

Predictors of resistance to brood parasitism within and among reed warbler populations

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In the coevolutionary arms race between avian brood parasites and their hosts, several adaptations have evolved on both sides, the most prominent and important host defense being rejection of the parasitic egg. In the present study, we investigated possible predictors of egg rejection in 14 populations of reed warblers *Acrocephalus scirpaceus* across Europe differing in risk of parasitism by the common cuckoo *Cuculus canorus*, providing a test of factors associated with geographic variation in host resistance to parasitism. In a binomial general linear mixed model procedure, we quantified the possible influence of host clutch size, cuckoo parasitism in population (yes/no), height of the nest above ground, height of vegetation in the vicinity of the nest and distance to nearest vantage point on rejection of an experimentally added nonmimetic cuckoo sized egg. In addition, we entered “population” into the models as a random factor. Rejection rate varied significantly among populations (range 4.8–68.9%). The most parsimonious model, based on selection by the Akaike information criterion, included cuckoo parasitism in the population (yes/no) and host clutch size; rejection rate was the highest in parasitized populations, and individuals laying larger clutches were the best rejecters. Furthermore, rejecters tended to breed in higher vegetation than acceptors. These findings suggest that spatial variation in the level of host resistance to brood parasitism may depend on current and/or past selection pressure due to the parasite and individual differences linked to abilities for egg rejection. *Key words:* *Acrocephalus scirpaceus*, brood parasitism, clutch size, coevolution, common cuckoo, *Cuculus canorus*, egg rejection, metapopulation, reed warbler. [*Behav Ecol* 19:612–620 (2008)]

A metapopulation is defined as a population that is made up of subpopulations of the same species occupying separate patches or habitats (Gilpin and Hanski 1991; Hanski and Gilpin 1997; Hanski 1999). The metapopulation approach has been applied by both ecologists and conservationists as a tool for understanding the dynamics and local adaptations in subdivided populations (e.g., Hanski and Thomas 1994; Esler 2000; Hokit et al. 2001; Marsh and Trenham 2001; Robert et al. 2003).

A particularly interesting model for studying metapopulation dynamics is the coevolutionary interactions between parasites and their hosts. In such interactions, traits evolved on one side are countered by the other (Dawkins and Krebs 1979). Obligate avian brood parasites significantly reduce the reproductive success of their hosts (Rothstein and Robinson 1998). Therefore, there is strong selection for evolving antiparasite adaptations, of which egg rejection is one of the main host defenses (Davies and Brooke 1989a, 1989b; Moksnes et al. 1990; Langmore et al. 2005). This will in turn favor parasites laying eggs that mimic those of the host, leading to a coevolutionary arms race with adaptations and counteradaptations evolving on both sides (Davies 2000; Stokke et al. 2005). Recently, several models have been developed for predicting the outcome of host–parasite interactions when taking into account the principles of metapopulation theory. Such models have traditionally included interactions between species that

have a completely overlapping distribution (e.g., Gandon et al. 1996; Gandon, van Zandt 1998; Gandon 2002; Nuismer et al. 1999, 2000; Gomulkiewicz et al. 2000). However, in many host–parasite systems, including avian brood parasites and their hosts, coevolutionary interactions typically occur only in parts of the host geographical range (Thompson 1994; Lindholm 1999; Soler et al. 1999; Brodie et al. 2002; Thompson and Cunningham 2002; Stokke, Hafstad, et al. 2007). Accordingly, recent investigations into host–parasite systems have acknowledged that hosts and parasites may only have partially overlapping distribution and that the magnitude of local adaptations in coevolutionary interactions also depend on the geographic structure of coevolutionary hot spots (where parasite–host interactions are reciprocal) and cold spots (where interspecific selection affects only one or neither of the species) (Nuismer et al. 2003). When host and parasite distributions do not overlap completely (e.g., Soler et al. 1999), or alternatively their range overlap but parasite utilization varies between geographic areas (e.g., Lindholm 1999; Stokke, Hafstad, et al. 2007), gene flow may theoretically distort coevolutionary interactions in specific populations even in coevolutionary hot spots (see e.g., Røskaft, Moksnes, Stokke, Moskát, Honza 2002, Røskaft et al. 2006). Therefore, there may be considerable variation among populations in expression of coevolutionary evolved traits in hosts, parasites or both, due to geographic structure of metapopulations (Endler 1986; Kaltz and Shykoff 1998; Thompson et al. 2002). Several studies have obtained support for spatial variation in parasitism and host resistance to parasitism (e.g., Thompson 1994, 1999, 2005; Hochberg and van Baalen 1998; van Baalen 1998; Gomulkiewicz et al. 2000; Brodie et al. 2002). However, there are only a couple of studies that have attempted to

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investigate what accounts for spatial variation in host resistance to avian brood parasitism (see below), and the aim of the present study was to contribute to this knowledge.

