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Research article

Can nest design hinder brood parasitism success?

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Avian nest design varies depending on environmental factors but may also be influenced by between-species interactions. In the brood parasitism context, hosts may evolve nest architectures that may limit parasite access to the nest cup, reduce parasite laying success or hinder parasite chick success. Therefore, nest characteristics may reduce the likelihood or minimise the costs of being parasitised. The common redstart *Phoenicurus phoenicurus* is a regular host of the common cuckoo *Cuculus canorus*, for which cuckoo eggs are often laid outside the nest cup, resulting in low effective parasitism rates. This allowed us to evaluate variation in host nest design and test whether nest design characteristics correlate with brood parasitism likelihood and cuckoo laying success (i.e. cuckoo egg laid in the nest cup versus outside the nest cup). While recording brood parasitism events in two distant redstart populations, we documented nest cup characteristics, such as internal dimensions, materials used and nest cup position, along with the nest-box dimensions. Cuckoo parasitism likelihood was lower for redstart nests in cavities with smaller entrances, for redstart nests with smaller nest cups and with nest cups that were built level to the rim material. For parasitised nests, cuckoo laying success was lower at redstart nests with nest cups placed further from the cavity entrance. Our results suggest a conditional process, where the cavity entrance size first prevents brood parasites access, then the cup size and the cup level in reference to the rim material affect the cuckoo choice, and finally, the nest cup position hinders cuckoo's laying success. The use of multiple nest design strategies may explain the current low effective parasitism rates in this system. Host nest design may serve as a frontline defence that could shape parasite's preferences, and consequently host nest characteristics.

Keywords: defence strategy, evolutionary arms-race, individual variation, nest characteristics, nest choice-



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Introduction

The use of materials found in the environment to build structures for protection and reproduction is a regular practice for animals (Barber 2013, Mainwaring et al. 2014a, Cornelissen et al. 2016). For birds, nest construction involves several decisions starting from the selection of a site and materials, and the manipulation of materials into a structure (Hansell 2000). These decisions influence the outcome of reproductive events (Mainwaring et al. 2014a, Breen et al. 2021). Nest concealment, for example, can be improved by selecting inconspicuous sites (Kleindorfer 2007), while nest materials or characteristics can make nests harder to depredate (Russell et al. 2001, Mezquida 2004, Buehler et al. 2017, Liu et al. 2021). Nest design can therefore enhance the breeding output by diminishing the risk of selective forces (Caro 2005, Feeney et al. 2012).

In the coevolutionary battle between brood parasites and their hosts (Davies 2000), early defence strategies are potentially the most advantageous, as they can protect the host's entire breeding attempt and minimize future costs (Britton et al. 2007, Patten et al. 2011, Feeney et al. 2012). Hosts can reduce the likelihood of brood parasitism and its costs by building nests that inhibit parasite access, limit its laying success and/or reduce the success of the parasite chick (Feeney et al. 2012, Moreras et al. 2021, Noh et al. 2021). For example, the steepness of the nest cup prevents cuckoo chicks from evicting the host eggs/chicks (Grim et al. 2009a), leading to a cohabitation of mixed broods with often lethal results for the young parasite (Hauber and Moskát 2008, Grim et al. 2009b, 2011). However, while there is occasional evidence that brood parasites may non-randomly select nests to parasitise (Soler et al. 1999a, Langmore and Kilner 2007), there is no clear evidence that selecting host nests with certain characteristics may enhance brood parasite breeding success. Nevertheless, host nest design may play a role in the parasite host-nest selection, where brood parasites should prefer nests easier to access and nests enhancing the success of the parasite chick.

Several characteristics of the nest can vary within species, populations and even at the individual level between seasons depending on different environmental aspects and individual experiences (Liljeström et al. 2009, Muth and Healy 2011, Mainwaring et al. 2012, 2014b, Tabib et al. 2016). Such variation is referred to in the literature as nest design. Previous research has shown that nest design acts in mate attraction, micro-climate control and inhibition of ectoparasites (Mainwaring et al. 2014a). The understanding in how variation in nest design may mitigate costs from negative species interactions is mainly focused on nest predation. Studies have shown that the nest cup size, nest materials and covering eggs with nest material reduce predation risk (Biancucci and Martin 2010, Prokop and Trnka 2011, Mainwaring et al. 2015, Liu et al. 2021) and conceal information from competitors (Loukola et al. 2014, Slagsvold and Wiebe 2021). However, in the brood parasitism context there have been a limited number of studies testing

nest size (Soler et al. 1999a, Hackemack et al. 2016) and only few recently tested brood parasitism likelihood considering host nest design as a whole (Murcia et al. 2020).

The common redstart *Phoenicurus phoenicurus* (hereafter 'redstart') is a regular host of the common cuckoo *Cuculus canorus* (hereafter 'cuckoo'; Rutila et al. 2002, Samaš et al. 2016, Thomson et al. 2016). As a cavity nester, the redstart is a good model to study the impact of nest design on brood parasitism risks because both nest sites and nest characteristics could potentially reduce cuckoo laying and parasitism success. Cavity nesting bird species commonly prefer cavity entrances not much larger than themselves (Politi et al. 2009), and with redstarts being much smaller than cuckoos (12–16 g versus 86–143 g; British Trust for Ornithology 2020), the cavities chosen by redstarts may force cuckoos to lay from the entrance (Kysučan et al. unpubl.). As a result, cuckoo eggs in this system are often 'misaid' and end up outside the nest cup on the rim of the nest, or even on the ground below the nest cavities (Rutila et al. 2002, Samaš et al. 2016, Thomson et al. 2016) and will not be incubated by the host. Restricted access for the cuckoo to the redstart nest cup means that variation in the redstart nest cup size and location within the cavity may further impact cuckoo laying success (i.e. the ability to lay the egg into the nest cup). Eviction of redstart eggs/nestlings may also be limited/prevented by placing the nest cup close to the cavity walls (Grim et al. 2009b, Thomson et al. 2016, Grim and Rutila 2017) or by lining nest cups with feathers which makes the cup surface unstable, slippery and difficult to grip by cuckoo nestlings attempting evictions (Grim et al. 2009a). In both cases this leads to cohabitation between redstart and cuckoo nestlings. Importantly, redstarts do not eject naturally laid cuckoo eggs from the nest cup or rim (Grim and Rutila 2017; in contrast to Daurian redstarts *P. aureoreus*, Yang et al. 2016), which makes redstarts an excellent model to extensively document all successful or unsuccessful brood parasitism attempts.

