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## Research

# Early-life environmental conditions influence parasitism at adulthood and life-history of a cuckoo host

**Jesús Miguel Avilés, Marta Precioso, Mercedes Molina-Morales and Juan Gabriel Martínez**

*J. M. Avilés (https://orcid.org/0000-0002-1463-8393)* ✉ *(javiles@eeza.csic.es), Depto de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas, CSIC, Almería, Spain. – M. Precioso (https://orcid.org/0000-0002-2030-5966), M. Molina-Morales (https://orcid.org/0000-0001-8669-6624) and J. G. Martínez, Depto de Zoología, Facultad de Ciencias, Univ. de Granada, Granada, Spain.*

Environmental conditions experienced by individuals early in life can extend into adult phenotypes with potential fitness consequences. Such environmental effects can be relevant for host species affected by parasitism, because poor early life conditions may lower parasite recognition or anti-parasite defenses and increase the risk of future parasitism. Here we provide a first test of this possibility by using data from a 16-year study of individually marked female magpie *Pica pica* hosts for which we know natal and adult environments, occurrence of great spotted cuckoo *Clamator glandarius* parasitism, egg discrimination ability and life history in detail. Females born in warmer years were more likely to be parasitized at adulthood and produced fewer offspring throughout their life. Egg discrimination behavior and lifespan of magpies were not influenced by the quality of natal environments. Our results provide support for the hypothesis that annual environmental variation promotes cohort effects in magpie hosts that may have an impact on cuckoo–host co-evolutionary dynamics.

Keywords: cohort effects, cuckoo parasitism, egg discrimination, fitness, life-history, magpies, natal environmental effects

## Introduction

In vertebrates, including humans, biotic and abiotic environmental conditions that individuals experience during their early life influence their growth and early development, and can translate into differences in adult phenotypes with important ecological and evolutionary consequences (reviewed by Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002). Several empirical studies with different taxa including reptiles (Madsen and Shine 2000, Marquis et al. 2008, Baron et al. 2010, Le Galliard et al. 2010), birds (Reid et al. 2003, Van de Pol et al. 2006, Saino et al. 2018) and mammals (Albon et al. 1987, Forchhammer et al. 2001, Descamps et al. 2008, Hamel et al. 2009, Pigeon et al. 2017) have shown that early life differences in weather conditions, population density or food availability can translate into cohort effects on fitness in the wild (i.e. differences in adult performance among individuals born in different years). Identifying how pervasive these cohort effects are, and, what

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are their lifetime consequences, is a cornerstone for predicting evolutionary dynamics in the wild (Mousseau and Fox 1998, Beckerman et al. 2003, Monaghan 2008).

Interspecific brood parasitism is a reproductive strategy in which the brood parasites lay their eggs in the nest of another species, the host, which carries out the parental duties, from the incubation of parasite eggs to feeding parasitic chicks (Rothstein 1990, Davies 2000, Payne 2005, Feeney et al. 2014). Brood parasitism often imposes large costs to hosts (Rothstein 1990, Soler 2014), and, in response, natural selection has favored the evolution of host behavioral defenses preventing parasitism such as parasite egg discrimination and rejection (Davies and Brooke 1988, Soler and Moller 1990, Aviles et al. 2010, Spottiswoode and Stevens 2010).

Cohort effects can be relevant for host species affected by parasitism. The study of host–parasite evolutionary dynamics has historically been framed into the boundaries of coevolution, where the patterns of adaptation are thought to mostly occur in response to reciprocal selection on the phenotypic traits between parasites and their hosts (Dawkins and Krebs 1979, Clayton et al. 1999, Thompson 2006). However, environmental conditions could also affect parasite–host dynamics (Kutz et al. 2005, Brooks and Hoberg 2007, Hoberg and Brooks 2015) by influencing parasite virulence, host defenses and the specificity of host–parasite interactions (Raffa et al. 2013, Brunner and Eizaguirre 2016). The mechanistic basis behind such environmental effects can be changes in host and/or parasite phenology (Brooks and Hoberg 2007, Moller et al. 2011, Avilés et al. 2014b, Cohen et al. 2018), or, in resource availability for hosts, and thus in their capacity to produce costly anti-parasite defenses (Altizer et al. 2006, Martin et al. 2010). However, the potential long-term consequences of early-life environmental effects on hosts, and how they are modulated by variation in adult environmental conditions remain unstudied in the wild.

