



Host density predicts presence of cuckoo parasitism in reed warblers

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In some hosts of avian brood parasites, several populations apparently escape parasitism, while others are parasitized. Many migratory specialist brood parasites like common cuckoos, *Cuculus canorus*, experience a short breeding season, and in order to maintain local parasite populations host densities should be sufficiently high to allow efficient nest search. However, no studies have investigated the possible effect of host density on presence of cuckoo parasitism among populations of a single host species. Here, we investigated possible predictors of common cuckoo parasitism in 16 populations of reed warblers, *Acrocephalus scirpaceus*, across Europe. In more detail, we quantified the effect of host density, number of host breeding pairs, habitat type, mean distance to nearest cuckoo vantage point, predation rate and latitude on the presence of cuckoo parasitism while controlling for geographical distance among study populations. Host density was a powerful predictor of parasitism. We also found a less pronounced effect of habitat type on occurrence of parasitism, while the other variables did not explain why cuckoos utilize some reed warbler populations and not others. This is the first study focusing on patterns of common cuckoo-host interactions within a specific host species on a large geographic scale. The results indicate that if host density is below a specific threshold, cuckoo parasitism is absent regardless of the state of other potentially confounding variables.

Most studies on avian brood parasitism have focused on single populations (Rothstein and Robinson 1998, Davies 2000). However, spatially heterogeneous environments are likely to influence both distribution of populations and their dynamics (Hanski 1999). Therefore, spatial differentiation of various populations of

hosts and parasites (metapopulation scenario) may lead to local adaptations and spatial variation in coevolution of parasites and their hosts (Thompson 1994, 2005). The investigation of host–parasite dynamics in a metapopulation context has so far mainly been applied to plants and their pathogens (reviewed by Kaltz and

Shykoff 1998). Recently, the metapopulation approach has been applied to coevolutionary interactions between great-spotted cuckoos (*Clamator glandarius*) and their black-billed magpie (*Pica pica*) hosts (Soler et al. 1998, 1999b, Martínez et al. 1999, Soler and Soler 2000). Lindholm (1999) used a similar approach to investigate common cuckoo (hereafter cuckoo) (*Cuculus canorus*) – reed warbler (*Acrocephalus scirpaceus*) interactions within Great Britain. In addition, Røskaft et al. (2002, 2006) have shown that spatial habitat structure is important for the evolution of rejection behavior in hosts and parasite counter-adaptations in cuckoo-host metapopulations. Such investigations can reveal the underlying causes of coevolutionary interactions in host–parasite systems (Soler and Soler 2000).

The cuckoo is an obligate brood parasite laying its eggs in the nests of at least 125 species of European passerines (Wyllie 1981, Moksnes and Røskaft 1995, Davies 2000). About 20 of these species are parasitized frequently and a similar number are considered to be occasionally parasitized. At least 17 distinct cuckoo gentes, specializing on and mimicking the eggs of one or a few host species, have previously been described in Europe (Wyllie 1981, Alvarez 1994, Moksnes and Røskaft 1995, Gibbs et al. 2000, Antonov et al. in press a). The reed warbler is the most frequently parasitized cuckoo host in Europe (Moksnes and Røskaft 1995), but the level of parasitism is highly variable both in space and time (Moksnes et al. 1993a, Davies et al. 1996, Brooke et al. 1998, Lindholm 1999, Stokke et al. 1999). Furthermore, the reed warbler is widespread and common throughout Europe (Cramp 1992), but nevertheless sub-populations are well defined within the metapopulation as a whole. This is due to the reed warblers' breeding habitat, which is mainly reedbeds surrounding lakes, ponds and ditches (Cramp 1992). Such habitats are scattered as isolated patches over large parts of the continent, making metapopulation theory applicable (Foppen et al. 2000, Hansson et al. 2002).

In the present study, we investigated the prevalence of cuckoo parasitism in 16 reed warbler populations across Europe. Our aim was to investigate the effect of potentially important parameters for occurrence of cuckoo parasitism among reed warbler populations while controlling for inter-population geographical distances. Specifically, we tested for the effect of six variables that could theoretically affect host usage by the cuckoo; host density, local host population size, habitat type, mean distance to nearest vantage point, predation rate, and latitude.