In this study our aim was to explore the correlation between cuckoo parasitism likelihood and redstart nest design to evaluate which aspects of nest design can reduce cuckoo parasitism risk and successful laying. To address this, we first quantified variation in host nest design and any correlations with nest site selection, in this case the cavity dimensions. We predicted nest-boxes with more volume to have bigger nest cups. Second, we assessed cuckoo parasitism likelihood and various cavity dimensions. The entrance hole size can restrict the cuckoo access to the nest cup and the cavity inner dimensions can reduce the cuckoo laying distance (i.e. distance from the entrance hole to the nest cup). Therefore, we expected nest-boxes with less volume and nest-boxes with bigger entrance holes to show higher parasitism probability. We then assessed if cuckoo parasitism likelihood is correlated with redstart nest design. Cuckoos should prefer to parasitise nests with cups that allow easier laying; therefore, we predicted cuckoo parasitism would be higher in bigger cups and cups closer to the entrance hole. However, it is worth considering that cuckoo eggs may also roll in the cavity after being laid. Feathers placed to protrude out of the lining of

nest cups can serve as a barrier that prevents the cuckoo egg from rolling into the nest cup. This is also the case for nest cups where the edge is higher than the rim material. We expected nest cups made mainly with feathers and/or with the cup edge higher than the rim material to be less likely to be parasitized. Finally, we tested what aspects of redstart nest design explained cuckoo laying success (i.e. cuckoo egg laid in the nest cup versus outside the nest cup). If cuckoos are adaptively selecting host nests, we expected that nest design characteristics affecting brood parasitism likelihood to be same ones affecting cuckoo laying success.

Material and methods

Study area and general protocol

Our study was conducted in two study sites ca. 400 km apart: near Oulu, northern Finland (65°0'40"N, 25°50'48"E), between 2013 and 2019, and near Ruokolahti, south-eastern Finland (61°24'00"N, 28°37'38"E), in 2015 and 2016. Approximately 350 nest-boxes were monitored each year per study site to collect data on redstarts breeding and cuckoo brood parasitism as part of long-term studies (Samaš et al. 2016, Thomson et al. 2016). Nest-boxes in Oulu were placed 120–200 m apart, while in Ruokolahti they were 50–350 m apart. All nest-boxes were placed in Scots pines *Pinus sylvestris* approximately 1.5 m above the ground. Nest-boxes from Oulu had the same inner dimensions: 13.0 × 13.0 × 28.0 cm (length, width and height), and entrance hole diameters of 3.0–7.0 cm, while nest-boxes from Ruokolahti were more variable: 10.0–16.0 × 9.0–13.0 × 25.0–32.0 cm (length, width and height), and entrance hole diameters of 3.0–8.5 cm. In 2015, to better standardise box types between study sites, 40 nest-boxes were permanently exchanged between study sites. The internal dimensions of nest-boxes were measured (to the nearest 0.5 cm) to account for those differences in the statistical analyses (below). It is important to note that cavity dimensions were not considered part of the redstart nest design but as a factor that could affect it.

We checked nest-boxes every 2–5 days from early May until late July (Samaš et al. 2016, Thomson et al. 2016). A nest-box was considered occupied when at least one redstart

egg was laid in it. To avoid pseudoreplication, only the first breeding attempt per season in each nest-box was included in analyses. For all nests we recorded any predation (i.e. host eggs disappearing or found broken) and brood parasitism events. At each visit we checked if a nest was parasitized and we recorded where the cuckoo egg was found: 'cup' for eggs within the redstart nest cup, 'rim' for egg outside of the redstart nest cup but within the nest-box or 'ground' for eggs found on ground below the nest-box (Thomson et al. 2016). Nests that were predated before the fifth redstart egg was laid (i.e. the time when parasitism is more likely) were excluded, as we could not be certain if those nests were or were not parasitized before being predated.

To evaluate different attributes of the nest design, we measured specific nest characteristics of each nest during the redstart egg laying period. New nest characteristics were added in later years, therefore sample sizes varied (Table 1). In the field we measured: the level of the nest cup in relation to the rim material (hereafter 'cup level', in three categories: even, higher and lower, Fig. 1a), the vertical distance from the entrance lower edge to the rim material (hereafter 'vertical distance', to the nearest 0.5 cm, Fig. 1b) and the nest cup depth (to the nearest 0.5 cm, Fig. 1b). We also estimated by eye the percentage of different materials used to build the nest cup (i.e. bark, dried grass, feathers, hair, lichen and moss, to the nearest 10%); this measure only considered the visible surface of the cup viewing from above.

