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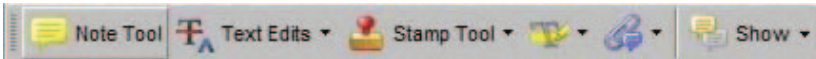
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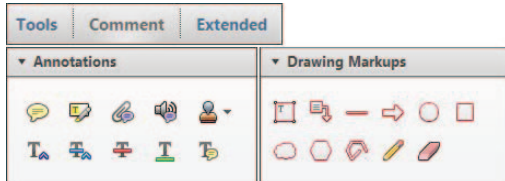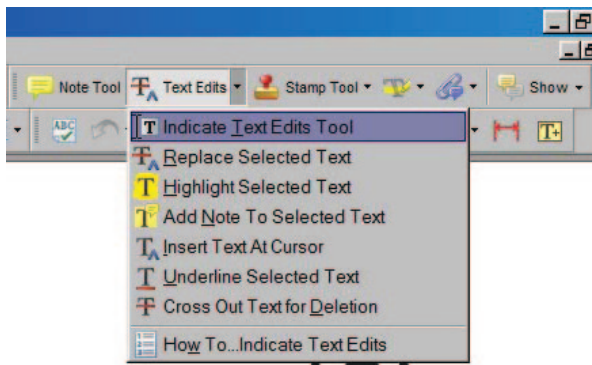

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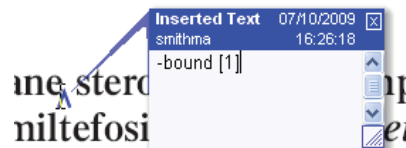
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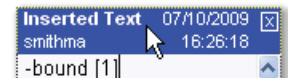
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Original Article

Geographic variation in egg ejection rate by great tits across 2 continents

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Hosts of brood parasites may vary geographically in their ability to resist parasitism. In contrast, geographic variation in defenses, such as egg rejection, is not expected to be present or vary geographically in unsuitable hosts. We examined spatial patterns of resistance in the great tit *Parus major*, a passerine that is a textbook example of an unsuitable host for brood parasites because of its hole-nesting habits. We experimentally tested for spatial variation in foreign egg rejection in 382 nests across latitudinal gradients in China (5 populations) and Europe (7 populations). In China, egg rejection rates were very high but showed a latitudinal gradient from 100% in the south to 52% in the north. In Europe, rejection rates were very low (on average only 4%) and did not vary latitudinally. The egg ejection rate patterns matched geographic patterns of parasitism risk with rejection probabilities decreasing with latitude (a surrogate measure of the diversity of brood parasites). The present study for the first time challenges the idea that hole-nesting birds did not evolve resistance mechanisms against brood parasites and highlights the importance of large-scale geographic comparisons in ecological research.

Key words: allopatry, conspecific parasitism, interspecific parasitism, life history traits, sympatry, trait loss.

INTRODUCTION

Parasites exploit variable numbers of hosts, ranging from strict specialists to generalists that may parasitize more than 100 different host species. Such patterns arise from coevolutionary interactions between hosts and parasites (Combes 2001). However, parasites may not exploit potential hosts if such hosts occupy niches that exclude parasites. For example, small-sized cavities used by birds as nest sites may prevent parasitism by larger parasitic cuckoos that

cannot enter the nest hole, and small hole-nesters prefer smaller cavities as nest sites over larger ones (van Balen et al. 1982; Carlson et al. 1998). A parallel case of avoidance of parasitism is the close association between potential bird hosts and human habitation that can reduce the risk of brood parasitism because most parasitic cuckoos avoid close proximity to humans, especially in urbanized areas (Grim et al. 2011; Liang et al. 2013; Møller et al. 2016).

Host resistance to parasitism is often consistent among populations (e.g., Grim et al. 2011). Thus, Moksnes et al. (1991), Moksnes and Røskaft (1995), and Davies (2000) classified most hole-nesting bird species as "unsuitable" for cuckoo parasitism, with the sole

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exception of the hole-nesting redstart *Phoenicurus phoenicurus* that is a common cuckoo host, apparently because cavities used by this species generally have large entrances that allow the cuckoo female to enter the nest and the cuckoo chick to fledge (von Haartman 1981; Grim et al. 2009). In contrast, a recent comparative analysis by Medina and Langmore (2015) showed that nest type was not predictive of egg rejection rates in hosts of brood parasites, and even tits and other hole-nesters often use natural cavities with large entrances (van Balen et al. 1982) that should readily allow a cuckoo to lay its egg in such nests. Tits sometimes even reuse open nests of other species (Monrsós et al. 1999) although such instances are rare.

