

Climatic effects and phenological mismatch in cuckoo–host interactions: a role for host phenotypic plasticity in laying date?

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Climatic effects on breeding phenology vary across organisms and therefore might promote a phenological mismatch in ecologically interacting species, including those engaged in coevolutionary interactions such as brood parasites and their hosts. Recent studies suggest that climatic induced changes in migration phenology may have mismatched cuckoos and their hosts in Europe. However, it is currently unknown whether cuckoo–host phenological mismatch results from different degrees of phenotypic plasticity or to different speeds of microevolutionary processes affecting hosts and parasites. Here we performed 1) cross-sectional correlations between climate conditions and population level of phenological mismatch between the migratory brood parasite great spotted cuckoo *Clamator glandarius* and its main resident host in Europe, the magpie *Pica pica*; and 2) a longitudinal analysis to study within-individual variation in breeding phenology for individual hosts experiencing different climate conditions over a period of nine years (2005–2013). Cross-sectional analyses revealed independent and contrary effects of winter and spring temperature on magpie phenology: magpie hosts tend to breed earlier those years with lower February temperatures, however, high temperature in the first half of April spur individuals to lay eggs. Breeding phenology of cuckoos was tuned to that of their magpie host in time and duration. However, annual phenological mismatch between cuckoos and magpie hosts increased with NAO index and January temperature. Longitudinal analyses revealed high individual consistency in magpie host phenology, but a low influence of climate, suggesting that the climatic-driven phenological mismatch between cuckoos and magpies at the population-level cannot be explained by a host plastic response to climatic conditions.

Organisms adapt to spatio-temporal environmental variation by modifying their breeding phenology (sensu Parmesan and Yohe 2003, Nussey et al. 2007, Charmantier et al. 2008, Porlier et al. 2012). Phenological responses to environmental variation, however, are not consistent across species (Visser and Both 2005), and, thereby, a fundamental challenge of current evolutionary biologists is to understand how differences among species in their phenological responses to environmental conditions might affect species interactions (Visser et al. 1998), and the direction and strength of local coevolutionary processes (Brooks and Hoberg 2007, Dobson et al. 2008, Møller 2010, Toju et al. 2011).

An ideal system for studying how climate may promote phenological mismatch involves the specialized interaction between some obligate avian brood parasites (hereafter cuckoos) and some of their favourite hosts (Saino et al. 2009, Møller et al. 2011). Cuckoo females lay their eggs in the nests of host species, and leave parental care of their offspring to unrelated foster parents (Davies 2000). Brood parasites usually reduce (often drastically) their host's breeding success (Rothstein 1990, Davies 2000, Payne 2005) resulting in strong selection pressures on the hosts favouring

the evolution of defences against parasitism (Rothstein 1990, Davies 2000), which in response have selected for further counter-defences in the parasite side, thus giving rise to a coevolutionary arms race. In this highly specialized interaction cuckoos must finely adjust their phenology to that of their favourite hosts, because otherwise the cuckoo will not be able to reproduce in the absence of that host.

So far, evidence of climatic effects promoting trait mismatch in cuckoo–host interactions came from studies showing that the degree of egg mimicry between European cuckoos *Cuculus canorus* and their favourite reed warbler *Acrocephalus scirpaceus* hosts was affected by climatic conditions both at local (Avilés et al. 2007), and wider continental spatial scales (Avilés et al. 2012). Also a recent study has shown that annual variation in climatic conditions might result in asymmetric effects on great spotted cuckoos *Clamator glandarius* and magpie *Pica pica* hosts with respect to probability of ectoparasitism, immunity and growth in a single population (Soler et al. 2014). Climate may also affect migration phenology of the European cuckoo and/or their hosts promoting phenological mismatches (Saino et al. 2009, Møller et al. 2011). Indeed, a recent study

revealed that short-distance, but not long-distance, migratory European cuckoo hosts have advanced their arrival to spring quarters in response to climate change more than cuckoos (Saino et al. 2009), which has led to an increase of the frequency of cuckoo parasitism of long-distance migratory hosts at a continental scale (Møller et al. 2011). Climatic induced effects on time of breeding of dunnocks *Prunella modularis* and reed warblers hosts also led to changes in the availability of host nests with eggs for cuckoos, although it did not result in changes in cuckoo abundance in the UK (Douglas et al. 2010).

Changes in phenological matching between cuckoos and their hosts may result from a number of mechanisms that may act in conjunction or in isolation and that have not been previously investigated. Phenological mismatch might reflect a micro-evolutionary process due to changes in allele frequency of hosts and/or cuckoos due to selection within the population, and/or due to gene flow by dispersal of individuals (either cuckoos or hosts) adapted to breed relatively earlier or later in the year (Przybylo et al. 2000). In addition, cuckoo–host phenological mismatch may arise if either individual hosts and/or cuckoos show variable levels of phenotypic plasticity and/or if plastic responses of cuckoos and their hosts rely on different environmental cues (Charmanier et al. 2008, Brommer et al. 2008, Porlier et al. 2012). Previous studies reporting changes in the time of breeding of the European cuckoo and/or its hosts relied on cross-sectional data reported at a regional and/or continental spatial scale (Saino et al. 2009, Douglas et al. 2010, Møller et al. 2011), which cannot discriminate among these mechanisms.