Many studies have investigated the effect of local host density and absolute number of hosts on spatial heterogeneity in the level of parasitism, especially in insect host–parasitoid systems. These investigations have obtained support for a range of scenarios from

positive density dependence to inverse density dependence or independence of host density on parasitism (Lessells 1985, Stiling 1987, Walde and Murdoch 1988, Darrouzet-Nardi et al. 2006, Thiel and Hoffmeister 2006). Migratory specialist avian brood parasites like cuckoos often experience a short breeding season, and therefore host densities should be sufficiently high to allow efficient nest searching and ultimately to maintain local parasite populations (Takasu et al. 1993). However, no studies have tested for the effect of host density on presence of cuckoo parasitism among populations of a single host species.

Populations of specific host species can occupy a range of habitat types, and host densities, parasite nest searching preference and efficiency or other characteristics could therefore be habitat-specific (Vogl et al. 2002, Thiel and Hoffmeister 2006). Furthermore, edge-effects could be more pronounced in certain habitat types than in others (Patten et al. 2006). This scenario could lead to a situation of variation in patch quality assessment by brood parasites depending on habitat (Thiel and Hoffmeister 2006), and therefore a relationship between occurrence of parasitism and habitat type or quality (Strausberger 2001, Røskaft et al. 2002, Burhans and Thompson 2006, Tewksbury et al. 2006).

Avian brood parasites like cuckoos and brown-headed cowbirds (*Molothrus ater*) depend on vantage points in trees or other elevated structures when searching for host nests (Alvarez 1993, Clotfelter 1998, Honza et al. 2002), and host pairs breeding close to trees are often more prone to parasitism than pairs breeding further away from such vantage points (Øien et al. 1996, Clotfelter 1998, Hauber and Russo 2000, Moskat and Honza 2000, Antonov et al. 2006, in press b). Therefore, potential host populations breeding where vantage points are scarce or absent might be expected to suffer less parasitism than populations breeding where vantage points are abundant (Røskaft et al. 2002).

Egg and nestling predation can seriously impair reproductive success in birds (Ricklefs 1969, Bosque and Bosque 1995, Martin 1995). Potential host populations experiencing high nest predation rates could lead to a situation where a parasite population will be unable to establish or alternatively maintain itself and thus become locally extinct. Therefore, the occurrence of cuckoo parasitism might be expected to be associated with nest predation rates (Avilés et al. 2006), i.e. presence of cuckoo parasitism should be determined by the level of nest predation experienced by their potential hosts.

Finally, differences in geographical distributions of host and parasite could lead to large-scale geographical variation in parasitism pressure. For example, because great-spotted cuckoos are only found in southern

Europe, magpies in northern Europe escape great spotted cuckoo parasitism while populations in southern Europe are prone to parasitism (Martínez et al. 1999, Soler et al. 1999b). Such latitudinal effects may theoretically also be of importance in other host–parasite interactions. Thus, meadow pipits (*Anthus pratensis*) breeding on Iceland and Faeroe Islands are allopatric with brood parasites while those breeding in England are sympatric, with important consequences for the presence of anti-parasite defenses (Davies and Brooke 1989, Avilés and Møller 2003).

Methods

Data collection

The 16 study sites were distributed throughout Europe (Appendix 1, Fig. 1), being representative of reed warbler distribution on the continent. In more detail, the study populations were Albufera de Adra (Almería), Spain (36°45' N, 2°57' W); Rio Guadiana (Badajoz), Spain (38°51' N, 7°02' W); Los Albardales (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), UK (51°56' N, 3°16' W); Ventes Ragas (Baltic Sea coast), Lithuania (55°22' N, 21°13' E); Arresø (Zealand), Denmark (55°57' N, 12°04' E) and Hellesjøvannet/Hemnessjøen (Akershus), Norway (59°44' N, 11°27' E).

