# Reducing cuckoo parasitism risk via informed habitat choices

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RESEARCH ARTICLE

# Reducing cuckoo parasitism risk via informed habitat choices

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## ABSTRACT

Brood parasitism incurs severe fitness costs for hosts. Diverse host adaptations to avoid parasitism exist at various stages of the host breeding cycle, but the literature suggests that egg-stage defenses are the most evolved. Fitness costs of parasitism would be minimized if hosts avoided parasitism prior to egg laying, but it remains unclear whether hosts are able to reduce parasitism risk via informed habitat choices. We conducted a playback experiment to examine the capability of forest passerine birds to perceive vocal cues of the Common Cuckoo (*Cuculus canorus*) to estimate local parasitism risk and adjust their breeding-habitat choices accordingly. The density of open-nesting host species was considerably lower in sites of high perceived parasitism risk than in control sites. Hosts thus seem able to reduce parasitism risk through informed breeding-habitat choices, but this behavior is restricted to open-nesting hosts. Cavity-nesting hosts did no+t respond to the simulated increase in parasitism risk, nor did bird species that are not known as regular Common Cuckoo hosts. Informed habitat selection as an adaptation against parasitism may have important implications for parasite–host coevolutionary interactions, via reduced selection for later-stage host adaptations, and for bird community structure in general.

*Keywords:* brood parasitism, coevolution, Common Cuckoo, eavesdropping, front-line defenses, informed habitat selection

## Reducción del parasitismo por parte de cucos por medio de escogencia de hábitat informada

### RESUMEN

El parasitismo de cría causa costos severos para la aptitud de los hospederos. Existen diversas adaptaciones de los hospederos para evitar el parasitismo en varias etapas de su ciclo reproductivo, pero con base en la literatura existente, las defensas en la etapa de incubación de los huevos parecen ser las más evolucionadas. Los costos que el parasitismo causa en la aptitud se minimizarían si los hospederos evitaran el parasitismo antes de la puesta de los huevos, pero aún no es claro si los hospederos son capaces de reducir el riesgo de parasitismo por medio de la escogencia de hábitat informada. Hicimos un experimento de reproducción de sonidos previamente grabados para examinar la capacidad de aves canoras de bosque de percibir pistas vocales de *Cuculus canorus* para estimar el riesgo local de parasitismo y ajustar su escogencia de hábitat reproductivo. La densidad de especies hospederas de nidos abiertos fue considerablemente menor en sitios con percepción de alto riesgo de parasitismo que en los sitios control. Los hospederos parecen ser capaces de reducir el riesgo de parasitismo mediante la escogencia informada del hábitat reproductivo, pero este comportamiento está restringido a las aves con nidos abiertos. Los hospederos que anidan en cavidades no respondieron al incremento simulado en el riesgo de parasitismo, al igual que las especies de aves que no son hospederas frecuentes de *C. canorus*. La selección informada de hábitat es una adaptación contra el parasitismo que puede tener implicaciones importantes para las interacciones coevolutivas reduciendo la selección a favor de adaptaciones en etapas más tardías del ciclo de vida del hospedero, y para la estructura de comunidades de aves en general.

*Palabras clave:* co-evolución, *Cuculus canorus*, defensas de primera línea, espionaje, parasitismo de cría, selección informada de hábitat

## INTRODUCTION

As a model system for coevolutionary interactions between species, the arms race between obligate brood parasites and their hosts has interested researchers for centuries (Rothstein 1990, Davies 2000, Feeney et al. 2014, Soler 2014). A wide range of birds suffer severe fitness costs due to parasitism; for example, Common Cuckoos (*Cuculus canorus*; hereafter "cuckoos") regularly parasitize as many as 30 avian species (Davies 2000). To deter parasites and

salvage their own reproduction, hosts possess diverse adaptations that, in turn, have selected for counteradaptations in parasites. Particularly well studied are traits that occur during the egg-laying stage (e.g., Davies and Brooke 1989, Langmore et al. 2005, Avilés et al. 2006, Spottiswoode and Stevens 2010, Igic et al. 2012), but host antiparasite adaptations exist in all stages of the breeding cycle (Feeney et al. 2014, Soler 2014).

The capability to collect information about local parasite abundance and to select breeding sites of lower parasite abundance (i.e. parasitism risk) would be especially beneficial for hosts. Such "front-line defenses" (Feeney et al 2012) early in the breeding cycle would enable hosts to prevent, or at least minimize, the costs of parasitism. Consequently, front-line defenses may reduce the selection pressure for, or block the evolution of, later-stage host adaptations and, thus, affect the whole sequence and outcome of the parasite–host coevolutionary arms race (Britton et al. 2007, Feeney et al. 2014). Host breeding-habitat selection as an adaptation against brood parasitism, however, has been neglected (but see Forsman and Martin 2009).

Acquiring information about relative habitat quality, in terms of resources or threats affecting individual fitness, is widespread in animals (Seppänen et al. 2007, Schmidt et al. 2010). Birds may assess ambient nest-predation risk by perceiving cues of predators and use that information in adjusting breeding-habitat choices and investment decisions (Eggers et al. 2006, Mönkkönen et al. 2009, Emmering and Schmidt 2011, Zanette et al. 2011, Forsman et al. 2013). Parallel strategies in relation to parasitism could be expected. Spatial variation in parasitism risk (Øien et al. 1996, Lindholm 1999, Moskát and Honza 2000, Antonov et al. 2007), coupled with parasites' preference for certain habitats in searching for host nests (Vogl et al. 2002), further emphasizes the potential for hosts to avoid parasitism via informed breeding-habitat selection.