Here, we combine cross-sectional and longitudinal analyses on individuals to investigate possible climatic effects on the phenology of a non-migratory magpie host population parasitized by the great spotted cuckoo in the south of Spain over a period of nine years (2005–2013). Previous studies have reported adaptations and counter-adaptations of both magpies and cuckoos at different stages of the reproductive cycle suggesting that these two species have been engaged for a long time in a coevolutionary arms race (reviewed by Soler and Soler 2000), but have neglected the possibility that abiotic factors, such as climate, may affect the dynamic of the interaction (see however Soler et al. 2014). Specifically, we were interested in the following points: 1) whether host breeding phenology and cuckoo–host phenological mismatch had changed in that population over that period; 2) whether those changes were associated with changes in local and regional climatic conditions; 3) whether host responses to climatic conditions at the individual level may contribute to explain population patterns of phenological mismatch. If the latter was the case, it would constitute a strong evidence for a previously neglected role of host phenotypic plasticity in determining cuckoo–host phenological mismatches.

Material and methods

Study area and system

The study was conducted in La Calahorra (37°10'N, 3°03'W, Granada, southern Spain) during the years 2005–2013 in

the frame of a long-term project on the interaction between great spotted cuckoos and magpies (Molina-Morales et al. 2012, 2013). Landscape is a patchy mosaic of groves of almond and olive trees, cereal crops and meadows. Magpies preferentially built their nests in almond trees. Magpies are territorial, sedentary and socially monogamous long-lived passerines (Birkhead 1991). This population was separated from other nearby populations in the area by arable lands with few or no potential nest sites for magpies (Martín-Gálvez et al. 2007). Furthermore, previous work has shown that our population differed from nearby populations in ecological conditions (i.e. phenology, breeding synchrony, density of nests and parasitism level, Martínez et al. 1996), which suggests it can be treated as a distinct unit for this study.

In our study area, magpies lay one clutch during April–May, and are the main host of the great spotted cuckoo. Cuckoo parasitism reduces magpie reproductive success by 80.0% through early hatching and effective competition for parental food delivery of cuckoo nestlings (Soler et al. 1996, 1997). This fact has selected for host recognition and rejection of cuckoo eggs by magpies (Soler and Møller 1990), which in turn has selected for punitive cuckoo behaviours promoting parasitism acceptance (Soler et al. 1995). In fact, the interaction between magpies and great spotted cuckoos is considered a classical example of coevolution (Soler and Soler 2000). Unlike magpies, great spotted cuckoos are migratory birds wintering in tropical Africa (i.e. trans-Saharan) and arriving to the breeding grounds in Guadix in late February or early March (Soler and Soler 2000).

Individual marking and monitoring

Some of the adult magpies were individually marked by unique combinations of colour rings, and subsequently monitored (see Molina-Morales et al. 2012 for further details). Monitoring of non-ringed females was based on parentage analyses (Molina-Morales et al. 2012). We assigned breeding attempts in different years to the same female when the nestlings in those broods were full siblings to each other. Also, we could assign early breeding attempts to later marked females using paternity analyses (Molina-Morales et al. 2012). Most sampled individuals were caught with adult plumage according to Birkhead (1991), and we did not know their exact age, thus we assigned them a two-level relative minimum age: females were coded as 1, if they were breeding at the first sighting and in the following year and 2, if they were breeding two years or more after the first sighting.

Nest monitoring

Magpie nests were monitored from 1 March to the beginning of July each breeding season between 2005 and 2013. We found 675 nests across the nine years of the study, but could estimate laying date only in 424 nests (63%) because some nests were abandoned during the early stage of building or predated before host clutch was completed. The average number of sampled nests with laying date information was 52.44 nests per year (range 31–70), and the

average number of parasitized nests was 20.11 nests per year (range 7–37). Nests were found by careful inspection of all trees in the breeding area, and georeferenced using GPS device. Each nest was observed with telescope or binoculars from a hide around 100 meters away during the nest building stage in order to identify marked birds involved in each nesting attempt. All nests were monitored at 5 days intervals during the breeding season. During egg laying nests were monitored at shorter (2–3 day) intervals which allowed estimating the date of laying of the first magpie egg, as magpies lay one egg per day (Cramp 1998), and knowing whether the nest was parasitized by great spotted cuckoos. Nests were categorized as parasitized if at least one great spotted cuckoo egg was detected in the nest.

Every year we calculated median and range (i.e. max–min) of laying dates of all magpie nests and of the subset of parasitized nests to estimate temporal variation in the phenology of magpie hosts and cuckoos at the population level. Annual differences in median laying date of cuckoos and magpies were then used as an index of phenological mismatch. Years with a high phenological mismatch were thus years in which clutches parasitized with great spotted cuckoo eggs were more delayed compared to the median laying date of magpie nests.

Between 2007 and 2011 we monitored the nests till fledging, which allowed us to test for an effect of laying date on probability of magpie nest failure (in all nests, and in the subset of parasitized nests) and on magpie fledgling success (calculated as the percentage of fledglings relative to the number of host eggs laid in the nest). In addition, in 2009 and 2010 we took body mass measurements of all great spotted cuckoo nestlings in the population at day 14 with a spring balance with a precision of 0.1 g. Analyses on this subset of nests and nestlings thus allowed estimating seasonal effects on magpie (i.e. host nest failure and fledgling success) and cuckoo (i.e. nest failure of cuckoo parasitized nests and body mass at fledging) fitness surrogates.