Different populations of the same species were often found to be consistently acceptors or rejecters of model cuckoo eggs (Davies 2000). However, Møller and Soler (2012) recently reviewed the literature on consistency in host responses to brood parasites and found large intraspecific variation in resistance in several host species (Cruz and Wiley 1989; Nakamura 1990; Soler 1990; Soler and Møller 1990; Briskie et al. 1992; Lindholm 1999; Soler, Martínez, et al. 1999; Moskát et al. 2002; Martín-Gálvez et al. 2006, 2007; Moskát et al. 2008; Stokke et al. 2008; Avilés et al. 2011; Soler et al. 2011; Langmore et al. 2012). These studies indicate that species-specific consistency in resistance is far from the rule. This finding may also cast doubts on traditional categorization of host species as either suitable or unsuitable.

A prime example of a group of apparently unsuitable hosts is species belonging to the families of tits (Paridae), flycatchers (Muscicapidae), treecreepers (Certhiidae), and nuthatches (Sittidae): these birds have an insect diet that should be optimal for raising a cuckoo chick (but see Yang et al. 2013), but they breed in holes which may not be accessible to cuckoos (Davies 2000). In a recent compilation of cases of brood parasitism by the common cuckoo *Cuculus canorus* in Europe (Møller et al. 2011), only 112 cases of parasitism in these hole-nesters were detected from a sample of 57 957 cases of parasitism (see also Grim et al. 2014). Within the above-outlined subset of hosts, the most common host species is the pied flycatcher *Ficedula hypoleuca* with 59 cases of parasitism, almost exclusively from Finland from the first half of the 20th century (Stokke et al., unpublished data). Although cuckoo eggs found in pied flycatcher nests are blue when perceived with human sight, such as those of the sympatric host race of the redstart, cuckoo eggs are in fact spectrally, perceptually, and chemically more similar to redstart than flycatcher eggs (Igic et al. 2012). This and the absence of rejection of even highly nonmimetic eggs by the pied flycatcher (von Haartman 1976; Davies and Brooke 1989) suggest that the recent reduction in the frequency of cuckoo parasitism in the pied flycatcher is caused by a large increase in the number of nest boxes for flycatchers that do not allow the cuckoo to lay its egg (Grim et al. 2014). This suggests that similar patterns may apply to other hole-nesters, like tits. Davies and Brooke (1989) documented a low rate of egg rejection by great tits *Parus major* (17%, $N = 12$ nests). However, all eggs rejected by great tits in this experiment were deserted. Because Davies and Brooke (1989) did not use nonmanipulated control nests, their data cannot be used to support the hypothesis that tits recognized and rejected foreign eggs. Indeed, Kempenaers et al. (1995) showed that desertion was similar in experimental and control tit nests (12% and 19% nests, respectively). Therefore, desertion cannot be considered an antiparasitic response in tits in this case, and these findings suggest that it is very likely that tits, at least in Europe, are pure acceptors of cuckoo eggs.

However, the great tit's range includes Asia and nothing is known about Asian tits responses to brood parasitism. Recent experimental evidence (Grim et al. 2014) shows that tits have better capacity to raise the cuckoo chick (measured as growth rate) than any other currently *suitable* cuckoo host (Grim 2006). Also the number of cuckoo chicks that successfully fledged from naturally parasitized tit holes with large entrances is not negligible (Grim et al. 2014). These patterns, taken together, suggest that there is a potential for tits to be involved in interactions with cuckoos, especially in areas where smaller body-sized cuckoos live and where natural holes with large opening do not prevent cuckoos from parasitizing tits. This suggests that studying non-European tit populations may provide important insights into tit–cuckoo interactions specifically and host selection by parasitic birds generally.

