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RESEARCH ARTICLE

Reducing cuckoo parasitism risk via informed habitat choices

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Running head: Reducing parasitism via habitat choices

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 based on existing literature, egg-stage defenses appear 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. Density of open-nesting host species was considerably lower in sites of high perceived parasitism risk than in control sites. Hosts thus seem to be able to reduce parasitism risk through informed breeding habitat choices, but this behavior is restricted to open-nesting hosts. Cavity-nesting hosts did not respond to the simulated increase in parasitism risk, nor did bird species that are not known as regular cuckoo hosts. Informed habitat selection as an adaptation against parasitism may have important implications for parasite-host co-evolutionary interactions via reducing selection for later-stage host adaptations, and for bird community structure in general.

Keywords: brood parasitism, co-evolution, front-line defenses, eavesdropping, informed habitat selection, Common Cuckoo

INTRODUCTION

As a model system for co-evolutionary 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*) regularly parasitize up to thirty species of birds (Davies 2000). To deter parasites and salvage their own reproduction, hosts possess diverse adaptations that in turn have selected for counter-adaptations in parasites. Particularly well-studied are traits occurring 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 anti-parasite adaptations exist in all stages of the breeding cycle (Feeney et al. 2014, Soler 2014).

Especially beneficial for hosts would be the capability to collect information about local parasite abundance and select breeding sites of lower parasite abundance, i.e. parasitism risk. 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. Front-line defenses may consequently 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 co-evolutionary arms race (Britton et al. 2007, Feeney et al. 2014). Host breeding habitat selection as an adaptation against brood parasitism has however been neglected (but see Forsman and Martin 2009).

Acquiring information about relative habitat quality regarding resources or threats affecting individual fitness is wide-spread in animals (Seppänen et al. 2007, Schmidt et al. 2010). Birds may assess ambient nest predation risk via 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 emphasize 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 common 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 common cuckoo are expected to show lower abundance and 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. Eight forest patches, 5.5–11 ha in size, on average 1.4 km apart, were selected, and nest boxes were provided for the Common Redstart (*Phoenicurus phoenicurus*, hereafter redstart; a frequently used cuckoo host in the study area (Thomson et al. 2016)) and other cavity-nesting birds (12-13 boxes with 7.0 cm entrance diameter, 5-6 with 3.2 cm entrance, and 2-3 Spotted Flycatcher nest platforms). Patches were paired in respect of spatial proximity, size and habitat similarity and randomized within pairs to two treatments. Four patches were assigned the 'cuckoo' treatment: perceived risk of brood parasitism was increased using playbacks of cuckoo vocalizations. The other four patches

served as silent controls (no playback). We used the same patches in both years, but with reversed treatments in 2012.

We decided to use a silent control instead of a control with playback of singing of a presumably neutral sympatric species. The reason for this is that multiple studies have shown that individuals collect information about the environment by observing the behavior of other species, also 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 wide-spread 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 is neither a perfect solution because we do not know how birds interpret it; it may be considered as a potential threat or a novel object that may affect behavior. We acknowledge that a silent control is not a perfect control. By using a silent control we avoid the potential problems mentioned above, but on the other hand cannot rule out the possibility that the mere playback (increased vocal activity in a site) or the presence of a playback machine affects the behavior of individuals in the playback sites. However, taking into account the scale of our experiment (average patch size 8 ha), the effects of these things 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 (see also Farrell et al. 2012, Hua et al. 2013 for similar arguments). Similar experimental designs using silent controls have been extensively applied 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 mere increased vocal activity due to the playback, or the presence of a playback machine, repels birds, a consistent negative

effect on bird abundance across sites and species irrespective of the status as cuckoo hosts could be expected.

Cuckoo vocalization playbacks were started before or during the settlement of resident and arrival of migratory birds, and *ca.* two weeks before the arrival of the first cuckoos (on 27th April in 2011 and on 1st May in 2012). Playbacks continued throughout the settlement period of birds and were terminated during the first week of June. We started the playbacks prior to natural arrival of cuckoos to ensure that the experimental manipulation of perceived parasitism risk affects all forest passerines, both resident and migratory birds. Starting the playbacks before the arrival of cuckoos should not have flawed the results, since even though the earliest arriving host individuals in the study area may settle in breeding sites before cuckoos, most hosts nevertheless settle in breeding sites (i.e. start nest building) after the arrival of first cuckoos. Playback machines were constructed using car radios (Emax, product number 3147), speakers and built-in timers with car batteries as power supplies. Playbacks included male 'cu-coo' calls of four cuckoo individuals (one per patch; sound files downloaded from xeno-canto) and were played for 4.5 hours per day 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 instead of female calls, even though they do not imply parasitism risk directly. They do however indicate parasitism risk indirectly, i.e. are reliable cues, because male singing territories and female laying territories overlap (Nakamura and Miyazawa 1997; pers. obs.). In addition to the reliability, also the availability of a cue affects its biological value for a cue-user. Male 'cu-coo' calling is much more frequent and therefore more easily available for cuckoo hosts than the female calls. The better availability of cues based on male calls,

coupled with them being indirectly reliable 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, nest success) of 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 done between 6th and 14th June and 4am - 8am in fair weather by walking through each site in parallel transects about 50 m apart and recording all bird individuals heard or seen onto site maps.