Climatic variables

We used the winter (December to March) North Atlantic oscillation index (NAO) as a natural large-scale proxy of the climatic condition that may affect laying date in the Mediterranean region. Negative winter NAO values are associated with increased precipitation in the Mediterranean region (Stenseth et al. 2003), including the Iberian Peninsula (Gordo et al. 2011). A number of studies have reported a relationship between the NAO-index and timing of breeding in birds including long-distance migrants (Przybylo et al. 2000, Møller et al. 2006). We obtained the winter NAO index from the web site (<www.cgd.ucar.edu/cas/jhurrell/indices.html>).

We also used total daily rainfall and average temperature calculated on a daily basis (hereafter rainfall and temperature) during the previous winter months (i.e. January and February) collected at a nearby meteorological station (Supplementary material Appendix 1 Table A1) as a proxy of the local winter climatic conditions generally affecting the studied population. We target on January and February climate conditions because at that time, but not before, most of magpie pairs are already in their breeding territories

in La Calahorra (Molina-Morales unpubl.). Therefore, climatic conditions in January and February are likely to influence the ability of female magpies to accumulate resources for egg laying. Rainfall and temperature records were retrieved from the website (<www.juntadeandalucia.es>) managed by the regional governments of Andalucía. Preliminary correlation analyses revealed that the NAO index was strongly correlated with rainfall (January rainfall vs NAO index: $r_p = -0.69$, $p = 0.039$; February rainfall vs NAO index: $r_p = -0.84$, $p = 0.009$), but not with temperature (January temperature vs NAO index: $r_p = 0.41$, $p = 0.26$; February temperature vs NAO index: $r_p = -0.07$, $p = 0.85$) in our study area. Therefore, we disregarded using rainfall information in subsequent analyses about winter climatic condition influence on phenology because most of its variation is retrieved by the NAO index.

In addition, because magpie and cuckoo phenology might also be affected by short-term weather effects we also investigated immediate spring temperature effects on phenology. The effect of spring temperature on breeding phenology has been demonstrated in many birds species included the magpie in UK (Crick and Sparks 1999). Most magpies in our population start laying in the second half of April (Supplementary material Appendix 1 Fig. A1), therefore we used total daily average temperature calculated on a daily basis during the first half of April as a surrogate of short-term weather effects likely affecting cuckoo and magpie individual decisions to lay eggs. Spring temperature was not related to the winter NAO index (April temperature vs NAO index: $r_p = -0.38$, $p = 0.312$) nor to winter temperature (April temperature vs January temperature: $r_p = -0.40$, $p = 0.281$; April temperature vs February temperature: $r_p = 0.02$, $p = 0.954$) in our study area, suggesting that both winter and spring temperature effects may independently affect magpie and cuckoo phenology.

Statistical analyses

Population-level analyses

In a first step, we used a linear mixed model (LMM hereafter) for studying variation in magpie laying date in relation to study year (i.e. 2005–2013) and parasitism status (i.e. parasitized versus non-parasitized) as random and fixed categorical effects, respectively. The interaction between study year and parasitism status was entered as a random factor in the model aiming to describe whether differences in the breeding phenology of parasitized and non-parasitized magpie nests changed between years.

Aiming to study the relationship between magpie and cuckoo fitness surrogates and laying date we first modeled probability of nest failure for all magpie nests studied between 2007 and 2011 as a binary dependent variable. We constructed a generalized linear mixed model (GLMM hereafter) where the fact that the nest was parasitized (cuckoo parasitized versus non-parasitized) was treated as fixed effect, and the year was treated as a random effect. Laying date and clutch size were included as covariates. In addition, we entered the interaction between laying date and parasitism which allowed us to test whether the effect of cuckoo parasitism on magpie host nest failure was mediated by laying date. Secondly we used a LMM to test the

influence of the same factors (i.e. parasitism as fixed effect, and year as a random effect) and covariates (i.e. laying date and clutch size) on fledging success of magpie hosts. This analysis was performed on the set of magpie nests in which at least one nestling fledged. These models thus responded the specific questions of whether breeding late increased host nest failure and decreased host productivity in our population.

In a second GLMM we modeled nest failure probability of cuckoo parasitized nests in relation to laying date and clutch size while entering year as random factor. In addition, we used a LMM to test the influence of laying date on cuckoo body mass at fledging while accounting for the non-independence of nestling raised in the same year and nest (i.e. year and nest as random effects). These models thus respond the question of whether being late increases nest failure of magpie nests holding a cuckoo egg and affects cuckoo nestling development. Temporal trends in magpie phenology and climatic conditions over the 2005–2013 period were analyzed with linear regression models weighted by number of nests using year as a continuous predictor. Similarly, we performed cross-sectional analyses to test changes in annual laying date of magpies and degree of cuckoo–host phenological mismatch in relation to regional and local climatic conditions using linear regression models. As the existence of temporal autocorrelation in time series analyses may artificially inflate the estimates of regression coefficients and their significance levels we checked for the presence of temporal autocorrelation in all the climatic variables and in laying date and in the residuals of linear models of these variable on year as a continuous predictor using the Box and Ljung *Q*-test as described in Statistica (StatSoft ver. 1995). Neither climatic indices nor magpie laying date or residuals were temporally autocorrelated at time lags of 1, 2, 3 and 4 years (Supplementary material Appendix 2 Table A2), suggesting that temporal autocorrelation would have a negligible effect in our cross-sectional analyses.