Data on cuckoo presence, cuckoo parasitism rate, host density, local host population size, mean distance to nearest trees, predation rate and latitude were collected for each site (Appendix 1). In each area, we searched systematically for nests during about three weeks of the breeding season of the reed warbler 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 found (usually building-stage or early egg-laying stage) until fledging. In this way, we were able to assess presence of cuckoo parasitism, level of parasitism, and predation rate. Predation rate refers to complete loss of eggs or

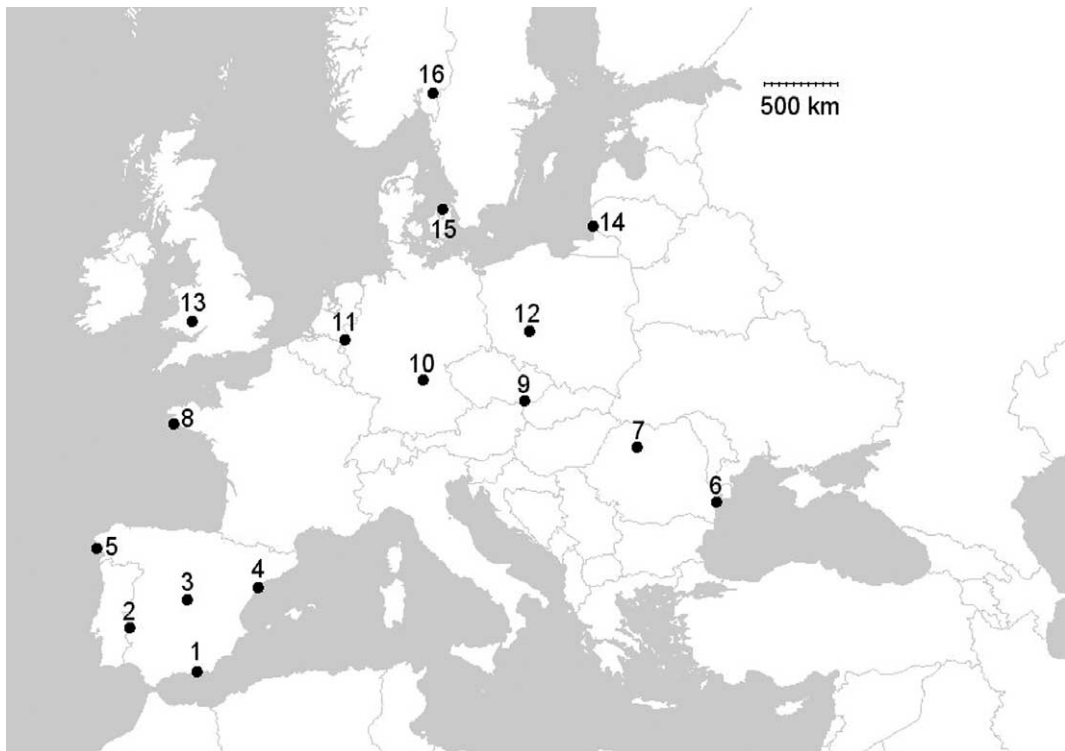


Fig. 1. Map of Europe showing the 16 reed warbler study populations (see Appendix 1 for details; the numbers correspond to numbers in the Appendix 1).

chicks from nests monitored from the egg-laying stage onwards. Host density (pairs ha^{-1}) was calculated by systematically counting the number of all simultaneously active nests in a representative area of suitable vegetation (i.e. where reed warbler nests were found). Estimates of approximate number of host breeding pairs in each study area were obtained from censuses made by local contact persons or from literature surveys. We set an arbitrary value of 2000 breeding pairs as a minimum in three populations where it was impossible to obtain reliable estimates of number of breeding pairs (Appendix 1). The true number of pairs in these three populations is likely to be significantly larger than 2000 pairs. Distance to nearest vantage point (tree, bush, power line or other possible perch sites for cuckoos more than 3 m above ground level) was estimated for all nests found in each study area, and the mean distance for all active nests was used in the analyses. Furthermore, all populations were classified into three different habitat type categories; (1) artificial fish ponds, (2) natural lakes or along rivers, and (3) natural lagoons or river deltas (Appendix 1).

We estimated the inter-population geographical distance between the 16 study areas to the nearest km by employing the distance tool in MapSource ver. 6.8.0.