We experimentally investigated whether forest passerine birds are able to use vocal cues of cuckoo presence to estimate local parasitism risk and adjust their breeding-habitat selection and investment decisions accordingly. If birds perceive such cues and use them in habitat selection, species that are hosts of the cuckoo are expected to show lower abundance and lower breeding investment in sites of high perceived parasitism risk than in low-risk sites, whereas no differences are expected in non-hosts.

## METHODS

We conducted the experiment in pine-dominated forests near the city of Oulu in northern Finland (64°60′N, 25°42′E) in 2011–2012. We selected 8 forest patches, 1.4 km apart on average and 5.5–11.0 ha in size. In each patch, we provided 12 or 13 nest boxes (with 7.0 cm entrance diameter) for Common Redstarts (a frequently used cuckoo host in the study area; Thomson et al. 2016), 5 or 6 nest boxes (with 3.2 cm entrance diameter) for other cavity-nesting birds, and 2 or 3 nest platforms for Spotted Flycatchers (for scientific names of species, see Table 1). Patches were paired according to spatial proximity, size, and habitat similarity and were randomized within pairs to 2 treatments. Four patches were assigned the "cuckoo treatment," in which the perceived risk of brood parasitism was increased by playbacks of cuckoo vocalizations. The other 4 patches served as silent controls (no playbacks). We used the same patches in both years, but with reversed treatments in 2012.

We decided to use a silent control, rather than a control with playback of a presumably neutral sympatric species singing, because multiple studies have shown that individuals collect information about the environment by observing the behavior of other species (including apparently neutral species) and use that information in their own decision making (e.g., habitat selection; Seppänen et al. 2007, Goodale et al. 2010). This behavior appears to be widespread among animals, though detailed knowledge is still scarce, and therefore it is difficult to identify a species that would not affect at least some other species within the bird community. Using a vocalization of an exotic allopatric species would not be a perfect solution either, because we do not know how birds would interpret it; it might be considered a potential threat or a novel object that could affect behavior. We acknowledge that a silent control is also not a perfect solution. By using a silent control, we avoided the potential problems mentioned above, but on the other hand we cannot rule out the possibility that the playback (increased vocal activity in a site) or merely the presence of a playback machine affected the behavior of individuals in the playback sites. However, taking into account the scale of our experiment (average patch size = 8 ha), any such effects are most likely negligible—and probably far weaker than the potential effects of, for example, heterospecific attraction or avoidance had the playback control been used instead of the silent control (for similar arguments, see Farrell et al. 2012, Hua et al. 2013). Similar experimental designs using silent controls have been applied extensively in studies of avian habitat selection (e.g., Hahn and Silverman 2006, Farrell et al. 2012, Hua et al. 2013, Ware et al. 2015). Nonetheless, if the increased vocal activity due to the playback—or the mere presence of a playback machine—repels birds, one could expect a consistent negative effect on bird abundance across sites and species, irrespective of the latter's status as cuckoo hosts.

Cuckoo vocalization playbacks were started before or during the settlement of resident birds and the arrival of migratory birds, and ~2 wk before the arrival of the first cuckoos (on April 27, 2011, and May 1, 2012). Playbacks

**TABLE 1.** List of forest passerine species observed in our study area in northern Finland during 2011–2012, classified as hosts or non-hosts, with the estimated number of pairs observed during the experiment (estimates based on the "average method"; see text).

| Species | Classification | Estimated number of pairs |
|---|---|---|
| Common Chaffinch (*Fringilla coelebs*) | Host | 46.5 |
| Common Redstart (*Phoenicurus phoenicurus*) | Host | 39.0 |
| Spotted Flycatcher (*Muscicapa striata*) | Host | 29.5 |
| Tree Pipit (*Anthus trivialis*) | Host | 23.0 |
| Willow Warbler (*Phylloscopus trochilus*) | Host | 20.0 |
| European Robin (*Erithacus rubecula*) | Host | 5.5 |
| Brambling (*Fringilla montifringilla*) | Host | 2.5 |
| Dunnock (*Prunella modularis*) | Host | 1.0 |
| Pied Flycatcher (*Ficedula hypoleuca*) | Non-host | 62.5 |
| Great Tit (*Parus major*) | Non-host | 36.0 |
| Eurasian Siskin (*Carduelis spinus*) | Non-host | 20.0 |
| Goldcrest (*Regulus regulus*) | Non-host | 2.5 |
| Song Thrush (*Turdus philomelos*) | Non-host | 2.0 |
| Willow Tit (*Poecile montanus*) | Non-host | 1.5 |
| Crested Tit (*Lophophanes cristatus*) | Non-host | 1.5 |
| Eurasian Bullfinch (*Pyrrhula pyrrhula*) | Non-host | 1.5 |
| Redwing (*Turdus iliacus*) | Non-host | 1.0 |
| Mistle Thrush (*Turdus viscivorus*) | Non-host | 0.5 |
| Eurasian Blackbird (*Turdus merula*) | Non-host | 0.5 |
| Coal Tit (*Periparus ater*) | Non-host | 0.5 |

continued throughout the settlement period of birds and were terminated during the first week of June. We started the playbacks prior to the natural arrival of cuckoos to ensure that the experimental manipulation of perceived parasitism risk affected all forest passerines, both resident and migratory birds. Starting the playbacks before cuckoos arrived was unlikely to affect the results; although the earliest-arriving host individuals in the study area may settle in breeding sites before cuckoos arrive, most hosts settle in breeding sites (i.e. start nest building) after the arrival of first cuckoos (pers. obs.). Playback machines were constructed using car radios (Emax, product no. 3147), speakers, and built-in timers with car batteries as power supplies. Playbacks included male *"cu-coo"* calls of 4 individual cuckoos (1 patch$^{-1}$; sound files downloaded from http://www.xeno-canto.org) and were played for 4.5 hr day$^{-1}$ with alternating playback and silent periods. Playbacks were audible throughout patches but were moved to different positions every few days to prevent habituation of birds. We decided to use male calls rather than female calls. Although male calls do not directly imply parasitism risk, they do indicate it indirectly (i.e. are reliable cues) because male singing territories and female laying territories overlap (Nakamura and Miyazawa 1997, J. Tolvanen et al. personal observation). In addition, the availability of a cue affects its biological value for a cue-user, and male *"cu-coo"* calling is much more frequent— and, therefore, more easily available to cuckoo hosts—than the female calls. The better availability of cues based on male calls, coupled with their reliability as indirect cues of parasitism risk, make them potentially more valuable cues for cuckoo hosts than female calls.