We took a photo of each occupied nest during the redstart egg-laying phase. This was done from directly above, keeping the camera perpendicular to the nest-box bottom and making sure that the nest-box entrance hole was visible to avoid losing the orientation of the nest cup. Using ImageJ software (Rasband 2018) and the length of the nest-box as a scale, we determined: the nest cup width (to the nearest 0.5 cm), the nest cup area (hereafter, 'cup area', to the nearest 0.5 cm²), the distance from the mid-point of the front wall to the closest cup edge (hereafter 'horizontal distance', to the nearest 0.5 cm, Fig. 1b) and the location of the nest cup centroid within the nest cavity in x and y coordinates (where both coordinates were zero in the mid-point of the nest-box front wall, hereafter 'x coordinate' and 'y coordinate', to the nearest 0.1 cm). We extracted all photo measurements twice and used the average values in analyses. We scaled the nest

Table 1. Summary of the redstart nest design characteristics measured. Sample sizes varied between different nest characteristics as in later years new nest characteristics were added. The feather cover includes only the visible nest cup surface viewing from above.

Variable	Range	Mean	SD	n
Cup area (cm ²)	18.0, 42.5	27.6	4.0	792
Cup steepness	0.4, 1.2	0.7	0.1	490
Vertical distance (cm)	4.0, 16.5	8.2	1.2	577
Horizontal distance (cm)	4.0, 16.0	5.5	1.7	792
Cup centroid x coordinate	-0.6, 0.7	0.0	0.2	784
Cup centroid y coordinate	0.2, 0.8	0.6	0.1	784
Feather cover (%)	0, 100	37.2	31.2	441
Cup level	Higher, Even, Lower	–	–	474
Laying distance (cm)	5.5, 17.5	10.0	1.8	520
Laying angle (degrees)	8.8, 61.9	33.5	8.0	520

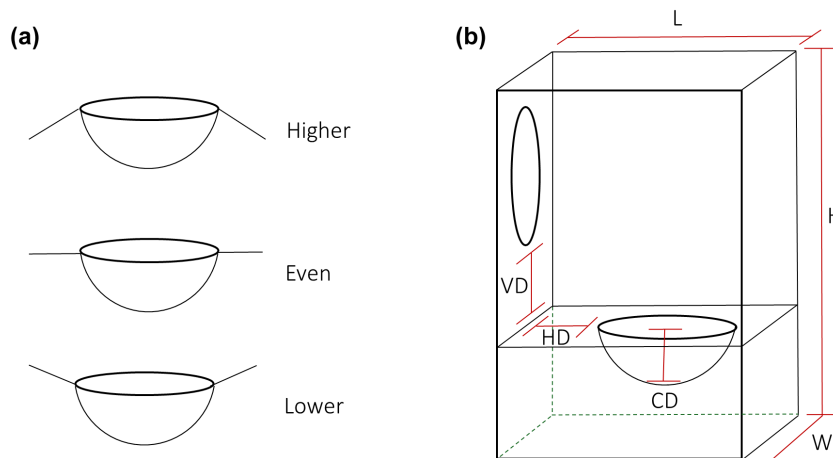


Figure 1. Redstart nest and cavity dimensions measured in the field. (a) Nest cup level. (b) Cup depth (CD), vertical distance (VD) and horizontal distance (HD), nest-box height (H), width (W) and length (L).

cup centroid coordinates to the nest-box size by dividing the x and y coordinates by the inner width and length of the nest-box, respectively. These relative coordinates describe the nest cup location within the nest cavity, irrespective of the cavity size. We calculated the nest cup steepness index by dividing the nest cup width by the nest cup depth (Grim et al. 2009a). Using the Pythagorean theorem, and the vertical and horizontal distance, we calculated the cuckoo female laying distance (i.e. distance from the lower inner edge of the entrance hole to the nearest nest cup edge, hereafter 'laying distance', to the nearest 0.5 cm). We also calculated the angle between the laying distance and the vertical distance (hereafter 'laying angle', in degrees).

Statistical analyses

All statistical analyses were conducted using R (ver. 3.6.2, www.r-project.org). We ran a Pearson correlation test for all nest characteristics, and we did not fit variables with $\rho > |0.7|$ correlation (i.e. strong linear relationship; Ratner 2009, Supporting information) within the same model. The horizontal distance was strongly positively correlated with the y coordinate, laying distance and laying angle ($r_{(310)}$: 0.82, 0.73 and 0.73, respectively, $p < 0.01$). The vertical distance was also strongly positively correlated with the laying distance ($r_{(310)}$: 0.90, $p < 0.01$), as was the y coordinate with the laying angle ($r_{(310)}$: 0.72, $p < 0.01$). For all the other nest characteristics correlations were $\rho < |0.7|$ (Supporting information). We discarded the horizontal and vertical distance to avoid collinearity. However, we kept the y coordinate and the laying angle and tested them in separate models in further analyses. We also tested the nest cup depth in separate analyses from the steepness index (to avoid collinearity). The results were similar for both, but here we present results only for the steepness index.

We analysed if the cavity dimensions affected nest design by using linear mixed models (LMMs, using the 'lme4' package, Bates et al. 2015). We built a full model separately

for each nest characteristic (cup area, nest cup steepness, laying distance, laying angle, x and y coordinates). Each nest characteristic was set as the response variable and nest-box dimensions (length, width and entrance diameter) were set as continuous fixed effects. We added the year data were collected (2013–2019) as a random intercept to account for possible temporal variation. The nest-box ID was also added as a random intercept to control for using the same nest-boxes over the years.