In several host species of the common cuckoo (hereafter cuckoo) *Cuculus canorus*, the majority of individuals within the population are apparently able to reject both naturally and experimentally added eggs from their nests. Furthermore, in such species there is little or no variation in rejection behavior among populations, and hosts will reject all eggs as long as they can be distinguished from their own clutch (e.g., Honza et al. 2004; Stokke et al. 2004, 2005; Antonov et al. 2006b). Therefore, it is reasonable to assume that rejection behavior in such “rejecter” species is more or less genetically fixed with negligible influence of conditional stimuli, age, or quality differences (Øien et al. 1999; Amundsen et al. 2002; Røskaft, Moksnes, Stokke, Bicík, Moskát 2002; Røskaft, Moksnes, Stokke, Moskát, Honza 2002; Stokke et al. 2005). Also in other hosts, like the dunnock *Prunella modularis*, there is apparently no variation in rejection behavior, but here all individuals are acceptors rather than rejecters (Davies 2000). In contrast, some host species show a much more pronounced variation in rejection behavior among individuals within populations. Here, some individuals reject foreign eggs, whereas others accept them even in cases where the parasitic egg apparently should be easily distinguished from host eggs (Stokke et al. 1999, 2005). Furthermore, as described above, it is well known that spatial differences in distribution of hosts and parasites may lead to variation in coevolutionary interactions between them (e.g., Thompson 1994, 2005). Røskaft, Moksnes, Stokke, Moskát, Honza (2002; Røskaft et al. 2006), and Barabás et al. (2004) have obtained support for spatial habitat structure and flow of genes among populations being of importance for the evolution of adaptations and counteradaptations in cuckoo–host metapopulations. Comparisons of several populations simultaneously have been carried out on great spotted cuckoos *Clamator glandarius* and their hosts, black-billed magpies *Pica pica* (Soler et al. 1998, 1999; Martínez et al. 1999; Soler JJ and Soler M 2000). In this system, it was found that gene flow among populations significantly affected local rejection rates (Soler et al. 2001a). Furthermore, Lindholm (1999, 2000) and Lindholm and Thomas (2000) compared cuckoo–reed warbler *Acrocephalus scirpaceus* interactions among several populations within Great Britain and found a significant variation in host egg rejection rate between populations.

Reed warblers have a widespread distribution and are common breeders in reedbeds surrounding lakes, ponds, and ditches throughout Europe (Cramp 1992). They typically inhabit clearly defined patches of marshland, often surrounded by large areas of unsuitable habitat. Such patches can vary much in size, but typically their size is fairly restricted, leading to local extinctions and recolonization in a source–sink system (Foppen et al. 2000). The distance between different suitable patches is often greater than daily reed warbler movement distances but shorter than maximum dispersal range. The majority of reed warblers have a very restricted natal and breeding dispersal (Paradis et al. 1998), which correspond well with what is found for the closely related great reed warbler *Acrocephalus arundinaceus* (Hansson et al. 2002). Therefore, the reed warbler is a suitable model species for studies of metapopulation dynamics. Furthermore, this species rank among the most commonly used cuckoo hosts in Europe (Moksnes and Røskaft 1995), but there is both spatial and temporal variation in levels of parasitism and host defenses among different populations (Davies and Brooke 1988; Moksnes, Røskaft, Bicík, et al. 1993; Davies et al. 1996; Brooke et al. 1998; Lindholm 1999; Stokke et al. 1999; Stokke, Hafstad et al. 2007). Reed warbler rejection rate of foreign eggs have

been found to be higher in parasitized populations than in nonparasitized populations (Lindholm and Thomas 2000).

The present study can be considered as an extension of the investigations carried out by Lindholm (1999) and Lindholm and Thomas (2000) because we are focusing on a larger set of populations and a broader geographical scale. In addition, we are investigating the influence of possible predictors on egg rejection rate that have not been considered in previous studies. Here, we investigated the influence of possible predictors on the state of an antiparasite adaptation within and among 14 reed warbler populations across Europe. In more detail, we analyzed the influence of presence of cuckoo parasitism in population, clutch size, height of vegetation in the vicinity of the nest, nest height, and distance to nearest vantage point on variation in egg rejection among and within the 14 populations. These possible predictors were selected because variation in rejection behavior within and among reed warbler populations can theoretically be explained in several ways. Firstly, some of the variation in egg rejection at the intrapopulation level could be due to gene flow of “acceptor” alleles from nonparasitized populations or rejecter alleles from parasitized populations. Therefore, there will be some individuals rejecting foreign eggs in nonparasitized populations and, although locally maladaptive, even acceptors of parasitic eggs in parasitized populations (Soler et al. 2001a; Røskaft, Moksnes, Stokke, Moskát, Honza 2002; Røskaft et al. 2006). Secondly, some individuals within populations are apparently able to adjust their antiparasite behavior according to specific conditional stimuli like observing a parasite in the vicinity of the nest or other cues indicating increased risk of parasitism (Davies and Brooke 1988; Moksnes, Røskaft, Korsnes 1993; Lindholm 2000; Moksnes et al. 2000). Therefore, theoretically, a genotypic variability in adjustment of conditional response could exist. For instance, some individuals could be “true acceptors,” others could be “true rejecters,” whereas individuals possessing a third genotype could be termed “conditional rejecters” (Lotem and Nakamura 1998). In any case, these scenarios indicate that rejection of foreign eggs should be higher in populations sympatric with parasites than in those that are allopatric. It is important to notice that these 2 scenarios (gene flow and flexible behavior) are not mutually exclusive but could take place simultaneously. Furthermore, variation in rejection behavior within populations may theoretically be influenced by clutch size and/or specific habitat characteristics. Individuals laying consistently large egg clutches are investing more into their current reproduction than those laying consistently small clutches and could therefore theoretically be more likely to reject parasitic eggs. Alternatively, because clutch size in many species is often larger in older birds than more inexperienced ones (e.g., Røskaft et al. 1983; Sæther 1990; Geslin et al. 2004; Garamszegi et al. 2004), rejection behavior can be influenced by correlates of age, like number of breeding attempts (Lotem et al. 1992, 1995; Grim 2002). This is due to that older birds know the variation of their own eggs through previous breeding attempts, whereas inexperienced individuals may need a prolonged learning period in order to get familiar with the variation in own egg appearance (see e.g., Lotem et al. 1992, 1995; Stokke, Takasu, et al. 2007). In any case, according to these scenarios, individuals laying larger clutches should also be the best rejecters. Furthermore, both general nest predation and brood parasitism could be related to specific habitat characteristics (e.g., Øien et al. 1996; Báldi and Batáry 2005; Antonov et al. 2007). Avian brood parasites depend on vantage points in elevated structures when searching for host nests (Alvarez 1993; Clotfelter 1998; Honza et al. 2002), and host pairs breeding close to potential perches are often more prone to be parasitized than pairs breeding further away from these vantage

