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1   Breeding near heterospecifics as a defence against brood parasites: can redstarts

2   lower probability of cuckoo parasitism using neighbours?

3

4   Angela Moreras[1], Jere Tolvanen[2], Risto Tornberg[2], Mikko Mönkkönen[3,4], Jukka T. Forsman[2,5],

5   Robert L. Thomson[1,6]

6

7   [1] FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape

8   Town, Rondebosch, 7701, South Africa

9   [2] Department of Ecology and Genetics, University of Oulu, 90014 Oulu, Finland

10   [3] Department of Biological and Environmental Sciences, University of Jyvaskyla, FI-40014

11   Jyväskylä

12   [4] School of Resource Wisdom, University of Jyvaskyla, FI-40014 Jyvaskyla, Finland

13   [5] Natural Resources Institute Finland (LUKE), 90014 Oulu, Finland

14   [6] Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland

15

16   Corresponding author:

17   Angela Moreras, email: AngelaMorerasResearch@gmail.com, tel: +57 350 4926782

Abstract

Breeding habitat choice based on the attraction to other species can provide valuable social information and protection benefits. In birds, species with overlapping resources can be a cue of good quality habitats; species with shared predators and/or brood parasites can increase joint vigilance or cooperative mobbing, while raptors may provide a protective umbrella against these threats. We tested whether the migratory common redstart (*Phoenicurus phoenicurus*) is attracted to breed near active nests of the great tit (*Parus major*), a keystone-information source for migrant passerine birds, or a top predator, the northern goshawk (*Accipiter gentilis*). This system is unique to test these questions because the redstart is a regular host for the common cuckoo (*Cuculus canorus*). Therefore, we also evaluated other possible benefits coming from the heterospecific attraction, especially in terms of reducing brood parasitism risk. We monitored redstart occupancy rates, onset of breeding, reproductive investment, and followed nest outcomes in terms of brood parasitism, nest predation risk and overall reproductive success. Redstarts avoided breeding near goshawks, but showed neither attraction nor avoidance to breed next to great tits. Both neighbours neither reduced brood parasitism risk nor affected overall nesting success in redstarts. Redstarts may not use heterospecific attraction for settlement decisions, as associations with other species can only exist when some benefits are gained. Thus, environmental cues may be more important than social information for redstarts when breeding habitat choice. Other front-line defence strategies may have a better impact reducing breeding negative interactions, such brood parasitism.

Introduction

Breeding habitat selection is used to enhance reproductive outcomes. Occurring at the start of the breeding cycle, these decisions determine the breeding site and have a large influence on the likelihood of offspring survival (Rosenzweig 1981; Reynolds 1996; Mayor et al. 2009; Chalfoun and Schmidt 2012; Boualit et al. 2019). Adaptive location decisions should account for negative interactions (i.e., predation, brood parasitism and competition), food availability, and other environmental factors (Banks and Beebee 1987; Martin 1993, 1995; Morris 2003). Assessment is crucial as each location may present different risks and benefits (Goodenough et al. 2009; Lehtonen et al. 2013). However, because personal assessment is costly, the number of possible sites that can be sampled is limited (Doligez et al. 2003; Danchin et al. 2004; Nocera et al. 2009). One strategy to overcome this dilemma, given the spatial and temporal variation in habitat quality (Mayor et al. 2009), could be to use information about the habitat quality based on the choices of other individuals, coined social information use (Reed et al. 1999; Doligez et al. 2002; Danchin et al. 2004).

Social information can be gathered from conspecific or heterospecific individuals (Mönkkönen et al. 1990; Doligez et al. 2003; Parejo et al. 2005; Seppänen et al. 2007). Settlement decisions can be based on the presence or absence of others and their breeding success (Valone 2007; Forsman and Seppänen 2011; Pizzatto et al. 2016). Conspecifics should provide relevant information due to a shared niche (Danchin et al. 2004; Loukola et al. 2012), however, for the same reason, associating with or copying conspecifics will likely carry fitness costs associated with competition (Seppänen

63   et al. 2007; Szymkowiak et al. 2016). To decrease such costs, the use of heterospecifics with an

64   overlapping yet not identical niche, should sometimes be preferred over conspecifics as sources

65   of information (Parejo et al. 2005; Seppänen et al. 2007; Szymkowiak 2013). Moreover, direct

66   information about the success of conspecifics is not available for the current breeding attempt,

67   making heterospecifics that settle earlier an important information source (Seppänen et al. 2007;

68   Tolvanen et al. 2020).

69

70   Attraction to, or associations with other species could also provide defence or protection benefits

71   (Quinn and Ueta 2008, see also heterospecific flocks, Morse 1977; Colorado 2013). Heterospecific

72   attraction should indirectly benefit the information user when the information source selects

73   habitats with lower predator or brood parasite abundance. Direct benefits such as increased

74   shared vigilance or cooperative mobbing can come from less-aggressive species (Hurd 1996;

75   Forsman et al. 1998; Polak 2014), while more aggressive or top predator species may provide a

76   protective umbrella effect for heterospecifics settling nearby (Quinn and Ueta 2008). For example,

77   raptors (or "aggressive" species) may prey on potential nest predators thereby decreasing nest

78   predation risk of neighbouring birds (e.g., Marti et al. 1993; Blanco and Tella 1997; Ueta 2007).

79   However, trade-offs need to be considered, as raptors may prey on nestlings and adult birds (Ueta

80   1999; Quinn and Kokorev 2002; Mönkkönen et al. 2007). Even though the use of heterospecific as

81   a source of information, and the attraction to predators/aggressive species for protective

82   associations are well supported, very few empirical tests have considered them in the brood

83   parasitism context (e.g., Grim 2008).

