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Cuckoo parasitism in a cavity nesting host: near absent egg-rejection in a northern redstart population under heavy apparent (but low effective) brood parasitism

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24 **Abstract**

25 Brood parasite - host systems continue to offer insights into species coevolution. A notable system
26 is the redstart *Phoenicurus phoenicurus* parasitized by the “redstart-cuckoo” *Cuculus canorus* gens.
27 Redstarts are the only regular cuckoo hosts that breed in cavities, which challenges adult cuckoos in
28 egg laying and cuckoo chicks in host eviction. We investigated parasitism in this system and found
29 high overall parasitism rates (31.1% of 360 redstart nests), but also that only 33.1% of parasitism
30 events (49 of 148 eggs) were successful in laying eggs into redstart nest cups. The majority of
31 cuckoo eggs were mislaid and found on the rim of the nest; outside the nest cup. All available
32 evidence suggests these eggs were not ejected by hosts. The effective parasitism rate was therefore
33 only 12.8% of redstart nests. Redstarts responded to natural parasitism by deserting their nests in
34 13.0% of cases, compared to desertion rates of 2.8% for non-parasitized nests. Our egg parasitism
35 experiments found low rates (12.2%) of rejection of artificial non-mimetic cuckoo eggs. Artificial
36 mimetic and real cuckoo eggs added to nests were rejected at even lower rates, and were always
37 rejected via desertion. Under natural conditions, only 21 cuckoo chicks fledged of 150 cuckoo eggs
38 laid. Adding to this low success, is that cuckoo chicks are sometimes unable to evict all host young,
39 and were more likely to die as a result compared to cuckoo chicks reared alone. This low success
40 seems to be mainly due to the cavity nesting strategy of the redstart which is a challenging obstacle
41 for the cuckoo. The redstart-cuckoo system appears to be a fruitful model system and we suggest
42 much more emphasis should be placed on frontline defences such as nest site selection strategies
43 when investigating brood parasite-host coevolution.

44

45 **Keywords:** coevolution, frontline host defences, nest site selection, interspecific parasitism, model
46 egg experiments

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48

49

50 **Introduction**

51 Conflict between obligate brood parasites and their hosts is a model system for studying
52 coevolution (Rothstein 1990, Davies 2000). Brood parasitism is a major selective force shaping the
53 life history of host species due to costs of lost reproductive output (Krüger 2007). Hosts have
54 acquired a range of strategies to counter-act parasitism (reviewed by: Soler 2014, Feeney et al.
55 2014): using habitat selection decisions (Forsman and Martin 2009), nest defence (Davies et al.
56 2003, Welbergen and Davies 2009), recognition and rejection of parasite eggs (Rothstein 1975,
57 Stokke et al. 1999, Spottiswoode and Stevens 2010) or nestling discrimination (Langmore et al.
58 2003, Grim 2007, Sato et al. 2010). Anti-parasitism defences may be costly, and lost once
59 parasitism risk decreases (Lahti et al. 2009); however, in some cases defences remain long after
60 parasitism risk has ceased (Rothstein 2001, Lahti 2006, but see Samaš et al. 2014).

61

62 Complete brood loss is a common fate for hosts successfully parasitized by the common cuckoo
63 (*Cuculus canorus*; hereafter, cuckoo). Cuckoo chicks gain an advantage through early hatching and
64 are efficient at evicting host eggs and chicks (Anderson et al. 2009). The cuckoo is the only
65 interspecific brood parasite in northern Europe, where it parasitizes a wide-range of host species
66 (Soler et al. 1999, Davies 2000). The cuckoo has evolved distinct cuckoo gens specializing on
67 specific host species, and female cuckoos produce eggs that specifically mimic the eggs of this host
68 species (Moksnes and Røskoft 1995, Gibbs et al. 2000). Coevolution in each cuckoo gens and host
69 system are likely to produce novel outcomes, therefore these systems may prove fruitful for
70 investigating different host strategies to counter-act parasitism.