points (Øien et al. 1996; Moskát and Honza 2000). In addition, nest or vegetation height might be important for the risk of parasitism simply due to that more concealed nests (i.e., nest low in vegetation and/or with high vegetation in the vicinity) are less prone to be detected by parasites or predators (Honza et al. 1998; Batáry and Báldi 2005; Antonov et al. 2007). Therefore, in order to minimize the risk of nest predation and parasitism, individuals should choose to breed in “safe” places far away from vantage points (Øien et al. 1996) and build well-concealed nests low in the vegetation and in high overall vegetation cover. If we assume that those individuals choosing to breed in safe places are better able to assess the risk of parasitism than those that breed in more “unsafe” places, we should also predict the former ones to be better able to reject parasitic eggs. Alternatively, individuals breeding in unsafe places could be more sensitive to the increased possibility of parasitism and therefore reject foreign eggs at a higher frequency than individuals breeding in safe places.

MATERIALS AND METHODS

Data collection

The 14 study sites were distributed throughout Europe (Table 1) and were representative of reed warbler distribution on the continent. In more detail, the study populations were Rio Guadiana (Badajoz), Spain, (38°51'N, 7°02'W); Los Albarales (Madrid), Spain (40°13'N, 3°33'W); Canal Vell (Ebro Delta), Spain (40°44'N, 0°47'E); Laguna de Vixán (Galicia), Spain (42°33'N, 9°02'W); Grindul Lupilor (Danube Delta), Romania (44°37'N, 28°43'E); Lake Sic (Transylvania), Romania (46°56'N, 23°54'E); Etang de Trunvel (Brittany), France (47°54'N, 4°22'W); Lužice (Southern Moravia), Czech Republic (48°50'N, 17°04'E); Mohrhof (Bavaria), Germany (49°40'N, 10°51'E); Diergardtsche Fischteiche (Rhineland), Germany (51°14'N, 6°06'E); Milicz (Silesia), Poland (51°32'N, 17°22'E); Llangorse Lake (Wales), United Kingdom (51°56'N, 3°16'W); Ventas Ragas (Baltic Sea coast), Lithuania (55°22'N, 21°13'E); and Arresø (Zealand), Denmark (55°58'N, 12°04'E).

Data on rejection of an experimentally added, nonmimetic parasitic egg, presence of cuckoo parasitism (yes/no), parasitism rate, distance to nearest vantage point, vegetation and nest height, and clutch size were collected at each site (Table 1 and Appendix). In each population, nests were searched systematically, during approximately 3 weeks of the reed warbler breeding season in 2002–2005. Each population was visited once, and all data used in the analyses were collected during this period. Nests were followed from the day when found (building stage or early egg-laying stage) until fledging. In this way, we were able to assess clutch size and absence or presence of cuckoo parasitism. Distance to nearest vantage point (tree, bush, power line, or other possible perch sites for cuckoos more than 3-m high) was estimated to the nearest meter for all nests found on each study site (Øien et al. 1996; Honza et al. 2002). Height of vegetation in the vicinity of the nest (centimeter) was measured as the vertical distance from the ground or water to the top of the highest herb above the nest in a radius of 5 m from the nest, and nest height (centimeter) was measured as the vertical distance from the ground or water to the nest.

We experimentally parasitized reed warbler nests with a real Chinese quail *Coturnix chinensis* egg painted pale blue resembling the redstart *Phoenicurus phoenicurus* cuckoo egg type (Stokke et al. 1999) on the day after the last host egg was laid ($N = 409$, Table 1). The parasitic eggs selected for experiments had approximately the same size as real cuckoo eggs. No experimentally parasitized nests were naturally parasitized

Table 1

Data on rejection rate of an experimentally added nonmimetic cuckoo-sized egg (% with sample size in brackets), presence or absence of cuckoo parasitism (yes/no), and rate of natural parasitism (% with sample size in brackets) for 14 European reed warbler populations (see Materials and Methods for a detailed description of the populations studied)

