Choice of nest attributes as a frontline defense against brood parasitism

Abbreviated title: Nest attributes as a defense against brood parasitism.

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ABSTRACT

Breeding- and nest-site choice is a behavioral strategy often used to counter negative interactions. Site choices prior to breeding prevents costs of predation and competition but has been neglected in the context of brood parasitism. For hosts of brood parasites, the earlier brood parasitism is prevented in the breeding cycle the lower the future costs. Suitable nest-sites for cavity-nesting common redstarts (*Phoenicurus phoenicurus*), a host of the common cuckoo (*Cuculus canorus*), are a limited resource, but their cavity-nesting strategy could potentially deter predators and brood parasites. We altered the entrance size of breeding cavities and investigated redstart nest site choice and its consequences to nest predation and brood parasitism risk, while accounting for potential interspecific competition for nest sites. We set-up paired nest-boxes and let redstarts choose between 7 cm and 5 cm entrance sizes. Additionally, we monitored occupancy rates in nest-boxes with 3 cm, 5 cm and 7 cm entrance sizes and recorded brood parasitism and predation events. We found that redstarts preferred to breed in 5 cm entrance size cavities, where brood parasitism was eliminated but nest predation rates were comparable to 7 cm entrance size cavities. Only in 3 cm cavities were both brood parasitism and predation rates reduced. In contrast to the other cavity-nesting species, redstart settlement was lowest in 3 cm entrance size cavities, potentially suggesting interspecific competition for small entrance size cavities. Nest site choice based on entrance size could be a front-line defense strategy that redstarts use to reduce brood parasitism.

Keywords: evolutionary arms-race, breeding-site choice, co-evolution, defense strategy, interspecific competition, nest predation.

INTRODUCTION

Breeding and nest site choice has profound fitness consequences because many crucial biotic factors (e.g. food resources and predation rates, Martin 1995) vary spatially (Schmidt et al. 2006; Thomson et al. 2006; McCaffery et al. 2014; Lino et al. 2019). Informed breeding site choice that considers different biotic variables could increase the likelihood of reproductive success and adult survival (Cody 1985; Reynolds 1996; Seppänen et al. 2007; Chalfoun and Schmidt 2012; Lehtonen et al. 2013; Ibáñez-Álamo et al. 2015; Cayuela et al. 2017). Safe breeding sites are essential (Fontaine and Martin 2006; Russell et al. 2009), and are usually well-hidden and difficult to reach, making them challenging for predators and parasites to locate or access (Mezquida 2004; Buehler et al. 2017). Therefore, breeding site selection is an adaptive response to enhance breeding outcome.

In birds, nest predation risk is a strong force in determining nest site choice at many spatial scales (Martin 1993). Birds avoid habitat patches with high predator densities (Schmidt et al. 2006; Chalfoun and Schmidt 2012), or may nest in concealed locations within habitat patches of high risk (Mezquida 2004; Eggers et al. 2006; Buehler et al. 2017). Nest site characteristics can also reduce predation pressure (Martin and Pingjun Li 1992; Chalfoun and Schmidt 2012) but suitable or safe sites are often a limited resource (Newton 1994; Aitken and Martin 2012, however, see Wesołowski 2007). For example, secondary cavity-nesters often prefer small entrance sizes and deep cavities that limit predator access (Wesołowski and Rowiński 2004; Koch et al.

2008; Lambrechts et al. 2010; Cockle et al. 2015), but at the cost of higher intra- and interspecific competition (Wiebe 2011; Aitken and Martin 2012).

Brood parasitism represents a significant cost for some bird species (Davies 2000). Hosts get exploited for parental care, which imposes long-term energetic costs of rearing parasite offspring, in addition to the loss of host progeny, which are often killed by the young brood parasite (Davies 2000). The fitness costs of brood parasitism, in terms of lifetime reproductive output, may be even higher than the costs stemming from predation (Pease and Grzybowski 1995; Schmidt and Whelan 1999; Krüger 2007). Yet, the impact of brood parasitism as a selective force for shaping breeding site choice in these systems is largely unknown. Understanding if nest-site choice is an adaptative defence strategy is needed to allow better interpretations of the arms-race in parasite-host systems.

The study of the arms-race between brood parasites and their hosts has mainly focused on adaptations at the egg-laying and nestling stages of the breeding cycle (Feeney et al. 2012). For a host, however, the best strategy would be to avoid being parasitized in the first place, since all post-parasitism defences carry costs (Patten et al. 2011). Strategies at the frontline of the arms-race (prior to the parasite egg being laid), such as nest site choice in location or characteristics, may be subject to strong natural selection (Patten et al. 2011). At the habitat patch scale, nest-site decisions relative to brood parasitism risk have been documented (Forsman and Martin 2009; Tolvanen et al. 2017), while previous experience with brood parasites influence future nest-site choice of individual hosts (Hoover 2003a; Expósito-Granados et al. 2017). Nevertheless, nest placement and nest architecture have been poorly explored as strategies against brood parasitism. It has been suggested that cavity-nesting could be an adaptive response to brood parasitism risk (Avilés et al. 2005). However, there is no empirical evidence supporting this idea.