Therefore, the objectives of the present study were to reexamine the egg rejection capacity of the great tit, which constitutes a textbook example of an unsuitable host due to its use of holes as nest sites. We 1) tested for spatial heterogeneity in rejection behavior across 2 large-scale latitudinal gradients, which differed in number of sympatric brood parasites (China with multiple cuckoo species of various body sizes and Europe with a single cuckoo species of large body size); 2) assessed the extent to which different species of brood parasites affected the rates of egg rejection across multiple tit populations; and 3) tested whether ejection rate increased with the diversity of cuckoo species. We tested for rejection behavior in 382 nests of great tits across 16 populations from the Czech Republic, Norway, and Denmark in the west to China in the east. We recorded the presence or the absence of the 3 most common species of cuckoos at our study sites in China and the only cuckoo species in Europe to test whether rejection behavior could be predicted by the presence or the absence of any specific cuckoo species. In addition, we tested if ejection behavior could be predicted by the local diversity of cuckoo species estimated as the total number of cuckoo species in each study site. We also included latitude as an additional predictor for 5 reasons. First, a recent study showed that latitude is a good predictor of egg rejection behavior in general (Medina and Langmore 2015). Second, cuckoos are typically very secretive and hard to detect (Erritzøe et al. 2012), and thus our estimates of local cuckoo presence may be imprecise (underestimated). Third, hosts typically show some dispersal and thus their responses in any particular study site (which we sampled) would reflect larger-scale geographical patterns of cuckoo diversity (which we did not sample) (Soler, Martínez, et al. 1999). Fourth, brood parasite–host interactions are typically dynamic, with repeated local extinction and recolonization of both parasites and hosts. Therefore, point estimates of parasite presence often may not reflect relevant long-term evolutionary pressures: currently parasitized populations may in fact be allopatric, whereas currently parasite-free population may in fact be sympatric at coevolutionary time scales (Thorogood and Davies 2013). Fifth, many factors other than brood parasitism may affect geographic patterns of host response to brood parasitism, and hence we included latitude as an additional variable to control for such potentially confounding effects. Therefore, we believe that latitude better represents potential parasite pressures on hosts than empirically but unreliably detected parasite presence/absence. As any particular population may be deviant and not typical of general patterns, we focused on meta-replication, i.e., replication across multiple populations within species (Johnson 2002; Stokke et al. 2008; Grim et al. 2011). We predicted that egg rejection should be detected in China but not in Europe, and that population-level rejection rates should positively covary with cuckoo species diversity.

MATERIALS AND METHODS

Study sites

In 2008–2010, we collected extensive data in 12 populations in Norway, Denmark, the Czech Republic, and China (Figure 1; Supplementary Table 1). All study sites were forests or open woodland, sometimes bordering on urban environments. For detailed descriptions of all the study sites, see Kleven et al. (2007), Krist (2009), Yang et al. (2012, 2013), and Matrková and Remeš (2012).

Potential host species

We experimentally tested the egg discrimination abilities of great tits (Figure 2; Supplementary Table 2). We sampled populations of *P. major minor* (Zuojia, Xiaolongmen, and Dongzhai), *P. major*

commixtus (Qiandaohu), and *P. major hainanus* (Diaoluoshan) in China and *P. major major* in Europe (Figure 1; Kvist et al. 2003; Päckert et al. 2005; Pavlova et al. 2006; Zhao et al. 2012; Johansson et al. 2013). The actual body sizes of the tits and their subspecies (Li et al. 1982; Cramp and Perrins 1993) are provided in Supplementary Table 3, as a recent study has shown that egg rejection is more likely to evolve when the parasite is relatively large compared with its host (Medina and Langmore 2015). We did not resolve whether *P. major minor* should be classified as a separate species from *P. major*.

Potential brood parasites

In Europe, only the common cuckoo was sympatric in some populations. In China, the 3 most common sympatric brood parasites were the common cuckoo, Himalayan cuckoo *Cuculus saturatus*, and

Figure 1
Locations of study sites. Circles and squares refer to study sites in Europe and Asia, respectively.

Legend: Vikhammer, Stjørdal, Røros, Brovst, Aalborg, Sumperk, Velky Kosir; Zuoujia, Xiaolongmen, Dongzhai, Qiandaohu, Diaoluoshan

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Figure 2
Example of an experimental nest of the great tit with host eggs and a blue nonmimetic model egg. Photo by P. Kovařík.

little cuckoo *C. poliocephalus*. We recorded their presence/absence in the study sites in China. The actual sizes of the cuckoos and their subspecies (Cheng et al. 1991) are provided in Supplementary Table 3. Other cuckoo species are present in some of the study sites (Yang et al. 2012, 2013); therefore, we in addition estimated diversity of brood parasites as the number of cuckoo species in each of our study sites.

