

1 **Disappearance of eggs from non-parasitized nests of brood**
2 **parasite hosts – the evolutionary equilibrium hypothesis revisited**

3

4 BÅRD G. STOKKE^{1*}, EIVIN RØSKAFT¹, ARNE MOKSNES¹, ANDERS PAPE
5 MØLLER², ANTON ANTONOV^{1†}, FRODE FOSSØY¹, WEI LIANG³, GERMÁN LÓPEZ-
6 IBORRA⁴, CSABA MOSKÁT⁵, JACQUI SHYKOFF², MANUEL SOLER⁶, JOHAN R.
7 VIKAN¹, CANCHAO YANG³ and FUGO TAKASU⁷

8

9 ¹*Department of Biology, Norwegian University of Science and Technology (NTNU),*
10 *Trondheim Faculty of Natural Sciences and Technology, NO-7491 Trondheim, Norway*

11

12 ²*Laboratoire Ecologie, Systematique et Evolution UMR 8079 CNRS-Université Paris-Sud XI-*
13 *AgroParisTech, F-91405 Orsay Cedex, France*

14

15 ³*Ministry of Education Key Laboratory for Tropical Animal and Plant Ecology, College of*
16 *Life Sciences, Hainan Normal University, Haikou 571158, P. R. China*

17

18 ⁴*Departamento de Ecología/IMEM Ramon Margalef, Universidad de Alicante, Apartado 99,*
19 *E-03080 Alicante, Spain*

20

21 ⁵*MTA-ELTE-MTM Ecology Research Group of the Hungarian Academy of Sciences, c/o*
22 *Biological Institute, Eötvös Lóránd University, Pázmány Péter sétány 1/c., H-1117 Budapest,*
23 *Hungary, and Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary*

24

25 ⁶*Grupo Coevolución, Unidad Asociada al CSIC, Departamento de Biología Animal, Facultad*
26 *de Ciencias, Universidad de Granada, E-18071 Granada, Spain*

27

28 ⁷*Department of Information and Computer Sciences, Nara Women's University, Kita-Uoya*
29 *Nishimachi, Nara 630-8506, Japan*

30

31 † *To the memory of A. Antonov who died much too young 20 May 2012*

32

33 * *Author for correspondence (bard.g.stokke@ntnu.no). Phone: +47 73596128 / Fax: +47*

34 *73596100*

35

36 **RUNNING TITLE: DISAPPEARANCE OF EGGS**

37

38

39 **ABSTRACT**

40 The evolutionary equilibrium hypothesis was proposed to explain variation in egg rejection
41 rates among individual hosts (intra- and interspecific) of avian brood parasites. Hosts may
42 sometimes mistakenly reject own eggs when they are not parasitized, i.e. make recognition
43 errors. Such errors would incur fitness costs and could counter evolution of host defences
44 driven by costs of parasitism, i.e. creating equilibrium between acceptors and rejecters within
45 particular host populations. Here, we report disappearance of host eggs from non-parasitized
46 nests in populations of 7 European passerine species. Based on these data we calculate the
47 magnitude of the balancing parasitism rate given that all eggs lost are due to recognition
48 errors. Importantly, since eggs are known to disappear from nests for other reasons than
49 erroneous host rejection, our data represent maximum estimates of such costs. Nonetheless,
50 disappearance of eggs was rare events and incurred low costs compared to the high costs of
51 parasitism. Hence, costs due to recognition errors are probably of minor importance as
52 opposing selective pressure to evolution of egg rejection in most hosts. We cannot exclude the
53 possibility that intermediate egg rejection rates in some host populations may be caused by
54 spatiotemporal variation in occurrence of parasitism and gene flow, creating variable
55 influence of opposing costs due to recognition errors and costs of parasitism.

56

57 **KEYWORDS:** Co-evolution; cuckoo; fitness cost; host defence; host-parasite interactions;
58 disappearance of eggs

59

60 INTRODUCTION

61 In hosts of avian brood parasites, costs of parasitism impose strong selection for evolution of
62 defensive traits because successful parasitism in many cases leads to total loss of host
63 reproductive output. Therefore, many hosts have evolved fine-tuned egg rejection abilities,
64 which in several cases have been countered by parasites evolving mimetic eggs (e.g. Payne,
65 1967; Brooke & Davies, 1988; Davies & Brooke, 1989a; Moksnes *et al.*, 1991; Antonov *et al.*
66 2006a; Starling *et al.* 2006; Spottiswoode & Stevens 2010; Stoddard & Stevens, 2010, 2011;
67 Begum *et al.*, 2011). In some species, there is apparently no variation in rejection abilities
68 either within or between populations, and rejection rates are more or less fixed at 100% (i.e.
69 all individuals are capable of rejection) as long as the appearance of the parasitic egg is
70 cognitively recognizable for the individuals in question (Stokke, Moksnes & Røskaft, 2005).
71 However, even rejection rates of non-mimetic eggs are only moderate in several other host
72 species, often showing prominent temporal and/or spatial variation (Brooke, Davies & Noble,
73 1998; Soler *et al.*, 1999; Stokke *et al.*, 2008), relying on additional cues other than egg
74 appearance when deciding to reject parasitic eggs (i.e. conditional responses (Brooke *et al.*,
75 1998; Davies, 2000)). Such co-occurrence of acceptors and rejecters (either as fixed or
76 flexible strategies) within a single host population is often explained by costs of making errors
77 in recognition and rejection of foreign eggs, which could outweigh the benefits of egg
78 rejection under specific circumstances (Rothstein, 1982a; Marchetti, 1992; Lotem, Nakamura
79 & Zahavi, 1995; Davies, Brooke & Kacelnik, 1996; Takasu, 1998). Specifically, host
80 individuals attuned to reject foreign eggs may mistakenly reject one of their own eggs in nests
81 that are not parasitized (Stokke *et al.*, 2005; Røskaft *et al.*, 2002a). These costs obviously
82 have fitness consequences because the resulting clutch size will be smaller than the optimal
83 one. In theory, such errors are most likely to occur in hosts that have high variation in egg
84 appearance within clutches (Davies & Brooke, 1989b; Lotem *et al.*, 1995; Stokke *et al.*,