Based on the two censuses we derived density estimates for forest passerine species. Due to 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 two 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 was treated as an additional “census” in a way that nest box data provided the absolute minimum pair number. If both community surveys implied higher pair number 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 higher pair number 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. In order to ensure that the results did not depend on the specific details on how the census data was 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 two censuses, or across the three “censuses” (bird surveys and nest box data) for cavity-nesting species. We performed the analyses using both density estimation methods, but since the results were qualitatively identical, we present only the results based on the “average method”.

We classified the species into two groups relative to 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, since detailed knowledge about the host status of some of these species is not available specifically for the study area. At least redstart, Brambling *Fringilla montifringilla*, Willow Warbler *Phylloscopus trochilus* and Spotted Flycatcher *Muscicapa striata* are present cuckoo hosts, and also the other species classified as hosts probably at least have 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) implying that they could be current cuckoo hosts in Finland too. Therefore, we are confident that the classification distinguishes the (potential) hosts from non-hosts as well as is currently possible.

Detectability of individuals/pairs is an essential issue in bird community censuses, and differences in detectabilities between species or experimental treatments may lead differences in census results to be erroneously interpreted as density differences. Since our community surveys were based on two censuses without explicit information about identities of individual birds, we could not estimate true detectabilities, i.e. the probability of an existing individual/pair to be observed in a specific census. We nevertheless attempted to evaluate the

effect of the treatments on the behavior of different species groups (hosts, non-hosts) regarding their detectability in the bird surveys by calculating a proxy of detectability by comparing the minimum census result to the maximum result within the two 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 of the apparent cuckoo to locate their nests via 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 higher) in the 'cuckoo' treatment compared to the 'control' treatment.

For statistical analyses we used GLMMs in Program R (version 3.2.4; R Core Team 2016). We analyzed response variables including total number and density of species, number and density of host species, non-host species and densities of the eight most abundant species (at least 10 pairs observed each year; redstart, Spotted Flycatcher, Chaffinch, Tree Pipit, Willow Warbler, Pied Flycatcher, Great Tit, Eurasian Siskin). Breeding parameters of the redstart were also analyzed. Data on redstart nest success (successful/predated) was too scarce for analyses, but simple nest success rates are reported. We assumed a normal (Gaussian) error distribution for the density variables and the redstart laying date, and a Poisson error distribution (with log link function) for the species richness variables and the 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 redstart clutch size analysis. Both variables were mean-centered. The validity of the full model regarding 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 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 AICc, and the model structure with the lower AICc value was adopted as the full model. Biologically relevant alternative models within the full models were fitted and AICc was used to determine the most parsimonious model. Variable ‘Treatment’ was retained in all models and 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 AICc, models were fitted using maximum likelihood (ML), but the model validation and the reported model statistics are based on models fitted using restricted maximum likelihood (REML). In case of the analyses with Poisson distribution Laplace approximation was always used.

RESULTS

During the experiment 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 the density of non-host species did not differ between treatments (Table 3; Figure 1A), but the density of host species was 0.39 pairs/ha (26%) lower in ‘cuckoo’

compared to control treatment (Table 3). Species-specific analyses of the most abundant species revealed that densities of all open-nesting host species were lower in ‘cuckoo’ treatment (relative decrease 16%-56%), though the decrease was not statistically significant in any of the species due to relatively low sample sizes (Table 3). The density of redstarts, the only cavity-nesting host, did not differ between treatments (relative increase 8%; Table 3, 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 redstart. Density of open-nesting hosts was 0.41 pairs/ha (33%) lower in ‘cuckoo’ treatment (Table 3, 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 seven 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 seven sites, not just due to exceptional effects in only a few sites. In non-hosts, the playback effect was negative in four sites (7%–35%), positive in two sites (7%–35%) and zero in two sites. The effect in non-hosts also contrasted the effect in open-nesting hosts in five of eight sites (negative in non-hosts and positive in open-nesting hosts in one site and zero or positive in non-hosts and negative in open-nesting hosts in four 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.