The common redstart (*Phoenicurus phoenicurus*, hereafter "redstart") is an excellent model to test nest-site choice as an adaptative defence against brood parasitism. It is a cavity-nesting species and regular host (32% of nests are parasitized, Thomson et al. 2016) of the common cuckoo (*Cuculus canorus*, hereafter ''cuckoo''). Cuckoos appear to struggle to lay in cavity nests based on the high proportion of cuckoo eggs mislaid outside of the host nest cup in nest-box studies (Rutila et al. 2002; Samaš et al. 2016; Thomson et al. 2016). If entrance size choice is an adaptive response to parasitism risk, redstarts should prefer to breed in cavities with entrance sizes that hinder cuckoo access. Redstarts also suffer nest predation and entrance size choice may be an adaptive response to decrease nest predation rates. Indeed, separating the role of nest predation and brood parasitism on the host nest site choice of hosts is difficult because nest site characteristics selected may similarly impact these processes. Lastly, redstart may compete with other cavity-nesting species for limited optimal cavity nest-sites (Lambrechts et al. 2010; Aitken and Martin 2012; Charter et al. 2016). Therefore, we also consider the nest site decisions of two common cavity nesting species that may compete for cavities with redstarts: the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*). Great tits are residents that start breeding before redstarts; while migrant pied flycatchers arrive at a similar arriving time to redstarts. Great tits sometimes kill pied flycatchers to steal nest boxes (Samplonius and Both 2019), and pied flycatchers are known to build their nest on top of other existing nest, taking over cavities that way (Slagsvold 1975).

Our main aim was to test the choice of nest characteristics, specifically preference for certain cavity entrance sizes, and then follow the consequences on breeding success. We used nest-boxes with three different entrance diameters: 3 cm, 5 cm and 7 cm in diameter, to understand redstart preference and choice for nest-site cavity size. We also followed the cavity entrance size preferences of pied flycatcher and great tit, to account for their potential competitive influence on redstart choice. Given the potential trade-offs between different selective forces acting simultaneously, (1) redstarts will prefer breeding in smaller entrance-size cavities, that represent a safer place to breed since they restrict entry of cuckoos and large predators. We predict higher occupation of redstarts in the smaller entrance cavities, while expecting decreased nest predation and parasitism rates in those cavities. However, (2) interspecific competition with other birds of the community may cause redstarts to use bigger entrance-size cavities, make them more vulnerable to cuckoo parasitism and nest predation. We expect higher preference for the smallest entrance-size in other species (i.e., great tits and pied flycatchers), while redstart will then have higher occupation rates in mid entrance-size nest-boxes, where brood parasitism rates are lower, but nest predation rates remain similar as the biggest entrance-size.

METHODS

Study Area and General Protocol

Our study was conducted near Oulu, Northern Finland (65°N, 25° 50´ E), between 2012 and 2019, in a study area of approximatively 60 km^2 that consisted of open scots pine (*Pinus sylvestris*) forests. Natural cavities in our study site vary from large entrances made by black woodpeckers (*Dryocopus martius*, ca. 9 cm, Rolstad et al. 2000), medium-sized cavities of great spotted woodpecker and three-toed woodpecker (*Dendroscopus major* and *Picoides tridactyla*, ca. 5 cm and 4.5 cm, Gorman 2004; Kosiński and Ksit 2007), to small cavities made by willow and crested tits (*Parus montanus* and *P. cristatus*, ca. 3 cm, Denny and Summers 1996; Wesolowski 2002). Cavities are used by different secondary cavity-nesters.

Studies of redstarts as subjects usually used nest-boxes with 6-8 cm diameter entrances (Samaš et al. 2016; Thomson et al. 2016); while for great tits and pied flycatchers nest-boxes with 3-4 cm diameter entrances are used (Thomson et al. 2003; Forsman and Seppänen 2011). In our study area, great tits and pied flycatcher annually occupy about 25% and 60% of small entrance size nest-boxes, respectively. However, great tits and pied flycatchers are considered non-hosts of the cuckoo, while redstarts are a common host (Grim et al. 2014; Grim and Samaš 2016; Samaš et al. 2016; Thomson et al. 2016).

As residents, great tits choose where to breed first, leaving the rest of the cavities to migrant, pied flycatchers and redstarts (Kristensen et al. 2013; Ouwehand et al. 2016). The earliest redstarts arrive at the breeding patches before pied flycatchers, but the settlement periods overlap for most of the populations (unpublished data). Redstarts initiate breeding in our study site between May 15 and June 15, while pied flycatchers initiate breeding between May 17 and June 23.

We placed nest-boxes in pines approximately 1.5 m above the ground and 100–220 m apart since 2011. All nest-boxes had the same dimensions: 17.5 x 17.5 x 28 cm (width, depth and height), and an entrance hole diameter of 7 cm. However, to simulate the entrance sizes of different natural cavities, we altered the size of the entrance hole of the nest-boxes using wooden covers screwed onto the box to cover the existing entrance hole (Figure 1). Using this manipulation three different nest-box entrance diameters: 3 cm, 5 cm, 7 cm (hereafter referred to as 3 cm box, 5 cm box and 7 cm box, respectively) were available to birds. Similar box manipulations in a pied flycatcher study resulted in meaningful differences in predation rate and incubation behavior (Morosinotto et al. 2013).

Annually, we checked nest-boxes every 2 to 4 days from early May until late-June (Thomson et al. 2016). Approximately 400 nest-boxes were monitored each year to collect data on redstarts breeding and brood parasitism rates by cuckoos as part of a long-term study. For all occupied nest-boxes we recorded: laying date, clutch size, brood size and any parasitism or predation events. A nest-box was considered occupied when at least 1 egg was laid in it. Only the first breeding attempt in each nest-box was considered for analyses. Nest-box occupancy by other species (mainly great tit and pied flycatcher) was recorded. We captured adult redstarts breeding in the nest-boxes between 2014 and 2017, however, return rates were very low: 1 of 237 ringed redstart females and 7 of 133 redstart males were recaptured. This suggests that the turnover in the breeding population across years is high.