We monitored the nest boxes regularly to record breeding parameters (laying date, clutch size, and nest success) of Common Redstarts. During the site visits, we also recorded the presence or absence of real cuckoos in order to estimate the natural abundance of cuckoos in the experimental sites. After the settlement period, passerine communities in the forest patches were each surveyed twice using an applied territory-mapping method (Koskimies and Väisänen 1988). Surveys were conducted during June 6–14, between 0400 and 0800 hours, in fair weather by walking through each site in parallel transects ~50 m apart and recording (on site maps) all individual birds heard or seen.

We derived density estimates for forest passerine species from the 2 censuses. Because of the low number of censuses per patch, we applied a conservative approach and defined species-specific density estimates as the average number of observed individuals across the 2 censuses divided by the patch area (the "average method"). The (average) number of observed individuals in a patch was assumed to reflect the number of breeding pairs in that patch. For species breeding in nest boxes, nest box data were treated as an additional "census" that provided the absolute minimum number of pairs. If both community surveys implied a greater number of pairs than the nest box data (some pairs may have been breeding in natural cavities), the density estimate was taken in the same way as for the rest of the species. If the nest box data implied a greater number of pairs than either or both of the surveys, the density estimate was taken as the average of the nest box data and the maximum survey result or simply as indicated by the nest

box data, respectively. To ensure that the results did not depend on the specific details of how the census data were interpreted to obtain the density estimates, we also applied another density estimation method, the "maximum method," which defined the density estimate as the maximum value across the 2 censuses, or across the 3 "censuses" (bird surveys and nest box data) for cavity-nesting species. We performed the analyses using both density estimation methods; however, because the results were qualitatively identical, we present only the results based on the "average method."

We classified the species into 2 groups based on their potential risk of being parasitized by the cuckoo. The species listed as main cuckoo hosts in Europe by Davies (2000) were classified as hosts and the rest as non-hosts (Table 1). This broad, European-scale classification was applied because detailed knowledge about the host status of some of these species is not available specifically for the study area. At minimum, Common Redstart, Brambling, Willow Warbler, and Spotted Flycatcher are present cuckoo hosts; and the other species classified as hosts have probably, at minimum, been relatively frequent hosts in the past. According to Davies (2000), Tree Pipits and European Robins are common hosts in neighboring countries (Sweden and Russia, respectively), which implies that they could also be current cuckoo hosts in Finland. Therefore, we are confident that the classification distinguishes the (potential) hosts from non-hosts as well as is currently possible.

Detectability of individuals and pairs is an essential issue in bird community censuses. If there are differences in detectability between species or experimental treatments, differences in census results may be erroneously interpreted as density differences. Because our community surveys were based on 2 censuses without explicit information about identities of individual birds, we could not estimate true detectability (i.e. the probability of an existing individual or pair to be observed in a specific census). Nevertheless, we attempted to evaluate the effects of the treatments on the behavior of different species groups (hosts and non-hosts), in regard to their detectability in the bird surveys, by calculating a proxy of detectability by comparing the minimum census result to the maximum result within the 2 censuses per forest patch per year (detectability index = minimum census value/maximum census value). If, for example, hosts of the cuckoo react to the *"cu-coo"* playbacks by behaving more cryptically (in order to decrease the chances that the apparent cuckoo will locate their nests by cueing on their behavior) and thereby becoming less likely to be observed in the surveys, the detectability index could be expected to be lower (i.e. variation in the census results within a patch being higher) in the cuckoo treatment compared to the control treatment.

For statistical analyses, we used generalized linear mixed models in R 3.2.4 (R Development Core Team 2016). We analyzed response variables, including total number and density of species, number and density of host species and of non-host species, and densities of the 8 most abundant species (i.e. $\geq 10$ pairs observed each year: Common Redstart, Spotted Flycatcher, Common Chaffinch, Tree Pipit, Willow Warbler, Pied Flycatcher, Great Tit, Eurasian Siskin). Breeding parameters of the Common Redstart were also analyzed. Data on Common Redstart nest success (successful or depredated) were too scarce for analyses, but simple nest success rates are reported. We assumed a normal (Gaussian) error distribution for the density variables and the Common Redstart laying date, and a Poisson error distribution (with log link function) for the species richness variables and the Common Redstart clutch size.

The full models included the main effects of "Treatment" and "Year" and their interaction. Additional covariates included patch area in species richness and density analyses, and laying date (both linear and quadratic effects) in Common Redstart clutch-size analysis. Both variables were mean-centered. The validity of the full model in relation to the model assumptions was investigated graphically by using histograms of standardized residuals and by fitting the standardized residuals against the fitted values and all explanatory variables. In the case of the Gaussian response variables, if the model validation indicated heterogeneity of variances among treatment groups or years, treatment- or year-specific variances were fitted. The models with and without the group-specific variances were compared using Akaike's Information Criterion corrected for small sample size ($AIC_c$), and the model structure with the lower $AIC_c$ value was adopted as the full model. Biologically relevant alternative models within the full models were fitted, and $AIC_c$ was used to determine the most parsimonious model. The variable "Treatment" was retained in all models, and the variable "Patch" was included as a random effect in all models. The model validation procedure was repeated for the most parsimonious model, and inferences were based on models that adequately fit the data and met the model assumptions. When selecting the most parsimonious model using the $AIC_c$, models were fitted using maximum likelihood, but the model validation and the reported model statistics are based on models fitted using restricted maximum likelihood. Laplace approximation was always used in the analyses with Poisson distribution.