84

85   The evolutionary arms-race between host and brood parasites has produced several host

86   strategies to combat brood parasitism (Davies 2000; Krüger 2007). Recently research has been

87   focused on "front-line" strategies (i.e. defences before parasite egg-laying, Feeney et al. 2012),

88   such as nest-site choice (Forsman and Martin 2009; Tolvanen et al. 2017a; Expósito-Granados et

89   al. 2017). Previous studies have found that host nests far from neighbours appear more likely to

90   suffer from brood parasitism (Brown and Lawes 2007; Feeney et al. 2012; Ma et al. 2018b; but see

91   Kelly et al. 2019). Conspecific neighbours can be attracted by alarm calls, deterring cuckoos that

92   avoid being mobbed by a larger group of individuals (Feeney et al. 2013; Ma et al. 2018a).

93   Moreover, by breeding near to heterospecific host species, birds can reduce brood parasitism

94   rates (Clark and Robertson 1979). However, whether non-host heterospecific neighbours can

95   deter brood parasites and decrease the probability of hosts being parasitized remains to be

96   explored.

97

98   In northern boreal forests, migrant songbirds that face short breeding seasons have been shown

99   to select breeding locations near to both resident tits and breeding raptors to gain various

100   breeding benefits (Mönkkönen and Forsman 2002; Thomson et al. 2003, 2006; Mönkkönen et al.

101   2007). The redstart (*Phoenicurus phoenicurus*) is part of this migrant forest bird community and is

102   a regular, cavity-nesting host for the cuckoo (*Cuculus canorus*). In Finland, redstarts suffer

103   relatively high brood parasitism rates (20% - 32%, Rutila et al., 2002; Samaš et al., 2016; Thomson

104   et al., 2016), yet show weak egg-stage anti-parasitic strategies (Avilés et al. 2005; Grim et al. 2009;

105   Thomson et al. 2016). Redstarts may evade cuckoo parasitism through front-line defences, for

106   example, choosing nest-sites inaccessible for the cuckoo (Moreras et al. 2021). However, other

107   front-line strategies are largely unexplored (but see, Tolvanen et al. 2017a), as is also the case for

108   many other brood parasite-host systems with apparent lack of host defence strategies.

109

110   Redstarts can be attracted to heterospecifics with overlapping niche and to protective raptors to

111   get breeding benefits. Here we used the great tit (*Parus major*) and northern goshawk (*Accipiter*

112   *gentilis*) as neighbours. Great tits can serve as an information source of good quality breeding

113   habitats to redstarts. As residents and cavity nesters, great tits have more time to select where to

114   breed (e.g., Forsman et al. 2002, Thomson et al. 2003), they also overlap in resources used during

115   breeding (Van Balen et al. 1982; Valtonen et al. 2017; Baroni et al. 2020) and share both adult and

116   nest predators (e.g., sparrowhawks, *Accipiter nisus,* woodpeckers, small rodents and mustelids)

117   with redstarts (Nilsson 1984; Gotmark and Post 1996; Wesołowski 2002; personal observation).

118   On the other hand, goshawks should act as a protective umbrella from predators and possibly

119   cuckoos (Mönkkönen et al. 2007; Tornberg et al. 2015). It is known that occasionally goshawks

120   prey upon cuckoos (Toyne 1998; Nielsen and Drachmann 1999; Rebollo et al. 2017, R. Tornberg,

121   unpublish data), potentially making cuckoos avoid the proximity to active goshawk nests.

122

123   Great tis can plausibly inform redstarts about habitats with low cuckoo density. Great tits tend to

124   avoid places where they have seen cuckoos (Davies and Welbergen 2008) and may also avoid

125   breeding in habitats with high cuckoo density given that cuckoos have a hawk-like appearance

126   resembling the sparrowhawk (Gluckman and Mundy 2013). Parids generally are attracted by

127   others' alarms calls (Sieving et al. 2004), and may mob cuckoos, either due to their hawk-like

128   appearance (Gluckman and Mundy 2013) or due to their potential history as a past host of the

129   cuckoo (Grim et al. 2014; Liang et al. 2016). Although great tits are currently believed to be a non-

130   suitable host for the cuckoo, this might be biased information, because almost all knowledge about

131   great tits comes from nest-box populations, where only nest-boxes with small entrances (ca. 3 cm

132   in diameter) that prevent cuckoo parasitism are used (Grim et al. 2014; Moreras et al. 2021).

133   Indeed, great tits can be naturally parasitized in cavities with larger entrances (e.g. 5 to 7 cm in

134   diameter, woodpecker cavities, Grim et al. 2014). Moreover, some great tit populations still show

135   high egg rejection rates (Liang et al. 2016), suggesting a co-evolutionary history with cuckoos.

136

137   In this study, we tested heterospecific attraction in redstarts, its impact on the breeding cycle (e.g.,

138   timing of breeding, nest predation rates, reproductive investment, and reproductive success) and

139   its possible influence as a front-line defence against brood parasitism. If heterospecific attraction

140   exists, we expect redstarts to preferentially nest in the neighbourhood of great tits, as well as,

141   within goshawks territories. Moreover, for heterospecific attraction as a strategy should be

142   adaptive, therefore, we expect benefits to redstarts in terms of earlier breeding time, larger clutch

143   size, number of nestlings and lower predation rates in redstart having great tits and goshawks as

144   neighbours. Finally, if the heterospecific attraction acts as an anti-parasite front-line defence, we

145   expect redstarts breeding close to great tits to have lower parasitism rates, and the likelihood of

146   cuckoo parasitism to increase as the distance from the goshawk nest increases.