Nest Cavity Entrance Size Choice Experiment

We conducted a cavity entrance size choice experiment in 2012 and 2013. In each experimental set-up redstarts could select between a 5 cm box and a 7 cm box approximately at 5 – 15 m apart (Table 1). We placed 59 choice set-ups: 29 in 2012 and 30 in 2013 (different locations between years). Only one redstart pair settled in each set-up.

Potential Factors Influencing Nest Choice

Parasitism and predation rates

We explored brood parasitism and nest predation rates in 5 cm vs 7 cm boxes in 2012 and 2013 using all nests in the experimental set-ups and the general box population (Table 1). To account for environmental conditions, we divided the study area into two main subareas, “Isokangas” and “Other”. Isokangas consists of a non-fragmented forest (approx. 6 km^2), while “Other” consists of an aggregation of several smaller patches of forest (approx. 5 km^2 combined). When calculating predation rates, we only consider predation events during the egg-laying period, since we were interested in the factors affecting nest site choice at the very early breeding phase. Therefore, most nests were partly protected from predation from early incubation by placing wire cages over the entrance of nest-boxes (Thomson et al. 2016). This also ensure that enough redstarts and cuckoos survive to make other concurrent studies possible. Nests, where predation occurred before the fifth redstart egg was laid, were not considered for the parasitism rate, since it was impossible to determine if the nest was previously parasitized or not.

Nest entrance size choice in heterospecific communities

We explored preferences of different entrance size nest-boxes for the common cavity-breeders in our area (redstart, great tit and pied flycatcher). During the breeding seasons of 2014-2017, and 2019, we used two dedicated areas of non-fragmented forest within Isokangas, and a new patch of forest called Pilpakangas (ca. 1 km^2 each and ca. 8 km apart). Nest-boxes with different entrance sizes were interspersed (Table 1), keeping approximately 90-150 m apart. These boxes were available to redstarts, pied flycatchers and later-breeding great tits and were regularly monitored as described above.

Between 2014 and 2017, we used 7 cm and 3 cm boxes (hereafter referred to as 3 cm vs. 7 cm box design); while in 2019, we placed all three different entrance size nest-boxes (hereafter referred to as 3 cm vs. 5 cm vs. 7 cm box design). For the 3 cm vs. 7

cm box design, entrance covers were placed between May 12-14 (before redstart settlement, 2014-2017). For 3 cm vs. 5 cm vs. 7 cm box design, all entrance sizes were available from May 14 onwards, except for the Isokangas area where 5 cm boxes were only available from May 21. However, only 3 redstart nests were initiated before May 21, thus this slight delay did not impact the nest site decisions for the vast majority of redstarts. In addition, our Cox regression models used to analyze this data account for the availability of the entrance sizes (see below for details).

We used brood parasitism and nest predation rates to analyze how multiple selective pressures can contribute to the entrance size choice. We calculated brood parasitism for redstarts, and nest predation rates for each species, as described above (see *Parasitism and predation rates*). However, due to other concurrent studies, for most nest-boxes occupied by pied flycatcher the initial entrance size was altered before the 3rd egg was laid having 7 cm diameter for most of the laying period. These nests were not considered for calculating nest predation or parasitism rates. The resulting low numbers of nests and low variation in predation rates prohibited any statistical analyses for this data (see Table 2).

Natural Cavities

During 2011-2017 we found redstart nests in natural sites on an ad-hoc basis. When located, the nests were classified as ground or tree cavity nests. For tree cavity nests we measured the distance above the ground (to the nearest 0.1 m), and the dimensions of the cavity hole entrance, as the vertical and horizontal diameter (to the nearest mm).

Table 1. Overview of the different data collection procedures in nest boxes followed in this study.

Year	Type of boxes	Total number of boxes	Description	Statistical analysis
2012 -2013				
Experimental design	5 cm 7 cm	59 59	Experimental set-up consisted of two nest-boxes, one 5 cm box and one 7 cm box, placed 5 – 15 m apart within two main subareas (Isokangas and Other).	Bootstrap/ GLMM
General box population	7 cm	136	Nest-boxes not used in the experiment but available in the study area. These were used for estimating predation and parasitism rates.	GLMM
2014-2017				
Two subsets of the general box population	3 cm 7 cm	273 252	Two distinct areas, with approximately 70 boxes of 3 cm entrance (35 boxes in Isokangas/ 35 boxes in Pilpakangas) and 60 boxes of 7 cm entrance (32 boxes in Isokangas/ 28 boxes in Pilpakangas), interspersed within each site annually. Annual number of boxes varied due to losses and occupation by invertebrates. “Total number of boxes” refers to the total number over all four years.	Cox regression
2019				
Two subsets of the general box population	3 cm 5 cm 7 cm	41 37 41	The same two distinct areas populated with 3 cm, 5 cm and 7 cm boxes, interspersed within each site. To ensure that all sizes were available throughout the season, we changed the covers of some nest-boxes setting up different entrance sizes when needed.	Cox regression

Statistical Analyses

All statistical analyses were conducted using R (version 3.6.2; R Development Core Team 2019). For each analysis, the modelling procedure started with building a full model including all relevant explanatory variables and interactions (see below for details). We searched for the most parsimonious model by fitting a null model (no explanatory variables) and all subset models including the entrance size (the main variable of interest) within the full model (see supplementary Table S1 for the full list of fitted models). We used AICc criteria for ranking the models. We then followed Richards et al. (2011) and defined final model sets as those within 6 AICc units but excluding models that were more complex versions of a model with lower AICc. If there were more than one model in the final set, we focused on the best-ranking model but also note if the inferences based on the other model(s) in the final model set differ. We base our statistical inferences on the parameter mean estimates and their 95% confidence intervals. Collinearity between explanatory variables was acceptable in all models (variance inflation factors, VIF < 3 in all cases; Zuur et al. 2010). Statistical analyses performed for each set-up are shown in Table 1.