## RESULTS

We observed 297 pairs (estimate based on the "average method") of forest passerines (20 species; Table 1), of which 167 pairs belonged to host species (8 species) and

130 pairs to non-host species (12 species). The final models explaining host, non-host, and total species richness in the experimental forest patches included only the main effect "Treatment" (Table 2), with no differences between treatments (Table 3).

Total bird density and density of non-host species did not differ between treatments (Table 3 and Figure 1A), but the density of host species was 0.39 pairs ha$^{-1}$ (26%) lower in the cuckoo treatment than in the control treatment (Table 3). Species-specific analyses of the most abundant species revealed that densities of all open-nesting host species were lower in the cuckoo treatment (range of relative decrease: 16–56%), though the decrease was not statistically significant in any of the species because of relatively low sample sizes (Table 3). The density of Common Redstarts, the only cavity-nesting host, did not differ between treatments (relative increase = 8%; Table 3 and Figure 1B). To get a more precise treatment-effect estimate for the open-nesting host species, we performed a post hoc analysis of density of host species excluding the Common Redstart. Density of open-nesting hosts was 0.41 pairs ha$^{-1}$ (33%) lower in the cuckoo treatment (Table 3 and Figure 1C). Densities of the most abundant non-host species did not differ between treatments (Table 3).

Patch-specific effects of the cuckoo playback in open-nesting hosts were negative in 7 sites (range of relative decrease: 10–66%) and positive (relative increase = 60%) in only one site (Holtinkylä). The overall negative effect was therefore a general result from 7 sites, not just due to exceptional effects in only a few sites. In non-hosts, the playback effect was negative in 4 sites (7–35%), positive in 2 sites (7–35%), and zero in 2 sites. The effect in non-hosts also contrasted the effect in open-nesting hosts in 5 of 8 sites (negative in non-hosts and positive in open-nesting hosts in 1 site; zero or positive in non-hosts and negative in open-nesting hosts in 4 sites).

The detectability indexes were similar across treatments in all species groups: hosts (cuckoo = 46%, control = 49%), open-nesting hosts (cuckoo = 46%, control = 48%), and non-hosts (cuckoo = 41%, control = 40%). Therefore, the observed differences between the treatments most likely reflect density differences, not differences in behavior regarding the detectability of the birds.

Common Redstart laying date ($n = 36$) and clutch size ($n = 29$) did not differ between treatments (Table 3). Common Redstart nest success rate was 66.7% in the cuckoo treatment ($n = 18$ nests) and 44.4% in the control treatment ($n = 18$ nests). Five nests, 1 in the cuckoo treatment and 4 in the control treatment (3 of 4 in the Holtinkylä site), were parasitized, but 3 were subsequently depredated and 2 eggs were laid outside the Common Redstart nest cup, where eggs do not develop. Therefore, all Common Redstart breeding failures were due to predation. During the site visits to check nest boxes, we observed real cuckoos 6 times in the control (4 different sites) and 2 times (2 different sites) in the treatment sites (on average, 7.0 and 6.4 visits per control and treatment sites per year, respectively). Observations of real cuckoos corresponded with the parasitism rates of Common Redstart; real cuckoos were observed in all 3 sites where parasitism was also observed.

## DISCUSSION

Our results demonstrate that several hosts of the Common Cuckoo appear to use vocal cues of cuckoos to estimate local parasitism risk and to avoid settling in high-risk habitats. A similar study found that some, but not all, hosts of parasitic Brown-headed Cowbirds (*Molothrus ater*) were able to perceive vocal cues of the parasite and preferred the low-parasitism-risk habitats (Forsman and Martin 2009). Øien et al. (1996) found that density of breeding Eurasian Reed Warblers (*Acrocephalus scirpaceus*) was higher in sites of lower parasitism risk (i.e. farther away from perch trees that cuckoos use to search for host nests). The results of those studies suggest that adaptive breeding-habitat selection may be an important, but thus far neglected, host adaptation for countering parasitism (see also Møller et al. 2016).

By choosing breeding sites with low abundance of cuckoos, hosts may decrease the risk of being parasitized and therefore avoid the fitness costs related to brood parasitism. Breeding-site choice is also probably the earliest stage of the breeding cycle in which hosts can try to avoid cuckoo parasitism. The earlier during the breeding cycle the hosts succeed in avoiding parasitism, the lower their fitness costs. By avoiding parasitism during habitat selection, hosts would avoid the costs related to nest defense (energetic cost and risk of injury), the earliest antiparasite defense properly recognized to date. Therefore, the ability to adjust breeding-site choices on the basis of, for example, vocal cues of cuckoos (i.e. informed habitat selection) could provide an efficient adaptation against brood parasitism.