Materials and methods

Study site and basic protocol

The study was conducted near Oulu, Finland (65°N, 25° 50′ E), in scots pine (*Pinus sylvestris*) dominated forest patches suitable for redstarts, approximatively 60 km^2 in area combined. We placed nest-boxes (approximately 400 permanent nest-boxes), which were monitored each breeding season by checking redstart occupancy every three to five days. 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. We recorded the laying date of the first egg, events of brood parasitism and nest predation, and clutch size. Once the egg-laying was completed, nests were monitored once a week, and partly protected from nest predation by placing wire cages over the entrance of nest-boxes in early incubation (however, small predators can still enter the nest-box, Thomson et al. 2016). This was done to ensure that enough redstarts and cuckoos survive to make other concurrent studies possible. Therefore, for protected nests we only considered predation taking place during the *ca.* 7- 10 day laying and early incubation period (after which the nests were protected), underestimating the predation rates for the entire nesting period (*ca.* 35 days). Wire cages were only placed in nest-boxes with great tits as neighbours, but not in nest-boxes within goshawk territories (see below for details). For nests that were not protected (i.e., within goshawks territories), 29 predation events were documented in 416 redstart nests in 6 years. Nests that were predated before the fifth redstart egg was laid, were not considered for calculated parasitism rates, since it was impossible to determine if the nest was previously parasitized or not.

169   During the nestling period, we registered the number of nestlings. The number of fledglings was

170   derived by subtracting from the nestling number any dead chicks found in the nest after fledging.

171   A nest was defined as successful if at least one nestling fledged.

172

173   Nest-box experiment set-ups

174   Great tit as neighbour

175   Between 2014 and 2017, we selected 80 nest-boxes each year from the larger redstart nest-box

176   population. These nest-boxes had 7 cm diameter entrance hole (hereafter "redstart box"), while

177   nest-boxes with a 3 cm diameter entrance hole (hereafter "tit box") were used for settling great

178   tits. However, it is important to note that all species could freely choose any nest-box. We created

179   pairs of redstart nest-boxes (40 pairs per year), where we randomly assigned one control and one

180   neighbour nest-box. The 'neighbour' redstart boxes had one tit box placed approx. 25 m from the

181   redstart box, and the 'control' redstart boxes did not have a tit box placed nearby (Figure 1). To

182   control for habitat quality, the 'neighbour' and 'control' boxes of each pair were separated only

183   by approx. 200 m, while the different neighbour-control pairs of redstart boxes were separated by

184   at least 300 m. Between 2014 and 2015 the same 40 pairs of boxes were used, but treatments

185   were swapped between years. Then we selected 40 different pairs of boxes and used them in 2016

186   and 2017, where treatments were also swapped between years. We divided the study site into 10

187   different patches to account for possible spatial differences in habitat. Of the 40 'neighbour' boxes

188   in each year, only those that at the time of redstart settlement had a great tit pair actively breeding

189   in the tit box were considered in the analyses. "Control" boxes of the pairs where the "neighbour"

190   box was not considered were also excluded from the analysis. Finally, redstart boxes occupied by

191   other species (great tits or pied flycatchers, *Ficedula hypoleuca*) were not considered. We excluded

192   54 pairs of nest-boxes.

193

194   *Goshawk as neighbour*

195   Between 2011 and 2018, we placed redstart boxes around the nest sites of 15 active and

196   successfully breeding goshawk nests. A goshawk territory may include several nest sites, but only

197   one is used each year. We used 9 different nest sites in 5 territories. As goshawks tend to breed in

198   the same location over the years, some nest sites and territories were used for multiple years:

199   three territories for two, five and six years and two nest sites for three and five years. Redstart

200   boxes were placed at distances ranging from 20 to 2000 m from the active goshawk nest

201   (distribution shown in Figure 2). The location of each nest box was fixed within the breeding season

202   and between years. However, in some nest sites, the number of nest boxes varied as we added

203   some redstart boxes in later years. Depending on the habitat suitability for redstart, we set up

204   between 15 and 45 redstart boxes around each goshawk nest. The goshawk territories and nest

205   sites have been followed as part of a long-term study on goshawk ecology (see Tornberg et al.

206   2009; Tolvanen et al. 2017b). Based on local goshawk ecology, all territories had different goshawk

207   pairs, while within a territory the same pair was likely breeding for multiple years. In total, 7 out

208   of the 15 goshawk breeding attempts were known or likely to involve unique goshawk pairs (at

209   least one parent different). Redstart boxes were monitored as described above (see *Study site and*

210   *basic protocol*). Note that both set-ups (i.e., great tit as neighbour and goshawk as neighbour)

211   were in different areas and there was no overlap between them.

212

213 *Statistics*

214 All statistical analyses were conducted using R (version 3.6.2, R Development Core Team 2019).

215 We built full models evaluating the heterospecific attraction of redstarts and its consequences

216 with generalized linear mixed models (GLMMs) for great tit attraction and generalized additive

217 mixed models (GAMMs) for goshawk attraction. Full models included all relevant explanatory

218 variables (see below for details). Then we searched for a parsimonious final model sets by fitting

219 all subset models within the full model, without excluding the fixed explanatory variable of main

220 interest: the neighbour presence (in the great tit attraction) or distance to the goshawk nest (in

221 the goshawk attraction).

222

223 Instead of a single polynomial over the whole domain (i.e. transformation), one can rather use

224 piecewise polynomial curves (i.e. a spline curve) in regions defined by knot using GAMM models

225 (Wood 2017). The GAMM models are composed of a sum of smooth functions of covariates in

226 addition to the standard linear covariate effects to capture the non-linear relationships using a

227 basis function. A penalized estimation of the spline is used to find the best-fitting line, while

228 penalizing more complex smoothers, ensuring that the model fit is not too complex. If the data

229 does not support a non-linear trend the spline curve will reduce to a linear trend. In our case the

230 distance effect in goshawk attraction was modelled as a non-linear cubic regression spline. For the

231 cubic regression the x-axis (i.e., distance) is divided into a certain number of knots. In knot

232 intervals, a cubic polynomial is fitted (this is a model of the form: $Yi = \alpha + \beta 1 \times Xi +$

233 $\beta 2 \times Xi^2 + \beta 3 \times Xi^3$), and the fitted values per segment are then glued together to form the

234 smoothing curve using first-order and second-order derivatives (Zuur et al. 2009; Perperoglou et

235 al. 2019).