Nest cavity entrance size choice experiment

To test differences in the likelihood of occupation between 5 cm and 7 cm boxes we fitted a binomial generalized linear model (GLM) with logit link function. The choice between the 5 cm and 7 cm nest-boxes was used as the binomial response variable (occupancy of 5 cm boxes 0 and of 7 cm boxes 1). Only the intercept was fitted as an explanatory variable. Thus, if the intercept is significantly negative the 5 cm box was preferred; if it is significantly positive the 7 cm box was preferred.

Parasitism and predation rates

Due to the complete lack of parasitized nests in 5 cm boxes (see Results), we used a resampling approach to test if brood parasitism rates differed between 5 cm and 7 cm boxes. Using a statistical bootstrap (resampling technique, Mooney and Duval, 1994), we estimated the likelihood of nests in 5 cm boxes being parasitized, assuming equal parasitism probability irrespectively of the entrance size. This approach produces a distribution of the expected parasitism events relative to the entrance size to compare with our observed data. The process consisted of generating 10000 permutations of a random sample of nests (without replacement) from the original dataset (including both entrance sizes). Considering the unequal distribution of 5 cm and 7 cm boxes between the two subareas (Isokangas and Other), the resampling approach accounted for spatial variation in parasitism rate between subareas at each permutation. The random sample size matched the number of nests that were parasitized in the study area between 2012-2013 (a total of 38 nests parasitized). For every nest selected, we first generated a random number between 1 and 100, to simulate a parasitism event. The nest was considered parasitized, and was therefore kept in the random sample, only if the random number generated was equal or lower than the observed parasitism rate of the subarea where the nest was located (23% for nests located in Isokangas and 15% for nests located in Other). If the random number was higher than the observed parasitism rate, a new nest was randomly selected from the original data set and a new random number, between 1 and 100, was generated. This process was repeated until each new nest was parasitized (i.e., the random number generated was lower or equal than the observed parasitism rate for the specific subarea of the nest). Therefore, for each permutation, the random sample was consistently made of 38 parasitized nests. Then the number of nests parasitized within 5 cm boxes was extracted for each permutation, and the probability of having zero parasitized nests in 5 cm boxes within the 1000 permutations was derived.

We also compared the probability of nest predation in 5 cm and 7 cm boxes using a binomial GLMM with a logit link function. The predation occurrence (yes/no) was set as the response variable and the entrance size of the box (5cm/7cm) as a fixed explanatory effect. The full model also included the subarea (Isokangas/Other) and year (2012/2013) as fixed effects to account for potential spatio-temporal variation in predation rate. Finally, we included the ID of the nest-box as a random-intercept effect since some of the nest-boxes were used in both years.

Nest entrance size choice in heterospecific communities

We used Cox proportional-hazards regression models (hereafter Cox models, Cox and Oakes 1984; Therneau and Grambsch 2000) to estimate the preference of the passerine community (redstarts, pied flycatchers and great tits) for the different entrance sized boxes. Cox models are often used to model survival but can be used to model any time-to-event data (see Forsman and Seppänen 2011; Samplonius and Both 2017; Tolvanen et al. 2020). Cox models estimate the relative probability (hazard ratio) of the event over time, with the event here being the nest-box occupation. We used the function *cox.zph* (package *Survival*; Therneau 2020) to build models for each set-up: 3 cm vs. 7 cm box design, and 3cm vs. 5cm vs. 7cm box design. Redstart and pied flycatcher occupancy were analyzed for both study designs, but data for great tit was adequate only for the 3 cm vs. 7 cm box design. Occupancy date was defined as the estimated nest initiation date (see *Supplementary material*). Nest-box entrance size was set as an explanatory fixed effect in all models. For the 3 cm vs. 7 cm box model, the entrance size was fixed for each nest-box during the whole breeding season (time-independent variable). However, in the case of the 3 cm vs. 5 cm vs. 7 cm box design, the entrance size is a time-dependent variable because additional covers were placed onto a subset of the nest-boxes at different times along the season (see Table 1). Year (only for the 3 cm vs. 7 cm box model: 2014-2017) and forest patch (Isokangas/Pilpakangas) were included as additional fixed effects to account for possible weather, and other environmental conditions, that may vary over time and space. For the 3 cm vs. 7 cm box design, we also tried the interaction between Year and Patch, but such models did not pass the proportional hazards assumption test (important for valid Cox models). In addition, for the pied flycatcher 3 cm vs. 7 cm box analysis, Year as a fixed effect did not pass the proportionality assumption, and was thus fitted as a *strata* effect, that is, the model accounted for the Year effects by allowing variable baseline hazards for different years but did not produce a Year effect estimate. Since the same nest-boxes were used for multiple years we also fitted the full models with including the ID of the nest-box as a random effect, using the function *coxme* (package *coxme*; Therneau 2019), but these mixed models had clearly higher AICc than the ordinary Cox models without the random effect and qualitatively identical fixed effect estimates to the ordinary Cox models (results not detailed). We thus focused on the ordinary Cox models without the random effect. All the full and final models fulfilled the proportionality assumption (global tests, $p > 0.5$).