Despite the general and rather clear avoidance of sites with cuckoo playback by the open-nesting host species, a considerable proportion of individuals settled in those sites. Brood parasitism, though potentially a strong selective pressure, is only one of many factors that animals need to take into account in selecting breeding sites. A trade-off situation arises if spatiotemporal variation in one or more of the other factors affecting individual fitness counters that of brood parasitism, precluding adaptive behavior directed solely toward parasitism. For example, nest predation is another major cause of breeding failure in birds, particularly in open-nesting species (Martin 1993), which can affect birds' habitat choices (e.g., Fontaine and Martin 2006, Forsman et al. 2013). The nest success rate of

**TABLE 2.** $AIC_c$ statistics of models explaining variation in different response variables. The final models with the lowest $AIC_c$ values are in bold.

| Response | Model | $\Delta AIC_c$ [a] | Akaike weight |
|---|---|---|---|
| Total species richness | **Treatment** | **0.00** [b] | **0.72** |
| | Treatment + PatchArea | 3.46 | 0.13 |
| | Treatment + Year | 3.63 | 0.12 |
| | Treatment + Year + PatchArea | 7.81 | 0.01 |
| | Treatment * Year | 7.83 | 0.01 |
| | Treatment * Year + PatchArea | 13.02 | 0.00 |
| Host species richness | **Treatment** | **0.00** [c] | **0.73** |
| | Treatment + Year | 3.53 | 0.12 |
| | Treatment + PatchArea | 3.63 | 0.12 |
| | Treatment * Year | 7.61 | 0.02 |
| | Treatment + Year + PatchArea | 7.89 | 0.01 |
| | Treatment * Year + PatchArea | 12.95 | 0.00 |
| Non-host species richness | **Treatment** | **0.00** [d] | **0.69** |
| | Treatment + PatchArea | 3.14 | 0.14 |
| | Treatment + Year | 3.58 | 0.12 |
| | Treatment * Year | 6.42 | 0.03 |
| | Treatment + Year + PatchArea | 7.45 | 0.02 |
| | Treatment * Year + PatchArea | 11.42 | 0.00 |
| Total density | **Treatment + PatchArea** | **0.00** [e] | **0.50** |
| | Treatment | 1.51 | 0.23 |
| | Treatment + Year + PatchArea | 2.56 | 0.14 |
| | Treatment + Year | 3.21 | 0.10 |
| | Treatment * Year + PatchArea | 7.17 | 0.01 |
| | Treatment * Year | 7.20 | 0.01 |
| Host density, all species | **Treatment + Year** | **0.00** [f] | **0.53** |
| | Treatment | 1.08 | 0.31 |
| | Treatment + Year + PatchArea | 4.33 | 0.06 |
| | Treatment + PatchArea | 4.50 | 0.06 |
| | Treatment * Year | 5.01 | 0.04 |
| | Treatment * Year + PatchArea | 10.74 | 0.00 |
| Host density, open-nesters | **Treatment + Year** | **0.00** [g] | **0.43** |
| | Treatment | 0.55 | 0.32 |
| | Treatment + PatchArea | 2.65 | 0.11 |
| | Treatment + Year + PatchArea | 3.00 | 0.10 |
| | Treatment * Year | 4.94 | 0.04 |
| | Treatment * Year + PatchArea | 9.34 | 0.00 |
| Non-host density | **Treatment + PatchArea** | **0.00** [h] | **0.79** |
| | Treatment * Year + PatchArea | 3.56 | 0.13 |
| | Treatment + Year + PatchArea | 5.26 | 0.06 |
| | Treatment | 7.91 | 0.02 |
| | Treatment + Year | 12.17 | 0.00 |
| | Treatment * Year | 15.56 | 0.00 |
| Common Redstart density | **Treatment** | **0.00** [i] | **0.79** |
| | Treatment + PatchArea | 4.04 | 0.10 |
| | Treatment + Year | 4.29 | 0.09 |
| | Treatment + Year + PatchArea | 9.31 | 0.01 |
| | Treatment * Year | 9.60 | 0.01 |
| | Treatment * Year + PatchArea | 15.94 | 0.00 |
| Spotted Flycatcher density | **Treatment** | **0.00** [j] | **0.67** |
| | Treatment + Year | 2.16 | 0.23 |
| | Treatment + PatchArea | 4.34 | 0.08 |
| | Treatment * Year | 7.47 | 0.02 |
| | Treatment + Year + PatchArea | 7.48 | 0.02 |
| | Treatment * Year + PatchArea | 14.13 | 0.00 |
| Common Chaffinch density | **Treatment** | **0.00** [k] | **0.44** |
| | Treatment + PatchArea | 1.08 | 0.26 |
| | Treatment + Year | 1.50 | 0.21 |
| | Treatment + Year + PatchArea | 3.47 | 0.08 |
| | Treatment * Year | 6.72 | 0.02 |
| | Treatment * Year + PatchArea | 10.08 | 0.00 |

