

Evolution of tolerance by magpies to brood parasitism by great spotted cuckoos

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Hosts may use two different strategies to ameliorate negative effects of a given parasite burden: resistance or tolerance. Although both resistance and tolerance of parasitism should evolve as a consequence of selection pressures owing to parasitism, the study of evolutionary patterns of tolerance has traditionally been neglected by animal biologists. Here, we explore geographical covariation between tolerance of magpies (*Pica pica*) and brood parasitism by the great spotted cuckoo (*Clamator glandarius*) in nine different sympatric populations. We estimated tolerance as the slope of the regression of number of magpie fledglings (i.e. host fitness) on number of cuckoo eggs laid in non-depredated nests (which broadly equals parasite burden). We also estimated prevalence of parasitism and level of host resistance (i.e. rejection rates of mimetic model eggs) in these nine populations. In accordance with the hypothetical role of tolerance in the coevolutionary process between magpies and cuckoos we found geographical variation in tolerance estimates that positively covaried with prevalence of parasitism. Levels of resistance and tolerance were not associated, possibly suggesting the lack of a trade-off between the two kinds of defences against great spotted cuckoo parasitism for magpies. We discuss the results in the framework of a mosaic of coevolutionary interactions along the geographical distribution of magpies and great spotted cuckoos for which we found evidence that tolerance plays a major role.

Keywords: host–parasite interactions; egg rejection; parasite resistance; spatial coevolutionary interactions

1. INTRODUCTION

Parasitism selects for defensive traits in their hosts that counteract the negative effects of such interspecific relationships. Hosts may directly attack parasites and thereby reduce parasite loads, for example, by eating or destroying parasites [1], or they can accept parasitism but minimize or limit the harm caused by a given parasite burden. These two components of host defence have been recognized and studied by plant biologists for more than one hundred years ([2,3] and references therein), and they have called them resistance and tolerance, respectively. Both resistance and tolerance are likely to be costly traits for hosts, and while the former host response to parasitism implies considerable negative effects for parasites, tolerance does not inhibit the parasites' growth or reproduction, but minimizes the impact of parasite attacks [4].

Despite resistance and tolerance having different consequences for parasite–host coevolutionary relationships, the study of tolerance has traditionally been neglected by

animal biologists, who have mainly concentrated on detection and study of antagonistic coevolution between host defences and parasite counter-defences in an open-ended coevolutionary arms race. From an ecological and evolutionary perspective, distinguishing between resistance and tolerance response to parasitism is of prime importance for several reasons reviewed in Råberg *et al.* [3]. First, while the evolution of resistance should reduce parasite prevalence in the host population, tolerance would have neutral or positive effects [5,6]. Second, the evolution of resistance, but not that of tolerance may result in open-ended antagonistic coevolution [4,6]. Finally, while resistance genes tend to be polymorphic, those of tolerance are expected to go to fixation in host populations [7]. Therefore, by taking both host tolerance and resistance strategies into account, unexplored scenarios in animal enemy–victim coevolution may arise because the evolution of one would influence the evolution of the other, and, for instance, the interaction between two antiparasitic strategies can be antagonistic [8], independent, or have additive effects [9].

Given the theoretical importance of tolerance in animal host–parasite coevolution, two recently published reviews argued for the necessity of exploring the predicted role of tolerance in such relationships [3,10]. Particularly