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

DISCUSSION

We demonstrate that several hosts of the common cuckoo appear to use vocal cues of the cuckoo 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 also 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 Reed Warblers (*Acrocephalus scirpaceus*) was higher in sites of lower parasitism risk, i.e. further away from perch trees that cuckoos use to search for host nests. These studies suggest that adaptive breeding habitat selection may be an important, but thus far neglected, host adaptation to counter 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 where hosts can try to

avoid cuckoo parasitism. The earlier during the breeding cycle the hosts succeed in avoiding parasitism the lower the fitness costs are. By avoiding parasitism during habitat selection, hosts would avoid the costs related to nest defense (energetic cost, risk of injury), the earliest anti-parasite defense properly recognized to-date. Therefore, cueing on e.g. vocal cues of cuckoos and subsequently adjusting ones breeding site choices (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, still a considerable proportion of individuals settled in these sites. Brood parasitism, though potentially being 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 solely towards 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). Nest success rate of redstarts was 66.7% in 'cuckoo' and 44.4% in 'control' treatments implying 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 predation rate of redstarts breeding in nest boxes would not be representative of predation risk in general, but here the 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. Resulting

non-random 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 (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 high perceived cuckoo parasitism risk. Furthermore, majority of the cuckoo parasitism events in redstart nests and 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 manipulations. 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, three redstart nests were parasitized and also real cuckoos were observed in the site during the control year, whereas no parasitized nests nor real cuckoos were observed during the treatment year.

Instead of altering habitat choices, an alternative explanation to the observed results could be that cuckoo hosts behaved more cryptically in the cuckoo playback sites in order to decrease the chances of simulated cuckoos locating their nests. Our bird community survey could not reliably distinguish between these two 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 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 host egg laying period, therefore there is no reason for birds to behave cryptically against cuckoos during incubation. Since 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 regarding 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 use 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. Redstarts did not show any response in breeding habitat choices to the treatments (effect size was even slightly positive), nor in the timing of breeding (laying date) or in reproductive investment (clutch size). Given the absence of egg rejection behavior or anti-parasitism adaptations at the nestling phase in our and other populations (Rutilla et al. 2002, Grim et al. 2009a,b, 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. Redstarts may settle in any habitat patch where suitable cavities are available. Alternatively, redstarts either are not capable of perceiving cuckoo vocalizations as indication of high parasitism risk, or do not use such

information in habitat selection. Furthermore, due to cavity-nesting, cuckoos have considerable difficulties parasitizing redstarts; only a minority of the cuckoo eggs 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 anti-parasite 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 redstart is currently a frequently used host.

Informed habitat choice to counter brood parasitism may also affect the emergence of other counter-adaptations later in the breeding cycle. Current theory predicts that efficient defenses in an earlier stage of the co-evolutionary 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, and thus strategy blocking provides an additional explanation for the low prevalence of egg rejection behavior.

Besides the parasite-host co-evolutionary interactions, our results have important implications for the patterns of species coexistence and structure of bird communities. Inconsistent behavior within the bird community relative 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 costs of parasitism (Forsman and Martin 2009). In addition to the inherent co-evolutionary implications for parasite-host interactions, such phenomenon with asymmetric behavior depending on the host status of species may also influence the structure of bird communities in general. While most studies about host-parasite co-evolution have focused on phases during or after egg-laying, we clearly need a holistic consideration of host-parasite co-evolution 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 co-evolutionary interactions, the defenses preceding parasite egg-laying deserve more attention, with the habitat selection process being at the 'front-line of the front-line defenses'.