The interaction between avian brood parasites and their hosts provides a suitable model system for uncovering the pervasive effects of early life conditions on behavior and fitness in the wild. Firstly, host defensive behaviors and, their associated fitness consequences, can be easily measured in host nests (Rothstein 1990). Second, host behavioral defenses can be plastic (reviewed by Ruiz-Raya and Soler 2017, Welbergen and Davies 2009), and, are therefore inherently susceptible to environmental variation. Finally, host susceptibility to parasitism likely depends on wider host behaviors (e.g. activity close to the nest, mate choice, etc.) that are tractable to measure in the wild (Parejo and Aviles 2007).

In the south of Europe, Eurasian magpies *Pica pica* are the main host of an obligate brood parasite, the great spotted cuckoo *Clamator glandarius* (Soler 1990). As a defense against the great spotted cuckoo, magpies have evolved the ability of recognizing cuckoo eggs and ejecting them from their nests (Soler and Moller 1990, Soler et al. 1999). The acquisition of the capacities leading to reject eggs is a slow process that on average takes up to four years in magpies (Martínez et al. 2020). There is, however, huge variation among female magpies in the age at which rejection is expressed (Martínez et al.

2020), and in their propensity to suffer cuckoo parasitism at adulthood (Molina-Morales et al. 2013).

The effect of natal environmental stress can manifest into adult magpie performance through the impairment of cognitive function (Pravosudov et al. 2005, Fisher et al. 2006). Egg rejection requires the involvement of several cognitive processes as learning, long-term memory, and visual and motor controls (Rothstein 1974, Lotem et al. 1995, Davies 2000), and cognition might also be involved in behavioral decisions allowing magpies not to be parasitized by cuckoos.

Magpies are in their breeding territories during winter and start the activities leading to reproduction (nest building) at the end of winter (middle-March) (Molina-Morales unpubl.). Indeed, previous findings have shown that winter, but not spring temperature, is associated with magpie reproductive phenology and with the degree of phenological mismatching between cuckoos and magpies (Avilés et al. 2014b). Also, long-term population analyses in our magpie population have revealed a negative association between yearly winter temperature and clutch size (Supporting information), which suggests that a higher winter temperature is associated with a lower resource availability around reproduction for magpies. Besides differences between years potentially promoting cohort effects, quality of magpies' breeding environments may also vary within the same breeding season. Indeed, delayed breeding in the season may also affect the availability of resources for development and growth, because late hatched magpie nestlings have lower body mass (Soler et al. 2014).

This study takes advantage of a longitudinal study of individually recognizable Eurasian magpies *Pica pica* in which quality of natal and breeding environments, parasitism, level of resistance and life/history traits have been quantified to assess delayed consequence of early life environments on fitness of a host in the wild. Based on the premise that poorer natal environmental conditions may impair behaviours involved in cuckoo avoidance and impact on later survival we predict higher parasitism and lower discrimination abilities and fitness in magpies born in warmer years and late nests within a given year. The effect of natal conditions on adult phenotype and fitness can, however, also be influenced by the environmental conditions that magpies experience at adulthood (Monaghan 2008, Pigeon et al. 2019). We therefore consider the effects of breeding temperature and parasitism at adulthood when assessing the effect of natal conditions on magpies.

## Material and methods

### Breeding and parasitism data

Data used in this study were collected as a part of the long-term study of the interaction between great spotted cuckoos and magpies at La Calahorra (37°10′N, 3°03′W, Granada, southern Spain) during March–July of the years 2005–2019, as described elsewhere (Avilés et al. 2014b, Molina-Morales et al. 2014, 2015, Martínez et al. 2020).

Since 2005, every fledgling (15–18 days after hatching) magpie in the population has been individually marked using a unique combination of colour bands and/or alphanumeric-coded PVC bands. We also obtained blood samples that allowed to sex individuals using sex-specific markers (Molina-Morales et al. 2012).

Magpie nests were monitored from the first of March to the beginning of July each breeding season. In magpies, only females incubate (Birkhead 1991) and thus are assumed to be the sex that reject cuckoo eggs (Soler et al. 2002), therefore we focus on natal effects on females in this study. Nests were found by careful inspection of all trees in the area and they were observed with a telescope from a hide around 100 m away during nest building in order to assign marked females to each nesting attempt. Thus, we were able to link a number of breeding females (n = 47) with their exact places of birth.