71

72 A notable cuckoo-host system is brood parasitism of the redstart (*Phoenicurus phoenicurus*).
73 Redstarts are the only regular cuckoo host that breeds in cavities; other regular cuckoo hosts are

74 open-cup nesting species where the cuckoo lays directly into the nest cup (Davies 2000). Poorly
75 accessible nest sites represent a unique challenge to this cuckoo gens, and appear to hinder the
76 laying of cuckoo females. As a result, cuckoo eggs in this system are often mislaid outside the host
77 nest cup (Ruttila et al. 2002), and are found on the nest rim. All studies on this system have found no
78 evidence to suggest that mimetic eggs (either real or artificial) have been ejected from nest cups
79 (Ruttila et al. 2002, 2006, Avilés et al. 2005, Grim et al. 2009a, b, this study). Moreover, video
80 recordings at redstart nests confirm that these eggs originate by being mislaid by cuckoo females
81 during parasitism attempts at the cavity nests (R Thomson pers. obs.).

82

83 It has been suggested that cavity nesting is a recently evolved redstart trait to avoid cuckoo
84 parasitism (Avilés et al. 2005). For example, potential hosts escape brood parasitism solely due to
85 their cavity nesting life history (Moksnes and Røskft 1995, Grim et al. 2014). Cavity nesting
86 further hampers the cuckoo chick from evicting host eggs or nestlings (Ruttila et al. 2002, Grim et
87 al. 2009a), which is rare in other cuckoo-host systems. Cuckoo chicks often share the nest with
88 redstart nestlings and fledgling success of the cuckoos is poor or delayed (Ruttila et al. 2002; Grim
89 et al. 2009a, b). Overall, cavity nesting seems likely to decrease the costs associated with cuckoo
90 brood parasitism for redstarts, but the benefits of using cavities (or other inaccessible sites) as a
91 defence against brood parasites needs investigation.

92

93 Cuckoo parasitism of redstart nests appears restricted to Finland, and perhaps the Baltic states
94 (Vilks 1972, Ruttila et al. 2002). Blue cuckoo eggs have rarely been found outside this area,
95 although redstarts occur throughout Europe (Moksnes et al. 1995). Due to this restricted
96 distribution, this system is relatively poorly studied (Davies 2015). Early work was limited to brief
97 descriptive accounts (von Haartman 1976, 1981, Järvinen 1984, Davies and Brooke 1989). This
98 improved in the last decade following the study by Ruttila and colleagues (2002) that brought

99 attention to this peculiar system and resulted in studies of the system in Eastern Finland (Ruttila et
100 al. 2002, 2006, Avilés et al. 2005, Grim et al. 2009a, b, Hauber et al. 2014). However, little in-depth
101 population parasitism data or egg rejection rate data exists from elsewhere in the system's range. In
102 addition, the success of parasitism events and reproductive success of the cuckoo are poorly studied.
103

104 Egg rejection strategies have traditionally been the focus of host defences against cuckoos.
105 Common hosts are often able to recognise parasite eggs that are not good mimics of the host species
106 (or individual's) eggs. The "redstart-cuckoo" gens lay immaculate blue eggs that closely match
107 redstart eggs (Avilés 2008, Igic et al. 2012, Fig. 1a). Despite being larger in size, redstarts appear
108 unable to recognize these mimetic cuckoo eggs (Ruttila et al. 2002). Rejection of natural cuckoo
109 eggs is mainly through nest desertion (Ruttila et al. 2002, 2006, Avilés et al. 2005); although non-
110 mimetic eggs are sometimes ejected from the nest cup (von Haartman 1976, 1981, Järvinen 1984,
111 Ruttila et al. 2002, 2006, Hauber et al. 2014).
112

113 Here we present cuckoo parasitism data from a northern redstart population. Our aims were to
114 document natural parasitism rates and to investigate the success of brood parasitism events at the
115 relatively inaccessible cavity nests. We also experimentally investigated redstart recognition and
116 rejection behaviour of cuckoo eggs as a host defence in this system by conducting artificial
117 parasitism experiments with model and real cuckoo eggs. Lastly, we monitored cuckoo eggs for
118 hatching and all hatched cuckoos for fledging success.
119
120

121 **Material and Methods**

122 *Field site and nest boxes*

Field work was conducted around the city of Oulu in northern Finland (65°N 25°50'E) in 2002, 2003, 2005 and 2011 – 2014. The study site covers an area of approximately 60 km², and consists of three main nest box population areas connected by several smaller areas of open Scots pine *Pinus sylvestris* dominated habitat (trees generally >50 years). The number of nest boxes followed in this study has increased over the years, from about 80 in 2002 to 350 in 2014. Nest boxes were placed on pine trees about 1.5 m above the ground and between 70 and 180 m apart. Boxes were produced by Linnunpönttö Oy, approximately 17.5 x 17.5 x 28 cm (width, depth and height) with an entrance hole diameter of 70 mm.