Statistical analyses

Estimated number of breeding pairs had to be log-transformed to obtain an approximate normal distribution. However, none of the other independent continuous variables included in the multiple logistic regression analyses deviated significantly from a normal distribution (Kolmogorov–Smirnov test with Lilliefors significance correction, $p > 0.05$). Most variables included in the analyses were not strongly inter-correlated thus eliminating any problems of co-linearity (Pearson correlations, $r = -0.24$ to 0.24 , $n = 16$, $p > 0.05$). However, predation rate and latitude was significantly negatively correlated ($r = -0.53$, $n = 16$, $p = 0.034$). We ran analyses both with and without one or the other of these two predictors, but they were both omitted from all final models, because they failed to explain a significant proportion of the variance in occurrence of parasitism (Results). Furthermore, we ran models both including and excluding the three populations where no cuckoos were present (Appendix 1), because the absence of cuckoos in these areas could be due to characteristics of the area that were unrelated to the variables that we included in the analyses.

A forward stepwise (based on likelihood-ratio) multiple logistic regression procedure was applied to model the effect of the six predictor variables on the presence/absence of cuckoo parasitism (dichotomous response variable) (Hosmer and Lemeshow 2000). In

addition, we performed a forward linear regression analysis in order to investigate possible effects of the six predictor variables on cuckoo parasitism rate (%). 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, candidate predictors of cuckoo parasitism according to the logistic regression procedure (habitat type and host density) and occurrence of cuckoo parasitism. These tests were carried out by XLStat 7.5.3. All other analyses were carried out using SPSS 13.0 for Windows.

Results

Seven of the 16 populations turned out to be parasitized by cuckoos. The level of parasitism in the latter varied from 6 to 21%. Before the stepwise logistic regression procedure, only host density and habitat type provided significant scores as candidate predictors of cuckoo parasitism. Therefore, we also entered interactions between these two variables into the model (Table 1). In the final model, the only variable that was a significant predictor of cuckoo parasitism was host density (Table 2), and 87.5% of the cases were classified correctly by using this model. Exclusion of the three allotopic populations yielded the same final model (84.6% of cases classified correctly; Table 2). The fit of the final model was satisfactory in both situations (model including all populations: Hosmer–Lemeshow $\chi^2 = 4.94$, $df = 6$, $p = 0.55$; model excluding allotopic populations: Hosmer–Lemeshow $\chi^2 = 7.59$, $df = 8$, $p = 0.47$). Furthermore, removing host density from the model resulted in a significantly poorer fit of the model (model including all populations: change in $-2 \log$ likelihood = 13.17, $df = 1$, $p < 0.001$; model excluding allotopic populations: change in $-2 \log$ likelihood = 10.10, $df = 1$, $p = 0.001$).

The forward linear regression analysis confirmed what was found by the logistic regression approach. Only host density was retained in the final model and could thus explain variation in cuckoo parasitism rate among populations (Fig. 2; $R^2 = 0.40$, $F = 9.15$, $df = 1, 15$, $p = 0.009$; constant $\pm$ SE: $B = 0.47 \pm 2.18$, $t = 0.22$, $p = 0.83$, coefficient $\pm$ SE for host density: 0.21 ± 0.07 , $t = 3.03$, $p = 0.009$). Exclusion of the three allotopic populations yielded a similar final model ($R^2 = 0.34$, $F = 5.58$, $df = 1, 12$, $p = 0.038$; constant $\pm$ SE: $B = 1.52 \pm 2.80$, $t = 0.54$, $p = 0.60$, coefficient $\pm$ SE for host density: 0.20 ± 0.08 , $t = 2.36$, $p = 0.038$).

Results from Mantel and partial Mantel tests corresponded well with results from logistic regression analyses (Table 3). Host density correlated significantly with occurrence of cuckoo parasitism, both when

Table 1. Forward logistic regression model of the influence of host density (pairs ha^{-1}), estimated number of host breeding pairs (log-transformed), habitat type (3 categories), mean distance to vantage point (m), predation rate of eggs and nestlings (%), and latitude (degrees and minutes) on absence or presence of cuckoo parasitism in 16 European reed warbler populations (all populations) and after exclusion of three populations allotopic with common cuckoos. Significant variables in bold. Scores and estimates of parameters included in the final model (host density) are presented in Table 2.