236

237 Firstly, we evaluated neighbour attraction for redstarts by testing differences in probability of

238 redstart occupancy (yes/no) using a binomial GLMM/GAMM with logit link function. For the

239 goshawk as neighbour analysis, as some nest boxes were added in later years for some nest sites,

240 we added as a fixed effect a binary "new box" variable indicating whether the nest box was set up

241 in the beginning of the season (new box = yes) or had already been available in earlier year(s) (new

242 box = no). Then possible benefits gained from this attraction (i.e. lower brood parasitism and nest

243 predation rates, earlier laying date, higher clutch size and fledgling number, and higher success)

244 were also evaluated. We tested parasitism and predation rates using binomial GLMMs/GAMMs

245 with logit link function, with the laying date included as a fixed effect in the full model to account

246 for possible variation due to timing of breeding. However, for the great tit as neighbour, predation

247 events were too few for a statistical analysis (9 events in total: 4 cases registered in restart nests

248 with neighbours and 5 cases registered in nests without neighbour). We also compared laying

249 date, clutch size and number of fledglings, using Poisson GLMMs/GAMMs with log link function.

250 Finally, we compared the probability of success using binomial GLMMs/GAMMs with logit link

251 function, with the laying date and probability of being parasitized as fixed effects. Full models of

252 all response variables in the great tit as neighbours' analysis included the interaction of great tit

253 presence and the year the data was collected to account for possible weather and other conditions

254 that vary over the years and might contribute to the nesting choice made by redstarts. For the

255 goshawk as neighbour analysis, full models included year as a random-intercept effect.

256   Additionally, to account for potential spatial variation in the responses and for using the same

257   nest-boxes multiple times, for the great tit as neighbour analysis we tested random-intercept

258   effects of the forest patch where the boxes were placed (10 patches) and nest-box ID, but we used

259   only the one better supported (i.e. the model with the lower AICc). While for the goshawk as

260   neighbour analysis, we tested random-intercept effects of goshawk territory ID and nest site ID,

261   but we used only the one that was better supported (i.e. the model with the lower AICc).

262

263   For the model selection process, we ranked the models using the AICc criteria. We then followed

264   Richards et al. (2011) and defined final model sets including the models within 6 AICc units, but

265   excluding models that were more complex versions of a model with lower AICc (Table 1). If there

266   were more than one model in the final model set, we focused on the best-ranking one but also

267   note if the inferences based on the other model(s) in the final model set differ from the best one.

268   We based our statistical inferences on the parameter mean estimates and their 95% confidence

269   intervals. Collinearity between explanatory variables was acceptable in all models (variance

270   inflation factors, VIF < 3 in all cases; Zuur et al. 2010). Finally, we graphically checked that the

271   models did not violate other model assumptions using DHARMa package (Hartig 2018).

Results

Great tit as neighbour

Around half (51.2%) of the paired "neighbour-control" boxes were occupied by redstarts. Out of 160 pairs available during the four years of the study (2014-2017), 82 pairs of boxes were included in the analyses, and 77 redstart nests were recorded within these. Out of the 82 control boxes 38 were occupied by redstarts (46.3%) and out of the 82 neighbour boxes 39 were occupied by redstarts (47.6%, Fisher's Exact test: p= 1.0). For all the breeding parameters evaluated (i.e., occupancy, laying date, clutch size, number of fledglings, brood parasitism and success rates), the final model set included only one model (Table 1). Moreover, for most breeding parameters the final model included as random intercept effect the box ID, but for the occupation probability the forest patch ID was better supported than the box ID. Redstarts did not nest more frequently near to great tit nests (Table 2). However, we found differences in redstart occupancy rates between years (Table 2).

The mean laying date of the first egg was around the 30th of May (mean= 30.1 ± 6.6 days, n=77). Most nests produced at least one fledgling with a success rate of 76.1% (n=67). We recorded 19 nests parasitized (27.1%), 12 cases in nests with neighbours (17.1%) and 7 cases in nests without neighbour (10.0%). Only 9 cases of predation were recorded during the study (11.7%), 4 cases in restart nests with neighbours (5.2%) and 5 cases in nests without neighbour (6.5%). This made it impossible to test differences in predation rates between treatments. None of the redstart

294   breeding parameters tested (laying date, parasitism risk, clutch size, number of fledglings or

295   success rate) show any clear statistical trend whether great tits were neighbours or not (Table 2).

296

297   *Goshawk as neighbour*

298   Occupancy of redstarts varied between 13.6 % and 75% of the nest-boxes in the 5 different active

299   goshawk territories. In total 175 out of 487 nest boxes were occupied during the 7 years we

300   collected data (35.9%). Only one model was selected in the final model set for the occupancy

301   (Table 1). This model included the distance effect, the variable describing if the nest-box was a

302   new box or not, and the goshawk territory as a random intercept term (Table 1). Redstart

303   occupancy increased linearly with the distance from the goshawk nest (Figure 3A). Moreover, nest-

304   boxes placed in the beginning of the current season (i.e. new boxes), were more likely to be

305   occupied by redstarts (Table 3).

306

307   Similar to great tit as neighbour data, the mean laying date of the first egg was around 30th of May

308   (mean= 29.7 ± 8.7 days, n=174). Nest predation rate was 21.9% (n=160), while the brood

309   parasitism rate was 22.9% (n=157) for redstarts with goshawks as neighbours. Therefore, more

310   than half of redstart nests fledged at least one chick (success rate = 63.2%, n=155). For laying date,

311   nest predation rate, brood parasitism rate and success rate, the final model set consisted of only

312   one model including only the distance effect (Table 1). For clutch size and number of fledglings

313   the final model set included two models, with the best model including the distance effect and

314   laying date (Table 1). Moreover, for all breeding responses the best models included as random

315   factor the nest ID (Table 1). For nest predation, the model included a non-linear smoother with

316   predation rate being lowest between approximately 800 m and 1400 m from the goshawk nest

317   (Figure 3C), however the smoother was overall not statistically significant (Table 2). For parasitism

318   rate there was no clear trend (Figure 3B). The laying date had a complex pattern, where females

319   settling near to goshawk nest (200-800 m) tended to lay later than females settling far (> 800 m)

320   from it (Figure 4A), showing a difference around 5 days between them (Figure 4A). The clutch size,

321   the number of fledglings and nest success did not differ relative to the distance from the goshawk

322   nest (Figure 4B, 4C, 3D).