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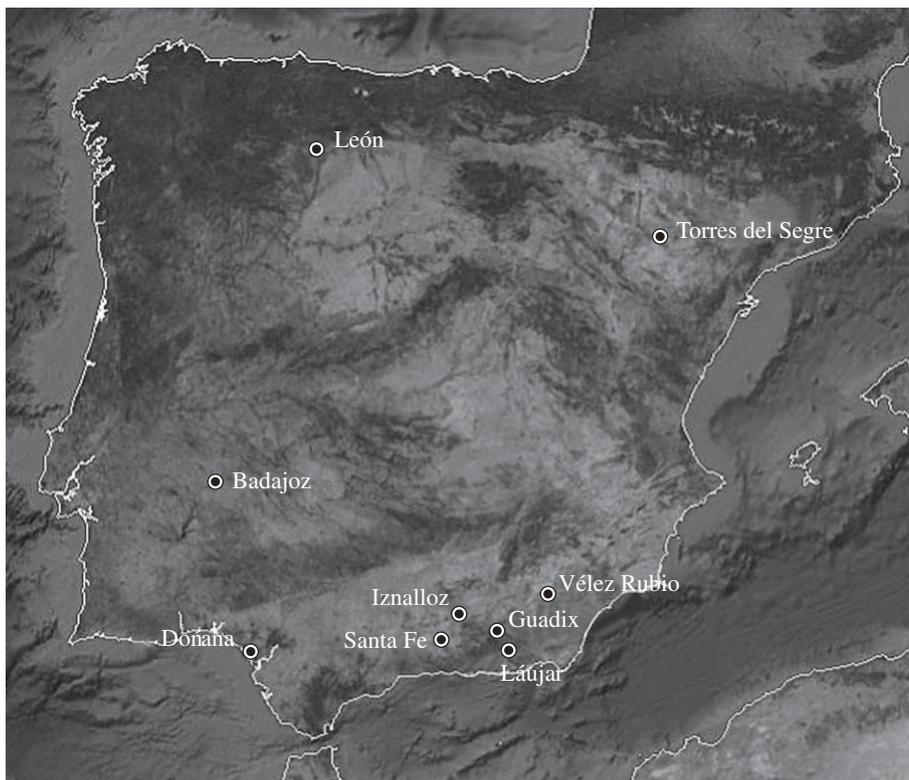


Figure 1. Location within the Iberian Peninsula of the nine study populations.

interesting is to detect variation in tolerance to parasitism of different host populations and to explore whether tolerance geographically covaries with selection pressure owing to parasitism (i.e. parasite prevalence) [10]. Furthermore, the study of geographical covariation between resistance and tolerance for different host–parasite systems will also help understand the possible antagonistic and/or additive nature of these antiparasitic responses [8,9,11].

Brood parasitism has been used as a model system for the study of antagonistic coevolutionary relationships [12], where the hosts (e.g. recognition and rejection of parasitic-eggs) and the brood parasites (e.g. mimetic eggs) evolve traits that confer resistance to each other [13,14]. In their review, Svensson & Råberg [10] suggested that tolerance could also play a role in the evolutionary dynamics of brood parasitism and they proposed the great spotted cuckoo (*Clamator glandarius*)–magpie (*Pica pica*) system as one where the evolution of tolerance might have fitness advantages. Here, we explore such relationships by quantifying both resistance and tolerance in several populations of magpies parasitized by the brood parasitic great spotted cuckoo. As an estimate of resistance to parasitism of different magpie populations, we quantified rejection rates of experimental mimetic eggs. We know that the ability of magpies to recognize and reject parasitic eggs is a defensive trait that has evolved as a consequence of selection pressure owing to parasitism and gene flow of genes that confer adaptive advantages [15–17]. As an estimate of magpie tolerance to brood parasitism in different populations we quantified the slope of the regression of host fitness (i.e. fledging success) against infection intensity (i.e. number of great spotted cuckoo eggs per host nest); the steeper the slope the lower the tolerance [3].

2. MATERIAL AND METHODS

(a) *Study areas and field procedures*

We studied nine different magpie populations (figure 1) in sympatry with its brood parasite, the great spotted cuckoo, where at least one parasitized nest did not fail owing to nest predation (table 1). Four of these populations (Doñana, Santa Fe, Guadix and Torres del Segre) were studied in 1992–1995, and have been described elsewhere [15], while the other five (Láujar, Badajoz, Vélez Rubio, Iznalloz and León) were sampled more recently (2007–2008).