We checked how the nest cup area was affected by its placement within the nest-box, using a generalized additive model (GAM, using the 'mgcv' package; Wood 2022) to capture the non-linear relationships of covariates along using a basis function. Instead of a single polynomial over the whole domain, GAM uses piecewise polynomial curves (i.e. a spline curve) in regions defined as knots (Wood 2017). The cubic regression function was fitted (a model of the form: $Y_i = \alpha + \beta_1 \times X_i + \beta_2 \times X_i^2 + \beta_3 \times X_i^3$) between each knot, then the fitted values per segment were glued together to form the smoothing curve using first-order and second-order derivatives (Zuur et al. 2009, Perperoglou et al. 2019). A penalized estimation of the spline was used to find the best-fitting line, which penalizes more complex smoothers, ensuring that the model fit was not too complex. If the data do not support a non-linear trend, the spline curve will be reduced to a linear trend. In this case the cup area was set as the response variable and a single smoother for both x and y coordinates (i.e. $s(x,y)$) was added as the only fixed effect.

Then we analysed if the cavity dimensions affected the probability of being parasitized (binary: yes/no) by building a generalized linear mixed model (GLMM, using the 'lme4' package) with logit link function. Nest-box dimensions (length, width and entrance diameter) were added as fixed effects. The study site (Oulu/Ruokolahti) was also added as a fixed effect because it could not be modelled as a random effect due to only having two levels (Harrison et al. 2018). The year that data were collected (2013–2019) and the nest-box ID were added as random intercept effects.

We further built a model evaluating how the probability of being parasitized (yes/no) was explained by the nest design using a generalized additive mixed model (GAMM, using the ‘*gamm4*’ package; Wood and Scheipl 2022) with logit link function. We used a GAMM model to allow a non-linear relationship of nest cup position using a single smoother for the x and y coordinates. The cup level (categorical; even/higher/lower), laying distance (continuous; cm), laying angle (continuous; in degrees), feather cover (ordinal; in percentage), x and y coordinates (continuous; in ratios), steepness (continuous; index) and cup area (continuous; cm²), as well as the study site (Oulu/Ruokolahti) were added as fixed effects. Additionally, the full model included the year data were collected (2013–2019) and the nest-box ID as random intercept effects. Given that brood parasitism events were highly unlikely in cavities with entrances smaller than 6 cm in diameter (only 1 out of the 291 parasitism attempts, over the seven years of the study), we excluded 77 nests from this and further analyses (i.e. all nest design related analyses).

Finally, we evaluated the probability of cuckoo laying success relative to nest design by including only redstart nests parasitized by cuckoos. We built a binomial GAMM model with the same fixed and random effect structure as used above but testing how nest design explained the likelihood of successful laying (cuckoo egg in cup) versus unsuccessful laying (cuckoo egg on rim). Nests where the cuckoo egg was found on the ground were excluded given its low occurrence (n = 11).

For all models, the explanatory continuous variables were centred to the mean (to have a meaningful interpretation of the intercept regarding the response variable, Zuur et al. 2009). For the model selection process, we first tested the random effects using full fixed effects structure with all combinations of the random terms (always including at least one random term), then selected the random effect structure with the lowest AIC_c. Using that random structure, we fit sub-models that included all combinations of the fixed effects and ranked the models using the AIC_c criteria. Further we used a threshold of $\Delta AIC_c \leq 6$ to select models within the final model set, excluding models that were more complex versions of the model with lower AIC_c (Burnham and Anderson 2002, Richards et al. 2011). When more than one model was included in the final model set, inferences from the best-ranking model, and any inference coming from the other model(s) that differed from the best-ranking model, were noted in the results. For the models testing cuckoo brood parasitism and successful laying, if none of the variables collected in the field were supported, we built a new model including only variables extracted from the photos (i.e. cup area, laying distance, laying angle, x and y coordinates) and ran the model selection process again. This was done to improve the sample size, as field measurements were missing from some nests. We based our statistical inferences on the mean parameter estimates and their 95% confidence intervals. Finally, we graphically checked that the models did not violate other model assumptions using the DHARMA package (Hartig 2018).

Results

Redstart nest design

Measurements of 733 nests in Oulu (2013–2019), and 133 nests in Ruokolahti (2015–2016) were collected. However, actual sample sizes varied depending on the data collected for each variable measured (Table 1). Redstart nest characteristics show substantial variation in multiple parameters (Table 1).

Redstarts start building their nest by filling the cavity with bark and moss. Next, they build the nest cup, using a combination of bark, dried grass, feathers, lichen and moss (Fig. 2). The most common material visible in nest cups was feathers: 80.3% of the cups contained feathers (n = 441); on average $46.3 \pm 28.1\%$ (SD) of the visible cup was feathers. Dried grass and moss were also common materials visible, as 67.8 and 51.7% of the cups, respectively, had those materials. Lichen (38.8%), hair (35.6%) and bark (29.7%) were less common. We further found that 56.5% of the nests had an even cup level, 31.6% had a higher cup level and 11.8% had a lower cup level (n = 474).

The relationship between the cup area and its location shows that nest cups placed close to the entrance hole and to the left side of the nest-box were slightly bigger than nest cups placed elsewhere (Fig. 3). The GAM model (n = 784) estimated degrees of freedom (edf) was 7.48, reflecting a highly non-linear relationship between the cup area and its location; however, the smoother was not statistically significant (p = 0.27).



Figure 2. Variation of redstart nest cup composition. Clockwise from top left: mostly feathers (from black grouse male, *Lyrurus tetrix*), mostly bark (from pine *Pinus* sp.), a complex mixture of bark (from birch, *Betula* sp.), pine needles, grass, feathers and a piece of plastic or paper (very rare, therefore it was not quantified), and finally mostly dried grass and roots (note that moss is not part of the nest cup lining but is used in the nest rim) Photos: TG.