Population	Rejection rate	Cuckoo parasitism	Parasitism rate
Spain, Badajoz	4.8 (21)	No	0.0 (27)
Spain, Madrid	20.0 (15)	No	0.0 (28)
Spain, Ebro Delta	27.3 (11)	Yes	21.1 (19)
Spain, Galicia	44.4 (36)	No	0.0 (39)
Romania, Danube Delta	59.0 (39)	Yes	5.8 (69)
Romania, Transylvania	32.1 (28)	No	0.0 (32)
France	33.3 (30)	No	0.0 (41)
Czech Republic	44.8 (29)	Yes	14.6 (82)
Germany, Bavaria	68.9 (45)	Yes	8.3 (72)
Germany, Rhineland	33.3 (24)	Yes	14.5 (55)
Poland	59.6 (52)	Yes	14.3 (105)
Wales	12.5 (16)	No	0.0 (49)
Lithuania	24.0 (25)	No	0.0 (61)
Denmark	47.4 (38)	Yes	8.1 (99)

by cuckoos, and no naturally parasitized nests were experimentally parasitized. Nests were visited every day or every second day for the next 6 days after experimental parasitism in order to assess whether the foreign egg was accepted or rejected by the hosts. If the parasitic egg was still in the nest and all eggs in the nest were warm at day 6, it was regarded as accepted. However, if the foreign egg disappeared or all eggs were cold and deserted within the 6-day limit, it was regarded as rejected.

Statistical analyses

The possible influence of the various predictors on egg rejection was tested by a binomial general linear mixed model (GLMM) with logit link (lmer function was used to fit the models by option “Laplace”), in which clutch size, cuckoo parasitism in population (yes/no), height of vegetation in the vicinity of the nest, nest height, and distance to vantage point were entered as fixed factors and “population” was entered as a random factor. An Akaike information criterion value (AIC) was calculated for all models, including interactions between various predictors (Table 2, Burnham and Anderson 2002). The AIC values in the final models were corrected for small sample sizes and thus selected based on AIC_c values. Models were then ranked using ΔAIC_c values ($\Delta_i = AIC_{c(i)} - AIC_{c(\min)}$), and Akaike weights (ω_i) were calculated from ΔAIC_c values in order to assess the likelihood of each model relative to others (Burnham and Anderson 2002). The final parameter estimates with approximated unconditional standard errors and 95% confidence intervals (CIs) of parameter estimates were calculated by model averaging (Table 3, Burnham and Anderson 2002). In order to confirm the fit of the model selection based on AIC_c values, we also ran separate tests of the influence of each possible predictor on rejection behavior among populations.

Mantel tests (Mantel 1967; Mantel and Valand 1970) and partial Mantel tests (Smouse et al. 1986) were employed to investigate the relationship between geographical distance, occurrence of cuckoo parasitism, and rejection rate of the experimentally added egg. These tests were carried out by XLStat 2006 (Addinsoft Inc. 2006, NY). All other statistical procedures were performed in R 2.5.1 (R Development Core

Table 2

Results from a mixed model logistic regression procedure aiming to explain variation in rejection behavior within and among 14 populations of reed warblers ($N = 409$ nests). Model selection based on AIC_c . Csize, total number of host eggs laid in a nest; Para, cuckoo parasitism in population (yes/no); Vheight, vegetation height in area where nest is situated (centimeter); Nheight, height of nest above ground (centimeter); and Dist, distance to nearest vantage point more than 3 m tall (meter). K , number of explanatory parameters in model; $\Delta_i = AIC_{c(i)} - AIC_{c(\min)}$; ω_i , Akaike weights. Interactions between predictors indicated by “:”. The most parsimonious model highlighted in bold (see Materials and Methods for a detailed description of the procedure)

Explanatory variable	K	AIC_c	Δ_i	ω_i
Csize + Para + Vheight + Para:Vheight	6	520.58	0.00	0.142
Csize + Para + Vheight + Nheight + Para:Vheight	7	520.64	0.05	0.139
Csize + Para + Vheight	5	521.32	0.73	0.099
Csize + Para	4	522.02	1.43	0.069
Csize + Para + Vheight + Nheight	6	522.08	1.49	0.068
Csize + Para + Vheight + Nheight + Para:Vheight + Para:Nheight	8	522.41	1.83	0.057
Csize + Para + Vheight + Nheight + Para:Nheight	7	522.42	1.83	0.057
Csize + Para + Vheight + Dist + Para:Vheight + Para:Dist	8	522.50	1.92	0.055
Csize + Para + Vheight + Dist + Para:Vheight	7	522.60	2.01	0.052
Csize + Para + Vheight + Para:Csize + Para:Vheight	7	522.60	2.02	0.052
Csize + Para + Vheight + Nheight + Para:Csize + Para:Vheight	8	522.64	2.06	0.051
Csize + Para + Vheight + Nheight + Dist + Para:Vheight	8	522.69	2.10	0.050
Csize + Para + Vheight + Nheight + Dist + Para:Vheight + Para:Dist	9	522.76	2.17	0.048
Csize + Para + Vheight + Nheight + Dist	7	523.89	3.30	0.027
Csize + Vheight	4	526.50	5.92	0.007
Full model including all interactions	11	526.53	5.94	0.007
Para:others	3	526.72	6.14	0.007
Csize	4	527.95	7.36	0.004
Csize + Nheight	4	528.31	7.72	0.003
Csize + Dist	4	528.65	8.07	0.003
Para + Vheight	3	529.04	8.45	0.002
Para	4	530.07	9.49	0.001
Para + Nheight	4	530.96	10.37	<0.001
Para + Dist	4	533.65	13.07	<0.001
Nheight + Vheight	3	535.67	15.08	<0.001
Vheight	2	535.78	15.20	<0.001
Intercept	3	535.80	15.22	<0.001
Nheight	4	537.16	16.58	<0.001
Dist + Vheight	3	537.36	16.78	<0.001
Dist	4	537.50	16.92	<0.001
Nheight + Dist				

Team 2007) and SPSS 15.0 (SPSS Inc., 2006, Chicago, IL). All tests were 2-tailed. Means are reported with standard deviations.