Briefly, at the beginning of the breeding season we intensively looked for magpie nests in the areas. Once a nest was located, we visited it at least once per week to detect brood parasitism by the great spotted cuckoo, to perform egg-recognition tests with mimetic model eggs (made with plaster of Paris) during the laying stage, and to record magpie response to experimental parasitism 4–7 days after experimental parasitism (for a more detailed description, see [15]). Afterward, nests were visited at the time of hatching and, later on, a few days before fledging (i.e. 18 days after hatching) to estimate fledging success. Some magpie nests with recorded responses to experimental parasitism were depredated before recording fledging success, while some other nests were detected after laying, and hence we did not perform egg-recognition experiments, but used all these nests for estimation of parasitism rates. Thus, sample sizes for different estimations are not identical (see table 1).

(b) *Statistical procedures*

We explored the relationship between fledging success of magpies and number of cuckoo eggs in their nests. The frequency distribution of the response variable (i.e. fledging success of magpies) contains more zero values than expected based on Poisson or negative binomial distributions (see the electronic supplementary material, appendix 1). We explore whether

Table 1. Percentage of brood parasitism by the great spotted cuckoo and rejection rates of experimental mimetic cuckoo eggs by magpies in nine different sympatric populations. (Values of tolerance to brood parasitism by magpies of the nine studied populations were estimated as the slope of the linear regression between fledging success plus one and number of cuckoo eggs that were laid in each magpie nest that did not suffer from predation. Intercepts of the regression lines are also shown. Total number of magpie nests used to estimate tolerance (N_t) and number of parasitized nests included (N_p) are also shown.)

population	latitude	longitude	% parasitism (N)	% rejection (N)	tolerance (s.e.)	intercept (s.e.)	tolerance N_t (N_p)
Doñana	37°08'N	6°56'W	11.5 (52)	43.5 (23)	-0.777 (0.171)	1.735 (0.044)	42 (4)
Santa Fe	37°11'N	3°43'W	85.7 (21)	33.3 (12)	-0.394 (0.218)	1.333 (0.425)	11 (10)
Guadix	37°18'N	3°11'W	51.8 (85)	63.6 (44)	-0.424 (0.060)	1.481 (0.065)	58 (35)
Torres del Segre	41°32'N	0°31'W	2.3 (43)	38.1 (21)	-0.952 (0.316)	1.767 (0.067)	23 (2)
León	42°35'N	5°34'W	4.9 (41)	26.8 (41)	-0.958 (0.252)	1.651 (0.057)	16 (2)
Izualloz	37°23'N	3°31'W	8.2 (49)	24.4 (41)	-0.750 (0.379)	1.443 (0.087)	19 (2)
Badajoz	38°52'N	6°56'W	13.0 (23)	59.1 (22)	-0.951 (0.176)	1.778 (0.073)	12 (3)
Vélez Rubio	37°39'N	2°04'W	20.6 (34)	12.1 (33)	-1.042 (0.535)	1.735 (0.126)	27 (8)
Láujar	37°00'N	2°52'W	17.6 (17)	33.3 (12)	-0.778 (0.246)	1.633 (0.116)	7 (1)

this zero-inflated distribution affects the relationship between response variable and the number of cuckoo eggs (fixed continuous factor) by using zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) models (see [18, ch. 11]). These are two-part models that include the count model (e.g. Poisson distribution and logistic link function) and the zero-inflation model (e.g. binomial function and logistic link function), allowing them to distinguish between the effects of independent variables on the binomial (more than expected zeros) and continuous (the effect of counts) distribution of the dependent variable (i.e. fledging success). Moreover, the relationship between fledging success of magpies and number of cuckoo eggs in their nests might follow a polynomial rather than a linear function [3], and we therefore included the quadratic term in the model. Finally, to control for among population variance, we included population identity as a discrete fixed factor in the model.