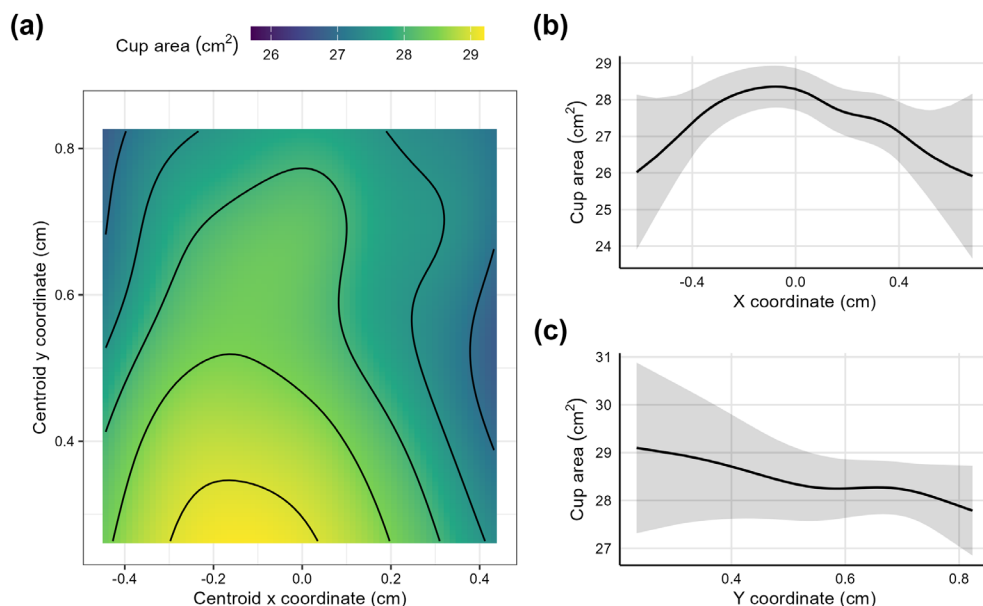


Figure 3. Predicted values of the redstart nest cup area in relation to the nest cup location. Relationship of the nest cup area with (a) both centroid coordinates combined, (b) the x coordinate and (c) the y coordinate. The nest-box entrance hole is placed at zero in both axes.

Redstart nest design was affected by the dimensions of the cavity (i.e. nest-box; Table 2). Bigger internal cavity dimensions contained bigger nest cups (β_{length} [95% CI]=1.00 [0.71, 1.30], β_{width} [95% CI]=0.40 [0.09, 0.68], $\sigma_{\text{Year}}=0.25$). The laying distance increased with cavity length (β [95% CI]=1.02 [0.89, 1.15], $\sigma_{\text{Box ID}}=0.78$, $\sigma_{\text{Year}}=0.47$). The laying angle increased along with the cavity width (β [95% CI]=0.82 [0.15, 1.46], $\sigma_{\text{Year}}=1.72$), but decreased as the entrance hole size increased (β [95% CI]=−0.90 [−1.78, −0.01]). When cavities had a bigger entrance hole, nest cups were smaller (β [95% CI]=−0.37 [−0.70, −0.03]). Moreover, for cavities with bigger entrance holes there was more variation in the nest cup y coordinate (x coordinate: $F_{1,777}=0.00$, $p=0.97$; y coordinate: $F_{1,777}=13.53$, $p<0.01$; Supporting information).

Nest design and cuckoo attempted parasitism

Out of the 816 nests measured, 291 had parasitism attempts (i.e. cuckoo egg found in redstart nest irrespectively of

its location: nest cup, rim or ground, Oulu=236/685, Ruokolahti=55/131). The study site was excluded from the final model because it was not informative (Table 3); therefore, it can be assumed that brood parasitism did not differ between sites. Nest-box width and length did not explain brood parasitism likelihood either; but parasitism likelihood increased along with the entrance hole size (β [95% CI]=0.94 [0.74, 1.62], $\sigma_{\text{Year}}=0.29$; Table 3, Fig. 4a).

After excluding nests in cavities with entrance holes smaller than 6 cm in diameter, the likelihood of cuckoo parasitism based on redstart nest design was explained by a final model set consisting of five models (Table 3). The best model had three explanatory variables: cup level, cup area and study site (Table 3). Nests with bigger nest cups were 36.6% more likely to be parasitised (β [95% CI]=0.09 [0.02, 0.16]; $\sigma_{\text{Box ID}}=0.30$, Fig. 4b). Nests with a higher cup level were 58.1% more likely to be parasitised than nests with an even cup level ($\beta_{\text{higher vs even cups}}$ [95% CI]=0.72 [0.19, 1.37]), but brood parasitism likelihood did not differ between

Table 2. Model statistics for the final model set explaining the variation of nest design given the internal dimensions of the nest-box (width, length and entrance hole diameter). The selected random effects are shown.

Response variable	Model parameters	Random	df	AIC _c	dAIC _c
Cup area (n=779)	Length + width + entrance diameter	Year	6	4352.9	0.0
	Length + width	Year	5	4353.9	1.0
	Length + entrance diameter	Year	5	4356.0	3.0
	Length	Year	4	4358.2	5.2
Laying distance (n=506)	Length	Year, box ID	6	1878.3	0.0
Laying angle (n=506)	Width + entrance diameter	Year	5	3541.4	0.0
	Width	Year	4	3543.6	2.1
	Entrance diameter	Year	4	3545.1	3.7
	Null	Year	3	−735.5	0.9
Steepness (n=521)	Width	Year	4	−736.4	0.0
	Null	Year	3	−735.5	0.9
Centroid x coordinate (n=775)	Null	Box ID	3	−10.42	0.0
Centroid y coordinate (n=775)	Entrance diameter	Year, Box ID	5	−1348.8	0.0
	Null	Year, Box ID	4	−1348.2	0.6

Table 3. Model statistics for the final model set of the likelihood of brood parasitism and the likelihood of cuckoo successful laying (binomial generalized additive mixed models, GAMMs) considering different nest characteristics (including the nest-box dimensions).