Nests were visited at 5-day intervals, although during egg laying and hatching they were visited every 2–3 days to check whether the nest was parasitized by great spotted cuckoos and to record all required data (such as clutch size, length and width of each egg used to estimate egg volume using the formula volume = length × width$^2$ × 0.515, or breeding success). Nests were categorized as parasitized if at least one cuckoo egg was detected in the nest. Cuckoo eggs can be easily discriminated from magpie eggs by a more rounded shape and general whiter ground colour as well as for their smoother texture (Molina-Morales et al. 2013, Martínez et al. 2020). The number of fledglings 16–18 days after hatching from each nest was used as a measure of the success of that female; an individual's total number of fledged offspring (LRS hereafter) was the sum of this figure for all sampled breeding attempts of a female in a lifetime. The last year that a female was recorded breeding in the population was considered the age of last reproduction and used as a reliable estimation of lifespan. Lifespan for females considered in this study was over four years (mean (± SE, range) lifespan = 4.57 (± 0.36, 1–10), n = 47 females).

## Egg rejection experiments

We tested magpie responses to model eggs made to resemble cuckoo eggs in appearance, size and mass (Molina-Morales et al. 2014). Models do not perfectly match the color of real great spotted cuckoo eggs and their rejection is higher than that of real cuckoo eggs (Molina-Morales et al. 2014), however, previous studies have consistently shown that they would provide a reliable estimate of magpie discrimination abilities selected by cuckoo parasitism (Soler and Moller 1990, Soler et al. 1999). Moreover, testing discrimination against model eggs is the most suitable procedure to get standardized rejection measures in hosts of avian brood parasites (Davies and Brooke 1989, Rothstein 1990). Swapping real great spotted cuckoo eggs might be problematic because the same female might be exposed by chance to cuckoo eggs differing in mimicry from their own eggs in differing years. Also, naturally laid cuckoo eggs are so rarely rejected in our system, that gathering sufficient samples to detect between-individual

differences in rejection of real cuckoo eggs would be exceptionally difficult. Finally, by using models we are not limited by the number of real cuckoo eggs available, and avoided affecting the reproductive success of magpies and cuckoo during the study, which would not be appropriate for estimating natal effects on magpie fitness. We introduced the model egg during magpie egg laying; the response to the model egg was regarded as rejection if the model egg disappeared from the nest or acceptance if the model egg was incubated with the host's clutch when we revisited the nest. If accepted, we removed the model egg 7 days after introducing it (Molina-Morales et al. 2014). Twenty-six out of 47 tested females were older than four years, which is the average age at which magpies start rejecting eggs (Martínez et al. 2020).

## Environmental variables

We used winter temperature before hatching and parasitism risk in the year of birth to describe cohort variation potentially affecting magpie development. Winter temperature is likely to influence the availability of resources for magpie reproduction. On the other hand, parasitism risk may affect the allocation priorities of magpies. In years with high risk of parasitism, parents may invest less in their offspring due to high chance of nest failure. Indeed, magpie parents can perceive parasitism risk in their territories before their reproduction and, in response, modulate their nest settlement decisions (Exposito-Granados et al. 2017a), potentially affecting the rearing conditions of their offspring (Exposito-Granados et al. 2017b).

Winter temperature was calculated by averaging temperature data collected on a daily basis during January and February at the nearby meteorological station of Iznalloz (Location: 37°25′03″N, 3°33′00″W. Altitude: 935 m). Temperature records were retrieved from the website <www.juntadeandalucia.es> managed by the regional government of Andalucía. Annual parasitism rate in the population (adult risk of parasitism hereafter), calculated as the percentage of magpie nests parasitized out of the total nests found each year, was used as an index to quantify the environmental quality in terms of cuckoo parasitism risk (Molina-Morales et al. 2014). Previous work has shown that parasitism rate is closely correlated with cuckoo abundance in our study area (Soler et al. 1998).

Neither parasitism risk nor winter temperature experienced any obvious linear trend over the sixteen years of study (linear regressions of parasitism rate and winter temperature on year; parasitism rate: slope (± SE) = −0.24 ± 0.25, $t_{14}$ = −0.94, p = 0.36, $r^2$ = 0.06; winter temperature: slope = 0.10 ± 0.26, $t_{14}$ = 0.38, p = 0.70, $r^2$ = 0.01). Moreover, winter temperature was unrelated to parasitism risk (Pearson correlations: $r_p$ = −0.10, p = 0.70, n = 16 years), suggesting that the two cohort variables can be simultaneously considered into models when assessing their effects on adult phenotype and fitness.