Longitudinal analyses

To assess whether magpie population responses to climatic conditions were due to individual variation in laying date, that is, plasticity we adopted the linear reaction norm approach (sensu Nussey et al. 2007) using those individuals that bred two or more years over the course of the study (we used 157 records from 58 females that bred at least twice during the period 2005–2013). We built different LMMs: one for each of the climatic variable affecting population-level variation in laying date (i.e. February and April Temperature) and cuckoo–host mismatch (i.e. NAO index and January temperature). Each model included laying date as the dependent variable, and age and one of the climatic variables as fixed effects. As random terms we included year, female identity (to test for variation between individuals in the average climatic conditions, i.e. elevations), and the interaction between female identity and the corresponding climatic variable (to test for between-individual variation in plasticity, i.e. slopes).

All models were fit using SAS 9.3. (PROC GLIMMIX procedure with link functions: identity and logit for LMMs and GLMMs, respectively), with type III tests of

fixed effects. Degrees of freedom for fixed effects were estimated using the Kenward–Roger approximation and significance of covariance parameters was tested with Wald *Z*-tests (SAS ver. 2013).

Results

Population level variation in host and parasite phenology and cuckoo–host mismatch

Laying date of magpies varied between years (random effect of year: $Z = 1.57$, $p = 0.05$) and in relation with cuckoo parasitism (fixed effect of parasitism: $F_{1,421.9} = 10.78$, $p = 0.001$), being late breeding magpies more likely cuckoo parasitized than earlier ones (mean (SE) = 26.3 of April (0.90 days) in 165 parasitized versus 22.5 of April (0.61 days) in 259 non-parasitized nests) (Supplementary material Appendix 1 Fig. A1). Differences in laying date between parasitized and non-parasitized magpie nests did not differ between years (interaction year \times parasitism: $Z = 0.55$, $p = 0.29$). No significant temporal trend was detected for the laying date of magpies (slope = 0.004 ± 0.02 , $t_7 = 0.18$, $p = 0.85$) and cuckoos (slope = 0.01 ± 0.02 , $t_7 = 0.51$, $p = 0.62$) over the nine years of study. However, breeding phenology of cuckoos was finely tuned to the breeding phenology of their magpie host: cuckoos tend to breed earlier those years in which their magpie hosts did it earlier (slope = 1.06 ± 0.26 , $t_7 = 3.96$, $p = 0.005$, $r^2 = 0.69$), also cuckoos tend to extend their breeding more time those years where magpie hosts extended more time their breeding (slope = 0.96 ± 0.09 , $t_7 = 10.52$, $p = 0.00001$, $r^2 = 0.94$).

Breeding success of magpies and cuckoos in relation to laying date

Nest failure probability of magpie host nests showed a year to year consistent pattern to increase seasonally (Fig. 1, Table 1). Among the nests with fledglings, however, host fledgling success decreased in parasitized nests, but did not change seasonally (Table 1). On the parasite side, nest failure probability of parasitized nests did not change seasonally (Table 1). However, cuckoo fledglings raised in late host nests were lighter than those raised in early host nests (Fig. 1, Table 1).

Climatic conditions and population level magpie host phenology and cuckoo–host mismatch

The NAO index was not related to the time of breeding of magpies (slope = -0.28 ± 0.53 , $t_7 = 0.54$, $p = 0.61$). January temperature (slope = 0.58 ± 1.15 , $t_7 = 0.50$, $p = 0.63$) was not significantly related with the laying date of magpies. However, magpies tends to breed earlier those years with low February temperatures (slope = 1.41 ± 0.57 , $t_7 = 2.55$, $p = 0.038$, $r^2 = 0.47$). April temperature alone did not significantly explain variation in laying date of magpies (slope = -0.71 ± 0.44 , $t_7 = 1.60$, $p = 0.15$). However, a multiple regression analysis in which we simultaneously assessed the effects of February and April temperature on magpie laying date revealed independent and contrary effects of winter and spring temperature on magpie