**TABLE 2.** Continued.

| Response | Model | $\Delta AIC_c$ [a] | Akaike weight |
|---|---|---|---|
| Tree Pipit density | **Treatment** | **0.00** [l] | **0.53** |
| | Treatment + PatchArea | 2.06 | 0.19 |
| | Treatment * Year | 2.67 | 0.14 |
| | Treatment + Year | 3.48 | 0.09 |
| | Treatment * Year + PatchArea | 5.88 | 0.03 |
| | Treatment + Year + PatchArea | 6.48 | 0.02 |
| Willow Warbler density | **Treatment + Year** | **0.00** [m] | **0.77** |
| | Treatment | 4.25 | 0.09 |
| | Treatment * Year | 4.89 | 0.07 |
| | Treatment + Year + PatchArea | 5.31 | 0.05 |
| | Treatment + PatchArea | 8.60 | 0.01 |
| | Treatment * Year + PatchArea | 11.55 | 0.00 |
| Pied Flycatcher density | **Treatment** | **0.00** [n] | **0.46** |
| | Treatment + PatchArea | 0.66 | 0.33 |
| | Treatment + Year | 2.99 | 0.10 |
| | Treatment + Year + PatchArea | 4.39 | 0.05 |
| | Treatment * Year | 4.46 | 0.05 |
| | Treatment * Year + PatchArea | 6.79 | 0.02 |
| Great Tit density | **Treatment + PatchArea** | **0.00** [o] | **0.73** |
| | Treatment + Year + PatchArea | 3.23 | 0.15 |
| | Treatment | 4.10 | 0.09 |
| | Treatment + Year | 7.00 | 0.02 |
| | Treatment * Year + PatchArea | 9.89 | 0.01 |
| | Treatment * Year | 12.31 | 0.00 |
| Eurasian Siskin density | **Treatment + PatchArea** | **0.00** [p] | **0.78** |
| | Treatment | 3.33 | 0.15 |
| | Treatment + Year + PatchArea | 5.31 | 0.05 |
| | Treatment + Year | 7.65 | 0.02 |
| | Treatment * Year + PatchArea | 11.47 | 0.00 |
| | Treatment * Year | 12.57 | 0.00 |
| Common Redstart laying date | **Treatment** | **0.00** [q] | **0.73** |
| | Treatment + Year | 2.46 | 0.21 |
| | Treatment * Year | 5.34 | 0.05 |
| Common Redstart clutch size | **Treatment** | **0.00** [r] | **0.58** |
| | Treatment + LayingDate | 2.66 | 0.15 |
| | Treatment + Year | 2.70 | 0.15 |
| | Treatment + LayingDate + LayingDate$^2$ | 5.60 | 0.04 |
| | Treatment + Year + LayingDate | 5.60 | 0.04 |
| | Treatment * Year | 5.61 | 0.03 |
| | Treatment * Year + LayingDate | 8.77 | 0.01 |
| | Treatment + Year + LayingDate + LayingDate$^2$ | 8.80 | 0.01 |
| | Treatment * Year + LayingDate + LayingDate$^2$ | 12.28 | 0.00 |

[a] $AIC_c$ values of the top models: [b] 75.66; [c] 65.94; [d] 64.07; [e] 40.24; [f] 30.63; [g] 28.17; [h] 10.99; [i] −20.24; [j] −18.48; [k] 0.93; [l] −6.70; [m] −9.99; [n] 2.58; [o] 1.44; [p] −32.47; [q] 232.41; [r] 117.91.

Common Redstarts was 66.7% in the cuckoo treatment and 44.4% in the control treatment, which implies equal or even higher nest predation risk in control sites. Some hosts may have treated predators as a more imminent threat than cuckoos and thus chose to settle in cuckoo playback sites. It could be argued that the predation rate of Common Redstarts breeding in nest boxes is not representative of predation risk in general, but in our study the Common Redstart nest boxes had a large enough entrance hole (7 cm in diameter) that any of the most usual nest predators (woodpeckers, small mustelids,

squirrels) in the study area could have entered the nest box. Alternatively, the capability of cueing on cuckoo vocalizations may not be innate but may require earlier experience with cuckoos. If that is the case, only older, experienced host individuals would be able to apply such cues in habitat selection. The resulting nonrandom spatial distribution of inexperienced and experienced hosts could have complex implications for parasite–host interactions (Grim 2002).

The effect of the cuckoo playback differed between species, as well as across experimental sites in some species

**TABLE 3.** Model statistics of the final models explaining variation in different response variables.

| Response | Parameter | Estimate | SE | df | t or z [a] | P |
|---|---|---|---|---|---|---|
| Total species richness [b] | Intercept | 2.29 | 0.11 | | 20.35 | <0.001 |
| | Treatment (Cuckoo) | −0.04 | 0.16 | | −0.24 | 0.81 |
| Host species richness [b] | Intercept | 1.68 | 0.15 | | 11.09 | <0.001 |
| | Treatment (Cuckoo) | 0.02 | 0.21 | | 0.11 | 0.92 |
| Non-host species richness [b] | Intercept | 1.50 | 0.17 | | 9.02 | <0.001 |
| | Treatment (Cuckoo) | −0.12 | 0.24 | | −0.49 | 0.63 |
| Total density | Intercept | 2.64 | 0.21 | 7 | 12.56 | <0.001 |
| | Treatment (Cuckoo) | −0.44 | 0.24 | 6 | −1.87 | 0.11 |
| | **PatchArea** | **−0.25** | **0.10** | **6** | **−2.56** | **0.04** |
| Host density, all species | Intercept | 1.71 | 0.18 | 7 | 9.29 | <0.001 |
| | **Treatment (Cuckoo)** | **−0.39** | **0.15** | **6** | **−2.62** | **0.04** |
| | Year (2012) | −0.36 | 0.15 | 6 | −2.42 | 0.05 |
| Host density, open-nesters | Intercept | 1.42 | 0.17 | 7 | 8.58 | <0.001 |
| | **Treatment (Cuckoo)** | **−0.41** | **0.18** | **6** | **−2.62** | **0.04** |
| | Year (2012) | −0.36 | 0.16 | 6 | −2.26 | 0.07 |
| Non-host density | Intercept | 1.11 | 0.08 | 7 | 13.37 | <0.001 |
| | Treatment (Cuckoo) | −0.05 | 0.10 | 6 | −0.54 | 0.61 |
| | **PatchArea** | **−0.18** | **0.04** | **6** | **−4.66** | **0.004** |
| Common Redstart density | Intercept | 0.29 | 0.06 | 7 | 5.11 | 0.001 |
| | Treatment (Cuckoo) | 0.02 | 0.02 | 7 | 1.10 | 0.31 |
| Spotted Flycatcher density | Intercept | 0.25 | 0.04 | 7 | 5.96 | <0.001 |
| | Treatment (Cuckoo) | −0.04 | 0.03 | 7 | −1.19 | 0.27 |
| Common Chaffinch density | Intercept | 0.44 | 0.07 | 7 | 6.70 | <0.001 |
| | Treatment (Cuckoo) | −0.12 | 0.09 | 7 | −1.38 | 0.21 |
| Tree Pipit density | Intercept | 0.24 | 0.05 | 7 | 4.56 | 0.003 |
| | Treatment (Cuckoo) | −0.10 | 0.06 | 7 | −1.49 | 0.18 |
| Willow Warbler density | Intercept | 0.31 | 0.05 | 7 | 6.07 | <0.001 |
| | Treatment (Cuckoo) | −0.12 | 0.06 | 6 | −2.21 | 0.07 |
| | **Year (2012)** | **−0.18** | **0.06** | **6** | **−3.23** | **0.02** |
| Pied Flycatcher density | Intercept | 0.50 | 0.07 | 7 | 7.29 | <0.001 |
| | Treatment (Cuckoo) | 0.01 | 0.10 | 7 | 0.11 | 0.92 |
| Great Tit density | Intercept | 0.33 | 0.06 | 7 | 5.50 | <0.001 |
| | Treatment (Cuckoo) | −0.04 | 0.09 | 6 | −0.48 | 0.65 |
| | **PatchArea** | **−0.07** | **0.02** | **6** | **−3.07** | **0.02** |
| Eurasian Siskin density | Intercept | 0.17 | 0.02 | 7 | 7.71 | <0.001 |
| | Treatment (Cuckoo) | −0.003 | 0.02 | 6 | −0.14 | 0.90 |
| | **PatchArea** | **−0.03** | **0.01** | **6** | **−3.06** | **0.02** |
| Common Redstart laying date | Intercept | 27.56 | 1.30 | 27 | 21.18 | <0.001 |
| | Treatment (Cuckoo) | −1.44 | 1.84 | 27 | −0.79 | 0.44 |
| Common Redstart clutch size [b] | Intercept | 1.94 | 0.10 | | 19.75 | <0.001 |
| | Treatment (Cuckoo) | −0.04 | 0.14 | | −0.30 | 0.76 |