Egg experiments

We used several treatments to robustly test for host egg discrimination abilities and to disentangle their origins (for specific rationales see below). We employed blue (Figure 2) or white model eggs made of clay of a size and mass similar to that of Asian emerald cuckoo *Chrysococcyx maculatus* eggs (21.1–24.0 × 15.7–17.4 mm; 3.1–3.8 g, N = 65 model eggs) (Figure 2). All models were manufactured by a single person and consistently painted with the same artificial nontoxic colors. Therefore, interpopulation differences we recorded cannot be an artifact of variation in the cues presented to birds—models were the same across all study populations. In European populations, it turned out that the clay models were almost always accepted (see Results for details). Acceptance of hard nonpuncturable models may represent a methodological artifact in hosts that are unable to both puncture the clay or grasp the models due to having small bills (Martín-Vivaldi et al. 2002). Therefore, we performed additional experiments where we painted a randomly chosen host egg dark blue with a nontoxic marker (following Hauber et al. 2014; hereafter blue conspecific treatment). Such experimental eggs were even more dissimilar to host eggs than blue and white artificial models but were puncturable and thus provided a strong test of host egg discrimination abilities. Further, we employed another treatment where we added a single conspecific egg to a focal host nest. Finally, some nests were only visited and eggs handled in the same way as in experimental nests (all treatments above) but no experimental eggs were added (hereafter: control nests).

Throughout we followed standard protocols to ensure that our results are quantitatively directly comparable with previous studies of the common cuckoo. Specifically, experimental eggs were added

to nests during the laying or early incubation period (most cuckoo hosts do not respond to foreign eggs differently between laying vs. incubation stages: Davies and Brooke 1989; Moksnes et al. 1991; Grim et al. 2011). We removed a single host egg (like cuckoos do) in nests where an artificial model or a conspecific egg was added; we note that such removal has no effect on host responses (Davies and Brooke 1989; this study). Although we visited some nests daily (depending on logistic constraints), we managed to revisit some other nests only after 6 days to check host responses (6 days is the standard criterion to assess egg acceptance: Davies and Brooke 1989; Moksnes et al. 1991; Grim et al. 2011). This prevented us from assessing exact latency to rejection but allowed us to score the host responses as follows: 1) ejection when the model egg was ejected from the nest and hence was missing, whereas the hosts' own eggs were incubated; 2) burial when the model egg was buried in the nest material; and 3) desertion when the clutch was left with cold eggs, and there were no signs of host presence.

We employed multiple experimental treatments because use of some particular egg types may fail to reveal a realistic picture of host egg discrimination abilities (Hauber et al. 2015). First, for puncture ejecter hosts hard plastic model eggs may be impossible to eject (Martín-Vivaldi et al. 2002). Second, eggs that are too similar to host eggs may be accepted by hosts despite the ability of hosts to reject more dissimilar eggs (e.g., Hauber et al. 2014). Therefore, the use of too "mimetic" experimental eggs can lead to the erroneous conclusion that the particular host did not evolve an ability to reject foreign eggs (Grim 2005). Third, a host species may reject relatively nonmimetic eggs, but this may just be a by-product of adaptations that evolved in the context of conspecific parasitism (López-de-Hierro and Moreno-Rueda 2010; Samas et al. 2014), although this latter problem is unlikely to be important in the present study species (Kempenaers et al. 1995; review in Griffith et al. 2002). Fourth, experimental nests may be deserted not because of the introduction of experimental eggs but due to any unrelated disturbance; therefore, it is necessary to use control (unmanipulated) nests to determine whether desertion represents a specific response to parasitism (Samas et al. 2014). For these reasons, it is necessary to use conspecific, mimetic and nonmimetic experimental eggs and

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control nests to reveal both host egg discrimination ability and the evolutionary origin of this ability (Grim 2005).