Discussion

We found no evidence of heterospecific attraction by redstarts to active nests of resident tits and predatory goshawks. Our results suggest that redstart nest site decisions are not obviously impacted by these species on a breeding territory scale, which is perhaps surprising given that resident tits and goshawks are regularly used in a similar context by other passerine species as cues of good quality habitat and/or safety (Forsman et al. 1998, 2002; Thomson et al. 2003; Mönkkönen et al. 2007; Quinn and Ueta 2008; Polak 2014). By tracking the consequences of redstart nest site decisions, our findings also showed that great tits and goshawks did not offer any protection from brood parasitism or nest predation risk. Other possible breeding benefits (i.e. earlier laying date, higher clutch size and fledgling number, and higher success) did not differ for redstart nests at different distances from these species, suggesting that redstarts do not use heterospecific attraction in breeding habitat decisions.

Great tit as neighbour

Breeding redstarts did not associate with nesting great tits, even when social information from these residents has proven to attract other nesting migrants (e.g., pied flycatcher and chaffinch, *Fringilla coelebs*) breeding in the deciduous forests (Forsman et al. 2002, Thomson et al. 2003). Social information about the quality of the environment has previously been shown to be important to migrants with limited time to sample the area (Doligez et al. 2002, 2003; Mönkkönen and Forsman 2002; Danchin et al. 2004; Nocera et al. 2009). However, redstarts did not avoid breeding close to great tits either, suggesting low competitive or other costly interactions between

345   both species (but see, Ahola et al. 2007; Samplonius and Both 2019, to see competition between

346   great tits and migrants). The breeding outcome of redstart nests supported this conclusion;

347   redstarts showed no clear benefits nor costs of breeding next to great tits in terms of their

348   reproductive investment and outcomes. Therefore, patches with or without great tits as

349   neighbours may represent the same quality for redstarts even when our results show variation in

350   occupancy rates between habitat patches.

351

352   Redstarts with great tit neighbours showed similar parasitism rates as those breeding alone. This

353   suggests that great tits do not provide either indirect (i.e. habitats with lower cuckoo densities)

354   nor direct defence (i.e cooperative vigilance and mobbing) against brood parasitism. However, as

355   previously found in yellow warblers (*Setophaga petechia*), by breeding in habitats with lower

356   brood parasite densities, birds may not ensure habitats with lower parasitism rates (Kelly et al.

357   2019). On the other hand, the direct defence of passerine heterospecific neighbours may vary

358   depending on the risk (Forsman and Mönkkönen 2001). The hawk appearance of cuckoos may

359   prevent great tits from responding to redstart alarm calls or from participating in cooperative nest

360   defence, as they may to not distinguish between cuckoos and hawks (Davies and Welbergen 2008;

361   Welbergen and Davies 2011), considering cuckoos as a real mortality threat.

362

363   *Goshawk as neighbour*

364   Redstarts tended to breed far from active goshawk nests, even when goshawks represent little

365   risk for small passerines (Solonen et al. 2019). Redstarts may fail to discriminate between different

366   hawk species; a recent study suggested that given the fact that male goshawks closely resemble

367   female Eurasian sparrowhawks (*Accipiter nisus*, which preys on small birds) at community level

368   small bird species avoid breeding near to goshawks (Burgas et al. 2021). We also found no support

369   for the idea that goshawk may provide protection against nest predators (Mönkkönen et al. 2007).

370   Given that nest predation risk was low overall in our study (18.6%, and completely absent in 2016),

371   small birds may not benefit from associating with goshawks, but redstarts may encounter a

372   negative outcome due to the attraction of mesopredators (Morosinotto et al. 2012). This is

373   supported by a higher nest predation rate within goshawks territories than in habitats with great

374   tits as neighbours (21.9% for goshawks as neighbours and 11.7% for great tits as neighbour).

375   Moreover, redstart clutch size, number of fledglings and success rate did not change relative to

376   the distance to the goshawk nest. Laying initiation date had a very non-linear pattern relative to

377   the distance to goshawk nest, but it was not clearly earlier or later closer to goshawk nest. The

378   lack of benefits of breeding near to goshawks may explain the lack of a positive association (Quinn

379   and Kokorev 2002; Lima 2009). Nevertheless, it is important to highlight that the suitability of the

380   habitat near to active goshawk nests was likely on average not as good for breeding redstarts as

381   the habitat further away, potentially affecting the nest-site choice. All in all, the possible negative

382   trade-offs of breeding near to goshawks support the avoidance pattern we found for redstarts,

383   rather than the random occupancy pattern shown previously by pied flycatchers (Mönkkönen et

384   al. 2007).

385

386   Redstarts breeding within goshawk territories did not experience a decrease in brood parasitism

387   risk, despite that goshawks prey on cuckoos (Toyne 1998; Nielsen and Drachmann 1999; Rebollo

388   et al. 2017, R. Tornberg, unpublished data). It is possible that redstarts breeding close to goshawks

389   would encounter goshawks more often and may become less attentive towards hawk-like birds

390   such as cuckoos; similar to the mechanism proposed in the risk allocation hypothesis (see Lima

391   and Bednekoff 1999; Thomson et al. 2011). This may facilitate brood parasitism events within

392   goshawks territories and possibly counteracts any goshawk protection benefits, as cuckoos willing

393   to seek host nests close within goshawk territories are not going to be perceived as a threat by

394   redstarts. However, many host species discriminate cuckoos from hawks (Trnka and Prokop 2012;

395   Trnka and Grim 2013; Li et al. 2015; Ma et al. 2018a), therefore, further research on redstart

396   discrimination of cuckoos is needed.