[a] t value for species density and Common Redstart laying-date variables, z value otherwise.
[b] Estimates in log (link function) scale.

(non-hosts). If the observed playback effects were merely due to the increased vocal activity or the presence of a single playback machine, all the species across all sites could have been expected to consistently avoid the playback sites. Therefore, it is most likely that the avoidance of playback sites by the open-nesting hosts reflects true avoidance of a high perceived risk of cuckoo parasitism. Furthermore, the majority of the cuckoo parasitism events in Common Redstart nests and the majority of the real cuckoos were observed in control sites. This implies that natural cuckoo abundance during the experiment was higher in control sites than in cuckoo playback sites, countering our experimental manipula-tions. Nevertheless, the abundance of open-nesting host species was lower in the year of cuckoo playback treatment in all but one site (Holtinkylä). The apparent positive playback effect in Holtinkylä could be explained by higher abundance of real cuckoos during the control year compared to the treatment year. Indeed, 3 Common Redstart nests were parasitized, and real cuckoos were observed in the site during the control year, whereas no parasitized nests or real cuckoos were observed during the treatment year.

Instead of altering habitat choices, an alternative explanation for the observed results could be that cuckoo hosts behaved more cryptically in the cuckoo playback
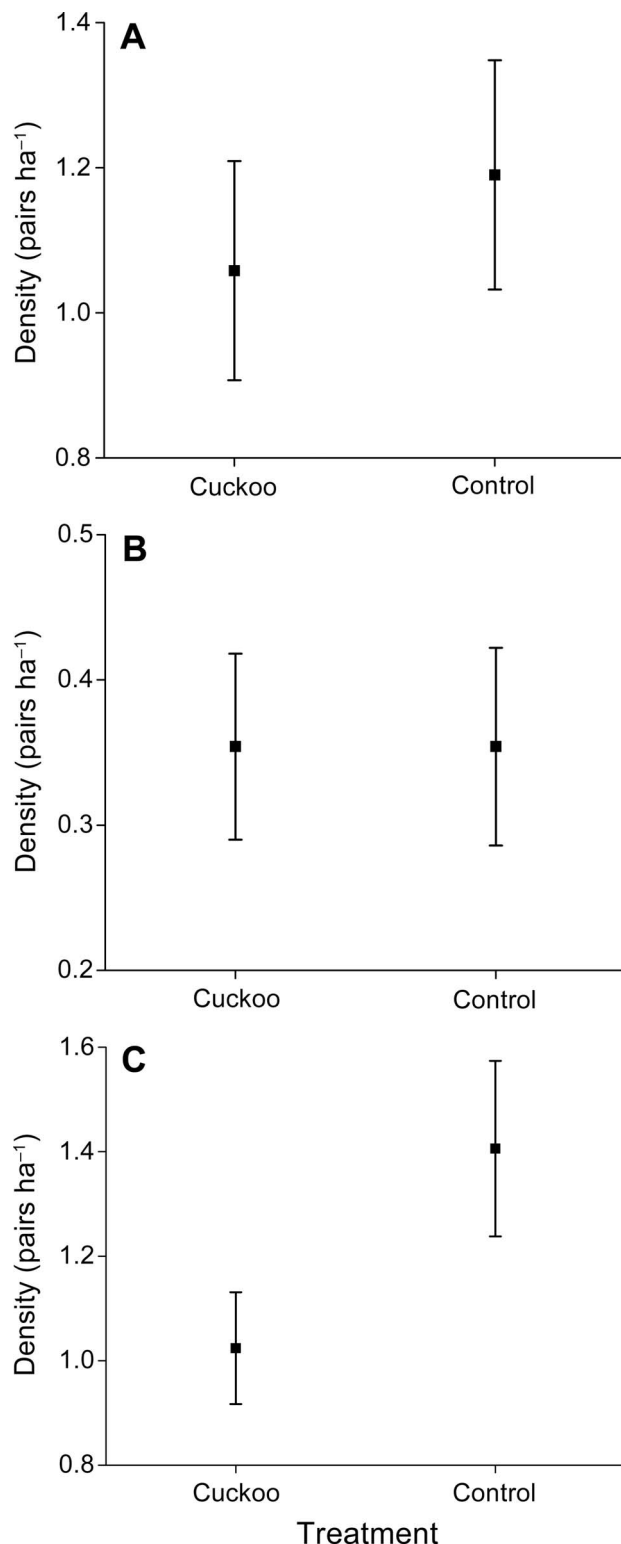
**FIGURE 1.** Mean densities ($\pm$ SE) of (**A**) non-hosts, (**B**) cavity-nesting Common Redstarts, and (**C**) open-nesting hosts in the cuckoo treatment (i.e. artificially increased cuckoo parasitism risk) and the control treatment in our study area in northern Finland, averaged over the 2 yr of the study (2011–2012).