Moreover, we consider laying date as an additional source of environmental variation with potential consequences at adulthood based on previous evidence suggesting that delayed

breeding results in poorer developmental conditions for magpie fledglings. Finally, because the effect of natal environmental conditions on magpie traits may exacerbate or vanish depending upon the environmental conditions experienced later in life (Monaghan 2008), we consider the risk of parasitism and the winter temperature that females experienced in all reproductive events as adults in our population (adult risk of parasitism and adult winter temperature hereafter).

## Statistical analyses

Analyses were performed using SAS ver. 9.4 statistical software. All continuous variables were z-standardized to improve interpretability (Schielzeth 2010). First, aiming to test for the effect of natal environmental conditions on the probability of parasitism and egg rejection we ran two generalized linear mixed models with binomial errors in which parasitism and egg rejection were the binary response variables (GLIMMIX procedure in SAS, link function: logit), respectively. So every breeding attempt was coded as parasitized (yes or not), or for each breeding attempt we considered whether the model egg was rejected (yes or not). Age of female at each breeding attempt was included as a covariate in the models because age is related with the probability of detecting parasitism and rejection in magpies (Molina-Morales et al. 2014, Martínez et al. 2020). As natal environmental effects we included in the models natal winter temperature and natal level of parasitism in the population (as two covariates). In addition, we entered laying date of the natal nest as a covariate to reflect differences in environmental conditions within the natal year. Finally, because females living in years with high parasitism rate are more likely parasitized (Molina-Morales et al. 2016), or may modify egg rejection based on perceived risk of parasitism (Moksnes et al. 1993, Thorogood and Davies 2013), we included adult risk of parasitism and adult winter temperature as two further covariates. The two models included as random intercepts the natal and the breeding year and female identity. However, the estimated Hessian matrix was not positive definite for the saturated model indicating that models converged to a solution where some of the random terms had not associated variation (i.e. breeding year for the model of parasitism and natal year for the model of rejection, Table 1). The random term with no associated variance was then removed from the models to obtain a definitive positive Hessian matrix (Kiernan et al. 2012).

In a second stage, we studied the influence of environmental conditions on female's life histories (i.e. LRS and lifespan). Data in these analyses are integrated across an individual's lifetime and hence restricted to one value for each female. First, we run a Zero-inflated Poisson regression model (GENMOD procedure in SAS) to test for the effects of level of parasitism and winter temperature at the natal year, laying date at the natal year, adult level of parasitism and winter temperature (calculated as the average parasitism and winter temperature for all the years a given female was sampled) on female's total number of produced fledglings. The model also included the number of sampled breeding attempts per female as a covariate to control for a possible effect of sampling effort. Second, we run a Poisson regression model (GENMOD procedure in SAS) to test the influence of the same predictors on magpie lifespan.

Standard model validation graphs (Zuur 2009) revealed that model assumptions of homogeneity of variance and normality of residuals were fulfilled.

## Results

### Temporal variation in cuckoo parasitism

On average a third of magpie nests have been parasitized by great spotted cuckoos over the 16 years (mean ($\pm$ SE) annual parasitism rate = 33.6% ($\pm$ 3.6), n = 1104 magpie nests). Parasitism rate varied strongly across years, ranging from 15.9% in 2007 to 65.5% in 2009 (Supporting information). At the individual level, we sampled on average 2.34 ($\pm$ 0.23, 1–7) ($\pm$ SE, range) breeding attempts of each female, and about a third of the sampled attempts of each female were parasitized (mean parasitized breeding attempts per female = 0.74 ($\pm$ 0.19, 0–3) ($\pm$ SE, range) (n = 47 females)).

### Natal and adult environmental conditions and parasitism and rejection in magpie adulthood

Natal winter temperature was positively associated with the probability of suffering parasitism at adulthood after accounting for yearly variation in parasitism rate (Table 1, Fig. 1A). Probability of suffering parasitism steadily increased from 16.6% for magpies that were born in the coldest years, to 83.3% for those females that were born in the hottest years (Fig. 1B). On the other hand, female age, the level of parasitism in the year of birth, natal laying date and adult winter temperature did not significantly influence the probability of suffering parasitism at adulthood (Table 1).