Statistical analyses

5.5 We performed generalized linear models (GLM) with a binomial error distribution and a logit link function. The binomial response variables were rejection, egg burial, and desertion with latitude and latitude squared (to account for nonlinear effects) as covari-
5.10 ates and country and presence or absence of each of the focal cuckoo species as fixed effects (see Table 1). Because many different variables may vary geographically and therefore correlate with host responses to cuckoo model eggs, we attempted to account for the potential effects of such confounding variables by inclusion of
5.15 latitude, but also presence or absence of individual cuckoo species and the total number of local cuckoo species at our study sites (see Table 2). Finally, we included color of model eggs, breeding stage (egg laying or incubation periods), clutch size, and year, as additional predictors to test for potential confounding effects of
5.20 these variables. Nonsignificant potential confounding effects were sequentially removed from full models. The estimation method for the GLM was the Firth adjusted maximum likelihood method. All analyses were performed in JMP (SAS 2012).

RESULTS

5.25 We detected 27 literature-reported cases of parasitism by the common cuckoo of the great tit in Europe (Møller et al. 2011, including cases of cuckoo chicks reported in Grim et al. 2014), but only a single case of common cuckoo parasitism of great tits in China.
5.30 We did not detect any cuckoo parasitism in any of the study nests in any study site during the present study. We found only 1 case of

Table 1

5.35
AQ8 **GLM model of ejection of model eggs in relation to linear and quadratic terms of latitude and presence or absence of the common cuckoo, Himalayan cuckoo, and Asian lesser cuckoo**

Term	χ^2	P	Estimate	SE
Intercept	38.695	<0.0001	−13.103	2.700
Latitude	19.774	<0.0001	0.162	0.043
Latitude squared	12.173	0.0005	0.006	0.002
Common cuckoo	3.045	0.081	0.660	0.392
Himalayan cuckoo	13.698	0.0002	7.375	2.279
Asian lesser cuckoo	0.675	0.412	−1.296	2.072

All degrees of freedom (df) = 1. The model had the likelihood ratio $\chi^2_5 = 198.41$, $P < 0.0001$, and the goodness of fit was $\chi^2_{389} = 411.77$, $P = 0.20$.

Table 2

5.50 **GLM model of ejection of model eggs in relation to number of cuckoo species, latitude, and latitude squared**

Term	χ^2	P	Estimate	SE
Intercept	29.952	<0.0001	−11.208	2.317
Number of cuckoo species	72.117	<0.0001	1.534	0.226
Latitude	13.210	0.0003	0.122	0.035
Latitude squared	11.728	0.0006	0.005	0.002

All degrees of freedom (df) = 1. The model had the likelihood ratio
5.60 $\chi^2_3 = 170.70$, $P < 0.0001$, and the goodness of fit was $\chi^2_{391} = 453.86$,
5.61 $P = 1.00$.

conspecific brood parasitism in China ($n = 294$ nests, 2008–2013) and a single case (2 eggs appeared in the nest in a single day) in the Czech Republic ($n = 174$ nests, 2009–2010).

5.65 Responses to conspecific eggs were in all cases acceptance
AQ9 ($n = 53$, Supplementary Table 2). These replicates were subsequently included in the global analysis because a dummy variable with conspecific eggs coded as 0 or 1 did not explain a significant amount of variation.

5.70 In control nests, we did not detect any cases of ejection (Supplementary Table 2). These replicates were subsequently included in the global analysis because a dummy variable with control nest coded as 0 or 1 did not explain a significant amount of variation.

5.75 The statistical model of ejection of eggs included 5 predictors (Table 1). Ejection rate decreased significantly in a nonlinear fashion with increasing latitude (Figure 3; Table 1). The rejection rate was significantly higher in study areas with Himalayan cuckoos (Table 1). In contrast, there were no significant additional effects of
5.80 color of model eggs, breeding stage (egg laying or incubation periods), clutch size, and year (results not shown). A statistical model for egg burial as response variable including latitude, latitude squared, and presence or absence of the 3 cuckoo species as predictor variables was not significant ($\chi^2_5 = 5.04$, $P = 0.07$), nor was a model
5.85 for nest desertion as response variable including latitude, latitude squared, and presence or absence of the 3 cuckoo species as predictor variables ($\chi^2_5 = 5.21$, $P = 0.39$).

Rejection rate increased with the number of cuckoo species (Figure 4). This effect of number of cuckoos species had a
5.90 $\chi^2_1 = 72.12$ (Table 2), whereas the combined effect for the 3 abundant cuckoo species only had a $\chi^2_3 = 17.42$ (Table 1).