Thus, before estimating within population associations, we studied the effect of frequency distribution and the possibility of a polynomial relationship after controlling for the effect of population identity. First, we found that Poisson distribution appropriately accounted for data overdispersion (`qcc.overdispersion.test` in *R*, $p < 0.0001$), since variance structure of the ZIP is equal to that of ZINB (likelihood ratio test, $\chi^2_1 = 0.001$, $p = 0.99$). Moreover, we did not find evidence of significant effects of zero-inflated distribution since neither cuckoo eggs (estimate (s.e.) = 7.90 (4.05), $z = 1.95$, $p = 0.051$) nor squared cuckoo eggs (estimate (s.e.) = -1.10 (0.67), $z = 1.65$, $p = 0.10$) significantly explained number of magpie fledglings in the zero-inflation submodel. Finally, we found that the squared terms did not significantly explain additional variance to that explained by the linear term, neither in the count submodel (effect of removal of the squared term, likelihood ratio test, $\chi^2_2 = 1.70$, $p = 0.43$) nor in the zero-inflation submodel (effect of removal of the squared term, likelihood ratio test, $\chi^2_2 = 5.18$, $p = 0.075$). Thus, for subsequent analyses we used Poisson generalized linear models (GLM) and corrected the standard errors by the dispersion parameter (see [18, ch. 9]). We used the interaction between population identity and number of cuckoo eggs to explore among population differences in the relationship between number of magpie fledglings and number of cuckoo eggs.

For each study area, we estimated tolerance as the slope of the regression of fledging success of magpies against the

number of great spotted cuckoo eggs laid in successful, non-depredated magpie nests; the steeper the slope, the lower the tolerance [3]. For one study population (Badajoz), none of the three parasitized magpie nests (with one, two and three parasitic eggs, respectively) produced magpie nestlings, and, therefore, the estimate of the slope when assuming Poisson distributions was not possible. Trying to solve this problem, we used number of magpie fledglings plus one to estimate the slopes in the nine studied populations. It should be mentioned here that the removal of the Badajoz population and the use of untransformed number of nestlings in the analyses of the remaining eight populations produces qualitatively identical results (i.e. identical significant factors, results not shown).

We used these estimated slopes as the dependent variable in regression analyses with parasitism rates and rejection rates as independent predictor variables. We take into account variation in reliability of slope values in our analyses by weighting regression analyses by the sample size used for each estimation (i.e. population). Using the inverse of the standard error of slopes as the weighting variable produced identical results.

We know from previous studies that gene flow among magpie populations in sympatry with the great spotted cuckoo is very high, resulting in non-structured magpie populations [19]. Moreover, we have also detected similar coevolutionary patterns between selection pressure owing to parasitism and rate of adaptive phenotypes (i.e. rejection rates), both at large and restricted geographical scales [15,20]. We statistically controlled the explored relationships between tolerance and resistance and parasitism selection pressure by the effect of geographical distances among populations by means of spatial autocorrelation analyses (Mantel tests with 10 000 permutations). For these analyses, we used the matrices of absolute differences among populations calculated for each variable and the matrix of geographical distances. These analyses however do not allow the use of weighted matrices because they are based on distance matrices and, thus, we were unable to take reliability of estimates of tolerance into account. Thus, we present the results from both weighted regressions and spatial autocorrelation analyses.

Except for weighed regression analyses that were performed in STATISTICS 9.0 (StatSoft, Inc.), all other statistics were performed in the 'R' ([21]; v. 2.11.1) environment.