Regarding egg rejection, neither natal nor breeding environmental conditions were significantly associated with the probability of rejecting model eggs after accounting for the significant effect of female age (Table 1, Supporting information).

### Natal and adult environmental conditions and magpie life history trait variation

The number of fledglings produced by females was predicted by winter temperature in their year of birth irrespective of natal and adult parasitism (Table 2): magpies that were raised in warmer years produced less offspring through their life (LRS, Fig. 2). LRS was not influenced by any of the remaining considered natal and breeding environmental variables (Table 2, Supporting information).

On the other hand, lifespan of females was not significantly associated with any of the considered environmental variables (Table 2), suggesting a negligible effect of natal and breeding conditions on female longevity.

Table 1. Influence of natal and adult environmental conditions on probability of parasitism and rejection in female magpies. Results of GLMMs testing for the effect of age of the female, level of parasitism and winter temperature at the natal year, laying date at the natal year and level of parasitism and winter temperature at the breeding year on probability of parasitism and rejection per breeding attempt as binary dependent variables. Models included as random intercepts the natal and the breeding year and female identity. Significant terms (95% confidence interval does not include the null) are highlighted in bold and predictors were standardized to improve interpretability.

| Probability of parasitism (n=100 breeding attempts of 47 females) | | | | | | | |
|---|---|---|---|---|---|---|---|
| Fixed effects | | | | | | | |
| Effect | Estimate | SE | df | F | p | Lower 95% CL | Upper 95% CL |
| Intercept | −0.24 | 0.52 | 79 | −0.46 | 0.657 | −1.46 | 0.98 |
| Age of female | −0.12 | 0.12 | 79 | 0.95 | 0.334 | −0.35 | 0.12 |
| Adult winter temperature | 0.01 | 0.24 | 79 | 0.01 | 0.968 | −0.48 | 0.50 |
| **Adult risk of parasitism** | **0.60** | **0.27** | **79** | **5.01** | **0.028** | **0.07** | **1.13** |
| Natal risk of parasitism | 0.32 | 0.37 | 79 | 0.73 | 0.397 | −0.43 | 1.07 |
| **Natal winter temperature** | **0.89** | **0.39** | **79** | **5.23** | **0.025** | **0.12** | **1.67** |
| Natal laying date | 0.22 | 0.24 | 79 | 0.83 | 0.366 | −0.26 | 0.70 |
| Random effects | | | | | | | |
| Subject | Estimate | SE | Z | p | | | |
| Natal year | 0.16 | 0.57 | 0.29 | 0.39 | | | |
| Breeding year[†] | 0.00 | . | . | . | | | |
| Female ID | −0.06 | 0.10 | −0.56 | 0.57 | | | |
| Probability of rejection (n=81 breeding attempts of 41 females) | | | | | | | |
| Fixed effects | | | | | | | |
| Effect | Estimate | SE | df | F | p | Lower 95% CL | Upper 95% CL |
| Intercept | −3.56 | 0.99 | 62 | −3.61 | 0.011 | −5.97 | −1.15 |
| **Age of female** | **0.63** | **0.19** | **62** | **11.07** | **0.002** | **0.25** | **1.00** |
| Adult winter temperature | −0.67 | 0.34 | 62 | 3.87 | 0.054 | −1.35 | 0.01 |
| Adult risk of parasitism | −0.52 | 0.56 | 62 | 0.85 | 0.359 | −1.63 | 0.60 |
| Natal risk of parasitism | 0.02 | 0.42 | 62 | 0.01 | 0.959 | −0.82 | 0.86 |
| Natal winter temperature | −0.69 | 0.46 | 62 | 2.26 | 0.138 | −1.60 | 0.23 |
| Natal laying date | 0.19 | 0.33 | 62 | 0.34 | 0.564 | −0.47 | 0.86 |
| Random effects | | | | | | | |
| Subject | Estimate | SE | Z | P | | | |
| Natal year[‡] | 0.00 | . | . | . | | | |
| Breeding year | 0.07 | 0.52 | 0.14 | 0.45 | | | |
| Female ID | 0.38 | 0.20 | 1.91 | 0.06 | | | |

[†] Breeding year was removed from the models to obtain a definitive positive Hessian matrix. Probability of parasitism of a breeding event did not vary in relation to breeding year once covariates and the two other random terms were excluded (estimate (SE): 0.19(0.32), Z=0.59, p=0.27).