Model parameters	df	AIC _c	dAIC _c	R ² (%)	edf
Parasitism versus nest-box dimensions (n = 799)					
Entrance size of the nest-box	3	996.37	0.00	16.80	–
Parasitism versus nest design (n = 275)					
Cup area + cup level + site	6	358.68	0.00	8.63	–
Cup area + site	4	361.06	2.38	5.49	–
Cup area + cup level	5	361.90	3.21	6.07	–
Cup level + site	5	363.57	4.89	5.17	–
Cup area	3	364.56	5.88	2.90	–
Successful laying versus nest design (n = 176)					
s(x coordinate, y coordinate) + Site	6	196.22	0.00	17.30	2

Note: The s() refers to the smoother of the generalized additive mixed model (GAMM) model. The estimated degrees of freedom (edf) reflect the degree of non-linearity of the smoother: an edf of 1 is equivalent to a linear relationship, an edf > 1 and ≤ 2 is a weakly non-linear relationship, and an edf > 2 indicates a highly non-linear relationship (Zuur et al. 2009).

nesses with a lower cup level and those with an even cup level ($\beta_{\text{lower vs even cups}}$ [95% CI] = 0.11 [−0.82, 0.99], Fig. 4c). Given that there was no statistically significant difference in the parasitism rates between study sites when considering only the nest-box dimensions (an analysis with a larger sample size; see above), differences between study sites in this and further models may be due to a reduction in sample size (Table 3).

Nest design and cuckoo laying success

Cuckoo laying was successful for only 30.2% of all cuckoo parasitism attempts (88 of 291 parasitised nests), while in

66.0% (192 of 291) of parasitism attempts the cuckoo egg was on the rim material, and in 3.8% of cases the cuckoo egg was found on the ground outside the nest-box (11 of 291). The final model set evaluating nest design and cuckoo laying success included only one model, which had the nest cup position and the study site as explanatory variables (Table 3). The smoother for the cup position (x and y coordinates combined) was highly statistically significant ($p < 0.01$), with an edf of 2, reflecting a weakly non-linear relationship between the cup position and cuckoo laying (Fig. 5). The x coordinate was not related to cuckoo laying success (Fig. 5b); while the y coordinate had a non-linear pattern, where the likelihood

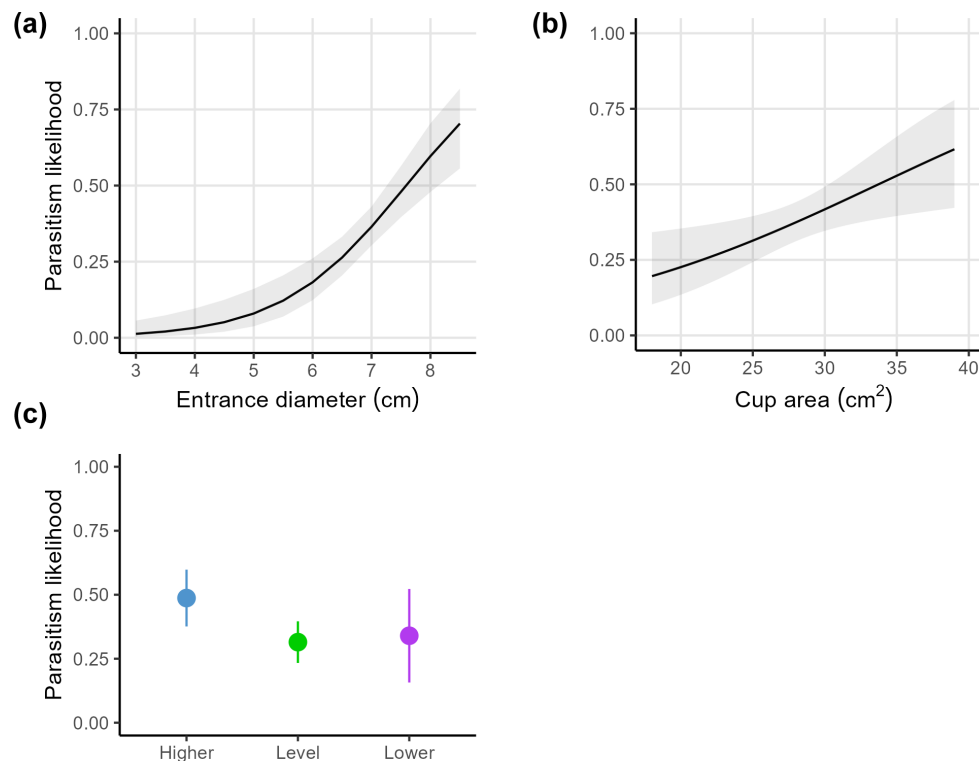


Figure 4. Predicted values of the probability of cuckoo parasitism in relation to the relevant redstart cavity characteristics and nest design: (a) cavity entrance hole size, (b) nest cup area and (c) nest cup level. The black line and points represent the mean estimate, while the ribbon and coloured lines are the 95% CIs. Note: When testing the probability of cuckoo parasitism in relation to nest design (b) and (c), nests in cavities with entrance holes < 6 cm were excluded (n = 77).