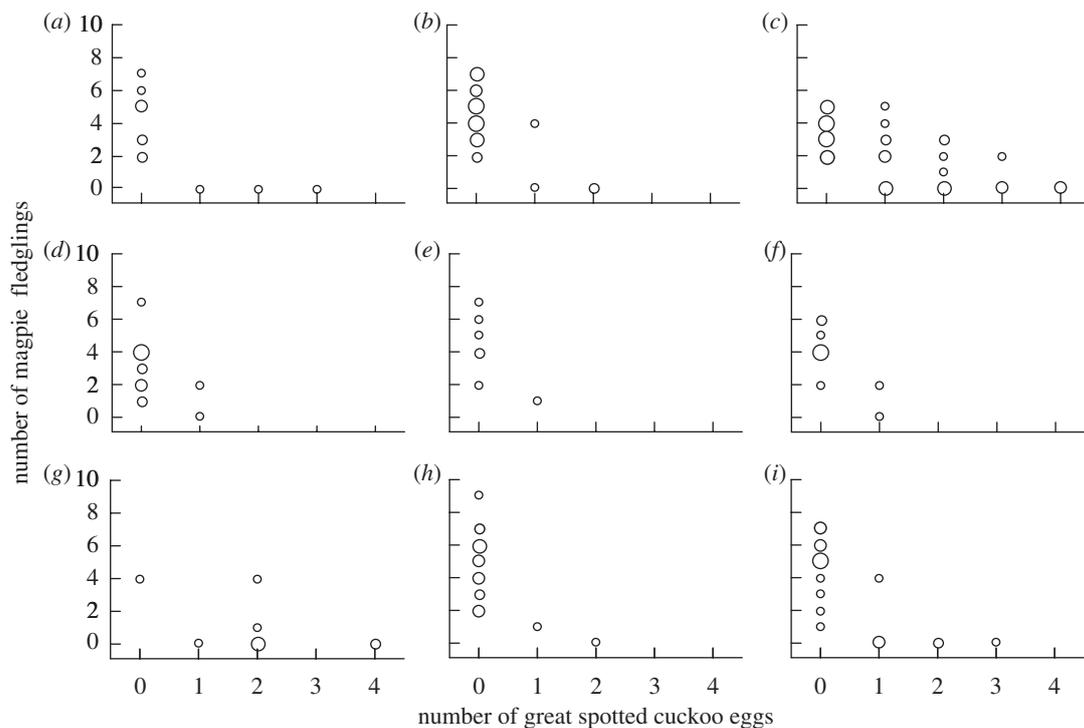


Figure 2. Relationships between number of magpie fledglings per nest and number of great spotted cuckoo eggs laid per magpie nest in each one of the nine sympatric populations. (a) Badajoz; (b) Doñana; (c) Guadix; (d) Iznalloz; (e) Láujar; (f) León; (g) Santa Fe; (h) Torres del Segre; and (i) Vélez Rubio.