[‡] Natal year was removed from the models to obtain a definitive positive Hessian matrix. Probability of rejection in a breeding event did not vary in relation to natal year once covariates and the two other random terms were excluded (estimate (SE): 0.43(0.49), Z=0.86, p=0.19).

## Discussion

Our results provide support for the idea that environmental conditions experienced early in life have pervasive long-term effects on risk of suffering cuckoo parasitism at adulthood, life history and fitness in magpie hosts. Females that were born after warmer winters were more likely affected by great spotted cuckoo parasitism. In the south of Spain, winter temperature influences the phenology of the interaction between cuckoos and magpies (Avilés et al. 2014b), and warmer winters likely associate with lower resource availability around reproduction for magpies. The effect of warm winters did not arise because temperature in the natal year covaried with other traits known to affect parasitism, including female age (Lotem et al. 1995, Martínez et al. 2020), adult risk of parasitism (Thorogood and Davies 2013) or climatic conditions

when breeding (Table 1), and was independent of the fact that females breeding in years with high risk of parasitism were more likely parasitized (Table 1). The ability to express egg rejection at adulthood and female lifespan were not influenced by natal or breeding environmental conditions. However, females produced less young over their lifetime (i.e. LRS) when they were born after warmer winters (Table 2).

### Natal environmental conditions and parasitism and egg rejection

Probability of a magpie of being parasitized at adulthood depends on environmental conditions experienced in the year of birth. Recent findings have shown a trend that longer-lived females are less likely to be parasitized (Martínez et al. 2020), which raises the possibility that the link found between
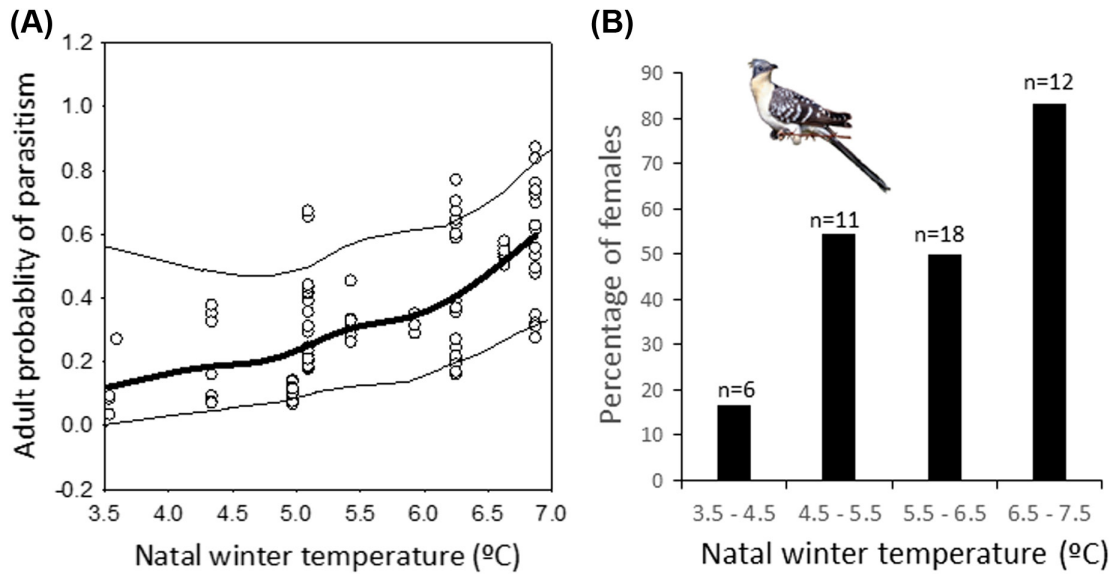
Figure 1. Parasitism in relation to natal environmental conditions in magpies. (A) The bold-black line show predictions from model on parasitism in Table 1; their 95% CL are represented by corresponding lighter colors. Data points are breeding events and are shown in gray. (B) Parasitism in relation to winter temperature at birth. Black bars show the percentage of magpies that were cuckoo parasitized at adulthood in relation to winter temperature at the year of birth. Numbers above bars are sample size for each temperature class. For graphical purposes winter temperature was classed in one-degree intervals, but analyses were done on continuous values (panel A). Illustration credits for the great spotted cuckoo picture taken from Macaulay Library at the Cornell Lab of Ornithology (Jorge Safara (ML 26072261)).

winter temperature in the year of birth and parasitism was mediated by female age. However, this possibility can be discarded because female age was controlled for in the analyses, and, because we found no evidence of an effect of natal environmental conditions on longevity of recruited females (Table 2). Unexpectedly, being born early or late within a breeding season had no influence on the risk of being parasitized at adulthood.