RESULTS

The most parsimonious model (the model with the smallest number of parameters of those with $\Delta AIC_c < 2$), based on selection by the AIC, included cuckoo parasitism in the population (yes/no) and clutch size (Table 2); rejection rate was higher in parasitized populations, and individuals laying larger clutches were also the best rejecters. However, the ΔAIC_c values among the 8 top candidate models were < 2 , all showing moderate to low ω_i values, and the best model

Table 3

Parameters explaining variation in egg rejection behavior within and among 14 reed warbler populations based on AIC_c model selection with model averaging. Model averaged estimates of parameters (β), unconditional standard errors (SE) and 95% CIs for all parameters (95% CI) are included. Csize, total number of host eggs laid in a nest; Para, cuckoo parasitism in population (yes/no); Vheight, vegetation height in area where nest is situated (centimeter); Nheight, height of nest above ground (centimeter); and Dist, distance to nearest vantage point more than 3 m tall (meter). “Parameter:Parameter” indicates interactions between specific parameters

Parameter	β	SE	95% CI
Intercept	-4.785	1.169	-7.076, -2.493
Csize	0.595	0.210	0.183, 1.007
Para	2.117	0.912	0.330, 3.905
Vheight	0.007	0.003	0.001, 0.013
Nheight	-0.005	0.005	-0.013, 0.004
Dist	0.001	0.003	-0.004, 0.006
Para:Vheight	-0.007	0.004	-0.014, 0.001
Para:Nheight	-0.007	0.008	-0.022, 0.008
Para:Dist	-0.006	0.004	-0.015, 0.002
Para:Csize	-0.083	0.399	-0.864, 0.698

(lowest AIC_c value) also included vegetation height and the interaction between parasitism and vegetation height. Therefore, we found it appropriate to use model averaging in order to obtain reliable parameter estimates (Table 3). Both cuckoo parasitism and clutch size were still significant predictors of egg rejection. In addition, the parameter estimate for vegetation height was positive, indicating that rejecters placed their nests in taller vegetation than acceptors. All other predictors and interactions between parasitism and the specific predictors had parameter estimates with 95% CIs including 0.

The mean rejection rate varied significantly among populations (range 4.8–68.9%, Pearson’s $\chi^2 = 52.73$, degrees of freedom [df] = 13, $P < 0.001$, Table 1). It turned out that 7 populations were parasitized by cuckoos while 7 populations apparently escaped parasitism (Table 1), and the mean rejection rate was significantly higher in parasitized than in nonparasitized populations (mean = 49.19% \pm 14.91, $N = 7$ vs. 25.53 \pm 13.38%, $N = 7$, respectively, analysis of variance, $F = 9.76$, df = 1,13, $P = 0.009$). Furthermore, there was a statistically significant correlation between parasitism rate and rejection rate (Spearman rank correlation, $r = 0.54$, $N = 14$, $P = 0.047$).

Mean clutch size was larger in rejecters than acceptors in 11 of the 14 populations and in 8 of 10 populations if taking into account only those populations where $N > 5$ in each group (acceptors vs. rejecters) (Wilcoxon signed ranks test, $Z = 2.33$, $N = 10$, $P = 0.02$, Appendix). Mean clutch size was larger in rejecters than acceptors in 5 of 7 parasitized and 6 of 7 nonparasitized populations and in 5 of 6 parasitized and 3 of 4 nonparasitized populations if taking into account only those populations where $N > 5$ in each group (Fisher exact test, $P = 1.00$).

Mean vegetation height in the vicinity of the nest was taller in rejecters than acceptors in 11 of the 14 populations and in 7 of 10 populations if taking into account only those populations where $N > 5$ in each group (Wilcoxon signed ranks test, $Z = 1.27$, $N = 10$, $P = 0.21$, Appendix). Mean vegetation height in the vicinity of the nest was taller in rejecters than acceptors in 5 of 7 parasitized and 6 of 7 nonparasitized populations and in 4 of 6 parasitized and 3 of 4 nonparasitized populations if taking into account only those populations where $N > 5$ in each group (Fisher exact test, $P = 1.00$).