DISCUSSION

5.95 We used large continental-scale data to examine patterns of antiparasite responses in a potential host of avian brood parasites that have traditionally been claimed to be unsuitable. Despite the presumed unsuitability as host due to its hole-nesting habit, some populations of great tits in China, but not in Europe, showed
5.100 very high egg rejection rates (up to 100%). Data from 382 great tit nests revealed large variation in the rate of ejection of model eggs among populations decreasing with latitude and increasing with the presence of Himalayan cuckoos. In fact, ejection rate increased strongly with the diversity of all parasitic cuckoo
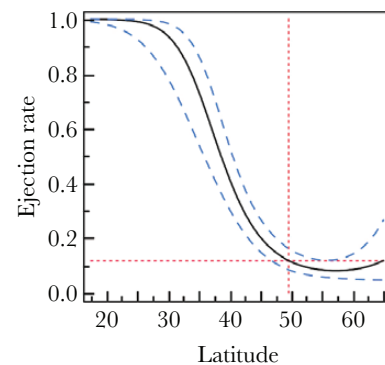5.105 species.

Figure 3

5.120 Predicted rejection rates (with 95% confidence intervals) of model cuckoo eggs in relation to latitude.
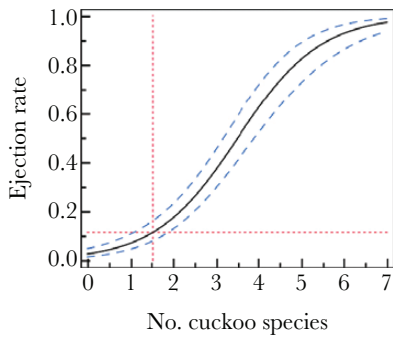5.122

6.5

6.10

Figure 4
Predicted rejection rates (with 95% confidence intervals) in different host species in relation to the number of cuckoo species.

6.15

Although great tits are common breeding birds in natural and managed forests in China, there is only a single record of cuckoo parasitism of the great tit, although this is likely to be due to the scarcity of data on cuckoo parasitism rather than an absence of parasitism (Grim et al. 2014). Studies of avian brood parasitism in China are rare, although the incidence of brood parasitism in China seems to be just as high as in Europe (Erritzøe et al. 2012). Consistent with this claim, Soler (2014) reported a similar mean (SE) rejection rate of model eggs from Asian cuckoo hosts (47% (12), $\mathcal{N} = 14$ species), as for European hosts (59% (5), $\mathcal{N} = 52$).

Great tits in Europe are some of the most commonly studied birds in the world and still cases of brood parasitism by cuckoos are extremely rare (Grim et al. 2014; this study). This may represent a methodological artifact. Specifically, in Europe, great tits are typically studied only when they breed in nest boxes with tiny holes that effectively prevent brood parasitism by the single large-body-sized interspecific parasite, and this may also prevent successful fledging by the cuckoo chick (reviewed in Grim et al. 2014). The rejection rate in 1 European population of great tits was relatively high, and we hypothesize that this may be the result of interspecific competition among different hole-nesters such as great tits and pied flycatchers over scare nest cavities. However, great tits in Europe and China commonly use natural cavities with large entrances (mean [SE] width of natural cavities according to van Balen et al. (1982) for Europe: 3.9 cm [0.68], range 2.0–6.5 cm, $\mathcal{N} = 33$ occupied holes; Liang et al. (2013) for China: 4.0 cm [1.23], range 1.8–6.5 cm, $\mathcal{N} = 61$ occupied holes]. Empirical data from redstarts confirm that cuckoo females are regularly able to enter boxes and cuckoo chicks easily fledge from boxes with entrances at the upper parts of this size range (Grim et al. 2009). Therefore, natural tit cavities should not prevent cuckoo parasitism in many cases and allow for coevolution between tits and cuckoos.

We did not find any cases of cuckoo parasitism in this study. This is most likely because we used standard tit nest boxes with small entrances (entrance diameter = 3.5 cm). Although cuckoo females are able to squirt the egg even into small entrance cavities (Davies 2000), such layings cannot establish a viable cuckoo gens (host race)—cuckoo chicks would not fledge from a small entrance cavity and the strain would go extinct in the very first generation (see also Grim et al. 2011; Samas et al. 2014). Therefore, a cuckoo gens specialized on parasitizing tits (or any other bird species) breeding in small cavities (natural or artificial) cannot exist in principle. However, *natural* nests of tits (which we did not study) are most likely open to cuckoo parasitism and such parasitism would select

for anti-cuckoo adaptations in the populations that also sometimes make use of nest boxes that we provided (see also Grim et al. 2014).