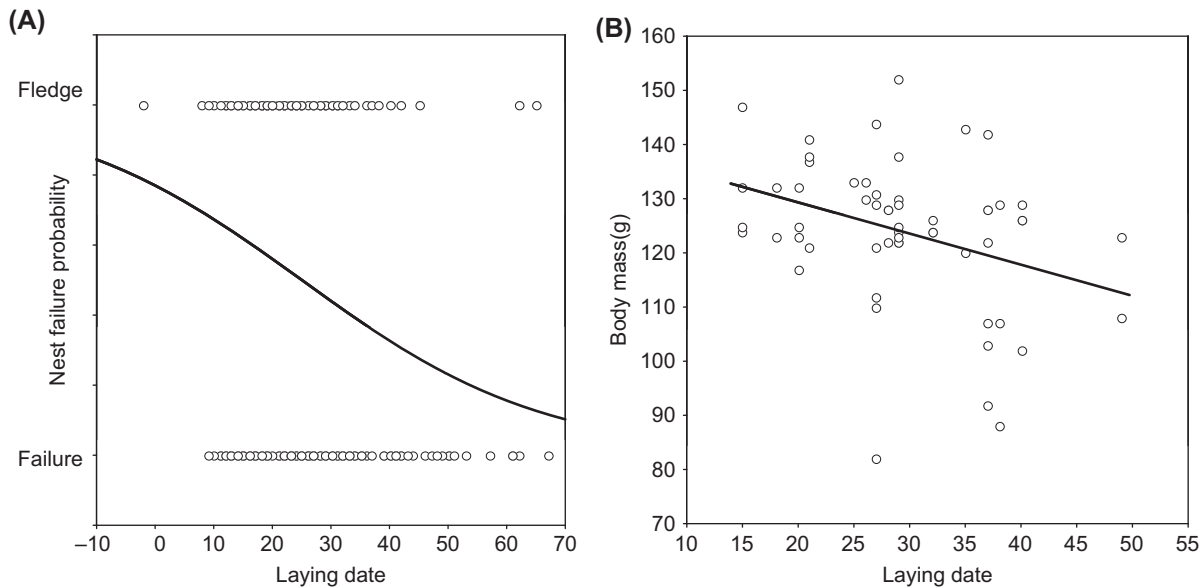


Figure 1. Magpie and cuckoo fitness surrogate in relation to laying date. (A) Magpie host nest failure probability in relation to laying date ($n = 238$ nests). (B) Cuckoo nestling body mass in relation to laying date ($n = 55$ nestlings raised in 34 nests).

phenology ($F_{2,6} = 9.16$, $p = 0.01$, $r^2 = 0.75$): magpie hosts tend to breed earlier those years with lower February temperatures ($\beta = -0.69 \pm 0.20$, $t_6 = 3.43$, $p = 0.01$; Fig 2); however, high temperature in the first half of April induced early laying in magpies ($\beta = -0.53 \pm 0.20$, $t_6 = 2.63$, $p = 0.04$; Fig 2).

Annual degree of phenological mismatching between great spotted cuckoos and magpies was related with regional and local winter climatic conditions: cuckoos delayed more their breeding time relative to magpies those years with a high NAO index (slope = 1.10 ± 0.36 , $t_7 = 3.04$, $p = 0.018$, $r^2 = 0.57$) and high January temperature (slope = 2.53 ± 0.71 , $t_7 = 3.54$, $p = 0.009$, $r^2 = 0.64$). February temperature (slope = 0.97 ± 0.70 , $t_7 = 1.37$, $p = 0.21$) and spring temperature (slope = -0.66 ± 0.46 , $t_7 = 1.42$, $p = 0.19$) were not related with the degree of phenological mismatch between cuckoos and magpies. In addition, when we reassessed the associations between winter NAO index and degree of phenological mismatch, and between January temperature and degree of phenological mismatch, by including spring temperature in multiple regression models results remained qualitatively identical and did not reveal any effect of spring temperature on cuckoo–host mismatch (multiple regression with NAO index and spring temperature as predictors: laying date vs NAO index: $\beta = 0.67 \pm 0.27$, $t_6 = 2.43$, $p = 0.05$; laying date vs April temperature: $\beta = -0.22 \pm 0.27$, $t_6 = 0.79$, $p = 0.45$; Multiple regression with January temperature and spring temperature as predictors: laying date vs January temperature: $\beta = 0.72 \pm 0.25$, $t_6 = 2.83$, $p = 0.03$; laying date vs April temperature: $\beta = -0.18 \pm 0.25$, $t_6 = 0.70$, $p = 0.51$; Fig 3).

Individual-level analyses of host phenology in relation to climatic conditions

Linear mixed-effects models revealed significant differences in laying date between different females (see the climate

variables in the fixed effects sections Table 2), but not evidence of an average plastic response to regional and local climatic conditions amongst magpie individuals (i.e. flat reaction norms; see interaction terms in the random effects sections of Table 2). In addition, individual female magpies did not exhibit plastic variation in laying date in response to the NAO index and winter or spring temperature (i.e. slopes) (Table 2). Hence, all results were concordant and suggested high variation in the laying schedule between females but low individual plasticity in laying date in response to the climatic conditions affecting our magpie population.

Discussion

Population-level analyses

The cross-sectional analyses performed in this study revealed that annual phenology of sedentary magpie hosts and the degree of phenological mismatch between migratory great spotted cuckoos and magpies is influenced by large-scale and local climatic conditions. Specifically, we found contrary and independent effects of winter and spring temperature on magpie phenology: magpies tend to breed earlier those years with low February temperatures, whereas high temperature in the first half of April favoured early laying. In addition, we found that cuckoos breed later relative to magpie hosts those years with a high NAO index and high January temperature. Previous studies have provided support for the existence of phenological mismatch between the European cuckoo and some of their main hosts at a continental scale due to changes in cuckoo and host migration phenology (Saino et al. 2009, Møller et al. 2011). Our results based on long-term monitoring of a single population extend previous findings and suggest that changes in breeding phenology due to climatic conditions may also apply to sedentary hosts, and may ultimately result

Table 1. Results of linear and generalized mixed-effects models of fitness correlates of magpie hosts and cuckoo parasites in relation to laying date. Significant terms are highlighted in bold. Degrees of freedom for fixed effects were estimated using the Kenward–Roger approximation.