sites in order to decrease the chances of simulated cuckoos locating their nests. Our bird community survey could not reliably distinguish between these 2 alternative explanations. However, predicting how hosts should respond to vocal cues of cuckoos is not straightforward. Nest defense is a common host behavior aimed at decreasing parasitism rates (Røskaft et al. 2002, Welbergen and Davies 2009), and therefore hosts could also be expected to be more attentive at their nests in the playback sites (cf. Davies et al. 2003), and to be more easily detected in bird surveys. Moreover, we performed the bird censuses in mid-June, when most breeding birds were incubating. Cuckoo parasitism is successful only if the female cuckoo matches its egg laying with the host's egg-laying period; therefore, there is no reason for birds to behave cryptically against cuckoos during incubation. Given that behaving cryptically probably decreases the efficiency of other duties such as foraging, birds should not be behaving that way unless there are clear fitness advantages. Also, the detectability indexes of hosts in overall and open-nesting hosts were similar between the treatments. Even though these indexes do not necessarily measure true detectability, they nevertheless suggest that host species did not behave differently in regard to their detectability in different treatments. Overall, our results suggest that open-nesting cuckoo hosts are capable of using cuckoo calls in assessing local parasitism risk, and of using that information in selecting safe breeding sites.

An intriguing contradiction to the consistent responses of the open-nesting host species was the lack of response in the only cavity-nesting cuckoo host. Common Redstarts did not show any response to the treatments in their breeding-habitat choices (effect size was even slightly positive), in their timing of breeding (laying date), or in their reproductive investment (clutch size). Given the absence of egg-rejection behavior or antiparasite adaptations at the nestling phase in our study population and in other populations (Rutila et al. 2002, Grim et al. 2009a, 2009b, Samaš et al. 2016, Thomson et al. 2016), avoidance of cuckoo parasitism via habitat choices could have been expected. One potential explanation for the lack of adaptive habitat choices could be the scarcity of, and competition for, suitable cavity nest sites. Common Redstarts may settle in any habitat patch where suitable cavities are available. Alternatively, Common Redstarts either are not capable of perceiving cuckoo vocalizations as an indication of high parasitism risk or do not use such information in habitat selection. Furthermore, because Common Redstarts are cavity-nesters, cuckoos have considerable difficulty parasitizing them; only a minority of the cuckoo eggs that are laid produce fledglings (Rutila et al. 2002, Samaš et al. 2016, Thomson et al. 2016). Consequently, the fitness costs of parasitism remain relatively low, potentially reducing the selection pressure

for antiparasite adaptations at other breeding stages. Indeed, the cavity-nesting habit per se has been suggested to have evolved in response to cuckoo parasitism (Avilés et al. 2005). The lack of adaptive habitat selection may also explain why the Common Redstart is currently a frequently used host.

Informed habitat choice to counter brood parasitism may also affect the emergence of other counteradaptations later in the breeding cycle. Current theory predicts that efficient defenses in an earlier stage of the coevolutionary cycle may inhibit the evolution of later-stage defenses, a process called "strategy blocking" or "rarer enemy effect" (Grim 2006, Britton et al. 2007). Many potential hosts of brood parasites show only low rejection rates of foreign eggs (Soler 2014). This has been attributed to evolutionary lag in hosts recently exploited by parasites or to parasites winning the arms race. In most cases, the existence of front-line defenses, especially informed habitat selection, has not been tested; thus, strategy blocking provides an additional explanation for the low prevalence of egg-rejection behavior.

Besides the parasite–host coevolutionary interactions, our results have important implications for patterns of species coexistence and bird community structure. Inconsistent behavior within the bird community in relation to cuckoo presence, with open-nesting host species avoiding cuckoos while other birds remain ignorant, results in variable community structures across the landscape. When modeling species distribution patterns and habitat selection of songbirds, spatial variation in abundance of brood parasites should be taken into account, in addition to the previously acknowledged interspecific interactions such as predation risk (Martin 1993), interspecific competition (Martin and Martin 2001), and heterospecific attraction (Seppänen et al. 2007).

In conclusion, our results suggest that open-nesting cuckoo hosts are able to use cues about cuckoo presence in adjusting their breeding-habitat selection and potentially avoiding, or at least reducing, the costs of parasitism (Forsman and Martin 2009). In addition to the inherent coevolutionary implications for parasite–host interactions, such phenomena—in which asymmetric behavior depends on the host status of species—may also influence the structure of bird communities in general. Although most studies of host–parasite coevolution have focused on phases during or after egg laying, we clearly need a holistic consideration of host–parasite coevolution across all stages of the arms race (Grim et al. 2011, Feeney et al. 2012, 2014). With the potential to shape the whole sequence and outcome of host–parasite coevolutionary interactions, the defenses preceding parasite egg laying deserve more attention—and the habitat-selection process is at the front line of these front-line defenses.

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