Table 4
Mantel and partial Mantel tests for variation in geographical distance between study populations (Geodistance), cuckoo parasitism (Parasitism) and rejection rate of an experimentally added Chinese quail egg (Rejection) among 14 reed warbler populations. Number of permutations is set to 1000 in all tests. Parentheses indicate variables that are controlled in the partial tests

Matrix comparison	<i>r</i>	<i>P</i>
Parasitism–rejection	0.281	0.007
Parasitism–geodistance	0.130	0.247
Rejection–geodistance	0.131	0.219
Parasitism–rejection (distance)	0.268	0.011

Mean nest height was smaller in rejecters than acceptors in 7 of the 14 populations and in 6 of 10 populations if taking into account only those populations where $N > 5$ in each group (Wilcoxon signed ranks test, $Z = 0.63$, $N = 10$, $P = 0.53$, Appendix). Mean nest height was smaller in rejecters than acceptors in 5 of 7 parasitized and 2 of 7 nonparasitized populations and in 4 of 6 parasitized and 2 of 4 nonparasitized populations if taking into account only those populations where $N > 5$ in each group (Fisher exact test, $P = 1.00$).

Mean distance to nearest vantage point was longer in rejecters than acceptors in 6 of the 14 populations and in 5 of 10 populations if taking into account only those populations, where $N > 5$ in each group (Wilcoxon signed ranks test, $Z = 0.00$, $N = 10$, $P = 1.00$, Appendix). Mean distance to nearest vantage point was longer in rejecters than acceptors in 3 of 7 parasitized and 3 of 7 nonparasitized populations and in 3 of 6 parasitized and 2 of 4 non-parasitized populations if taking into account only those populations, where $N > 5$ in each group (Fisher Exact test, $P = 1.00$).

Results from Mantel and partial Mantel tests corresponded well with results from the above analyses (Table 4). Variation in rejection rates between pairs of populations correlated significantly with variation in parasitism status, also when controlling for geographical distance between populations. Furthermore, variation in parasitism status and rejection rate between pairs of populations was not correlated with variation in geographical distance.

DISCUSSION

In this study, we have shown that both presence of cuckoo parasitism in a given population and clutch size are significant predictors of egg rejection in reed warblers. This finding was supported both by results from GLMMs and analyses of single predictors' influence on egg rejection. In addition, rejecters tended to breed in taller vegetation than acceptors.

The influence of cuckoo presence or absence on egg rejection behavior has been documented in previous studies both within (Davies and Brooke 1988; Moksnes et al. 2000) and among reed warbler populations (Lindholm and Thomas 2000) as well as in other hosts (e.g., Moksnes and Røskaft 1989; Moksnes, Røskaft, Korsnes 1993; Bártol et al. 2002; but see Soler et al. 2000). However, even in populations with cuckoo parasitism, there are obviously some individuals that accept foreign nonmimetic eggs regardless of presence or absence of conditional cues. Vice versa, in nonparasitized populations, there are individuals that apparently reject such eggs without the presence of conditional stimuli. These differences among individuals in rejection behavior could have a genetic basis as in magpies parasitized by great spotted cuckoos (Martín-Gálvez et al. 2006), but this possibility remains to be investigated. Spatial variation in the state of coevolved

traits is well known in host–enemy interactions (e.g., Brodie et al. 2002), and differentiation of neighboring populations in such traits is more likely when gene flow is low (e.g., Sistierson and Averill 2004). Interestingly, there was a significant correlation between rejection rate and level of parasitism among the 14 populations. Because the level of parasitism may be an indicator of how often individual reed warbler pairs encounter cuckoos close to their nests, the link between rejection rate and level of parasitism can partially be explained by triggering of a conditional response in individuals. In any case, reed warblers and cuckoos obviously have only partially overlapping distribution, thus potentially creating a mosaic of cold and hot spots of coevolution (Nuismer et al. 2003).

There was an overall significant positive relationship between clutch size and rejection of nonmimetic eggs, as in another brood parasite–host system (Soler et al. 2001b). Furthermore, this relationship was evident both in parasitized and nonparasitized populations. The influence of clutch size on egg rejection may theoretically be explained by age-specific variation in clutch size. In some passerines, first-year breeders on average lay smaller clutches than more experienced individuals (e.g., Røskaft et al. 1983; Garamszegi et al. 2004; Geslin et al. 2004; Mitrus 2005), and reproductive performance in general is known to improve with age (e.g., Sæther 1990; Robertson and Rendell 2001). The costs related to reproduction imply that effort in current reproduction must be seen as a trade-off between this event and future reproduction events (Williams 1966a, 1966b). A smaller clutch size in young individuals may therefore be a consequence of less investment in current reproduction in order to enhance odds of reproduction later in life (Stearns 1976; Røskaft 1985). Furthermore, if inexperienced reed warblers are more likely to accept foreign eggs as in great reed warblers (Lotem et al. 1992, 1995), the relationship between egg rejection and clutch size found in the present study is expected. However, our findings only suggest correlational support for such a relationship. Alternatively, the influence of clutch size on egg rejection could be due to variation in overall body condition reflecting quality. According to such a scenario, individuals in better condition or of better quality should be able to afford producing more eggs than low-quality individuals (e.g., Houston et al. 1983; Goodburn 1991; Pietiäinen and Kolunen 1993; Verhulst et al. 1995; Garamszegi et al. 2004), but it is not straightforward to envision which mechanisms should enable individuals of better quality to reject nonmimetic foreign eggs at a higher rate than low quality individuals. A third possibility is that there is close genetic linkage between clutch size and rejection behavior with no influence of age or quality per se. However, the results from this study do not allow us to distinguish between possible influences of these potentially influential parameters on rejection behavior.