Magpie host nest failure (n = 238 nests)					
Term	Covariance parameter	Random effects SE	Z	p	
Year	0.45	0.45	1.00	0.15	
Term	Coefficient	Fixed effects SE	F	DF	p
Clutch size	0.41	0.15	7.46	1,233	0.006
Laying date	−0.04	0.02	4.13	1,233	0.04
Parasitism	1.48	0.90	2.74	1,233	0.09
Laying date × Parasitism	0.02	0.03	0.47	1,233	0.49
Magpie host fledging success (n = 118 nests)					
Term	Covariance parameter	Random effects SE	Z	p	
Year	5.25	23.10	0.23	0.41	
Term	Coefficient	Fixed effects SE	F	DF	p
Clutch size	2.69	2.42	1.24	1,92.66	0.27
Laying date	−0.07	0.26	0.09	1,104.2	0.77
Parasitism	−49.51	17.74	7.79	1,112.7	0.006
Laying date × Parasitism	1.24	0.79	2.49	1,112.3	0.11
Cuckoo nest failure (n = 97 nests)					
Term	Covariance parameter	Random effects SE	Z	p	
Year	0.38	0.58	0.67	0.25	
Term	Coefficient	Fixed effects SE	F	DF	p
Clutch size	−0.14	0.20	0.46	1,94	0.50
Laying date	−0.02	0.02	0.58	1,94	0.44
Fledging cuckoo body mass (n = 55 nestlings)					
Term	Covariance parameter	Random effects SE	Z	p	
Nest	3.51	28.85	0.12	0.45	
Year	7.71	22.65	0.34	0.36	
Term	Coefficient	Fixed effects SE	F	DF	p
Laying date	−0.48	0.28	2.93	1,25.33	0.05

in phenological mismatch between parasitic cuckoos and their hosts.

There was no evidence of changes in local climatic conditions in our study site during the period 2005–2013 and not surprisingly magpie host population has not shown any shift in its time of laying during that time. This may simply reflect the short time period considered in these analyses. However, February and April temperature explained 75% of annual variation in magpie laying date, which still would suggest that temperature has a fundamental influence on breeding phenology of magpies in this population. We cannot discard, however, that the absence of any clear temporal trend in magpie phenology was due to the conflicting effects of winter (i.e. delayed) and spring (i.e. immediate) temperature on magpie laying dates.

Previous studies in other bird species (Dunn 2004, Both et al. 2004), included magpies in UK (Birkhead 1991), had found that high spring temperatures induced early

laying. Our results confirmed these findings as high April temperature triggered laying of magpies in our population once we control for winter temperature. However, the simultaneous consideration of winter and spring temperature also revealed a high influence of winter temperature on magpie phenology. Indeed, we found that, irrespective of the influence of spring temperature, magpies breed earlier those years with low winter temperature. This pattern was not confounded by concomitant temporal changes in climate and host phenology, and is contrary to the general pattern reported in birds (Crick and Sparks 1999, Dunn 2004), and also in magpies (Birkhead 1991, Crick and Sparks 1999), of advancing egg production time in response to the increase in spring temperature. Previous studies have shown that the effect of temperature on laying date may greatly vary both between (Dunn 2004, Torti and Dunn 2005) and within bird species (Visser et al. 2003, Husby et al. 2010) due to geographical and ecological

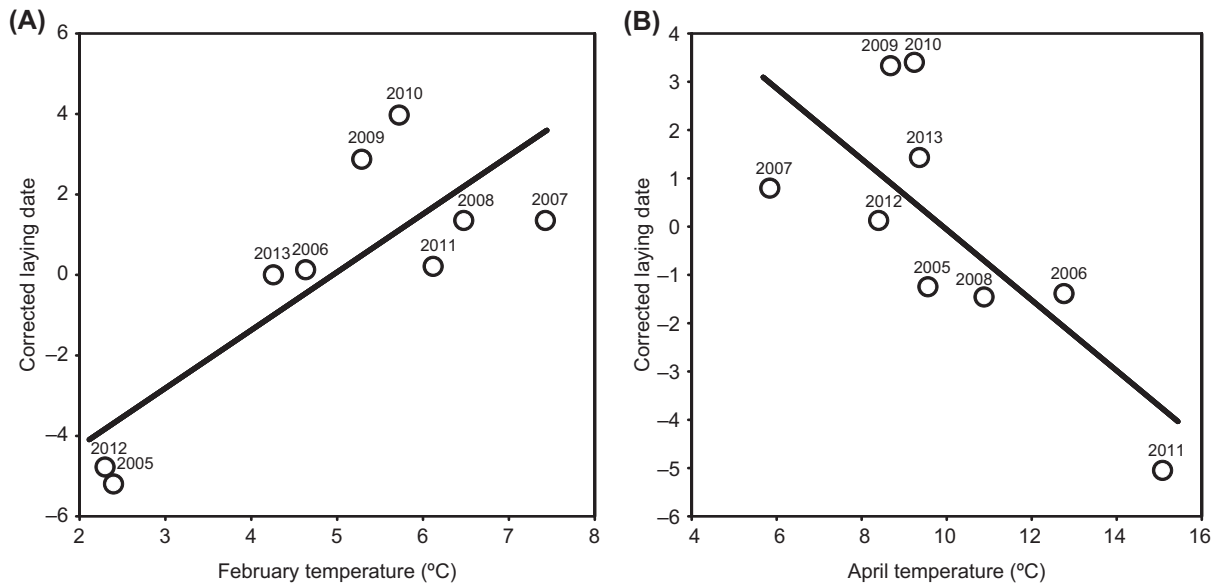


Figure 2. Relationship between the annual mean laying date of magpie hosts in each of the nine years and February (A) and April (B) temperature. Laying date is expressed as the residual of laying date on April (A) and February (B) temperature aiming to illustrate pure effects of winter and spring temperature in magpie population phenology.

differences. However, the simultaneous effect of winter and spring temperature on bird phenology has been rarely investigated.

