Year was included as a fixed effect, however, the model could not appropriately handle it, since the estimates for pair id were zero but different from zero if year was excluded from the model; so we decided to finally exclude year, also because it seemed to have little effect on provisioning rates (Table 1). This model included 49 marked individuals ($n = 39$ nests) involved in provisioning observations of which 26 ($n = 24$ nests) were observed breeding in the following season.

Secondly, we constructed a linear model (LM) in which laying date in the subsequent breeding season (year $t + 1$) was the dependent variable and parasitism status (non-parasitized = 0, parasitized = 1), provisioning rate (continuous variable) and laying date (continuous variable) in the previous breeding season (year t) were included as fixed effects. We also included a two-way interaction between parasitism status and laying date and another one between parasitism status and provisioning rate. This model included 23 of those 26 individuals found breeding in the following season. One individual was excluded because its breeding attempt corresponded to a replacement clutch. This data set included two pairs so one member of each pair was randomly excluded to

avoid pseudoreplication and we ran the same model excluding the other member of the pair (Supplementary information) and results remained qualitatively similar. Year and sex seemed to have little effect on provisioning rates (Table 1) and laying dates already accounted for the variability between years (they were mean-centered by year), so year and sex were not included in the model in order to avoid model over-fitting. We were unable to analyse other reproductive variables (i.e. clutch size) since a large proportion of those 23 individuals (43%) were parasitized in the following breeding season. Additionally, in the same data set, we tested whether the difference in laying date between two consecutive years (i.e. laying date in $t + 1$ minus laying date in t) differed according to parasitism status in year t . We then constructed a LM fitted by generalized least squares (GLS; R package nlme ver. 3.1-144 (Pinheiro et al. 2020)) with a variance structure that allowed different variance per parasitism status level (parasitism status showed residual heterogeneity), in which the difference in laying dates between both breeding seasons (year t and year $t + 1$) was the dependent variable and parasitism status (non-parasitized = 0, parasitized = 1), provisioning rate (continuous variable) and a two-way interaction between them were included as fixed effects. The same model was run excluding the other member of each pair as above (Supplementary information).

Results

Provisioning behaviour

Both sexes provisioned nestlings at similar rates regardless of the type of chick reared in the nest (interaction sex and parasitism status; female provisioning rates on non-parasitized nests: mean = 2.91, median = 3.17, SD = 1.43, parasitized nests: mean = 2.83, median = 2.5, SD = 1.56; male provisioning rates on: non-parasitized nests: mean = 3.74, median = 3.67, SD = 1.70, parasitized nests: mean = 2.82, median = 2.5, SD = 1.37; Supplementary information). In addition, there were no clear differences in provisioning rates between individuals that reared cuckoo nestlings (mean = 2.83, median = 2.5, SD = 1.45) and those that reared magpie nestlings (mean = 3.32, median = 3.33, SD = 1.61; Table 1), not even when controlling for brood size (interaction between brood size and parasitism status; Supplementary information). Provisioning rates increased with brood size and brood age (Table 1). The associations of nest volume and laying date with provisioning rates were not statistically significant (Table 1).

However, individual provisioning rates significantly differed between parasitized and non-parasitized nests when parasitized broods contained one or two cuckoo nestlings (mean = 2.57, median = 2.29, SD = 1.38) and non-parasitized broods four or more magpie nestlings (mean = 3.57, median = 3.50, SD = 1.59; Supplementary information; Fig. 2).

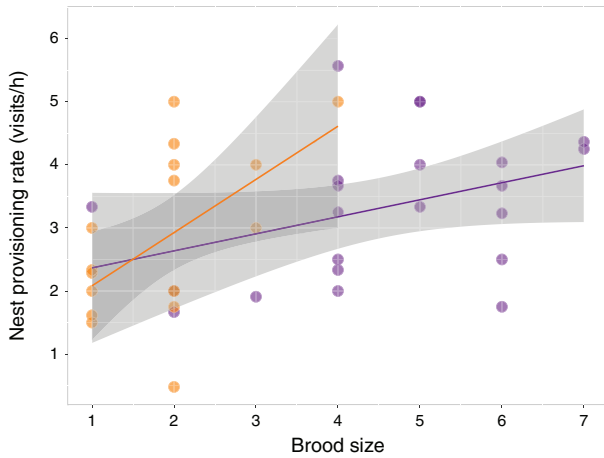


Figure 1. Nest provisioning rates (feeding visits/h) do not significantly differ regarding the nest parasitism status. Each point represents the mean provisioning rate per nest ($n=39$ nests). Solid lines represent regression lines and shaded areas represent the 95% confidence interval for non-parasitized (purple circles, $n=22$ nests) and parasitized nest (orange circles, $n=17$ nests).