131

132 *General methods*

133 Nest boxes were checked at least bi-weekly between 2002 and 2005; and at least weekly for seasons
134 2011 onwards, but often more frequently. Almost all nests were visited at least once during the egg
135 laying period to calculate the date when the first egg was laid (based on one egg laid per day). We
136 recorded if nests were parasitized by cuckoos. Cuckoo eggs were easily distinguished from redstart
137 eggs based on size (Fig 1).

138

139 For parasitized nests we recorded the site where the cuckoo egg was found. These were classified
140 as: i) 'cup' for eggs within the redstart nest cup (Fig 1a,c), ii) 'rim' for eggs outside the nest cup but
141 within the nest box (Fig 1b,c), or iii) 'ground' for egg found on the ground below nest boxes. We
142 also distinguished a category, iv) 'dumped' for cuckoo eggs that were laid in redstart boxes that
143 contained only partly built redstart nests (Fig 1d). This distinction for 'dumped' eggs was clear in
144 most cases, however in some the dumped egg appeared just prior to redstart eggs (see Results).

145

146 We followed incubated cuckoo eggs to determine if the eggs hatched, the result of the eviction
147 process of host eggs/chicks, and finally if the cuckoo chicks fledged. In 2013 and 2014 we protected

148 most redstart nests after incubation was initiated by placing a wire cage over the entrance hole (this
149 decreased but did not eliminate nest predation).

150

151 *Artificial brood parasitism experiment*

152 During 2005, and 2011 – 2014, we experimentally parasitized redstart nests with artificial and real
153 cuckoo eggs. Artificial eggs were the same size and weight as real cuckoo eggs and were made of
154 plaster painted with acrylic colour (following Rutila et al. 2002). We used two types of eggs;
155 mimetic eggs that closely matched the blue eggs laid by ‘redstart cuckoos’ (Fig 2a) and non-
156 mimetic eggs that matched the grey speckled eggs laid by the cuckoo gens that parasitizes
157 bramblings (*Fringilla montifringilla*, Fig 2b, Vikan et al. 2010). For experiments with real eggs we
158 used dumped eggs and eggs laid on the rim to parasitize nests (the same or different nest).

159

160 Artificial parasitism consisted of five treatments: i) artificial mimetic egg inserted, ii) artificial non-
161 mimetic egg inserted, iii) redstart egg from the nest handled and replaced (hereafter the “control”
162 treatment), iv) real cuckoo egg that originated from a different nest added (mostly dumped eggs or
163 second or third laid cuckoo eggs from multi-parasitized nest), and v) real cuckoo egg from rim of
164 the same nest put in the cup. Treatments were randomized in most years as suitable stage nests were
165 found; in 2011, however, only non-mimetic eggs were used. We mainly performed the treatments
166 during the egg-laying phase (between 1 and 6 eggs, 149 of 159 tests) and on a few occasions after
167 clutch completion on the first day of incubation (10 of 159). Each experimental egg (artificial or
168 real) was used only once per year.

169

170 Eggs were scored as accepted if they were incubated in the nest cup after at least 6 days from clutch
171 completion. If inserted eggs were found on the ground outside nest boxes, the rim of the nests or
172 damaged within the nest cup, we scored the egg as ejected. Similarly, if nests were found with the

eggs cold in consecutive visits, the nest was scored as deserted. Accepted artificial eggs were left in the nest and collected during the nestling phase.

Statistical analyses

We used Chi-square tests to investigate rejection rates of eggs in both naturally parasitized and artificially parasitized nests. We first compared rejection rates of naturally parasitized nests with natural non-parasitized nests not included in experiments. Second, we compared each artificial treatment separately to the control, and then pooled all mimetic treatments (all added blue cuckoo eggs, real or artificial) and compared that to the non-mimetic artificial egg treatment. Chi-square test was also used to examine the survival rates of cuckoo chicks that did or did not share the nest with host nestlings.