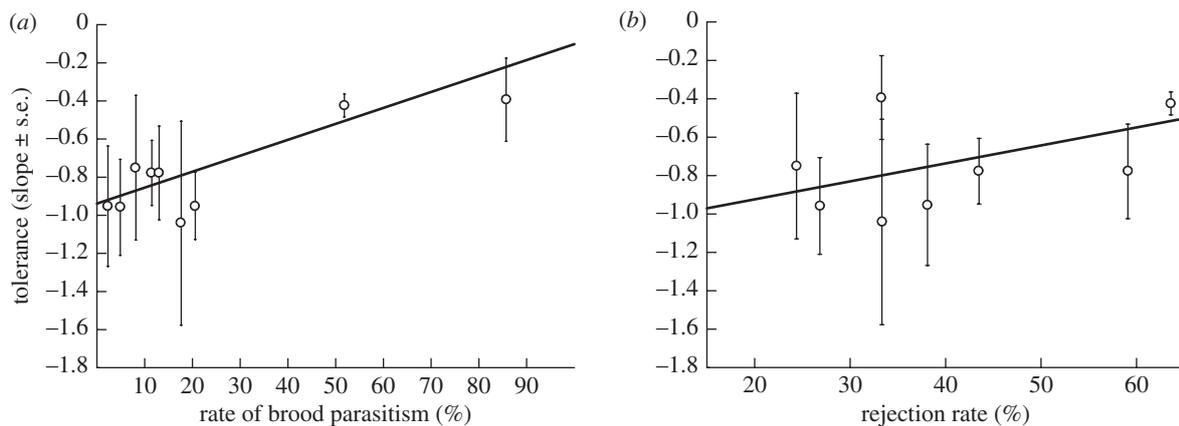


Figure 3. (a) Relationship between tolerance (estimated as the slope of the relationship between fledging success and number of cuckoo eggs in magpie nests in nine different populations \pm s.e.) and prevalence of brood parasitism (i.e. number of parasitized nests; tolerance = 0.008 (parasitism - 0.94)). (b) Rejection rates of experimental mimetic eggs of nine populations of magpies in sympatry with the great spotted cuckoo (tolerance = 0.009 (parasitism - 0.15)). The lines are the linear regression lines.

While 'glm' function (included in R, 'stats' package) was used for Poisson-GLM, the next R-packages: 'pscl' [22,23], 'lme4' [24], 'qcc'(scrucca [25]), 'ecodist' ([26]; v. 1.2.3) were, respectively, used for ZINB and ZIP analyses, overdispersion test, likelihood ratio test and Mantel tests.

3. RESULTS

We found considerable among-populations variation in estimates of tolerance of brood parasitism by magpies (Poisson-GLM, breeding success of magpies as a dependent variable; population identity as fixed factor and number of cuckoo eggs as covariate; effect of removing the interaction term: scaled deviance 17.68, $p = 0.024$; figure 2, table 1). Intercepts of the relationship between fledging success of magpies and number of cuckoo

eggs estimated for different population did not differ significantly ($F_8 = 1.62$, 206, $p = 0.12$, table 1).

Magpie populations with higher rates of brood parasitism by the great spotted cuckoo had higher tolerance to parasitism (figure 3a; weighted regression, β (s.e.) = 0.87 (0.19), $t = 4.65$, $N = 9$, $p = 0.0023$), even after statistically controlling for geographical distances among populations (spatial autocorrelation analyses; parasitism prevalence: partial Mantel $R = 0.74$, $p = 0.011$; geographical distances: partial Mantel $R = -0.06$, $p = 0.55$). Moreover, magpie populations with higher rates of resistance (i.e. rejection rates of experimental model eggs) have higher tolerance (figure 3b; weighted regression, β (s.e.) = 0.73 (0.26), $t = 2.86$, $N = 9$, $p = 0.024$). This tendency disappeared when statistically controlling for geographical distances among populations (spatial

autocorrelation analyses; rejection rates of mimetic eggs: partial Mantel $R = -0.03$, $p = 0.55$; geographical distances: partial Mantel $R = -0.21$, $p = 0.83$).

Finally, the effect of parasitism on the level of tolerance of magpies to brood parasitism was still statistically significant after statistically controlling for the effect of variance explained by rejection rates (weighted multiple regression, partial effect of parasitism prevalence: β (s.e.) = 0.67 (0.15), $t = 4.41$, $N = 9$, $p = 0.005$; partial effect of rejection rates: β (s.e.) = 0.42 (0.15), $t = 2.74$, $N = 9$, $p = 0.034$), even after controlling for geographical distances among populations (spatial autocorrelation analyses; parasitism prevalence: partial Mantel $R = 0.75$, $p = 0.011$; rejection rates of mimetic eggs: partial Mantel $R = 0.16$, $p = 0.19$; geographical distances: partial Mantel $R = -0.02$, $p = 0.49$).

4. DISCUSSION

We estimated tolerance as the slope of the regression line between fledging success of non-depredated and non-abandoned magpie nests against the number of parasitic eggs successfully (i.e. non-rejected) laid by cuckoos. Our main findings include the detection of geographical variation in estimated tolerance to brood parasitism among host populations. Furthermore, we found that levels of tolerance to brood parasitism by different magpie populations were positively related to parasite prevalence, but not to levels of resistance estimated for the same magpie populations. These associations suggest that tolerance is an adaptive response to brood parasitism, and that tolerance and resistance (i.e. cuckoo egg recognition and rejection) are probably not antagonistic, but rather independent adaptive responses of magpies to great spotted cuckoos.