Parents' presence and breeding phenology in the following season

The presence/absence of adults in a given breeding season was not affected by parasitism status, brood size, provisioning rate or laying date in the previous breeding season and there were no clear differences between males and females in their probability of being present at the study site in the following season (Table 2).

On the other hand, laying date in a given season was positively associated with the previous season's laying date, but it was not related to provisioning rates in that previous breeding

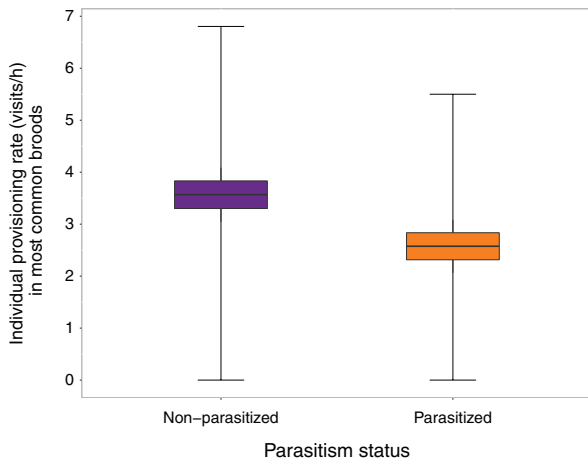


Figure 2. Magpie provisioning rates (feeding visits/h) are higher in non-parasitized nests that contain 4 or more magpie nestlings (purple box, mean=3.57, SE=0.27, $n=36$ observations, 18 nests) compared to parasitized nests that contain 1 or 2 cuckoo nestlings (orange box, mean=2.29, SE=0.26, $n=28$ observations, 14 nests). Boxes represent the mean and standard error of magpie provisioning rates. Error bars represent 95% confidence interval.

Table 2. Factors affecting adults' presence in the following breeding season ($t+1$) ($n=49$ individuals, 39 nests).

Fixed effects	β	Lower CI	Upper CI	df	LRT	p-value
Intercept	0.16	-0.53	0.85	1	0.23	0.63
Parasitism status in t	0.49	-1.59	2.57	1	0.21	0.64
Brood size in t	0.88	-0.36	2.12	1	2.56	0.11
Provisioning rate in t	0.1	-0.61	0.81	1	0.08	0.77
Laying date in t	-0.58	-1.42	0.26	1	2.49	0.11
Sex	-0.64	-2.14	0.85	1	0.87	0.35
Random effects	σ				LRT	p-value
Pair identity	0.53				0.01	0.92

Results of a GLMM (Binomial distribution, logit link function) testing the effect of parasitism status, brood size, provisioning rate, laying date, sex and pair identity on the presence/absence of the adult magpies in the subsequent breeding season. 95% CI were calculated by the Wald approximation; parameter estimates were calculated by the Gauss-Hermite approximation to the log-likelihood with 25 quadrature points; p-values for fixed and random effects were calculated by a likelihood ratio test. Marginal $R^2=0.22$; Conditional $R^2=0.28$ (calculated following Nakagawa and Schielzeth 2013; MuMIn package, ver. 1.43.15, Bartoń 2019).

season and individuals that reared cuckoo nestlings one season bred later in the following season than individuals that reared magpie nestlings (Supplementary information). Furthermore, differences in laying dates between two consecutive breeding seasons were not related to provisioning rates in the previous breeding season either, but were larger for parasitized magpies (mean=2.33, SD=3.08) compared to non-parasitized ones (mean=-2.29, SD=6.73; Table 3, Fig. 3).

Discussion

In this study we explored parental investment of male and female magpie hosts in naturally parasitized and non-parasitized nests, and tested whether parental investment and raising parasitic cuckoos affects future reproductive performance. Our results indicate that magpie provisioning rates were higher in nests with older nestlings and larger broods, which is consistent with Buitron (1988) and Moreno-Rueda et al.

Table 3. Factors affecting the difference in laying dates between two consecutive breeding seasons in magpies ($n=23$ individuals).

	β	Lower CI	Upper CI	df	F	p-value
Intercept	0	-0.39	0.39	1,20	3.36	0.081
Parasitism status in t	0.71	-0.02	1.44	1,20	4.81	0.040
Provisioning rate in t	-0.09	-0.42	0.24	1,20	0.27	0.606

Results of a LM fitted by GLS testing the effect of parasitism status and provisioning rate in year t on the differences in laying dates between year t and year t+1 (i.e. laying date in t+1 minus laying date in t). $R^2=0.15$ (piecewiseSEM package, ver. 2.1.0, Lefcheck 2016). Significant estimates are highlighted in bold.