Results

General parasitism rate and parasitism success

We found that 31.1% of redstart nests were parasitized by at least one cuckoo (Table 1). This figure is obtained from 360 redstart nests followed for this study (Table 1), but excludes 36 nests that were predated during the egg laying period (five of these nests were confirmed parasitized at the time of predation). Parasitism rates varied between years (Table 1). In total 18 redstart nests (16.1%) were parasitized multiple times (15 twice and 3 thrice), in addition one of the predated nests contained two cuckoo eggs when predated.

In four cases cuckoos laid in ready feather-lined cup nests, 1-2 days prior to redstart egg-laying (included in parasitism rate calculations). But we also documented an additional 11 cases where a cuckoo egg was dumped on an incomplete redstart nest with no eggs. These 11 boxes did not

198 progress to full nests, and were also not totalled into the overall parasitism rates. We detected three
 199 definite cases when cuckoos laid eggs after incubation was initiated. The majority of cuckoo eggs
 200 were therefore laid during the egg laying period.

201

202 Our study documented a total of 150 cuckoo eggs laid in our redstart population. We noted the
 203 placement of all these cuckoo eggs, except for two (laid in the same redstart nest in 2002). Of the
 204 remaining 148 cuckoo eggs, only 33.1% were laid into the nest cup (Table 2). The remaining
 205 cuckoo eggs were found on the nest rim, ground outside the nest box or were dumped on
 206 incomplete nest material (Table 2). We did not always check for cuckoo eggs on the ground below
 207 redstart nests and the number of these eggs was likely underestimated. Predators may also remove
 208 eggs on the ground prior to our box visits. Taking into account multiple parasitism events in some
 209 nests, only 12.8% of redstart nests were effectively parasitized during the laying procedure (Table
 210 1).

211

212 *Response to parasitism*

213 Of the nests that were effectively naturally parasitized (egg laid into nest cup), 13.0% were deserted
 214 by the redstarts; in two cases the cuckoo egg was also punctured (Table 3). No confirmed cases of a
 215 real cuckoo egg that was ejected out the nest cup were detected (Table 3). However, the nest
 216 desertion rate of naturally parasitized redstart nests was significantly higher than that of non-
 217 parasitized redstart nests (2.8% of 177; $\chi^2 = 8.13$, $df = 1$, $p = 0.004$).

218

219 Our artificial parasitism experiment detected low rates of egg ejection and nest desertion as an anti-
 220 parasitism strategy (Table 3). Only 2 of 69 artificial mimetic and real mimetic cuckoo eggs that
 221 were added to nests were rejected (both by nest desertion, Table 3). In nests that received non-
 222 mimetic artificial eggs, 12.2% of the artificial eggs ($n = 5$) were rejected. In two cases the non-

mimetic eggs were ejected and were found on the ground below the nest box; the other three nests were deserted. One control nest (2.5%) was also deserted. There was no clear difference in the probability of rejection between any of the artificial parasitism treatments and the control treatment (all $\chi^2 < 2.77$, $df = 1$, all $p > 0.096$). When we compared the non-mimetic treatment to all mimetic treatments combined there was a tendency of higher rejection probability for non-mimetic eggs ($\chi^2 = 3.73$, $df = 1$, $p = 0.053$). Low rejection rates did not allow us to test between and within year temporal effects, or effects of timing of parasitism.

230

231 *Cuckoo hatching and fledging success*

232 By transferring mislaid cuckoo eggs into nest cups of the same or different nests (Table 4), we were
 233 able to follow a total of 105 cuckoo eggs in redstart nest cups (Table 4). In total 78.1% were
 234 incubated to completion, of which 15.9% did not hatch. Of the 69 cuckoo chicks that hatched, 10
 235 (14.5%) died during the nestling stage. Therefore only 72.0% of the cuckoo eggs incubated to
 236 completion produced a fledgling (see Table 4 for details). Of the original 49 cuckoo eggs effectively
 237 laid into 46 redstart nests, only 59.2% hatched and only 42.9% produced a fledgling (see Table 4 for
 238 details).