RESULTS

Nest Cavity Entrance Size Choice Experiment

Out of the 59 choice set-ups, we recorded 29 redstart breeding site choices. In all but one case, redstarts chose to breed in the 5 cm box over the 7 cm box (96%; GLM, intercept = -3.33 [-6.21, -1.79]). The other set-ups (30 out of 59) were occupied by pied flycatchers (17 set-ups, all chose 5 cm box) or great tits (6 set-ups, all but one chose the 5 cm box) or were not occupied at all (7 set-ups).

Potential Factors Influencing Nest Choice

Parasitism and predation rates

Considering all nest-boxes occupied by redstarts in our study area in 2012-2013 (Table 2), none of the nests within 5 cm boxes (excluding 3 predated nests) were brood parasitized, while 33.6% of nests in 7 cm boxes (excluding 17 nests: 1 abandoned and 16 predated nests) were brood parasitized (Table 3). Under the assumption that the entrance size does not affect brood parasitism rates, the bootstrapped samples suggest that the likelihood of zero parasitism events in redstart nests in 5 cm boxes was 2 out of 10000.

Table 2. Number of nest-boxes occupied by each species or left unoccupied, for each study design. The proportion of occupied boxes in parentheses. *Nest-boxes in the 2012-2013 study are set-up paired and only one box could be occupied per set-up.

Year	3 cm	5 cm	7 cm
2012-2013 (experimental paired design)*			
Redstart	-	28 (0.47)	1 (0.02)
Pied Flycatcher	-	17 (0.29)	0 (0.00)
Great Tit	-	5 (0.08)	1 (0.02)
Empty	-	9 (0.15)	57 (0.97)
Total	-	59	59
2014-2017			
Redstart	19 (0.07)	-	149 (0.59)
Pied Flycatcher	217 (0.80)	-	0 (0.00)
Great Tit	26 (0.09)	-	8 (0.03)
Empty	11 (0.04)	-	95 (0.38)
Total	273	-	252
2019			
Redstart	7 (0.17)	19 (0.53)	17 (0.42)
Pied Flycatcher	27 (0.66)	2 (0.05)	3 (0.07)
Great Tit	6 (0.15)	0 (0.00)	0 (0.00)
Empty	1 (0.02)	16 (0.42)	21 (0.51)
Total	41	37	41

For nest predation in 2012-2013, only the null model was included in the final model set (Table 4). Therefore, there was no effect of entrance size on nest predation rate (entrance diameter, 7 cm vs. 5 cm, effect estimate: -0.07 [-0.98 – 0.83], see also R^2 in supplementary material Table S1); 25.8% of the nests in 5 cm boxes were predated (Table 3), while 24.4%; of the nests in 7 cm boxes (excluding 3 nests) were predated (Table 3). Between 2014-2019, in both set-ups (3 cm vs 7 cm box design and 3 cm vs 5 cm vs 7 cm box design), we found an absence of cuckoo parasitism in redstart nests placed in 3 cm and 5 cm boxes; all parasitic events occurred in 7 cm boxes (39.9% of nests in 7 cm boxes were parasitized, Table 3). Also, nest predation in redstart nests was absent in 3 cm and 5 cm boxes (Table 3), while the predation rate in 7 cm boxes occupied by redstarts was 14.5% between 2012 and 2019 (Table 3).

Table 3. Number of nests parasitized or predated for each species in each nest-box type. The total number of nests per entrance size are provided in parentheses. Nest-boxes were considered occupied when at least one egg was laid. For the calculation of the brood parasitism rate, nests where predation or abandonment occurred before the fifth egg was laid were excluded. No brood parasitism was observed in pied flycatchers and great tits.

		3 cm	5 cm	7 cm
Brood parasitism rate				
Redstart	2012-13	-	0 (28)	38 (113)
	2014-17	0 (6)	-	54 (133)
	2019	0 (3)	0 (8)	5 (15)
	Percentage	0% (9)	0% (36)	37.2% (261)
Nest predation rate				
Redstart	2012-13	-	8 (31)	31(127)
	2014-17	0 (6)	-	9 (146)
	2019	0 (3)	0 (8)	2 (16)
	Percentage	0 % (9)	20.5% (39)	14.5% (289)
Pied	2014-17	0 (14)	-	0 (0)
Flycatcher	2019	0 (7)	0 (0)	0 (3)
	Percentage	0% (21)	-	0% (3)
Great Tit	2014-17	0 (20)	-	0 (6)
	2019	0 (6)	0 (0)	0 (0)
	Percentage	0% (26)	-	0% (6)

For other cavity-nesting species in the community, nest predation was absent in 3 cm boxes (Table 3), and none of the three pied flycatcher nor six great tit nests in 7 cm boxes were predated (Table 3).