Parameter	All populations						Excluding allotopic populations					
	Step 0			Final step			Step 0			Final step		
	Score	df	p	Score	df	p	Score	df	p	Score	df	p
Host density	9.822	1	0.002				7.452	1	0.006			
Host number of breeding pairs	0.221	1	0.638	0.443	1	0.506	0.086	1	0.769	0.375	1	0.540
Habitat	7.641	2	0.022	2.376	2	0.305	5.154	2	0.076	1.452	2	0.484
Habitat (1)	4.390	1	0.036	2.321	1	0.128	1.935	1	0.164	1.449	1	0.229
Habitat (2)	6.857	1	0.009	0.255	1	0.614	4.952	1	0.026	0.249	1	0.618
Host density $\times$ habitat	6.450	2	0.040	2.571	2	0.276	4.655	2	0.089	2.076	2	0.354
Host density $\times$ habitat (1)	0.684	1	0.408	2.217	1	0.136	0.317	1	0.573	1.862	1	0.172
Host density $\times$ habitat (2)	6.447	1	0.011	0.251	1	0.616	4.633	1	0.031	0.244	1	0.621
Distance to vantage point	0.575	1	0.448	0.302	1	0.583	1.651	1	0.199	0.771	1	0.380
Predation rate	0.003	1	0.953	0.286	1	0.593	0.100	1	0.752	0.344	1	0.558
Latitude	0.488	1	0.485	0.254	1	0.614	0.002	1	0.965	0.089	1	0.766

including and excluding allotopic populations and when controlling for habitat type and geographical distance between populations. Habitat type also correlated significantly with occurrence of cuckoo parasitism, but when excluding allotopic populations that correlation was no longer significant. The same pattern was found when controlling for distance between populations, but when controlling for host density the correlations between cuckoo parasitism and habitat type were no longer significant. Host density correlated significantly with habitat type, but not when excluding allotopic populations. However, when controlling for distance the correlation between density and habitat was significant both when including all populations and when excluding allotopic populations. Occurrence of parasitism was not correlated with geographical distance in any of the correlations or partial correlations. Neither habitat type nor host density was significantly correlated with geographical distance.

Inspection of the data revealed that host density must be above a critical threshold for cuckoo parasitism

to take place, i.e. all except one population with a density above 15 pairs ha^{-1} were parasitized, and none with a density below 13 pairs ha^{-1} were parasitized. When host density was above the critical threshold there was no significant correlation between parasitism rate and host density ($r_{sp}=0.10$, $n=8$, $p=0.94$). Furthermore, there was a higher mean host density in artificial fish ponds than in natural lakes or rivers (Mann–Whitney U-test, $z=2.65$, $n=11$, $p=0.008$) and natural lagoons or river deltas ($z=2.21$, $n=9$, $p=0.027$). However, there was no statistically significant difference in density between the two natural habitats ($z=0.08$, $n=12$, $p=0.94$). Furthermore, there was a statistically significant difference in frequency of parasitized populations between artificial fish ponds and natural lakes or rivers (Fisher exact test, $n=11$, $p=0.015$). However, there were no significant differences in frequency of parasitized populations between artificial fish ponds and natural lagoons or river deltas (Fisher exact test, $n=9$, $p=0.17$), or between the two natural habitats (Fisher exact test, $n=12$, $p=0.52$).

Table 2. Final logistic regression model of the influence of host density (pairs ha^{-1}), estimated number of host breeding pairs (log-transformed), habitat type (3 categories), mean distance to vantage point (m), predation rate of eggs and nestlings (%), and latitude (degrees and minutes) on absence or presence of cuckoo parasitism in 16 European reed warbler populations (all populations), and after exclusion of three populations allotopic with common cuckoos. Scores of parameters not included in the final model are presented in Table 1. Parameter estimates (β) are presented with their standard errors (SE). Wald statistic $=\sqrt{(\beta/SE)}$. Odds-ratio $=\exp(\beta)$, represents the ratio-change in the odds of the event of interest for a one-unit change in the predictor.

