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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

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18 Abstract

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

38

39 Keywords: nest-site choice, frontline defence, heterospecific attraction, reproductive success,
40 interspecific interaction.

41 Introduction

42

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

56

57 Social information can be gathered from conspecific or heterospecific individuals (Mönkkönen et
58 al. 1990; Doligez et al. 2003; Parejo et al. 2005; Seppänen et al. 2007). Settlement decisions can
59 be based on the presence or absence of others and their breeding success (Valone 2007; Forsman
60 and Seppänen 2011; Pizzatto et al. 2016). Conspecifics should provide relevant information due to
61 a shared niche (Danchin et al. 2004; Loukola et al. 2012), however, for the same reason, associating
62 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; Wesółowski 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 unpublished data), potentially making cuckoos avoid the proximity to active goshawk nests.

122
123 Great tits 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' alarm 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.

147 **Materials and methods**

148

149 *Study site and basic protocol*

150 The study was conducted near Oulu, Finland (65°N, 25° 50' E), in scots pine (*Pinus sylvestris*)
151 dominated forest patches suitable for redstarts, approximately 60 km² in area combined. We
152 placed nest-boxes (approximately 400 permanent nest-boxes), which were monitored each
153 breeding season by checking redstart occupancy every three to five days. We placed nest-boxes
154 in pines approximately 1.5 m above the ground and 100–220 m apart since 2011. All nest-boxes
155 had the same dimensions: 17.5 x 17.5 x 28 cm (width, depth and height), and an entrance hole
156 diameter of 7 cm. We recorded the laying date of the first egg, events of brood parasitism and
157 nest predation, and clutch size. Once the egg-laying was completed, nests were monitored once a
158 week, and partly protected from nest predation by placing wire cages over the entrance of nest-
159 boxes in early incubation (however, small predators can still enter the nest-box, Thomson et al.
160 2016). This was done to ensure that enough redstarts and cuckoos survive to make other
161 concurrent studies possible. Therefore, for protected nests we only considered predation taking
162 place during the *ca.* 7- 10 day laying and early incubation period (after which the nests were
163 protected), underestimating the predation rates for the entire nesting period (*ca.* 35 days). Wire
164 cages were only placed in nest-boxes with great tits as neighbours, but not in nest-boxes within
165 goshawk territories (see below for details). For nests that were not protected (i.e., within
166 goshawks territories), 29 predation events were documented in 416 redstart nests in 6 years.
167 Nests that were predated before the fifth redstart egg was laid, were not considered for calculated
168 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: $Y_i = \alpha + \beta_1 \times X_i +$
233 $\beta_2 \times X_i^2 + \beta_3 \times X_i^3$), 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).

272 Results

273

274 *Great tit as neighbour*

275

276 Around half (51.2%) of the paired “neighbour-control” boxes were occupied by redstarts. Out of
277 160 pairs available during the four years of the study (2014-2017), 82 pairs of boxes were included
278 in the analyses, and 77 redstart nests were recorded within these. Out of the 82 control boxes 38
279 were occupied by redstarts (46.3%) and out of the 82 neighbour boxes 39 were occupied by
280 redstarts (47.6%, Fisher’s Exact test: $p= 1.0$). For all the breeding parameters evaluated (i.e.,
281 occupancy, laying date, clutch size, number of fledglings, brood parasitism and success rates), the
282 final model set included only one model (Table 1). Moreover, for most breeding parameters the
283 final model included as random intercept effect the box ID, but for the occupation probability the
284 forest patch ID was better supported than the box ID. Redstarts did not nest more frequently near
285 to great tit nests (Table 2). However, we found differences in redstart occupancy rates between
286 years (Table 2).

287

288 The mean laying date of the first egg was around the 30th of May (mean= 30.1 ± 6.6 days, $n=77$).
289 Most nests produced at least one fledgling with a success rate of 76.1% ($n=67$). We recorded 19
290 nests parasitized (27.1%), 12 cases in nests with neighbours (17.1%) and 7 cases in nests without
291 neighbour (10.0%). Only 9 cases of predation were recorded during the study (11.7%), 4 cases in
292 restart nests with neighbours (5.2%) and 5 cases in nests without neighbour (6.5%). This made it
293 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).

323 Discussion

324

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

336

337 *Great tit as neighbour*

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

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435 The authors declare that they have no conflict of interest.

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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
<i>Great tit attraction</i>						
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
<i>Goshawk attraction</i>						
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		

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

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	-	-		

702 note: where applicable intercept is New box, no.

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.