The positive effect of winter temperature on magpie phenology is intriguing, and could be explained by immigration of breeding individuals from colder populations. If magpies migrate into our population from colder areas, magpie population phenology may advance because migrants would experience earlier environmental cues for reproduction than in their original populations. As mentioned above, our magpie population is close to others differing in phenology (Martín-Gálvez et al. 2007),

and previous genetic studies have shown that they all form a metapopulation in which gene flow is frequent (Martín-Gálvez et al. 2007). However, it remains unstudied whether gene flow can or cannot be mediated by climate-dependent dispersal in magpies. Alternatively, this pattern might result from changes in the age pyramid of our population due to an effect of winter conditions on survival probability of first-year magpies. A similar mechanism was proposed to explain male shortening of tail length under favorable conditions in a Danish barn swallow *Hirundo rustica* population (Møller and Szép 2005). Magpie' highest mortality occurs during the first

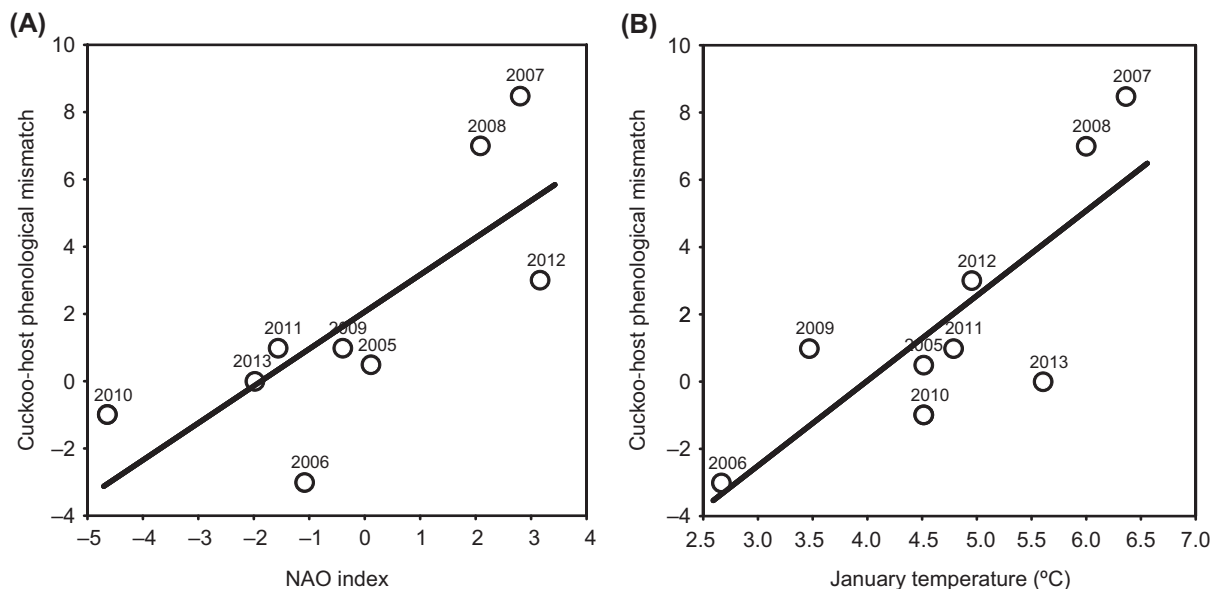


Figure 3. Relationship between the annual degree of phenological mismatch (i.e. differences in median laying date of cuckoos and magpie hosts) and NAO index (A) and temperature in January (B).

Table 2. Results of linear mixed-effects models of plasticity in magpie egg-laying date in response to regional (i.e. NAO index) and local winter climatic (January and February temperature) and spring (first half of April temperature) conditions. Analyses were done using 157 records from 58 females that bred at least twice during the period 2005–2013. Climatic variables were mean centered. Significant terms are highlighted in bold. Degrees of freedom for fixed effects were estimated using the Kenward–Roger approximation. Significant terms are highlighted in bold.

NAO index		Random effects			
Term	Covariance parameter	SE	Z	p	
Female	27.09	8.55	3.17	0.0008	
Year	11.27	8.43	1.34	0.09	
NAO index × Female	0.02	0.45	0.06	0.47	
		Fixed effects			
Term	Coefficient	SE	F	DF	p
Age	7.59	2.91	6.78	1,126	0.01
NAO index	−0.22	0.53	0.17	1,5.9	0.69
January temp		Random effects			
Term	Covariance parameter	SE	Z	p	
Female	27.14	8.41	3.23	0.0006	
Year	11.91	8.61	1.38	0.08	
January temp × Female	1.09	3.24	0.34	0.36	
		Fixed effects			
Term	Coefficient	SE	F	DF	p
Age	7.57	2.93	6.68	1,122.1	0.01
January temp	0.02	1.20	0.00	1,6.33	0.98
February temp		Random effects			
Term	Covariance parameter	SE	Z	p	
Female	24.98	7.85	3.18	0.0007	
Year	5.93	5.40	1.10	0.13	
February temp × Female	3.37	2.89	1.16	0.12	
		Fixed effects			
Term	Coefficient	SE	F	DF	p
Age	7.18	2.80	6.54	1,1112.7	0.01
February temp	1.16	0.73	2.49	1,10.15	0.14
April temp		Random effects			
Term	Covariance parameter	SE	Z	p	
Female	26.75	8.34	3.21	0.0007	
Year	9.14	7.29	1.25	0.10	
April temp × Female	2.28×10^{-17}		0.00	1.00	
		Fixed effects			
Term	Coefficient	SE	F	DF	p
Age	7.57	2.89	6.83	1,130.8	0.01
April temp	−0.52	0.47	1.25	1,5.90	0.30