Parameter in model	All populations					Excluding allotopic populations				
	Estimate (β)	SE	Wald χ^2	p	Odds ratio	Estimate (β)	SE	Wald χ^2	p	Odds ratio
Host density	-0.169	0.081	4.365	0.037	0.845	-0.149	0.077	3.788	0.052	0.861
Constant	3.798	1.781	4.545	0.033	44.608	3.083	1.720	3.212	0.073	21.818

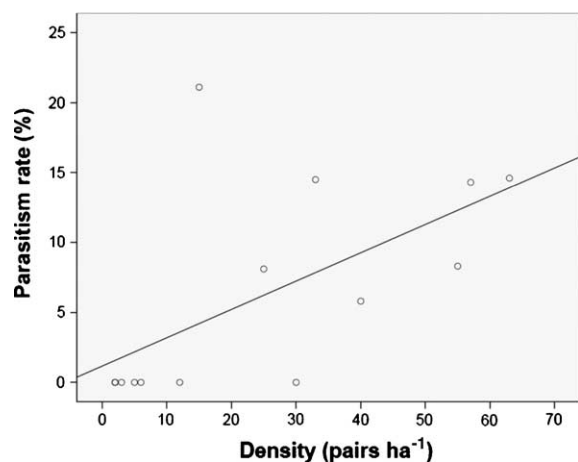


Fig. 2. The relationship between parasitism rate and host density among 16 European reed warbler populations. The fitted line is the linear regression line.

Discussion

In this study we have shown that host density is the best predictor of cuckoo parasitism in the reed warbler because below a specific threshold of reed warbler density (13–15 pairs ha^{-1}) there was no cuckoo parasitism. In only one apparently non-parasitized population (Madrid) did host density exceed the critical threshold of 15 pairs ha^{-1} . However, it is notable that in this particular population the mean distance to nearest vantage point for the cuckoo was large (Appendix 1), implying that cuckoos would have difficulties exploiting this population although overall host density

was sufficiently high. There was apparently also a less pronounced effect of habitat type on occurrence of parasitism. Furthermore, there was a correlation between host density and habitat type; artificial fish ponds had the highest densities of hosts and were also most susceptible to parasitism. Artificial fish ponds often have narrow belts of reeds compared to most natural habitats, which leads to an ideal situation for cuckoos with high densities of hosts with nests situated close to each other. However, when host densities are sufficiently high, populations will apparently be parasitized regardless of habitat type. Both the logistic regression procedure and the Mantel tests revealed that host density was the best predictor of cuckoo parasitism, and that the correlations between habitat type and parasitism were no longer significant when controlling for host density.

Host density thresholds are common in other host–parasite systems, and they are important for sustaining parasite populations (Jaffee et al. 1992). However, such thresholds have previously not been described in avian brood parasites and their hosts. Interestingly, however, Brooker and Brooker (2003) found that Horsfield's bronze cuckoos (*Chrysococcyx basalis*) in Australia appear to need a minimum of 12–20 host pairs within specific areas for successful breeding, but they did not estimate the threshold host density per se. Jensen and Cully (2005) described very marked variation in level of parasitism in dickcissels (*Spiza americana*) by a generalist parasite, the brown-headed cowbird in tallgrass prairie within a confined sub-region in USA, but could not attribute these differences to any other variable than local densities of the female parasite (but see Zimmermann

Table 3. Mantel and partial Mantel tests for correlation between variation in geographical distance between study populations, habitat type, host density and cuckoo parasitism among 16 reed warbler populations, and after exclusion of three populations allotypic with common cuckoos. Number of permutations is set to 1000 in all tests. Parentheses indicate variables that are controlled in the partial tests.