We hypothesized that ejection behavior in great tits would depend on the local diversity of brood parasites in our study sites. We used the number of cuckoo species, as a measure of diversity of brood parasites. In addition, we included latitude (and latitude squared to account for nonlinear effects) as an additional explanatory variable because it is well known that numerous factors other than the diversity of parasites show latitudinal variation (Rohde 1998). Hence, we controlled statistically for such a potentially confounding effect. There is a steep latitudinal gradient of increasing diversity of cuckoos from Northern to Southern China, with no similar cline in Europe, where the common cuckoo is the sole brood parasite on small-sized hosts. We found a similar pattern when relating ejection rate in response to the number of sympatric cuckoo species. Indeed, we found evidence of significant heterogeneity among study areas with a particularly steep latitudinal cline once the effects of latitude and parasite species had been considered (Table 1). The stronger effect of number of cuckoo species compared with the presence or the absence of the 3 most abundant cuckoo species suggests that interaction effects in addition to the main effects contribute to the evolution of egg ejection. These patterns were present for ejection rate, but not for egg burial or desertion, demonstrating that there was no concomitant selection for a diversity of resistance behavior against cuckoo parasitism, but for specific resistance based on egg ejection.

Finally, we documented no rejection of conspecific eggs in the present study (note that desertion was not a specific response to parasitism), which is in line with previous findings (Kempenaers et al. 1995). Likewise, there is an absence of genetic evidence for conspecific parasitism in tits according to parentage analyses of more than 12 500 nestlings (review in Griffith et al. 2002). In line with this, we found only 2 cases of conspecific brood parasitism across all study sites. This means that conspecific brood parasitism cannot explain our results and provides evidence for ejection of our experimental eggs being a specific antiparasite response that coevolved with locally abundant cuckoos, especially in Southern China.

Two mechanisms may account for spatial intraspecific variation in ejection rate among sites: gene flow and local adaptation. Soler, Martínez, et al. (1999, 2001) showed for magpie *Pica pica* hosts that allopatric populations retained significant levels of resistance to cuckoos with this level depending on distance from areas of sympatry. The data that we have analyzed here do not allow for discrimination between the 2 hypothetical mechanisms (see also Thorogood and Davies 2013). However, the gradual decay in ejection rate with distance that we have documented (Figure 3) is consistent with an effect of dispersal. In other words, gene flow between populations may maintain the egg rejection capacity to some extent in northern Chinese populations (with lower local cuckoo diversity and, by implication, parasite pressure), while local adaptation may lead to the high rejection in southern Chinese populations (with high diversity of cuckoos). Liang et al. (2013) have previously reported a strikingly similar case of strong ejection behavior against model cuckoo eggs in barn swallows *Hirundo rustica* from China, but not in Europe. The replication of these research findings in great tits suggests that sympatry of several species of cuckoos and the occurrence of 11 species of cuckoos in China alone may have resulted in the evolution of strong egg ejection. With the large number of cuckoo species in tropical South America, Africa, Asia, and Australia (Erritzøe et al. 2012), it is likely that similar cases will be revealed by future research.

In conclusion, high rates of ejection of model cuckoo eggs in great tits have evolved in sympatry with species of parasitic cuckoos in China with a gradually decreasing rate of rejection with increasing latitude as the species diversity of cuckoos decreases. Importantly, tits accepted all conspecific eggs excluding an alternative hypothesis that conspecific brood parasitism was the selective pressure behind the evolution of high rates of egg rejection in Asian tits. The present study highlights the importance of large geographic scale in ecological research: without studying multiple populations across 2 continents, it would not be feasible to challenge a traditional view, based on European field sites, that any hole-nesting birds are unsuitable cuckoo hosts and do not evolve any anti-cuckoo defenses. Great tit populations living in Europe either lost or even did not evolve specific anti-cuckoo adaptations in the ecological context where only a single large-sized cuckoo species does not represent a threat to great tits usually breeding in small-sized holes. This pattern provides an example of how general host ecology (general life history traits, Grim et al. 2011) may contribute to host escape from the burden of brood parasitism.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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