Nest entrance size choice in heterospecific communities

For preference of 3 cm vs. 7 cm box design, the final model set for redstarts included only one model (Table 4) that showed a clear preference of redstarts for 7 cm over 3 cm boxes (Table 5, Figure2A). Overall, 7 cm boxes were chosen 5 times more often than 3 cm boxes (Table 5). The model also suggested spatio-temporal variation in the overall occupancy rate (independent of the entrance size) between years and the two habitat patches (Table 5). For preference considering all three entrance sizes (3 cm vs. 5 cm vs. 7 cm design), the final model set included two models (Table 4). The best rated one suggesting that redstarts preferred 5 cm boxes over 3 cm or 7 cm boxes (Table 5, Figure 2B). Overall, redstarts were 2.7 times more likely to occupy 5 cm than 3 cm boxes. There was no clear difference between occupancy of 7 cm and 3 cm boxes (Table 5).

For other cavity-nesting species in the community, in both the 3 cm vs. 7 cm and 3 cm vs. 5cm vs. 7cm designs, we found a clear preference of 3 cm boxes for both pied flycatcher and great tit (Table 5). Few 3 cm boxes remained unoccupied (<4%), while almost half of 5 cm boxes remained unoccupied (Table 2). Note that great tits did not occupy any 5 cm boxes in 2019 (the only year including 5 cm boxes); while pied flycatchers only occupied two 5 cm boxes (Table 2).

Table 4. Model statistics of the final model sets for nest predation in redstart (binomial GLMs), and nest-box occupancy in redstart, pied flycatcher and great tit (Cox regression). The number observations (n) is given but for the Cox regressions refers to the number of events (i.e. occupation of a nest box). However, for the design of 3 cm vs 7 cm 516 nest boxes were included in the analysis, and for 3 cm vs 5 cm vs 7 cm was 2209 entries were considered. Note that the number of observations of the 3 cm vs 5 cm vs 7 cm design is so big because the entrance size is a time-dependent variable, therefore, each day for each box has a unique entry.

Factor	Model parameters	n	Df	AICc	dAICc	Akaike weight	R^2 (%)
Nest predation							
Redstart	Null	158	2	180.70	0.00	1.00	-
Occupation 3 cm vs 7 cm							
Redstart	Entrance size + Year + Site	165	5	1766.93	0.00	1.00	39.05
Pied flycatcher	Entrance size + strata(Year)	217	1	1446.08	0.00	1.00	86.43
Great tit	Entrance size	28	1	315.98	0.00	1.00	50.92
Occupation 3 cm vs 5 cm vs 7 cm							
Redstart	Entrance size	42	2	357.22	0.00	0.85	16.78
	Null	42	0	360.63	3.41	0.15	-
Pied flycatcher	Entrance size + Site	29	2	169.82	0.00	0.65	93.47
	Entrance size	29	1	171.07	1.24	0.35	92.62

Natural cavities

During the study period, we documented 10 natural redstart nests: eight in secondary cavities located on tree trunks (six in Scots pine trees, one in a birch and one in an aspen), and two on the ground (one within the root system of a fallen pine, the other below moss of a small mound). The tree cavity nests were on average 3.4 ± 0.4 m (range 1.7 m – 5 m) above ground, with cavity entrances having an average a horizontal diameter of 5.2 ± 0.2 cm (range 4.8 cm – 6.1 cm), and vertical diameter of 5.4 ± 0.3 cm (range 4.4 cm – 6.5 cm); all of them roughly round and assumed to be made by great spotted woodpeckers. Five cavity nests were checked during the chick phase and none contained a cuckoo chick. The two ground nests were also checked and one (the nest below the moss) had been parasitized. The cuckoo chick hatched and evicted all redstart' chicks but was predated prior to the next nest inspection.

Table 5. Final cox regression models for nest-box occupancy in heterospecific communities. The exponentiated coefficient column describes how much more/less likely a nest-box in the specific group was occupied compared to the baseline group. For example, redstarts were 5 times more likely to occupy a 7 cm than a 3 cm box; or occupancy was 0.83 times as likely (or 17% less likely) in 2015 than in 2014. Parameter estimates for which the 95% CI of the exponentiated coefficient excludes one, are in bold. Given the low occupancy (n=6) of great tits for the 3 cm vs 5 cm vs 7 cm design, we did not perform a cox regression on them. Sample sizes are given in Table 4.

Choice	Parameter	Coefficient	exp(Coefficient)	95% CI
3 cm vs 7 cm				
Redstart	Entrance size, 7 cm	**1.61**	**5.00**	**3.08, 8.14**
	Year, 2015	-0.19	0.83	0.55, 1.24
	Year, 2016	**-0.43**	**0.65**	**0.43, 0.99**
	Year, 2017	**-1.02**	**0.36**	**0.23, 0.58**
	Site, Pilpakangas	**0.46**	**1.59**	**1.17, 2.16**
Pied flycatcher	Entrance size, 7 cm	-20.10	<0.01	0, Inf
Great tit	Entrance size, 7 cm	**-2.06**	**0.13**	**0.04, 0.38**
3 cm vs 5 cm vs 7 cm				
Redstart	Entrance size, 5 cm	**0.98**	**2.71**	**1.09, 6.73**
	Entrance size, 7 cm	0.10	1.10	0.45, 2.68
Pied flycatcher	Entrance size, 5 or 7 cm	**-4.53**	**0.01**	**0.002, 0.05**
	Site, Pilpakangas	-0.76	0.47	0.22, 1.02

Note: baseline is the entrance diameter 3 cm and, where applicable, year 2014 and site Isokangas. For pied flycatcher in the 3 cm vs. 5 cm vs. 7 cm design, the 5 cm and 7 cm entrance sizes were combined to facilitate model fitting (no flycatchers settled in 7 cm boxes); while for the 3 cm vs. 7 cm design, the strong negative coefficient and practically zero exponentiated coefficient, but vast 95% CI, are due to all flycatchers settling into 3 cm boxes.