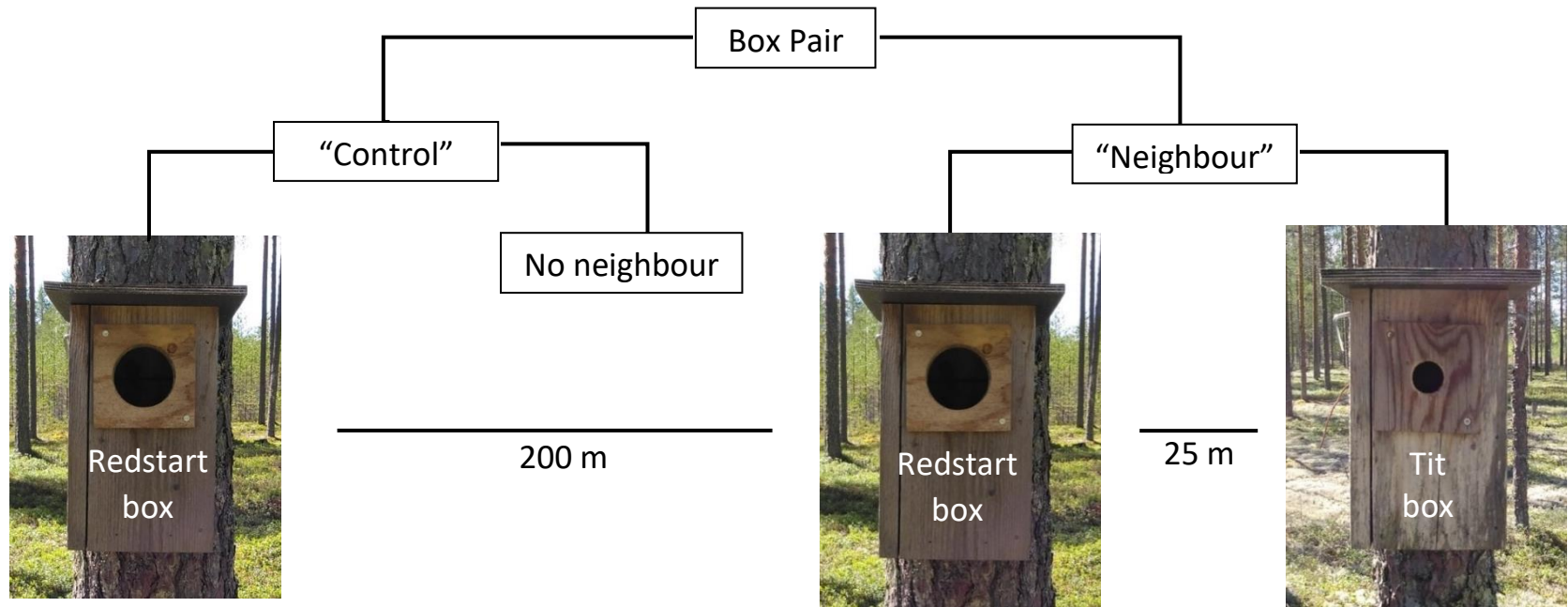


Figure 2.