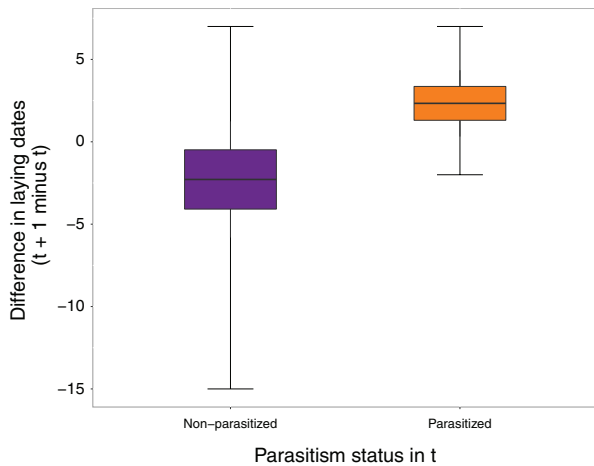


Figure 3. Magpies parasitized in year t delay their breeding in year $t+1$ compared to non-parasitized magpies ($n=23$ individuals). Boxes represent the mean and standard error of the difference in laying dates between two consecutive breeding seasons ($t+1$ minus t) for non-parasitized (purple boxes, mean = -2.29 , SE = 1.80) and parasitized magpies (orange boxes, mean = 2.33 , SE = 1.03). Error bars represent 95% confidence interval. Negative values correspond to an advance in laying dates and positive values correspond to a delay.

(2007), and with previous studies in passerines (Khwaja et al. 2017, Carr et al. 2019). Furthermore, our results show that, contrary to our prediction, there are no significant differences in the provisioning rates between parasitized and non-parasitized nests in general, and parasitism does not affect the relative contribution of sexes. Also, parasitism does not affect the presence/absence of individuals in the following year but, surprisingly, individuals that have been parasitized in a particular year breed later and delay their laying dates compared to non-parasitized individuals in the following year.

Nest provisioning rate and parasitism

Our analyses showed that magpie's provisioning rate did not statistically differ between parasitized and non-parasitized nests (Fig. 1), even though we expected to find a lower provisioning rate in parasitized nests since they contain fewer nestlings. Indeed, our analyses confirmed that, brood size is one of the main predictors of provisioning rate. Besides, Soler et al. (1995a) showed that broods parasitized with a single great spotted cuckoo nestling received less food than non-parasitized broods (mean brood size: 4.1 (SD = 0.3)) in the same area. The absence of clear differences in our first analysis (Table 1) could be due to the fact that our dataset included both non-parasitized nests with a small brood size (i.e. one to three magpie nestlings, 18.2% of the non-parasitized nests) and parasitized ones with a large brood size (i.e. three or four cuckoo nestlings, 17.6% of the parasitized nests), which occur naturally, but at low frequency in the population (26% and 17%, respectively). Indeed, when we analysed the subset of observations in nests with the most

common brood size (non-parasitized nests containing 4 or more nestlings and parasitized nests containing 1 or 2 nestlings; Supplementary information), individual provisioning rates were significantly smaller in parasitized nests (Fig. 2). This suggests that for most parasitized individuals (83% of the parasitized nests in the population contain one or two cuckoo nestlings) rearing a parasitized brood would suppose a smaller nest provisioning effort than rearing a non-parasitized brood (most frequently with 4 or more magpies chicks) although the net gain in terms of fitness would be zero.

In any case, our results are in accordance with the general pattern observed in brood parasite–host systems, suggesting that the consequences of parasitism on host provisioning rates seem to depend upon whether parasitic chicks are reared along with nest mates, increasing then brood size or not. In the case of brown-headed cowbirds *Molothrus ater* whose chicks commonly share the nest with host chicks, hosts respond to parasitism by increasing their provisioning rates (for example, indigo bunting *Passerina cyanea* (Dearborn et al. 1998), eastern phoebes *Sayornis phoebe* (Hauber and Montenegro 2002), prothonotary warbler *Protonotaria citrea* (Hoover and Reetz 2006) or red-winged blackbirds *Agelaius phoeniceus* (Grayson et al. 2013)). In contrast, in the case of parasites whose nestlings are reared alone in host nests, several studies have found that host provisioning rates were either similar between parasitized and non-parasitized broods (Brooke and Davies 1989, Kilner et al. 1999, Mark and Rubenstein 2013, Samaš et al. 2019, this study), or were lower in parasitized nests. For example, common cuckoo nestlings reared by rufous bush robins *Cercotrichas galactotes* received less food than a normal host brood (Martín-Gálvez et al. 2005), or were fed less frequently when they are reared by common redstarts *Phoenicurus phoenicurus* (Samaš et al. 2018).

Most of these studies are correlational, and as such, could be affected if parasitism was not random. Some parasites choose their hosts according to their characteristics. For example, Brooker and Brooker (1996) found that young or inexperienced splendid fairy-wren females *Malurus splendens* were more likely parasitized by the Horsfield's bronze cuckoo *Chrysococcyx basalis*. Only one of the studies above mentioned has discarded the effect of the host selection by parasites by testing whether provisioning rates differed between experimentally and naturally parasitized nests, finding no clear differences between them (Grayson et al. 2013). In this study we analysed data from naturally parasitized and non-parasitized nests, so our results may be influenced by host choice made by parasites.