239

240 Cuckoo chicks evict host eggs or chicks by pushing them onto the rim of the nest (personal
 241 observations). However, not all cuckoo chicks evicted all host young. In 10 of 67 (14.9%) cases, the
 242 cuckoo chick was unable to evict all host young and shared the nest with redstart chicks (for two
 243 cuckoo chicks, data on the fate of redstart chicks was missing). These ten nests with mixed broods
 244 (cuckoo and redstart chicks) fledged on average 3.6 redstart chicks (range 1–6). In comparison,
 245 unparasitized (and not predated) redstart nests fledged on average 6.0 redstart chicks (range 0–8).
 246 Cuckoos were significantly more likely to die when sharing the nest with redstart chicks ($\chi^2 = 15.6$,
 247 $df = 1$, $p = <0.001$). Of the 10 cuckoo chicks that shared the nest cup with redstart nestlings, half did

not fledge (five fledged, but five died), whereas 53 of 57 cuckoo chicks that did not share the nest with redstart chicks fledged. One of the cuckoo chicks that died with host chicks was from a nest which naturally hatched two cuckoo chicks, but only one survived (both excluded from the chi-square test).

Discussion

We found high rates of cuckoo parasitism in a northern redstart population, with 31.1% of nests parasitized at least once. Parasitism rates were higher than recorded for other redstart populations in Finland (between 0–23%, Rutila et al. 2002, 2006) and matched some of the highest rates for host populations parasitized by cuckoos: sedge warbler *Acrocephalus schoenobaenus* 27% (Kleven et al. 2004), marsh warbler *A. palustris* 45% (Kleven et al. 2004), great reed warbler *A. arundinaceus* 34–66% (Moskát and Honza 2000, Kleven et al. 2004). However, despite high parasitism rates many parasitism events failed because the cuckoo eggs did not reach the redstart nest cup. The effective parasitism rate was therefore only 12.8%.

Our data further shows that 13.0% of the effectively parasitized nests were deserted. In addition, some parasitized nests were predated or the cuckoo eggs failed to hatch. Even when the eggs hatched, 14.9% of cuckoo chicks were unsuccessful in evicting all host offspring. Mixed cuckoo-host broods are unusual but have been documented before in the cuckoo-redstart system; Rutila et al. (2002) found that almost half of cuckoo chicks failed to evict all host chicks. Mixed host-parasite broods are more characteristic of cowbird or *Clamator* cuckoo parasitism systems (Soler and Soler 1991, Kilner et al 2004), but in these examples the brood parasite chicks suffer little as a result. Common cuckoos instead suffer severe costs when raised in mixed broods (Grim 2009a, b), and in our population half of the cuckoo chicks raised with host offspring failed to fledge. In total, only 21 of 46 (45.7%) effectively parasitized redstart nests produced a cuckoo fledgling (only 18.8% of all

273 parasitized redstart nests). Therefore cuckoos' breeding success (number of young fledged per egg
274 laid) was only 14.0%. This success rate is lower than the 18% found by Rutila and colleagues
275 (2002).

276

277 Naturally laid cuckoo eggs found on the nest rim and ground (together 59.5% of cuckoo eggs) are
278 very unlikely to stem from host egg ejection (see also Rutila et al. 2002, 2006, Avilés et al. 2005).
279 Of the 16 real cuckoo eggs and 16 full mimetic artificial eggs introduced to redstart nests, none
280 were ejected (if egg ejection was the strategy used, at the rates of rim eggs documented, about 17 of
281 these added eggs should have subsequently been found on the rim). In addition, none of 37 mislaid
282 eggs that we introduced into the actual nest cup of the same nest re-appeared on the nest rim during
283 subsequent nest checks. A more likely explanation is that the cavity nesting strategy of the redstart
284 makes it a challenging host for the cuckoo to parasitize and therefore majority of the cuckoo's
285 laying attempts fail and the egg ends up on nest rim or on the ground. Indeed, redstarts appear to
286 gain large counter-parasitism benefits from nesting in cavities, which has been suggested to be a
287 recently evolved trait (Avilés et al. 2005).