Our findings suggest that the previous observation that some magpies in a given population consistently avoid being parasitized across their lives, whereas other do not (Molina-Morales et al. 2013), could be influenced by the quality of

Table 2. Influence of natal and adult environmental conditions on life history trait variation (LRS and lifespan) in female magpies. Results of the zero-inflated Poisson and Poisson regression models testing for the effect of level of parasitism and winter temperature at the natal year, laying date at the natal year, adult level of parasitism and winter temperature and number of breeding attempts on number of fledglings and lifespan of each female, respectively. Significant terms (95% confidence interval does not include the null) are highlighted in bold and predictors were standardized to improve interpretability.

| Effect | Estimate | SE | $\chi^2$ | p | Lower 95% CL | Upper 95% CL |
|---|---|---|---|---|---|---|
| LRS (n=39 females) | | | | | | |
| Intercept | 1.72 | 0.09 | 314.03 | <0.0001 | 1.53 | 0.91 |
| **Number of breeding attempts** | **0.20** | **0.08** | **5.25** | **0.02** | **0.03** | **0.38** |
| Adult winter temperature | 0.009 | 0.13 | 0.01 | 0.94 | −0.25 | 0.27 |
| Adult risk of parasitism | −0.20 | 0.10 | 3.83 | 0.050 | −0.40 | 0.0004 |
| Natal risk of parasitism | −0.19 | 0.10 | 3.69 | 0.054 | −0.39 | 0.003 |
| **Natal winter temperature** | **−0.34** | **0.12** | **7.49** | **0.006** | **−0.58** | **−0.09** |
| Natal laying date | −0.0008 | 0.10 | 0.01 | 0.99 | −0.20 | 0.20 |
| Lifespan (n=47 females) | | | | | | |
| Intercept | 1.51 | 0.07 | 456.02 | <0.001 | 1.37 | 1.65 |
| **Number of breeding attempts** | **0.29** | **0.07** | **17.45** | **<0.001** | **0.16** | **0.43** |
| Adult winter temperature | 0.02 | 0.08 | 0.07 | 0.79 | −0.15 | 0.19 |
| Adult risk of parasitism | −0.12 | 0.08 | 2.36 | 0.12 | −0.28 | 0.03 |
| Natal risk of parasitism | 0.01 | 0.08 | 0.02 | 0.88 | −0.16 | 0.18 |
| Natal winter temperature | 0.02 | 0.08 | 0.07 | 0.78 | −0.15 | 0.19 |
| Natal laying date | 0.07 | 0.07 | 0.93 | 0.33 | −0.07 | 0.21 |
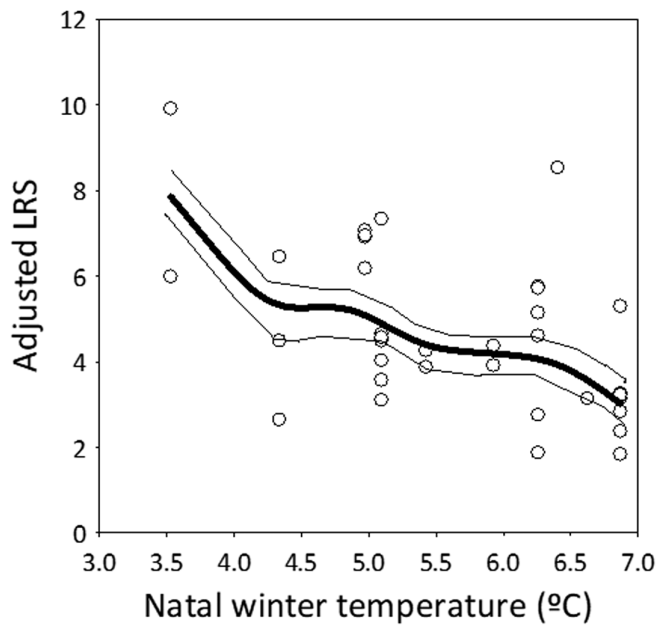
Figure 2. Lifetime breeding success of magpies in relation to natal environmental conditions. Predicted number of fledglings for an adult female magpie in relation to natal winter temperature. The bold-black line show predictions from model on LRS in Table 2; their 95% CL are represented by corresponding lighter colors. Data points are females and are shown in gray.