In the present study, there was an indication of a relationship between egg rejection and vegetation height; rejecters placed their nests in taller vegetation than acceptors. The possible effect of vegetation height was relatively weak because the parameter estimates with 95% CIs was close to include 0. However, Clarke et al. (2001) found that more visible reed warbler nests were more prone to be parasitized, and Moskát and Honza (2000) reported the same pattern in great reed warblers. Furthermore, in marsh warblers *Acrocephalus palustris*, parasitized nests were placed in shorter stands of vegetation than nonparasitized ones (Antonov et al. 2007). Support for a correlation between nest cover and general nest predation is however ambiguous. In reed warblers, for example, a previous study found no correlation between nest predation and nest cover, whereas in marsh warblers, there was a negative correlation between these 2 parameters (Ille et al. 1996). Furthermore, in great reed warblers, nests at sites with taller reed cover were

less prone to predation (Batáry and Báldi 2005). Given that nests in taller vegetation are more difficult to find for both predators and brood parasites (see also Honza et al. 1998), this relationship could reflect that rejecters breed in more safe places than acceptors. Again, this could indicate that rejecters are more experienced or of better quality than acceptors, and that they are able to attain the best nesting sites.

Variation in height of nests above ground or water did not explain variation in egg rejection within and among populations in the GLMM procedure. Furthermore, there was no difference in number of populations in which nest height was lower in rejecters than acceptors than the opposite. This makes sense because previous studies of cuckoo hosts have shown that there was no link between risk of parasitism and nest height (e.g., Moskát and Honza 2000; Antonov et al. 2007). Therefore, actual concealment of the nest in terms of vegetation height appears to be more important as a predictor of parasitism and egg rejection than nest height.

Several studies have found that distance to a potential parasite vantage point is important for the risk of parasitism. Both hosts of cuckoos and brown-headed cowbirds *Molothrus ater* are in many cases more prone to parasitism when they breed close to trees (Alvarez 1993; Øien et al. 1996; Burhans 1997; Clotfelter 1998; Hauber and Russo 2000; Moskát and Honza 2000; Antonov et al. 2006a), a pattern that has also been found in reed warblers within specific populations (Øien et al. 1996). Individuals should therefore avoid parasitism by breeding away from vantage points. Theoretically, such individuals could also be better able to assess the risk of parasitism and thus be better rejecters of cuckoo eggs. However, as the present study shows, there is apparently no significant link between egg rejection and distance to vantage points in reed warblers.

In conclusion, resistance to cuckoo parasitism varied greatly among host populations. On a large geographic scale, presence of cuckoo parasitism was an important predictor of egg rejection in reed warblers, suggesting that current and/or past

Appendix

Data on mean values (\pm SD, numbers in brackets) of clutch size, vegetation- and nest height (cm) and distance to nearest vantage point (m) in 14 European reed warbler populations. P = population, A = acceptors of the parasitic egg, R = rejecters of the parasitic egg (see Methods for a detailed description of the study sites, parameter definitions and experimental procedure)