397

398   *Brood parasitism and heterospecific neighbours*

399   Redstarts did not use heterospecific attraction to counteract brood parasitism. Neither aggressive

400   neighbours (i.e., goshawks) nor other passerine species (i.e., great tits) seem to contribute to

401   reduce brood parasitism risk. Other frontline defence strategies may be preferred for redstarts to

402   reduce brood parasitism. There has been speculation that redstarts moved from ground-cavity to

403   tree-cavity breeding due to cuckoo parasitism pressure (Avilés et al. 2005), and therefore, that

404   redstarts could face lower selection pressure to evolve other defence strategies. Cavity-nesting in

405   redstarts results in high rates of mislaid cuckoo eggs (around 70%, Samaš et al. 2016; Thomson et

406   al. 2016), reducing successful brood parasitism risk. A recent study also found that cavity choice

407   based on the entrance size is an adaptive strategy redstarts may use to prevent cuckoos to

408   access the nest cup (Moreras et al. 2021). Other frontline strategies such as nest placement,

409   breeding phenology and nest defence may be useful to reduce parasitism risk (see Feeney et al.

410   2012), yet, these have received little empirical research. Heterospecific attraction as a strategy to

411   reduce brood parasitism should be tested in other brood parasite-host systems, especially after

412   considering that conspecific attraction can reduce brood parasitism risk (Brown and Lawes 2007;

413   Feeney et al. 2012; Ma et al. 2018b; but see Kelly et al. 2019) and that communities can impact

414   the life history of the host, and therefore, the development of adaptations.

415

416   In conclusion, redstarts do not use great tits or goshawks as part of a frontline defence of nest

417   choice to prevent cuckoo brood parasitism. Redstarts seem to avoid breeding within goshawk

418   territories, while they do not avoid nor are attracted to great tits. There were no apparent

419   breeding benefits of having either as a heterospecific neighbour, and therefore, no need to be

420   attracted to breed near heterospecifics. Other frontline strategies, such as nest attributes (i.e.,

421   safer entrance size and cup location within the cavity for redstarts), and self-nest defence may

422   constitute better trade-offs for redstarts. Further research on such frontline strategies is needed

423   to better understand brood parasite-host co-evolution, especially in brood parasite-host systems

424   where it has been thought that hosts possess no defence strategies.

Declarations

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

Ethics approval

All animal experiments were approved by the Finnish Center for Economics Development, Transport and Environment (Elinkeino-liikenne-ja ympäristökeskus, ELY, permit numbers: POPELY/136/07.01/2014 and VARELY/921/2017).

Availability of data and material

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689   **Table 1.** AICc statistics of the final set of models explaining variation in different breeding factors.

690   Only models within 6 AICc units were included but excluding models that were more complex

691   versions of a model with lower AICc.

Response variable	Model parameters	n	Df	AICc	dAICc	Akaike weight
Great tit attraction						
Occupancy	Tit box + Year	164	6	218.8	0.00	1.00
Laying date	Tit box	77	3	508.4	0.00	1.00
Success rate	Tit box	62	3	64.4	0.00	1.00
Parasitism rate	Tit box	70	3	87.0	0.00	1.00
Clutch size	Tit box	68	4	271.3	0.00	1.00
Number of fledglings	Tit box	46	3	192.5	0.00	1.00
Goshawk attraction						
Occupancy	Distance + Box seniority	418	6	534.2	0.00	1.00
Laying date	Distance	154	5	1124.1	0.00	1.00
Success rate	Distance	137	5	187.0	0.00	1.00
Predation rate	Distance	141	5	140.7	0.00	1.00
Parasitism rate	Distance	142	5	163.5	0.00	1.00
Clutch size	Distance + Laying date	131	6	519.3	0.00	0.58
	Distance	131	5	519.9	0.62	0.42
Number of fledglings	Distance + Laying date	137	6	796.1	0.00	0.75
	Distance	137	5	798.3	2.26	0.25

692 **Table 2.** Summary of the generalised linear mixed model of redstart breeding parameters

693 depending on great tit attraction (present/absent). Parameter estimates for which the 95% CI

694 excludes zero are in bold.

Fixed effects	Estimate	95% CI	Random effect	Variance
Occupancy				
Intercept	**1.37**	**0.33, 2.41**	Patch ID	0.51
Tit neighbour, yes	-0.09	-0.76, 0.58		
Year 2015	-0.99	-2.02, 0.02		
Year 2016	**-1.92**	**-3.00, -0.85**		
Year 2017	**-1.97**	**-3.15, -0.79**		
Laying date				
Intercept	**3.41**	**3.34, 3.47**	Nest ID	0.01
Tit neighbour, yes	0.03	-0.06, 0.11		
Success rate				
Intercept	**1.24**	**0.03, 2.45**	Nest ID	0.50
Tit neighbour, yes	0.13	-1.09, 1.34		
Parasitism rate				
Intercept	**-1.29**	**-2.07, -0.50**	Nest ID	<0.01
Tit neighbour, yes	0.59	-0.47, 1.66		
Clutch size				
Intercept	**1.91**	**1.79, 2.03**	Nest ID	0.00
Tit neighbour, yes	0.01	-0.17,0.19		
Number of fledglings				
Intercept	**1.74**	**1.58, 1.91**	Nest ID	0.00
Tit neighbour, yes	0.05	-0.19,0.29		

note: intercept is Tit neighbour "no" and Year 2014

695

696 **Table 3.** Summary of the generalised additive mixed models of redstart breeding parameters in

697 the neighbourhood of active goshawk nest. Parameter estimates for which the 95% CI excludes

698 zero are in bold. The distance as fixed effect has the smoother characteristic from generalised

699 additive models. The estimated degrees of freedom (edf) reflect the degree of non-linearity of the

700 smoother: an edf of 1 is equivalent to a linear relationship, an edf > 1 and ≤ 2 is a weakly non-

701 linear relationship, and an edf > 2 indicates a highly non-linear relationship (Zuur et al. 2009).