DISCUSSION

Redstarts showed a clear cavity entrance size preference for 5 cm over both 3 cm and 7 cm cavities. This preference proved to decrease (even eliminate) cuckoo parasitism risk but had no consistent impact on nest predation risk in the early breeding phase. In our data, not a single redstart nest within a 5 cm box was parasitized by cuckoos, whereas 37.2% of nests in 7 cm boxes were parasitized. In contrast, nest predation rate was even marginally higher in 5 cm than in 7 cm. Redstarts breeding in natural cavities showed the same cavity use trend, with the occupied natural cavities having approximately 5 cm diameter entrance size. Our results also show that great tits and pied flycatchers prefer 3 cm nest boxes while redstarts appear to avoid them.

Entrance size Choice and Parasitism Risk

Our results show a clear impact of redstart nest cavity entrance size preference on cuckoo parasitism rates. Cavity entrances of 5 cm and 3 cm diameter reduced or even completely deterred cuckoo parasitism. An adaptation that prevents the parasite gaining access to the nest would seem advantageous for the host (Hoover 2003b). For example, prothonotary warbler (*Protonotaria citrea*) nests showed higher cowbird parasitism rates in cavities with large entrance size (Hoover 2001). In our study, a small entrance appears to represent a physical constraint for the cuckoo to lay her eggs. Even when cuckoos parasitize redstart nests with 7 cm entrance cavities, most of the cuckoo eggs are mislaid on the nest rim or even end up on the ground (Samaš et al. 2016; Thomson et al 2016). If 7 cm entrance cavities cause cuckoos to mislay, smaller cavity entrance sizes will pose a greater challenge and our data suggests may even exclude cuckoo parasitism completely. Given that birds generally prefer cavity entrances not much larger than themselves (Politi et al. 2009), cavity-nesting can represent an advantage when a substantial size discrepancy between parasite and host exists, as is the case for the redstart-cuckoo system (cuckoo about 10 times larger than redstart: 86-143 gr vs 12-16 gr; British Trust For Ornithology 2020). There are suggestions that a 5 cm entrance size could be large enough for the cuckoo chick to fledge (Löhrl 1979), but smaller cavities may preclude cuckoo fledging. Therefore, it would be maladaptive for cuckoos to parasitize nests with entrances smaller than 5 cm, which should drive host preference for smaller cavities.

Entrance Size Choice and Predation Risk

Predation rates of redstart nests did not consistently differ between 5 cm and 7 cm boxes, suggesting the presence of a predator guild that can still enter 5 cm cavities (e.g. squirrels, great-spotted woodpeckers and weasels, Wesolowski 2002; Baroni et al. 2020). The smallest cavity size (3 cm) showed an absence of nest predation events, suggesting these were inaccessible to the local nest predators. Smaller cavities should therefore be favored by redstarts (like other passerines, Remm et al. 2006; Kozma and Kroll, 2010; Fokkema et al. 2018), although they were mostly avoided. This suggests that nest predation does not drive nest entrance size choice for redstarts, even though nest predation is undoubtedly relevant (Martin 1993; Mezquida 2004;

Eggers et al. 2006; Buehler et al. 2017). Redstarts may use some other nest site characteristics, as the depth of the cavity, to prevent predation (Koch et al. 2008; Baroni et al. 2020).

Birds nesting in cavities show relatively high nest survival (Ricklefs 1969) and are potentially be under weaker selection from nest predation for their nest-site choice (Chalfoun and Schmidt 2012). Our estimates of nest predation rates (14.2% of nests) partially supported this, but it only considered predation taking place during the *ca.* 7-day laying period (after which the nests were protected), underestimating the predation rates for the entire nesting period (*ca.* 35 days). However, we were focus on nest-site choice, which is is based on cues present in the territory at the time of settlement, e.g. predator presence (Chalfoun and Schmidt 2012). Therefore, if redstart cavity choice was mostly determined by predation pressure, we would expect a clear preference for predator-safe 3 cm boxes. By preferring 5 cm entrance size, redstarts prevent larger nest predators but remain susceptible to most of the woodpeckers, small rodents and mustelids (see Wesolowski 2002). Further studies are needed to confirm our suggestion about entrance size not contributing to reduce nest predation in redstarts.

Entrance Size Choice and Interspecific Competition

Redstarts showed the lowest preference (occupancy rates) for the smallest cavities (3 cm boxes). Redstarts even preferred 7 cm over 3 cm entrance sizes, even when the larger cavities offer no protection from nest predation or brood parasitism. This apparently maladaptive behavior (in terms of costs of predation and parasitism risk) may be linked to higher interspecific competition for small entrance sizes, which are preferred by the other two species we followed. Even though our study excluded the main population of great tits that initiated breeding before our boxes were available, great tits and pied flycatchers occupied almost all 3 cm boxes available. This suggests that competition for 3 cm boxes may be stronger than for 5 cm or 7 cm boxes.