winter (Birkhead 1991, Molina-Morales and Martínez unpubl.), and it might be particularly high in cold winters. Furthermore, it is known that young magpies breed later than old ones (Birkhead 1991). Thus, in harsh conditions (i.e. in cold winters) selective mortality might eliminate young magpies and adults may have earlier or better access (i.e. lower competence) to resources and/or territories resulting in the advance of laying date. Winter temperature effects might thus induce changes in magpie phenology through their possible effects on migration and/or selective mortality which would ultimately determine the pull of magpies that will have a chance to breed in spring. In that time, individual decisions to lay would be more likely influenced by spring immediate temperature.

A critical point is to know how changes in climatic conditions may impact on the dynamic of the interaction

between great spotted cuckoos and magpies in our population. Unfortunately, we cannot compare the breeding outcome of magpies and great spotted cuckoos at the level of individual as we could not ascribe cuckoo eggs to females. However, the analyses of the relationships between laying date and breeding success of magpies and cuckoos provide some insight about the potential fitness consequences of breeding late for magpies and great spotted cuckoos. Being late penalizes magpies by increasing nest failure, but not fledging success, irrespective of parasitism, while late cuckoo fledglings were significantly lighter than those raised in early nests. Therefore, cuckoos laying late relative to magpies would face the double cost of nest failure of their hosts besides a lower fitness prospect due to reduction of body weight at fledging of their offspring.

Individual-level analyses of host phenology

Our longitudinal analyses performed on magpie individual hosts experiencing different value of climatic conditions over several breeding seasons allowed us to disentangle the potential role of plasticity and microevolution on the observed annual changes at population level. Magpie plasticity at the level of population was not due to individual plasticity in phenology in response to climate as magpies were relatively invariant to climatic conditions (see also Charmantier et al. 2008). Previous theoretical studies had suggested a higher potential for selection of phenotypic plasticity in more predictable environments (Gavrilets and Scheiner 1993). Indeed, a recent empirical study has shown that individual great tit plasticity was relatively lower in less food predictable populations (Porlier et al. 2012). We reported a low temporal autocorrelation for all climatic cues analysed in la Calahorra (Supplementary material Appendix 2 Table A2), which would suggest a low potential for selection on individual plasticity in our population.

Our study revealed a disagreement between cross-sectional and longitudinal analyses. We found population-level plasticity in host phenology in response to climatic conditions, but very little between-individual plasticity in response to climate. A previous study had documented a similar pattern in the colonial breeder common guillemot *Uria aalge* where selection imposed by a need of breeding synchronously might have limited selection on individual plasticity to climate (Reed et al. 2006). Knowing how magpies may show an annual tracking of local climatic conditions without phenotypic plasticity is intriguing. Magpie have a relatively short generation time (life expectancy of magpies in UK was 2.0 years, Birkhead 1991), an although animals may show evolutionary responses over short time scales (Grant and Grant 1995), it still seems unlikely that selection due to fluctuating climatic conditions caused the population to track the local climatic conditions every year. Alternatively, population tracking of local climatic conditions may arise if climatic conditions affected dispersal movements of magpies in our study area. Our magpie population is connected by gene flow and migration to other nearby populations (Martín-Gálvez et al. 2007). In this vein, marked gene drift due to departure or entrance of individuals selected to breed at different times of the year may induce the average population matching to climatic conditions and limited the potential of selection on individual plasticity.

Conclusion

Despite the fact our results should be considered with caution given the short study period considered, our study is the first providing support for the idea that both regional and local climatic conditions may impact on cuckoo-host interaction through their influence on cuckoo and host breeding phenology at the population scale. Although the mechanisms behind the link between temperature and phenology of cuckoos and magpies clearly deserve further investigation, if magpies and cuckoos differ in their sensitivities to temperature magpie hosts could be exposed to great spotted cuckoos earlier or later in the season as

climate changes with potential consequences for the dynamic of the interaction. Our longitudinal analysis based on a set of marked individuals that experienced different values of environmental conditions over several breeding seasons revealed that magpie host population plasticity in breeding phenology did not arise from individual plasticity in response to local climatic conditions. This finding might be related to the high genetic and migration connectivity of our magpie population with nearby ecologically different populations and the low predictability of climatic conditions that may favour selection to act on short dispersal rather than on plastic laying in response to climatic change. Our results, thus, emphasize the need of including climatic variables as factors potentially explaining the dynamic of interaction between parasites and its hosts, and illustrate the importance of considering studies at the level of individual in order to deepen in the knowledge of the evolutionary mechanisms shaping population responses to climatic variation.

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Supplementary material (available online as Appendix oik-01124 at <www.oikosjournal.org/readers/appendix>). Appendix 1–3.