Fixed effects	Estimate	95% CI	edf	p-value	Random effects	Variance
Occupancy						
Intercept	-1.19	-2.581, 0.036	-	-	Year	0.47
s(Distance)	-	-	1	**<0.01**	Territory ID	0.97
New Box, yes	**0.87**	**0.278, 1.488**	-	-		
Laying date						
Intercept	**3.41**	**3.309, 3.501**	-	-	Year	<0.01
s(Distance)	-	-	**4.13**	**<0.01**	Nest ID	0.01
Success rate						
Intercept	0.22	-0.836, 1.052	-	-	Year	0.00
s(Distance)	-	-	1	0.59	Nest ID	0.75
Predation rate						
Intercept	-0.99	-2.272, 0.391	-	-	Year	<0.01
s(Distance)	-	-	2.06	0.20	Nest ID	1.91
Parasitism rate						
Intercept	**-1.22**	**-1.996, -0.651**	-	-	Year	0.11
s(Distance)	-	-	1	0.40	Nest ID	0.00
Clutch size						
Intercept	**2.10**	**1.850, 2.356**	-	-	Year	0.00
s(Distance)	-	-	1	0.74	Nest ID	0.00
Laying date	-0.01	-0.014, 0.001	-	-		
Number of fledglings						
Intercept	**1.27**	**0.418, 1.987**	-	-	Year	<0.01
s(Distance)	-	-	1	0.09	Nest ID	0.69
Laying date	**-0.01**	**-0.026, -0.001**	-	-		

note: where applicable intercept is New box, no.

702

703   Figure legends

704   **Figure 1.** Redstart nest box pair design with one "control" and one "neighbour" box, set up

705   approximately 200 m apart. The neighbour box had a great tit nest box placed approximately 25

706   m away, while the control box had no great tit neighbour nearby. Redstart nest box pairs were

707   only included in the dataset if the tit box contained an active great tit nest.

708

709   **Figure 2.** Frequency distribution of the number of nest-boxes available for redstarts from 20 m to

710   2000 m from the active goshawk nest. The count bins are each 250 m.

711

712   **Figure 3**. The most supported generalized additive mixed model for redstart predicted relative

713   probability of (a) occupancy, (b) parasitism and (c) predation rates and (d) the probability of

714   success at different distance from an active goshawk nest. The dashed lines are the 95% CIs.

715

716   **Figure 4.** The most supported generalized additive mixed model for redstart predicted relative (a)