Contrary to our prediction and previous work on this species (Buitron 1988), we did not find significant differences between male and female provisioning rates, neither in non-parasitized nor in parasitized nests. Some authors have recently suggested that in bird species with biparental care where partners tend to stay together in long-term pair bonds, changes in the reproductive value of broods may induce a matching response of both sexes in parental care (Mariette and Griffith 2015). Magpies meet some of these conditions as they are long-lived and have long-term pair bonds (Birkhead 1991). Altogether, our results

suggest that cooperation between the sexes prevails in the species and parasitism does not substantially affect the relative contribution of males and females to parental care.

Parental effort and adults' presence and breeding phenology in the following season

Despite the fact that our sample size is modest, our analysis suggests that individual provisioning rates in a given year were unrelated with host's presence/absence at the breeding site or laying date in the following breeding season.

Extra costs imposed by brood parasitism on future reproduction have been reported in some hosts. For example, male and female rufous-and-white wrens that had reared a parasitic Central America striped cuckoo were less likely to breed in the following breeding season (Mark and Rubenstein 2013). In other systems, the effect of parasitism seems to be sex-dependent, hinging on which sex provides more care: prothonotary warbler males (Hoover and Reetz 2006) and great reed warbler females (Koleček et al. 2015) had reduced return rates when they had been previously parasitized by brown-headed cowbird and by common cuckoo, respectively. On the other hand, Samaš et al. (2019) reported that parasitism by common cuckoo does not seem to affect great reed warbler return rates. Our study system differs from those of hosts mentioned above, as magpies are sedentary and stay all year around in the area where they breed. Moreover, parasitism only affects interannual breeding dispersal of magpie males, reducing their dispersal distances (Molina-Morales et al. 2012); therefore the lack of differences in the presence/absence between the previously parasitized and non-parasitized individuals would suggest no costs of cuckoo parasitism in terms of adult magpie survival (Table 2).

Our results, however, have shown that, when accounting for the potential effects of previous year's provisioning rate and laying date, the laying date of individuals in the subsequent season was affected by their parasitism status in the previous year (Supplementary information). Specifically, non-parasitized magpies advanced their laying dates in the subsequent breeding season, while parasitized individuals delayed them (Table 3, Fig. 3). This is important since the individuals that breed earlier in the breeding season have higher fledgling success (Birkhead 1991, Soler et al. 1995b). Moreover, delaying reproduction may entail high costs for magpies because the risk of parasitism increases throughout the season in our magpie population (Molina-Morales et al. 2016). Thus, the delay in laying date in the subsequent season of magpies suffering parasitism would be a consequence of an extra cost of parasitism that seems to be independent of the nest provisioning rates. This effect of parasitism on future reproduction might be related to other stages of the parental care period that we have not considered in this study, such as the post-fledgling stage: Soler et al. (1995c, 2014) found that great spotted cuckoo fledglings are frequently fed by magpies other than their foster parents that had also reared cuckoo chicks that season. Feeding a greater number of cuckoo fledglings than those reared in the nest and maybe, other aspects of the post-fledgling caring period may raise the costs of parental care even further and have cumulative carry over effects that

may not affect magpies' apparent survival but their breeding phenology in the future. However, this latter result should be taken with caution due to the small sample size. Further studies should try to evaluate the possible fitness costs of delayed reproduction in magpies due to parasitism.

Conclusions

In summary, magpies' workload (estimated as provisioning rate) in parasitized and non-parasitized nests was similar overall, but smaller in parasitized nests when comparing the most common brood size of parasitized nests (1 or 2 cuckoo nestlings) versus the most common brood size of non-parasitized nests (4 or more magpie nestlings). Brood parasitism did not seem to modify the relative contribution of host males and females to nestling provisioning. Moreover, rearing parasitic broods did not influence hosts' apparent survival (neither for males nor females) but seemed to negatively affect their breeding phenology in the subsequent season by delaying breeding and possibly increasing the likelihood of being parasitized. This suggests the possibility of extra post-fledging costs of parasitism for magpies that would be worth investigating in the future. Our results stress the need of evaluating the costs of parasitism at all breeding stages as well as its effect on different hosts' life history traits. This study provides valuable information about the short- and long-term costs of parasitism in magpies, but further research about the long-term costs of parasitism should be done to draw stronger conclusions about the role of parental care on great spotted cuckoo and magpie interactions.

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Data deposition

Data and analysis script will be available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.8931zcrnw>> (Precioso et al. 2020).

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Supplementary information (available online as Appendix jav-02522 at <www.avianbiology.org/appendix/jav-02522>).