natal environments. Previous lab studies have shown long-term effects of developmental conditions on adult personality traits in vertebrates (Noguera et al. 2015, Krause et al. 2017), and theoretical work has suggested that differences in personality may explain variation in susceptibility to suffer parasitism (Barber and Dingemanse 2010, Aviles and Parejo 2011). In magpies, females escaping from cuckoos select areas with different characteristics and build their nests differently than those being parasitized (Molina-Morales et al. 2013). Moreover, egg rejection is positively associated with more aggressive behaviors across individuals (Avilés et al. 2014a), which provides a possible explanation for the inter-female variation in parasitism.

Regarding egg rejection, our findings corroborate previous results showing that proneness to discriminate model eggs was unaffected by perceived risk of parasitism in magpies (Soler et al. 2000, Molina-Morales et al. 2014), and previous findings showing a fundamental role of age in determining egg discrimination (Molina-Morales et al. 2014, Martínez et al. 2020). Innovatively, we also found that the expression of egg rejection was unaffected by variation in natal environmental conditions. This finding might suggest that learning to discriminate model eggs would not be impaired in females that were raised under poor environmental conditions. Perhaps the range of variation in natal environmental conditions experienced by females was not large enough to induce differences in learning, as did experimental work with captive birds (reviewed in Buchanan et al. 2013). Also, it cannot be excluded that learning played only a minor

role in egg discrimination in magpies compared to other cognitive processes such as long-term memory and visual or motor controls. A bad start may also affect learning through delaying the age at which females start to reject eggs.

The effect of a bad start in terms of avoiding cuckoo parasitism at adulthood might be exacerbated if magpies experience bad environmental conditions later in life, setting the scenario for the study of the interaction between natal and adult environmental conditions on parasitism (Monaghan 2008, Pigeon et al. 2019). The low number of recruited females despite 16 years of monitoring impedes us to formalize a test of this possibility, although we found that differences in probability of suffering parasitism and life-history variables between cohorts of magpies that have experienced different natal conditions persisted irrespective of variation in adult breeding conditions.

Mechanisms linking quality of natal environments and magpie parasitism at adulthood are unknown, and cannot be elucidated in our study. In the south of Spain warm winter conditions relate with resource restrictions for magpies (Soler et al. 2014, Supporting information). Therefore, a possible mechanism explaining our findings is the negative effect of food restriction on magpie brain development (Antonow-Schlorke et al. 2011), which might lead to a lower cognitive performance in terms of cuckoo avoidance. Alternatively, the pattern might be the consequence of an effect of natal environments on adult size (Forchhammer et al. 2001). It is possible that cohorts of magpies raised under poor environmental conditions were smaller and then less competitive as adults and relegated to the worst habitats in terms of avoiding cuckoos. Indeed, a captivity study has shown that body size correlates with dominance among juveniles in the close relative black-billed magpies *Pica hudsonia* (Komers and Komers 1992).

## Conclusions

Our findings illustrate long-term effects of early life environmental conditions on probability of suffering parasitism and life-history parameters in a wild vertebrate species. Females that fledged in years with unusual warm winters had a lower LRS. As females that are born in warmer winters are also more likely to be parasitized, our results suggest that winter warming reduces individual fitness in magpies via an increase in the risk of cuckoo parasitism at adulthood, and may thus potentially influence long-term magpie population dynamics (Beckerman et al. 2002). Therefore, ignoring the complexity of long-term effects of early-life environment will hinder our capacity to understand cuckoo–host coevolutionary dynamics. More specifically, as winter temperatures play a role in the probability of suffering parasitism since climate warming is becoming prevalent, the impact of avian brood parasites on host populations may become more apparent in the future.

## Author contributions

**Jesus M. Aviles**: Conceptualization (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Marta Precioso**: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Mercedes Molina-Morales**: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Juan G. Martínez**: Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the CSIC digital repository: <https://doi.org/10.5061/dryad.vx0k6djr7> (Avilés et al. 2021).

## Supporting information

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

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