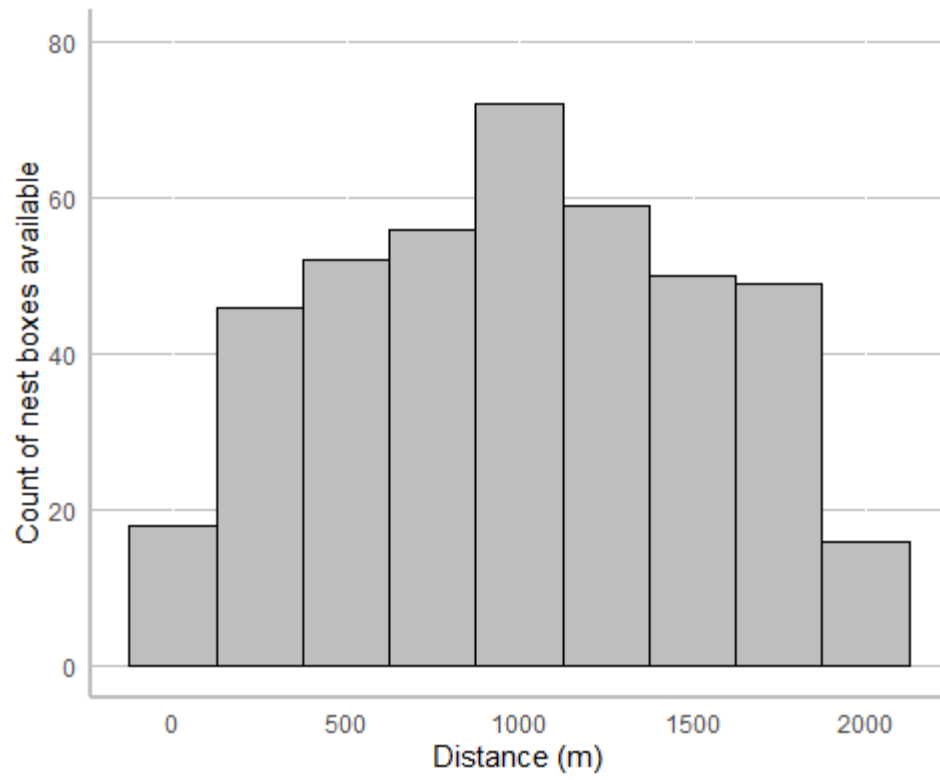
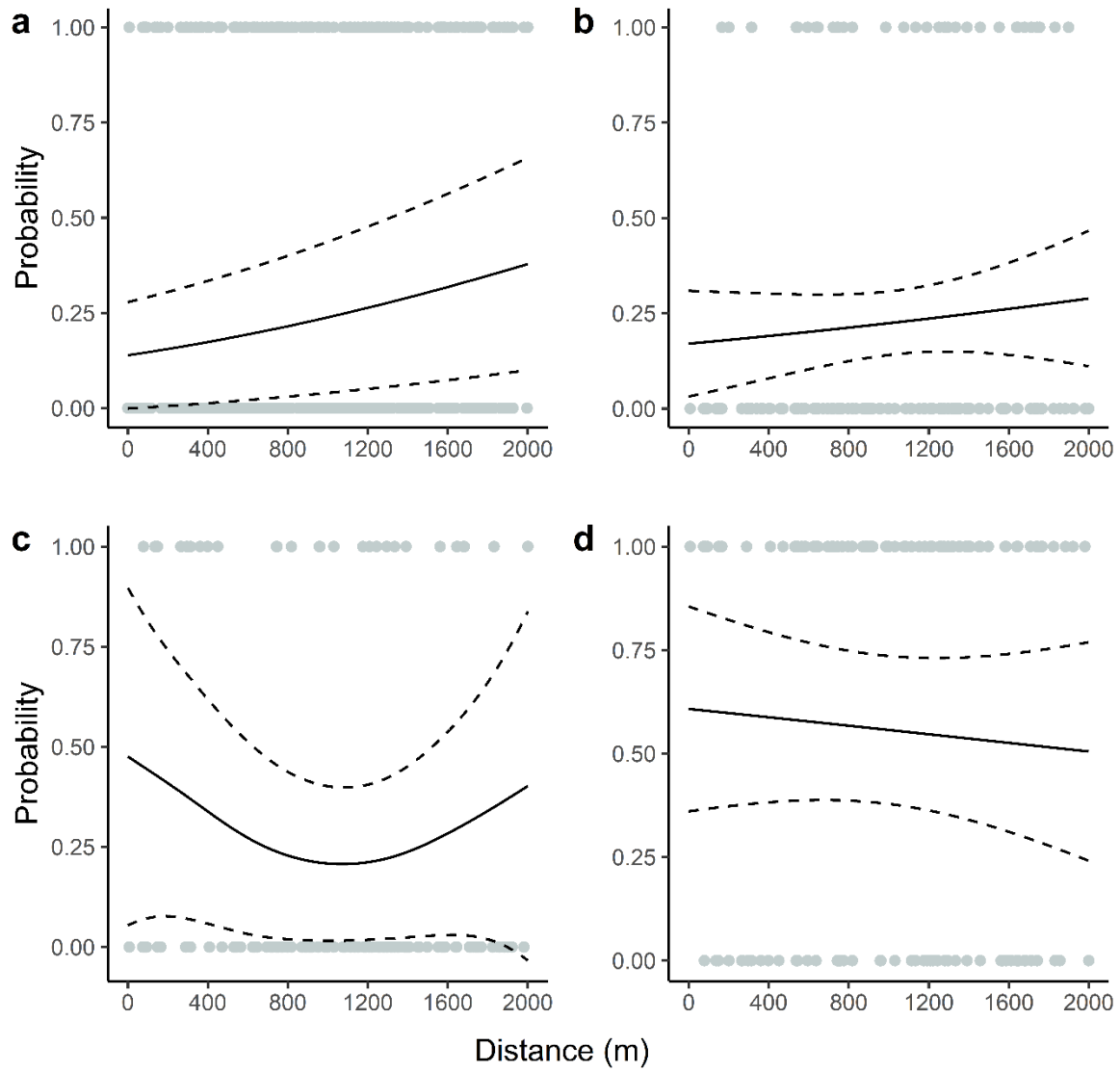


Figure 3.



Figure