Matrix comparison	All populations		Excluding allotypic populations	
	r	p	r	p
Parasitism-density	0.530	<0.001	0.453	0.015
Parasitism-habitat	0.285	0.026	0.163	0.097
Parasitism-distance	0.079	0.261	0.036	0.724
Density-habitat	0.367	<0.001	0.163	0.175
Density-distance	−0.019	0.852	−0.119	0.292
Habitat-distance	−0.040	0.660	−0.048	0.623
Parasitism-density (habitat)	0.513	<0.001	0.455	0.003
Parasitism-density (distance)	0.533	<0.001	0.465	0.005
Parasitism-habitat (density)	0.124	0.111	0.015	0.384
Parasitism-habitat (distance)	0.290	0.015	0.165	0.074
Parasitism-distance (density)	0.106	0.105	0.103	0.107
Parasitism-distance (habitat)	0.095	0.125	0.045	0.248
Density-habitat (distance)	0.367	0.004	0.329	0.012
Density-distance (habitat)	−0.005	0.485	−0.110	0.113
Habitat-distance (density)	−0.036	0.337	−0.009	0.582

1983). Furthermore, variation in brown-headed cowbird parasitism on plumbeous vireos (*Vireo plumbeus*) was related to distance to the parasite's feeding areas rather than to host density (Goguen and Mathews 2000). However, in song sparrows (*Melospiza melodia*) the absolute number of nests in an area was positively correlated with the level of brown-headed cowbird parasitism (Smith and Arcese 1994, Arcese et al. 1996). In generalist brood parasites, cumulative host density or density of a particularly conspicuous host species could have a significant effect on parasitism of specific host species. That is the case for black-capped vireos (*Vireo atricapillus*) parasitized by brown-headed cowbirds. Northern cardinals (*Cardinalis cardinalis*) are conspicuous birds, and parasitism of vireos was significantly correlated with cardinal densities (Barber and Martin 1997). Furthermore, parasitism of the critically endangered pale-headed brush-finch (*Atlapetes pallidiceps*) in southern Ecuador by another generalist brood parasite, the shiny cowbird (*Molothrus bonariensis*), varies among areas, probably due to differences in host availability (Oppel et al. 2004). In generalist brood parasites that require specific habitats for feeding, like brown-headed cowbirds, it is important to acknowledge that regional composition of habitats could directly influence the density of parasites and therefore also risk of parasitism (Robinson et al. 1995). Therefore, habitat fragmentation may reduce the number and density of hosts while increasing the density of brood parasites leading to very high levels of parasitism. On the other hand, larger patches of intact habitats without parasite feeding habitats may lead to higher densities of hosts but a lower density and level of parasitism by brood parasites (Hoover et al. 2006).

The cuckoo is a specialist brood parasite in that various female gentes utilize specific host species (Wyllie 1981, Moksnes and Røskaft 1995, Gibbs et al. 2000, Honza et al. 2001), and specialist parasites are particularly dependent on patterns of host distribution (Pacala and Hassell 1991). Obviously, the cuckoo needs a good supply of available host nests throughout the breeding season, and therefore it is no surprise that host density is an important predictor of cuckoo parasitism (Alvarez 2003). A previous comparative study of host selection among different host species of the cuckoo in Europe revealed that relative host population size affected parasitism rate more strongly than any other variable (Soler et al. 1999a, but see Avilés and Møller 2004). This makes sense, because a high relative population size on a large scale will arguably result in a higher density of hosts also on a local scale. A low relative population size often implies that local populations are small and host densities are too low for successful utilization of such species by specialist brood parasites, even when they may be suitable hosts in all other respects. However, the present

study has shown that even populations with a low absolute number of host breeding pairs are likely to be parasitized as long as host density is high.