Other species may occupy the smallest entrance size cavities first and leave redstarts only with the option of having the mid-size ones. However, even when great tits (as residents) can choose cavities first, redstarts still have access to nest sites with the smallest entrance size, since early breeding individuals arrive before most pied flycatchers (personal observation). Interspecific competition for cavities can, however, also occur once a breeding pair has already occupied a nest-box. For example, pied flycatchers are known to usurp cavities (Slagsvold 1975). During the study, there were 4 cases where pied flycatchers stole nest-boxes from redstarts, and only one case where the opposite happened. Previous experiences (e.g., having had a nest usurped) may restrain redstart from using the smallest entrance size cavities. Moreover, if redstarts choose the smallest entrance size, they may suffer severe costs, even mortality from great tits (Ahola et al. 2007).

Entrance Size Choice Based on Multiple Selective Forces

When choosing nest-sites, redstarts seem to face the trade-off of at least two different selective forces: brood parasitism and interspecific competition. After considering the combined trade-offs, the 5 cm entrance cavity could be optimal to prevent parasitism, while still avoiding competition costs. However, experimental studies are needed to properly identify the causes for observed preference in cavity entrance size. The role of interspecific competition could also be clarified by studying entrance size choice in areas where pied flycatcher and great tits are rare (e.g. northern Lapland).

Natural nests were predominantly found in woodpecker cavities of approximately 5 cm in diameter. Redstart preference for 5 cm entrance size nest-boxes, therefore, mirrors apparent preference found in nature. However, without data on the availability of different entrance sizes of natural cavities in the study area, we are unable to denote true preference in natural cavities. Nevertheless, there is a full community of cavity excavators in the study area, and other natural cavity creating processes also occur. It thus seems unlikely that the strong entrance size preference we observed is purely driven by familiarity with 5 cm entrance size cavities in the area. We have also shown that other secondary cavity nesters in these forests (great tits and pied flycatchers), which are not current cuckoo hosts but suffer nest predation, prefer the smallest entrance hole diameter. Future efforts should focus on natural cavity availability and follow natural redstart nests to determine preference and cause of reproductive losses.

Implications for Cuckoo-redstart Co-evolutionary Arms-race

The most studied adaptive strategies in cuckoo-host systems are egg recognition and ejection, or nest desertion (Pease and Grzybowski 1995; Krüger and Davies 2002; Krüger 2011). However, the redstart is a species that shows limited use of these anti-parasite adaptations (Rutila et al. 2002; Avilés et al. 2005; Grim and Samaš 2016; Samaš et al. 2016; Thomson et al. 2016; Tolvanen et al. 2017). Adaptative nest-site choice that decreases brood parasitism risk could be a game-changer. Cavity-nesting in redstarts results in high rates of mislaid cuckoo eggs (around 70%, Samaš et al. 2016; Thomson et al. 2016). The costs of brood parasitism for redstarts would be much higher in the absence of these nest site limitations (e.g. open-cup nesting reed warbler, 35% nest failure, Polačiková et al. 2009). Our results suggest that brood parasitism may elicit the selection of specific nest features.

For cuckoo-host systems, parasitism costs are mostly calculated after nest-site choice (i.e. from laying until fledging success, Avilés et al. 2005; Krüger 2011). This ignores how frontline defenses could potentially contribute to reduce the costs of brood parasitism. For example, given the low success of cuckoo egg-laying and hatching (Rutila et al. 2002; Samaš et al. 2016; Thomson et al. 2016), some authors have suggested that redstarts should not evolve any defense strategy (Avilés et al. 2005, see *evolutionary lag hypothesis* and *evolutionary equilibrium hypothesis*, Rothstein 1982; Rohwer and Spaw 1988; Davies 2000). Yet, our results are in line with a cavity entrance size preference potentially being a defense strategy to brood parasitism.

With nest-site choice as an anti-brood parasite adaptation, redstarts could have avoided the need to develop other strategies in later stages of the breeding cycle to minimize the costs of brood parasitism. There has been speculation that redstarts moved from ground-cavity to tree-cavity breeding due to cuckoo parasitism pressure (Avilés et al. 2005), especially considering the higher brood parasitism rates in ground-cavity nests (Rutila 2004). For example, in Britain, populations of redstarts are unparasitized and most nests are located in nest-boxes (usually designed for small hole-nesting passerines, e.g. great tits). Considering the low preference for ground-cavity nesting, it might be that in the past redstarts moved to tree-cavity nesting to avoid brood parasitism (Rutila 2004). Similarly, great tits have been considered a past cuckoo hosts (based on rejection behavior of foreign eggs, Grim et al. 2014; Liang et al. 2016) however, nowadays great tits tend to occupy nest-boxes with the smallest entrance size (Charter et al. 2016), possibly precluding cuckoo laying. If redstarts start breeding exclusively in cavities with small entrances the cuckoo gens parasitizing them may disappear, as possibly happened to the British population. Therefore, frontline strategies in parasite avoidance could have higher adaptive value for hosts than previously thought, and more focus on them is needed.

In conclusion, redstarts preferred to breed in cavities with 5 cm entrance size that may be the result of avoiding brood parasitism and interspecific competition. Breeding in smaller entrance size cavities may give a significant edge for the redstart against cuckoo parasitism, potentially explaining the current low effective parasitism rates in this system. Whether this is enough to "win" the co-evolutionary arms-race depends on the cuckoo's ability to evolve laying strategies that enable successful parasitism of small-entrance cavity nests. This also shows that further research on such front-line strategies is needed to better understand brood parasite-host co-evolution. Our study shows an example where multiple factors could have influenced the currently observed behavior in animals. Therefore, considering multiple factors in a single study is useful for understanding trait patterns in natural populations.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Moreras et al. (2021).

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