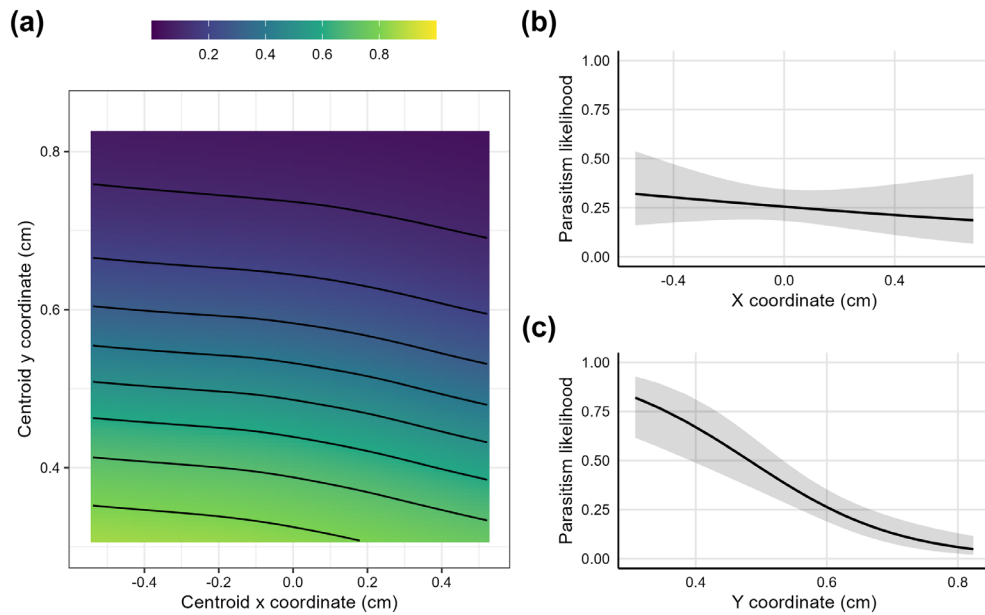


Figure 5. Predicted values of the probability of cuckoo successful laying in relation to redstart nest cup position. The nest cup position is examined in three ways: (a) both nest cup centroid coordinates combined, (b) the x coordinate and (c) the y coordinate. The nest-box entrance hole is positioned at zero in both axes. In (b) and (c), the black lines represent the mean estimate, while the ribbons are the 95% CIs.

of cuckoo laying success dropped rapidly from approximately 80% for nest cups located close to the front wall (entrance hole; y coordinate 0.3) to almost 10% for nest cups with a y coordinate of 0.7, thereafter levelling off to some extent (Fig. 5c). We also found a higher likelihood of successful cuckoo laying in Ruokolahti compared with Oulu ([95% CI] = 1.52 [0.68, 2.44]; $\sigma_{\text{Box ID}} = 0.00$), possibly given by the fact that Ruokolahti nest-boxes had bigger entrance holes (see section 'study area and general protocol').

Discussion

The present study reveals previously unknown details of the brood parasite–host coevolutionary arms-race based on host nest design. Redstarts showed large variation in their nest design, and some nest characteristics covaried with brood parasitism risk. Cuckoo parasitism showed no clear correlation with the width and length of the cavities, but cuckoos were more likely to select nests in cavities with bigger entrances. In terms of nest design, bigger nest cups and nest cups with edges higher than the rim material were more likely to be parasitized. Nevertheless, cuckoo females were able to successfully parasitize (i.e. cuckoo egg laid into nest cup) only 30.2% of all parasitism attempts. Only the nest cup position clearly affected cuckoo laying success; when the nest cup was closer to the entrance cuckoo laying was more successful.

Nest design variation

The size and position of the redstart nest cup was partly determined by the cavity dimensions. In longer cavities, nest cups were placed further from the entrance hole, which made the

laying distance longer for cuckoos, and may also prevent other enemies from reaching the nest cup (Wesołowski 2002). This perhaps allowed redstarts to build bigger nest cups in longer cavities. Redstarts built smaller nest cups in cavities with larger entrance holes (≥ 6 cm in diameter). Building smaller nest cups may be an alternative way to decrease the risk of parasitism for redstarts when breeding in cavities with larger entrances. Great tits *Parus major* have been observed to adjust the size and danger distance (which is the same as laying distance) of the nest cup to the height of the cavity (Mazgajski and Rykowska 2008). Cavity nesters may first select a cavity to breed in, and based on the cavity dimensions, then shape the attributes of their nest to prevent future costs (i.e. loss of offspring). However, for secondary cavity nesters, suitable or safe sites to breed are often a limited resource (Newton 1994, Wesołowski 2007, Aitken and Martin 2012). Thus, more experienced, or early arriving redstarts may choose larger cavities and build larger nest cups in places harder for enemies to reach.

Nest design and cuckoo parasitism

Cuckoo females appeared to prefer to parasitize redstart nests with bigger nest cups. Larger redstart nest cups should increase cuckoo laying success by increasing the probability of the cuckoo egg ending in the nest cup if cuckoos lay from the cavity entrance. However, the impact on laying success would not necessarily be meaningful for cuckoo gaining access to the nest cup. This result resembles the cuckoo preference for larger nests of great reed warbler *Acrocephalus arundinaceus* (Moskát and Honza 2000) and the oriental reed warbler *Acrocephalus orientalis* (Wang et al. 2022). Other brood parasites, such as the little bronze-cuckoo *Chalcites minutillus* and the great spotted cuckoo *Clamator glandarius*

have also shown a preference for larger nests (Soler et al. 1995, Noh et al. 2021). Previous studies noted that nest size is a sexually selected trait reflecting the willingness to invest in reproduction (De Neve et al. 2004, Tomás et al. 2013), but can also be positively correlated to breeding success (Alabrudzińska et al. 2003, Álvarez and Barba 2008), and the quality of the builders (Mainwaring et al. 2014a). Brood parasites may then cue on aspect of nest size to select high-quality hosts, to potentially impact the quality of the parasitic nestling. Higher brood parasitism rates for nests with bigger nest cups could also be a by-product of cuckoos' preference for some other host characteristic reflecting high-quality hosts that build bigger nest cups (Polačiková et al. 2009).