The results from our study fit nicely with predictions made by the theoretical models of Takasu et al. (1993). They predicted that below a certain host density threshold, the local cuckoo population could easily go extinct due to stochastic effects. Furthermore, Lindholm (1999) found that the frequency of cuckoo parasitism on reed warblers did not increase in direct proportion to host abundance (i.e. total population size) in reed warbler sub-populations within Great Britain. She also noted that some populations (including the Llangorse Lake population in Wales) were not parasitized although they apparently were neither too large nor too small in terms of total population size. Our analysis offers an explanation for this anomaly, because we found that host density in Llangorse Lake (12 pairs ha^{-1}) was slightly below the threshold required for a population to be utilized by cuckoos (13 pairs ha^{-1}), and this may explain why this population apparently escaped parasitism. In accordance with Lindholm (1999), we found that occurrence of suitable vantage points and reduced reproductive success (high predation rates) could not explain presence or absence of cuckoo parasitism among populations. Obviously, within parasitized populations, access to vantage points would enhance the risk of parasitism, but our study revealed that the occurrence of suitable vantage points is not the key factor if host density is below a specific threshold. This finding is also relevant in the context of the "spatial habitat structure hypothesis" proposed by Røskaft et al. (2002). This hypothesis suggests that the absence or presence of cuckoo parasitism is explained by differences in habitat characteristics between areas, i.e. availability of vantage points for the brood parasite. However, that hypothesis can be extended so that not only habitat structure, but also host density contributes to spatial differences in level of parasitism.

It could be argued that host egg rejection should be taken into account in a study like the present one. Firstly, it is likely that egg rejection is higher in parasitized than in non-parasitized populations (Moksnes and Røskaft 1989, Moksnes et al. 1993b, Lindholm and Thomas 2000, Bártol et al. 2002), and secondly it is a theoretical possibility that we could miss some parasitism events if cuckoo eggs were ejected before we were able to detect them. However, we also performed egg rejection experiments in all populations (real Chinese quail (*Coturnix chinensis*) eggs painted light blue), and the single most important parameter explaining variation in rejection rates among populations (4.8–68.9%,) was presence of cuckoo parasitism (Stokke et al., unpubl.). Furthermore, the majority of experimentally added eggs were rejected by desertion.

Therefore, it is highly unlikely that we failed to classify any parasitized populations as not being parasitized.

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Appendix 1. Data on sympatry with cuckoos (yes/no), presence of cuckoo parasitism, parasitism rate (%), number of nests in brackets), habitat type (see Methods for description), host density (pairs ha^{-1}), estimated number of breeding pairs in population, mean distance to vantage point (m), predation rate of eggs and nestlings (%), number of nests in brackets), and latitude (degrees and minutes) for 16 European reed warbler populations (see Methods for a detailed description of the study areas).

Number	Population	Sympatry	Cuckoo parasitism	Parasitism rate	Habitat type	Host density	Number of breeding pairs	Vantage point	Predation rate	Latitude
1.	Spain, Almería	No	No	0 (20)	2	13	150	25.0	42.1 (19)	36.45
2.	Spain, Badajoz	No	No	0 (27)	2	2	250	5.8	56.7 (30)	38.51
3.	Spain, Madrid	Yes	No	0 (28)	2	30	250	101.2	45.8 (24)	40.13
4.	Spain, Ebro Delta	Yes	Yes	21.1 (19)	3	15	50	90.2	40.9 (22)	40.44
5.	Spain, Galicia	Yes	No	0 (39)	3	3	50	32.6	13.5 (37)	42.33
6.	Romania, Danube Delta	Yes	Yes	5.8 (69)	3	40	2000	35.9	58.9 (56)	44.37
7.	Romania, Transylvania	Yes	No	0 (32)	2	2	200	63.6	41.4 (29)	46.56
8.	France	Yes	No	0 (41)	3	6	500	59.4	5.9 (34)	47.54
9.	Czech Republic	Yes	Yes	14.6 (82)	1	63	110	8.9	34.7 (72)	48.50
10.	Germany, Bavaria	Yes	Yes	8.3 (72)	1	55	300	90.0	13.9 (36)	49.40
11.	Germany, Rhineland	Yes	Yes	14.5 (55)	1	33	50	35.8	15.2 (46)	51.14
12.	Poland	Yes	Yes	14.3 (105)	1	57	2000	6.1	38.6 (83)	51.32
13.	Wales	No	No	0 (49)	2	12	200	75.8	2.6 (39)	51.56
14.	Lithuania	Yes	No	0 (61)	3	5	2000	45.5	23.1 (52)	55.22
15.	Denmark	Yes	Yes	8.1 (99)	2	25	700	36.6	5.7 (87)	55.57
16.	Norway	Yes	No	0 (58)	2	8	80	87.6	31.5 (54)	59.44