The possibility that hosts in general and magpies in particular show some degree of tolerance to their brood parasites was suggested by Svensson and Råberg [10], who argued that the high costs experienced by resistant (i.e. rejecter) magpies, which include nest destruction by cuckoos [27], could favour tolerance as an alternative defence mechanism. In fact, we have experimental evidence that magpies who had experimental eggs removed and suffered experimental nest predation, changed to accept experimental parasitism in subsequent breeding attempts [28]. Similarly, there exists evidence suggesting that the ant *Proformica logiseta* that tolerates brood parasitism by the slave-making *Rossomyrmex minuchae* may experience fitness advantage [29]. Therefore, tolerance of brood-parasitism would be of selective advantage for magpies and other hosts of brood parasites in parasitized populations. Based on our previous result that magpies breeding in sympatry with the cuckoo lay larger clutches than allopatric magpies [30], Svensson and Råberg [10] suggested that magpies laying larger clutch sizes would better tolerate brood parasitism by cuckoos.

The detected strong relationship between tolerance and parasitism prevalence among populations cannot be explained by the significant positive relationship between tolerance and resistance since the former appeared even after controlling for the effect of the latter (see §3). Thus, although host resistance (i.e. foreign egg recognition and rejection) is positively associated with

selection pressure owing to parasitism even after controlling for the large amounts of gene flow among magpie populations [16], the effect of brood parasitism on levels of magpie tolerance is independent of the degree of the antiparasitic resistance evolved in each magpie population. This association was not owing to among population differences in breeding success of non-parasitized nests of magpies since the intercept of the regression lines of each population did not differ among populations. All these pieces of evidence suggest that tolerance is an important defence of magpies to brood parasitism that covaries geographically with level of selection pressures imposed by parasitism.

The second main result is the lack of association between resistance and tolerance that magpies of different populations show to brood parasitism by great spotted cuckoos after the relationship is controlled by geographical distances. It is known that resistance of magpies against great spotted cuckoos has a strong geographical component [15], and thus, the effect of controlling for geographical distance might suggest that resistance and tolerance to brood parasitism covaried geographically. However, we did not find evidence of a relationship between geographical distance and tolerance and, consequently, this lack of association between resistance and tolerance should be better interpreted as evidence that tolerance and resistance are not traded-off, as detected in some other systems [8]. Resistant magpies may incur important costs owing to erroneous recognition of mimetic great spotted cuckoos eggs [31], or owing to cuckoos revisiting parasitized nests and destroying those where cuckoo eggs had disappeared [27]. This might prevent fixation of resistance in the host population [7]. However, such cuckoo behaviour implies important costs involved in revisiting magpie nests and possible misrecognition of own eggs that may impede the fixation of cuckoo counter-defences in the populations [7]. Tolerance traits would imply only low additional costs for hosts in parasitized populations (e.g. those related to increase clutch size), and, therefore, will tend to be driven to fixation by selection if they have a genetic basis [7]. Moreover, it is also known that if tolerance and resistance traits are not genetically correlated, as should be the case for those related to clutch size and parasitic-egg recognition ability [17], resistance and tolerance are not necessarily mutually exclusive [9] and, therefore, would respond to parasitism in different ways depending on selective pressures owing to parasitism and relative costs and benefits of defences [11], which may vary geographically.

Summarizing, we here report, to our knowledge, the first evidence of a geographical covariation between selection pressure owing to parasitism and tolerance of animal hosts under natural conditions that, additionally to the effects of parasitism-resistance related traits, might contribute to ameliorate negative effects of a given parasite burden.

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