We found no difference in brood parasitism rates based on the cup steepness or feather cover, but nests with a higher cup level were more likely to be parasitized over those with a nest cup even with or lower than the rim. From the laying point of view, a lower nest cup level should instead be preferred by cuckoos because cuckoo eggs mislaid on to the rim could roll into the nest cup. This may be why this type of nest was the least common in redstarts. Cuckoos may instead focus on enhancing the ability of their nestling to evict the host eggs/nestlings to increase their survival (Grim et al. 2009b). It might be easier for cuckoo nestlings to evict host eggs/nestlings downhill from cups built higher than the rim. Cuckoos may then prefer redstart nests that enhance nestling eviction over those that increase laying success. This preference could be expected for open-cup nesting hosts and for redstarts breeding in ground cavities, where cuckoo parasitism has higher effective parasitism rates (i.e. low laying error; Rutila et al. 2002, Avilés et al. 2005). The idea that redstarts shifted from ground-cavity to tree-cavity breeding may suggest that cuckoos' preference for nest cups built higher than the rim could be a residual selected trait from the recent past when most redstarts bred in ground cavities (Avilés et al. 2005).

Cuckoo parasitism probability was significantly reduced for cavities with smaller entrances. This pattern was mainly due to cavities with less than 6 cm entrance diameter having almost no parasitism attempts. In this study, cuckoos were more likely to parasitize both larger cavity entrances and larger nest cups, although these characteristics were negatively correlated: larger entrance cavities had smaller nest cups. This suggests that cuckoos may be confronted with a trade-off between entrance size and cup area. Alternatively, this reflects successive limitations on host choice, with entrance size first defining which nests are available for parasitism, and cup area affecting the final cuckoo choice among the available nests (see also Grim et al. 2011). This is supported by previous results showing redstart preference for cavity entrances of 5 cm, which completely excluded cuckoo parasitism (Moreras et al. 2021). Small cavity entrances then appear to represent a physical constraint for cuckoo laying or fledging (Löhr 1979), making them the safest breeding option for redstarts. However, due to the inter- and intraspecific competition for such safe breeding places, not all redstarts can choose cavities with small entrance holes (Moreras et al. 2021). Redstarts may then use nest design as a next stage to decrease cuckoo laying success.

Nest design and brood parasitism laying success

Nest cup placement seemed to be the most important characteristic preventing successful brood parasitism. Redstarts that placed their nest cups further from the entrance hole were less likely to have cuckoo eggs in the nest cup; this parallels the well-known pattern of decreasing parasitism risk with increasing distance between host nests and cuckoo female perches (Øien et al. 1996). A higher likelihood to escape parasitism for nest cups located further from the entrance also suggests that cuckoo females often lay from the entrance hole (which is confirmed via video recordings; Kysučan et al. unpubl.). If cuckoos could enter the nest-box to lay, it should be equally easy to lay into the nest cup irrespective of its location in the cavity. However, the position of the nest cup was not a relevant factor for cuckoo brood parasitism. Instead, cuckoos were more likely to parasitize cavities with larger entrance size, but these were related to smaller nest cups which do not seem to be located further from the entrance. Redstarts, therefore, do not seem to compensate for choosing unsafe cavities with cup placement, but rather build smaller nest cups that in turn seemed to be less preferred by cuckoos. This is similar to what was previously found in magpie *Pica pica* populations in sympatry with the great spotted cuckoo (Soler et al. 1999b). Overall, our observational results suggest a hierarchical process in redstart nest design based on brood parasitism risk. However, note that it is also possible that the nest cup placement for redstarts is meant to prevent predators that cannot access the cavity from reaching the nest contents from the cavity entrance (Wesołowski 2002, Czeszczewik and Walankiewicz 2003). Further studies on closely related species, as the Daurian redstart, may be necessary to confirm the use of hierarchical strategies on the genus.

In conclusion, intraspecific variation in nest design is usually attributed to differences in weather, reproductive investment or avoidance of nest predation; however, we suggest that it can also be due to costs imposed by brood parasitism. Cuckoo females seem to prefer redstart nests with larger nest cups, and nest cups with edges higher than the rim material. Redstarts can prevent brood parasites accessing the nest cup by first placing their nests in cavities with smaller entrance holes or by making their nest cup less appealing in size (smaller) to cuckoos. Then, by placing their nest cup far from the entrance hole redstarts may decrease the cuckoo's laying success. The use of multiple nest design strategies may explain the current low effective parasitism rates in this system. Frontline strategies of both the host and the brood parasite may shape host nest characteristics and the parasite's preferences, impacting the co-evolutionary arms-race between them. However, future experimental studies should test (via manipulating nest design) whether these correlations are just a by-product of natural variation of host nests (moulded by different selection pressures) or specific frontline defences.

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Data availability statement

Data are available from the ZibaHub Digital Repository: <https://doi.org/10.25375/uct.23057924.v1> (Moreras et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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