Population	Clutch size			Vegetation height		
	P	A	R	P	A	R
Spain, Badajoz	3.67 \pm 0.80 (21)	3.65 \pm 0.81 (20)	4.00 \pm 0.00 (1)	240.48 \pm 33.98 (21)	237.50 \pm 31.93 (20)	300.00 \pm 0.00 (1)
Spain, Madrid	3.33 \pm 0.72 (15)	3.17 \pm 0.72 (12)	4.00 \pm 0.00 (3)	246.33 \pm 47.04 (15)	245.42 \pm 48.55 (12)	250.00 \pm 50.00 (3)
Spain, Ebro						
Delta	4.00 \pm 0.00 (11)	4.00 \pm 0.00 (8)	4.00 \pm 0.00 (3)	227.27 \pm 11.91 (11)	225.00 \pm 11.95 (8)	233.33 \pm 11.55 (3)
Spain, Galicia	3.39 \pm 0.65 (36)	3.35 \pm 0.59 (20)	3.44 \pm 0.73 (16)	333.33 \pm 53.45 (36)	322.50 \pm 49.93 (20)	346.88 \pm 56.18 (16)
Romania,						
Danube Delta	4.56 \pm 0.60 (39)	4.44 \pm 0.51 (16)	4.65 \pm 0.65 (23)	193.08 \pm 19.49 (39)	191.25 \pm 21.87 (16)	194.35 \pm 18.05 (23)
Romania,						
Transylvania	3.89 \pm 0.50 (28)	3.79 \pm 0.54 (19)	4.11 \pm 0.33 (9)	209.64 \pm 28.61 (28)	210.00 \pm 27.89 (19)	208.89 \pm 31.80 (9)
France	4.13 \pm 0.51 (30)	4.00 \pm 0.46 (20)	4.40 \pm 0.52 (10)	216.17 \pm 20.24 (30)	212.75 \pm 19.70 (20)	223.00 \pm 20.58 (10)
Czech Republic	4.17 \pm 0.47 (29)	4.13 \pm 0.50 (16)	4.23 \pm 0.44 (13)	260.69 \pm 61.47 (29)	270.63 \pm 57.90 (16)	248.46 \pm 65.81 (13)
Germany,						
Bavaria	4.40 \pm 0.54 (45)	4.36 \pm 0.50 (14)	4.42 \pm 0.56 (31)	400.44 \pm 102.87 (45)	392.86 \pm 99.73 (14)	403.87 \pm 105.69 (31)
Germany,						
Rhineland	3.83 \pm 0.57 (24)	3.75 \pm 0.68 (16)	4.00 \pm 0.00 (8)	262.50 \pm 34.80 (24)	268.75 \pm 38.28 (16)	250.00 \pm 23.91 (8)
Poland	4.08 \pm 0.48 (52)	4.00 \pm 0.45 (21)	4.13 \pm 0.50 (31)	235.58 \pm 19.75 (52)	233.33 \pm 18.53 (21)	237.10 \pm 20.69 (31)
Wales	3.44 \pm 0.63 (16)	3.36 \pm 0.63 (14)	4.00 \pm 0.00 (2)	281.88 \pm 37.63 (16)	281.43 \pm 39.97 (14)	285.00 \pm 21.21 (2)
Lithuania	4.16 \pm 0.55 (25)	4.21 \pm 0.54 (19)	4.00 \pm 0.63 (6)	224.00 \pm 29.16 (25)	218.42 \pm 29.68 (19)	241.67 \pm 20.41 (6)
Denmark	4.00 \pm 0.47 (38)	4.00 \pm 0.46 (20)	4.00 \pm 0.49 (18)	285.79 \pm 33.50 (38)	282.50 \pm 31.93 (20)	289.44 \pm 35.72 (18)
Population	Nest height			Distance		
	P	A	R	P	A	R
Spain, Badajoz	111.81 \pm 35.01 (21)	110.40 \pm 35.30 (20)	140.00 \pm 0.00 (1)	6.05 \pm 6.27 (21)	6.20 \pm 6.39 (20)	3.00 \pm 0.00 (1)
Spain, Madrid	102.20 \pm 30.88 (15)	102.08 \pm 34.49 (12)	102.67 \pm 11.59 (3)	126.67 \pm 77.43 (15)	133.33 \pm 85.00 (12)	100.00 \pm 30.00 (3)
Spain, Ebro						
Delta	82.00 \pm 17.57 (11)	88.38 \pm 16.46 (8)	65.00 \pm 0.00 (3)	88.18 \pm 68.09 (11)	91.25 \pm 80.61 (8)	80.00 \pm 17.32 (3)
Spain, Galicia	127.50 \pm 32.83 (36)	126.00 \pm 26.14 (20)	129.38 \pm 40.53 (16)	34.00 \pm 33.60 (36)	41.05 \pm 35.86 (20)	25.19 \pm 29.27 (16)
Romania,						
Danube Delta	38.33 \pm 12.84 (39)	45.63 \pm 11.82 (16)	33.26 \pm 11.14 (23)	32.90 \pm 30.00 (39)	31.50 \pm 28.00 (16)	33.87 \pm 31.90 (23)
Romania,						
Transylvania	55.04 \pm 21.63 (28)	56.84 \pm 24.16 (19)	51.22 \pm 15.52 (9)	71.64 \pm 31.60 (28)	69.63 \pm 31.74 (19)	75.89 \pm 32.74 (9)
France	86.67 \pm 20.53 (30)	87.75 \pm 19.70 (20)	84.50 \pm 23.03 (10)	65.63 \pm 43.86 (30)	71.35 \pm 41.54 (20)	54.20 \pm 48.36 (10)
Czech Republic	78.62 \pm 28.25 (29)	72.50 \pm 26.71 (16)	86.15 \pm 29.31 (13)	8.79 \pm 9.68 (29)	9.81 \pm 9.87 (16)	7.54 \pm 9.67 (13)
Germany,						
Bavaria	85.56 \pm 20.84 (45)	87.86 \pm 20.54 (14)	84.52 \pm 21.23 (31)	103.20 \pm 89.36 (45)	133.36 \pm 81.14 (14)	89.58 \pm 90.78 (31)
Germany,						
Rhineland	75.21 \pm 21.14 (24)	77.81 \pm 21.98 (16)	70.00 \pm 19.64 (8)	35.79 \pm 28.86 (24)	38.88 \pm 30.24 (16)	29.63 \pm 26.69 (8)
Poland	66.06 \pm 24.13 (52)	75.81 \pm 28.11 (21)	59.45 \pm 18.75 (31)	6.13 \pm 10.76 (52)	5.19 \pm 2.82 (21)	6.77 \pm 13.80 (31)
Wales	87.50 \pm 21.06 (16)	87.50 \pm 22.08 (14)	87.50 \pm 17.68 (2)	83.56 \pm 108.43 (16)	69.07 \pm 98.60 (14)	185.00 \pm 162.64 (2)
Lithuania	84.28 \pm 23.54 (25)	83.26 \pm 24.02 (19)	87.50 \pm 23.80 (6)	50.28 \pm 64.44 (25)	30.89 \pm 35.14 (19)	111.67 \pm 97.66 (6)
Denmark	100.34 \pm 29.31 (38)	94.50 \pm 26.82 (20)	106.83 \pm 31.33 (18)	37.50 \pm 28.96 (38)	34.50 \pm 26.24 (20)	40.83 \pm 32.15 (18)

selection pressures from the parasite have increased the level of resistance, with additional influence of individual variation in resistance among hosts. These findings highlight the importance of considering both population and individual factors when investigating spatial heterogeneity in host resistance to parasitism.

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