288

289 A cavity nesting strategy may also introduce some costs for hosts. Ejecting identified brood parasite
290 eggs out of the nest cavity may be challenging for host individuals due to the difficulties of grasping
291 and puncturing the egg (although is possible: Rutila et al. 2002, this study). Therefore, the main
292 rejection option available for redstarts may be nest desertion. Nest desertion rate was indeed higher
293 in effectively parasitized redstart nests (13.0%) than in non-parasitized nests (2.8%) suggesting that
294 desertion is the main egg rejection strategy of the redstart. Similar evidence has been found in
295 studies that have experimentally added non-mimetic eggs in this system (Rutila et al. 2002, 2006,
296 Avilés et al. 2005, Hauber et al. 2014). However, no nest was deserted when mimetic eggs were
297 placed into non-parasitized nests (i.e. nests that had not hosted a cuckoo female laying visit)

298 implying that redstarts are unable to reliably detect mimetic cuckoo eggs. This raises the question,
299 how do the redstarts decide when to desert the nest if they cannot distinguish the mimetic cuckoo
300 egg from their own eggs?

301

302 Naturally parasitized nests where cuckoos succeeded to lay into the redstart nest cup showed the
303 highest overall nest desertion rates. In addition, two of the nests where cuckoo eggs that were laid to
304 the nest rim were placed in the nest cup were deserted. Egg rejection of mimetic cuckoo eggs in the
305 form of nest desertion therefore appears limited to cases where the redstart had the possibility to
306 observe the cuckoo laying at the nest. We speculate that the presence of the female cuckoo at the
307 nest may be a vital cue to redstarts that they have been parasitized. This presence cue may lead to
308 the nest desertion decisions recorded. Previous work has shown that the presence of a cuckoo
309 increases the probability of egg rejection in reed warblers (Davies and Brooke 1988, Moksnes et al.
310 1993, 2000). This hypothesis should be tested in the redstart-cuckoo system. Observer disturbance
311 may also elicit this response (Hanley et al. 2015), although it did not appear to affect desertion rates
312 in our study.

313

314 Despite being higher than in non-parasitized nests, nest desertion rate was still relatively low in
315 naturally parasitized nests, with majority of the redstart population accepting the cuckoo egg. Nest
316 desertion as a rejection strategy of foreign eggs is more costly than egg ejection, especially in
317 northern populations where the short breeding season may prevent successful renesting (Pakanen et
318 al. 2014). High costs of desertion in combination with low effective cuckoo parasitism rates and
319 further lowered parasitism costs due to unhatched cuckoo eggs may make acceptance of the cuckoo
320 egg a more beneficial strategy at the population level than abandoning the nesting attempt. In
321 addition, relatively low cuckoo eviction success (Rutla et al. 2002, Grim et al. 2009a, this study)
322 adds to the lowered costs of parasitism. On the other hand, if observation of a laying cuckoo at the

323 nest is a necessary cue of having been parasitized the low nest desertion rate may also reflect the
324 difficulty of observing the cuckoo laying event.

325

326 In artificial egg parasitism experiments, our redstart population exhibited low egg rejection rates
327 with only 12.2% of the artificial non-mimetic eggs rejected. This rejection rate did not differ from
328 control or other treatment groups. Low rejection rates of non-mimetic eggs in a common host seems
329 surprising, yet this matches the prediction of Moksnes et al. (2013) that current common hosts
330 would show less egg rejection behaviour due to the current stage of the co-evolutionary arms-race.
331 However, the rates of non-mimetic egg rejection have been far higher in other populations.
332 Rejection of non-mimetic eggs ranged from 38–50% (by either egg ejection or nest desertion), both
333 in populations with rather high natural parasitism rates up to 23% and also in populations without
334 cuckoo parasitism (Ruttila et al. 2002, 2006). Järvinen (1984) nevertheless reported full acceptance
335 of non-mimetic eggs artificially added to redstart nest in far north-western Finland.

336

337 Predominant acceptance of non-mimetic eggs implies a short history of cuckoo parasitism. On the
338 other hand, the highly mimetic cuckoo eggs of the redstart cuckoo gens (Igic et al. 2012) suggest a
339 long co-evolutionary history with strong selection from the host by rejecting non-mimetic eggs.
340 Contemporary redstart populations however show only low to moderate egg rejection rates
341 (Järvinen 1984, Ruttila et al. 2002, 2006, Avilés et al. 2005). The underlying mechanism may be
342 that, in relation to the potential benefits of egg ejection or nest desertion these strategies are too
343 costly due to mistakes made by hosts (Davies et al. 1996, Samaš et al. 2014). The benefits of egg
344 ejection or nest desertion depend on the costs of parasitism. Indeed, the current low utilization of
345 egg rejection by the redstarts may reflect the low reproductive costs of cuckoo parasitism to
346 redstarts (e.g. Grim et al. 2009b, this study).