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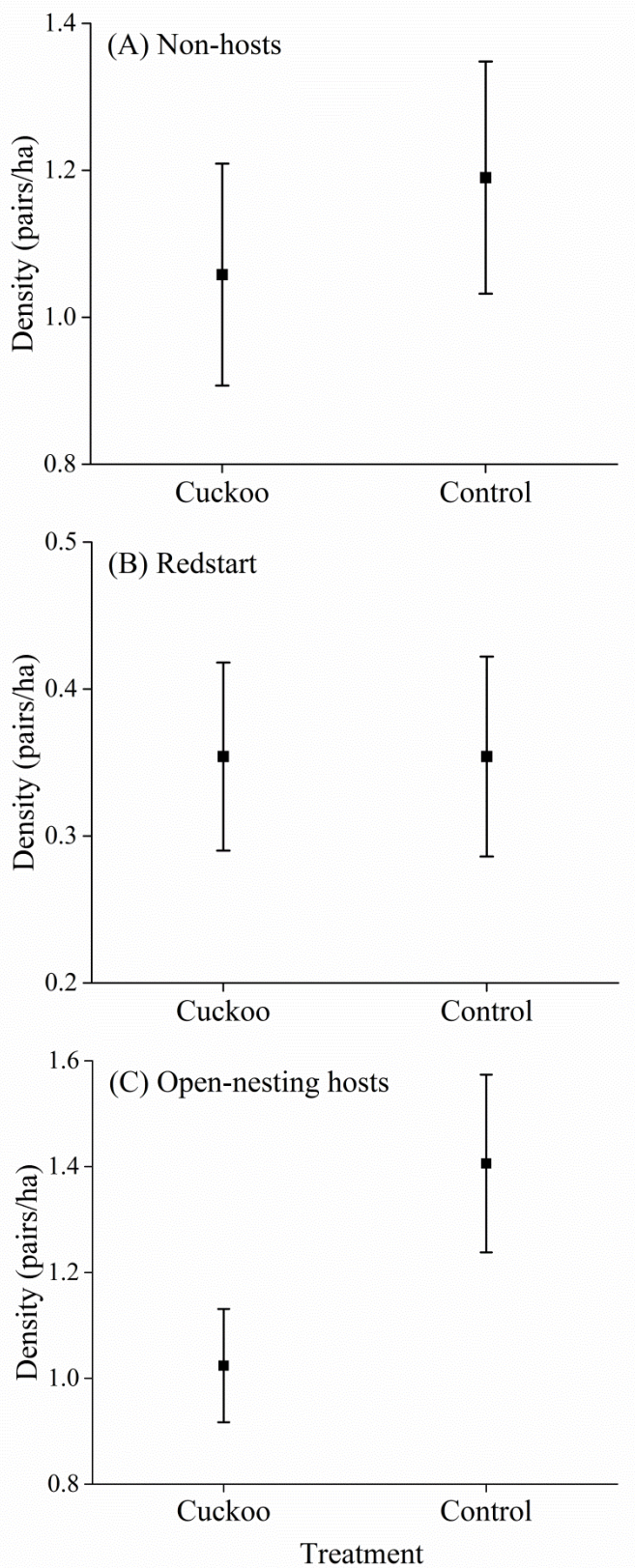


FIGURE 1. Mean densities of birds (\pm SE) in artificially increased cuckoo parasitism risk and control treatments, averaged over the two years. Density of **(A)** non-hosts, **(B)** cavity-nesting redstart and **(C)** open-nesting hosts.

TABLE 1. List of observed forest passerine species, the classification to hosts and non-hosts and the estimated number of pairs (estimates based on the “average method”, see methods for details) observed during the experiment.

Species	Host classification	Estimated number of pairs
Chaffinch (<i>Fringilla coelebs</i>)	Host	46.5
Common Redstart (<i>Phoenicurus phoenicurus</i>)	Host	39
Spotted Flycatcher (<i>Muscicapa striata</i>)	Host	29.5
Tree Pipit (<i>Anthus trivialis</i>)	Host	23
Willow Warbler (<i>Phylloscopus trochilus</i>)	Host	20
European Robin (<i>Erithacus rubecula</i>)	Host	5.5
Brambling (<i>Fringilla montifringilla</i>)	Host	2.5
Dunnock (<i>Prunella modularis</i>)	Host	1
Pied Flycatcher (<i>Ficedula hypoleuca</i>)	Non-host	62.5
Great Tit (<i>Parus major</i>)	Non-host	36
Eurasian Siskin (<i>Carduelis spinus</i>)	Non-host	20
Goldcrest (<i>Regulus regulus</i>)	Non-host	2.5
Fieldfare (<i>Turdus philomelos</i>)	Non-host	2
Willow Tit (<i>Poecile montanus</i>)	Non-host	1.5
Crested Tit (<i>Lophophanes cristatus</i>)	Non-host	1.5
Bullfinch (<i>Pyrrhula pyrrhula</i>)	Non-host	1.5
Redwing (<i>Turdus iliacus</i>)	Non-host	1
Mistle Thrush (<i>Turdus viscivorus</i>)	Non-host	0.5
Blackbird (<i>Turdus merula</i>)	Non-host	0.5
Coal tit (<i>Periparus ater</i>)	Non-host	0.5

TABLE 2. AICc statistics of models explaining variation in different response variables. The final models with the lowest AICc value are in bold.

Response	Model	Δ AICc ^a	Akaike weight
Total species	Treatment	0.00^b	0.72
richness	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	Treatment	0.00^c	0.73
richness	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	Treatment	0.00^d	0.69
richness	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,	Treatment + Year	0.00^f	0.53
all species	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,	Treatment + Year	0.00^g	0.43
open-nesters	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
Redstart density	Treatment	0.00ⁱ	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	Treatment	0.00^j	0.67
density	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
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
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	0.00ⁿ	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
Redstart laying date	Treatment	0.00^q	0.73
	Treatment + Year	2.46	0.21
	Treatment * Year	5.34	0.05
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 AICc 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.

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

Response	Parameter	Estimate	SE	df	t/z-value^a	P-value
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
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
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
Redstart laying date	Intercept	27.56	1.30	27	21.18	<0.001
	Treatment (Cuckoo)	-1.44	1.84	27	-0.79	0.44
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 redstart laying date variables, z-value otherwise

^b Estimates in log (link function) scale