717   laying date, (b) clutch size (c) number of fledglings at different distance from an active goshawk
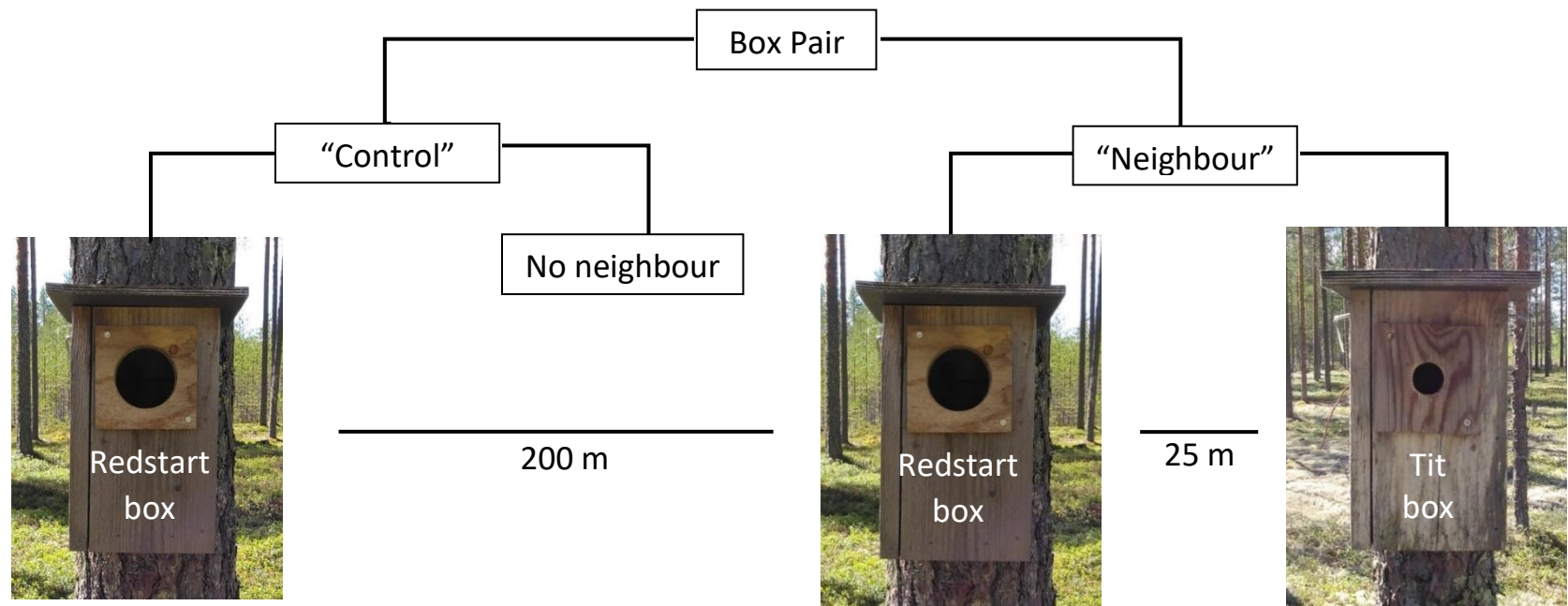
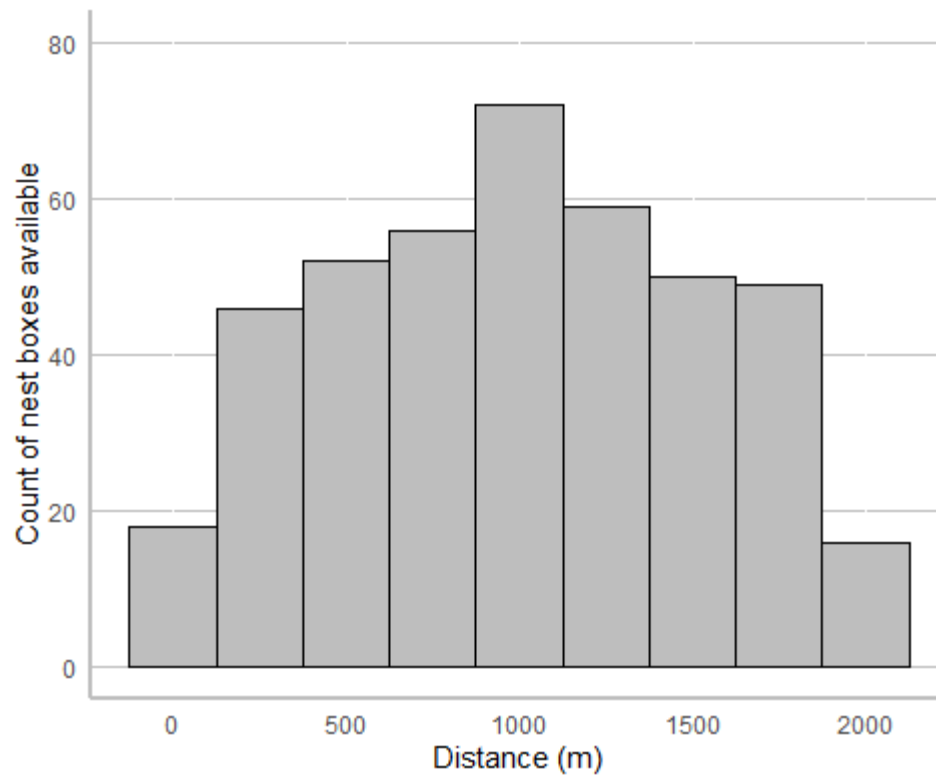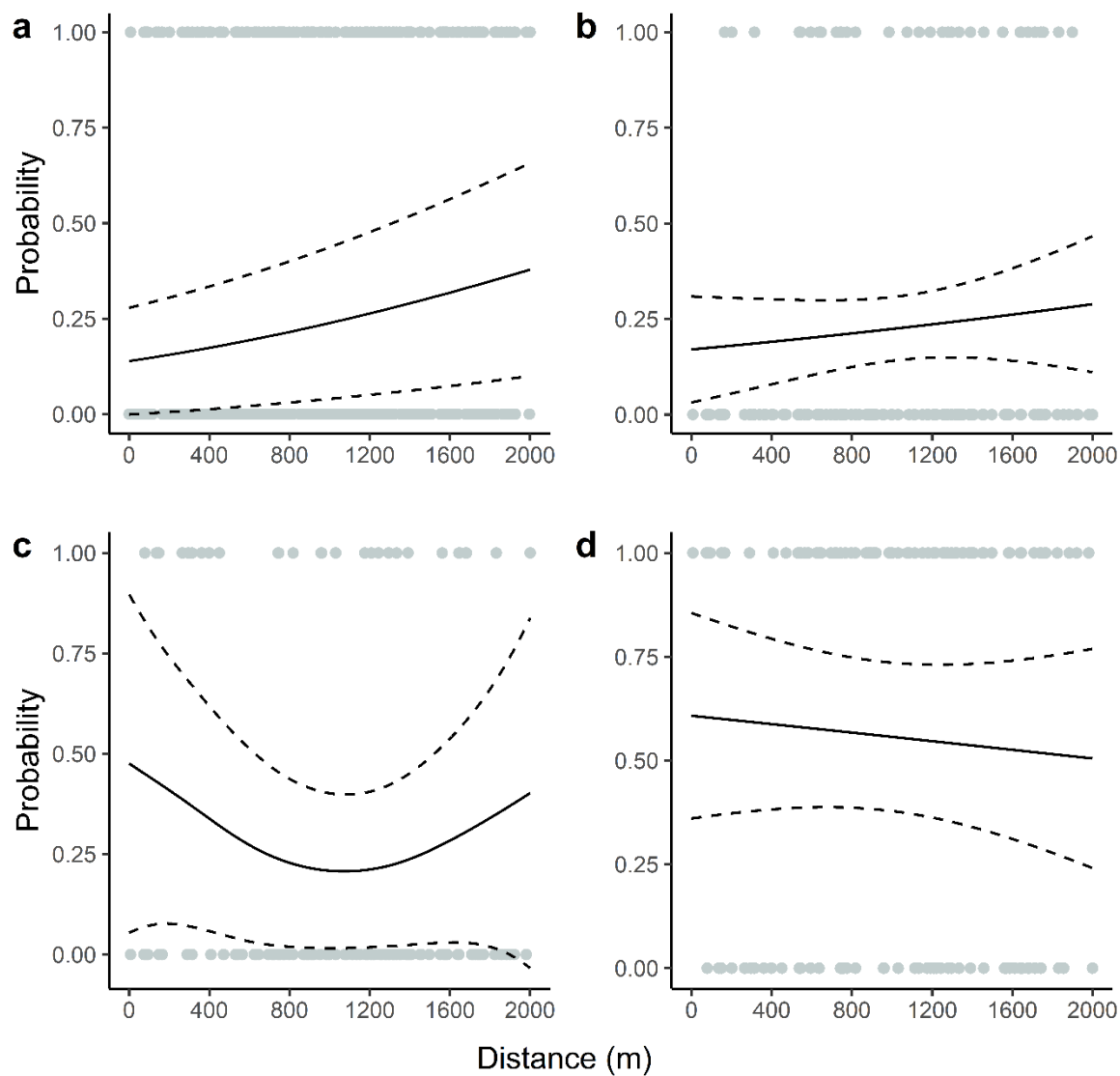718   nest. The dashed lines are the 95% CIs.

Figure 1.

Figure 2.

Figure 3.

Figure 4.