347

348 Breeding success of cuckoos in our population is low, even though the redstarts do not seem to
349 recognize cuckoo eggs and show only low levels of nest desertion in response to cuckoo parasitism.
350 Therefore, despite the high apparent parasitism rate, the true cost of parasitism in our redstart
351 population appears to be relatively low. Low cuckoo breeding success appears to stem from two
352 causes: low laying success of female cuckoos and relatively low eviction success of cuckoo chicks.
353 Both seem to be related to the redstart's strategy to breed in cavities. Cavity nesting may therefore
354 be seen as an important frontline defence (Avilés et al. 2005, Forsman and Martin 2009, Feeney et
355 al. 2012, 2014) that may reduce parasitism costs and weaken selection on defences (such as egg
356 rejection) later in the breeding cycle (Britton et al. 2007). We suggest that much more emphasis
357 should be placed on such frontline defences, and the redstart-cuckoo system would be a fruitful
358 model for investigating nest site selection as a defence against brood parasitism.

359

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490 Figure 1: Redstart nests parasitized by common cuckoos, a) cuckoo egg found within the nest cup,
491 b) cuckoo egg mislaid outside the nest cup, c) one mislaid and one correctly laid cuckoo egg, and d)
492 cuckoo egg dumped in a nest box with redstart nesting material but without a completed nest cup.

493 Figure 2: Redstart nests artificially parasitized using a) mimetic and b) non-mimetic model common
494 cuckoo eggs. In panel a) the mimetic model egg is indicated by the arrow, while a naturally laid real
495 cuckoo egg lies to the right.
496

497 Table 1. Number of redstart nests followed in each year and the number parasitized annually.

498

Year	Nests followed	Predated ¹	Nests used	Parasitized
2002	9	1	8	2 (25.0%)
2003	15	3	12	2 (16.7%)
2005	16	1	15	7 (46.7%)
2011	33	3	30	4 (13.3%)
2012	39	6	33	9 (27.3%)
2013	114	11	103	30 (29.1%)
2014	170	11	159	58 (36.5%)
		Total	360	112 (31.1%)
Effectively				
parasitized ²				46 (12.8%)

499 ¹nests predated during egg laying not allowing us to determine the parasitism status

500 ²parasitized nests where the cuckoo egg was laid in the nest cup

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505 Table 2. The laying site of each cuckoo egg documented in this study.

506

Site of cuckoo egg	N	%
Inside the nest box		
In the nest cup	49	33.1
On the nest rim	82	55.4
Dumped on incomplete nest	11	7.4
On the ground outside	6	4.1
Total	148	

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511 Table 3. The responses of redstarts to artificial egg parasitism experiments and natural parasitism
 512 events. All experimental nests are detailed with the number of ejected, deserted and accepted
 513 outcomes.

514

Treatment	Excluded ^a	N	Ejected	Deserted	Accepted
Manipulated nests					
Control (touch)	1	40	0	1	39 (97.5%)
Mimetic	1	16	0	0	16 (100%)
Non-mimetic	3	41	2	3	36 (87.8%)
Cuckoo egg	0	16	0	0	16 (100%)
Rim cuckoo egg put-in	3	37	0	2	35 (94.6%)
Non-manipulated nests					
Parasitized ^b		46	0	6	40 (87.0%)
Non-parasitized		177	0	5	172 (97.2%)

515 ^a excluded due to unknown fate caused by nest predation soon after treatment

516 ^b effectively parasitized nests where at least one cuckoo egg was naturally laid into the host nest cup

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520

521 Table 4. The fate of cuckoo eggs followed in relation to different origins.

522

	Total	Eggs incubated to completion	Hatched (Unhatched)	Fledged
Naturally laid into nest cup	49	31	29 (2)	21
Moved to new nest	16	16	11 (5)	11
Rim eggs put into cup	40	35	29 (6)	27
Total	105	82	69 (13)	59

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