85 2007), making it difficult for hosts to recognize and hence reject parasitic eggs. Thus, if
86 parasitism rates are low or variable, the costs of making recognition errors could sometimes
87 potentially be higher than the costs of parasitism. Such a scenario could result in equilibrium
88 between acceptors and rejecters within particular host populations or, if costs due to
89 recognition errors and rejection costs are high, even lead to acceptance being the optimal
90 strategy (the evolutionary equilibrium hypothesis, Lotem & Nakamura, 1998).

91 However, the importance of recognition errors as an opposing selective force to egg
92 rejection, at least in hosts of evicting parasites, has been questioned (Røskaft *et al.*, 2002a;
93 Stokke *et al.*, 2002a). In brood parasites like honeyguides (Indicatoridae) and cuckoos
94 (Cuculidae), the parasitic chick gets rid of all host eggs or young from the nest soon after
95 hatching (Davies, 2000; Anderson *et al.*, 2009; Grim *et al.*, 2009; Spottiswoode & Koorevaar,
96 2012), enforcing high costs on host reproduction and hence strong selection for evolution of
97 defences against parasitism, depending on the level of parasitism. Furthermore, estimating
98 occurrence of recognition errors is not straightforward. It is well known that partial egg losses
99 may be due to other causes than erroneous ejection of own eggs, like e.g. jostling or partial
100 predation (e.g. Rothstein, 1982b; Lerkelund *et al.*, 1993). Hence, only constant monitoring of
101 nests throughout the egg laying and incubation period can provide us with evidence for the
102 occurrence of recognition errors. Without such monitoring, we cannot rule out the possibility
103 that eggs may disappear for other reasons than erroneous host rejection and estimates of such
104 costs are therefore in many cases likely to be higher than what is actually the case.

105 The objective of the present study is to report the disappearance of own eggs in actual
106 and potential host species of common cuckoo *Cuculus canorus*. Based on these data, we
107 estimate maximum costs of recognition errors and the parasitism rate that should balance
108 these costs. We discuss our results in relation to current knowledge of co-evolutionary
109 adaptations in cuckoos and their hosts.

110

111 MATERIAL AND METHODS

112 ESTIMATE OF PARASITISM RATE BALANCING MAXIMUM RECOGNITION

113 ERRORS ESTIMATES

114 We acknowledge that the response to a parasitic egg may be conditional/plastic (Brooke *et al.*,
115 1998; Lindholm & Thomas, 2000; Soler, Martín-Vivaldi & Fernández-Morante, 2012).

116 Furthermore, we realistically assume that host egg rejection behaviour has a genetic basis
117 (Martín-Gálvez *et al.*, 2006). In the absence of parasitism, the frequency of rejecters in the

118 population **may** decline due to recognition errors, but also due to other costs related to
119 maintaining specific traits or due to stochasticity (Lahti, 2005, 2006). **In populations**

120 **experiencing parasitism above a certain threshold level**, selection will likely lead to rejecters
121 producing more offspring than acceptors because rejecters escape the costs of parasitism. We

122 use the model presented by Davies & Brooke (1989b) to derive average reproductive success
123 of acceptor and rejecter pairs (RS_{acceptor} and RS_{rejecter}) and the corresponding balancing

124 parasitism rate, p^* . Let p be the parasitism rate (probability of a host nest being parasitized).

125 Average reproductive success of acceptor pairs (both sexes are acceptors) is

126

$$127 \quad RS_{\text{acceptor}} = F(1 - p) + c(F - 1)p$$

128

129 where F is the average host clutch size and c is the proportion of host young reared together
130 with a parasitic chick ($0 \leq c \leq 1$). Typically, for evicting brood parasites like *Cuculus*

131 cuckoos, $c = 0$ (but see Rutila, Latja & Koskela, 2002), but for non-evicting parasites, c can
132 be larger. We assume that cuckoo females remove one host egg from the nest when

133 parasitizing the nest (Davies, 2000), even though removal of more than one egg is not

134 uncommon (Øien *et al.*, 1998). Average reproductive success of rejecter pairs (at least one
135 breeding individual is rejecter), where all parasite eggs are rejected is

136

$$137 \quad RS_{\text{rejecter}} = (F - \Delta F)(1 - p) + (F - \Delta F - 1) p$$

138

139 where ΔF denotes recognition errors expressed as the number of host eggs lost by rejecters.

140 Since only rejecters are likely to commit recognition errors, we need to take egg rejection

141 rates within the population into account when calculating ΔF as follows

142

$$143 \quad \Delta F = [\text{Proportion of host eggs lost from unparasitized nests in population}] [\text{Mean} \\ 144 \text{ clutch size in population}] / [\text{Egg rejection rate in population}] \quad (1)$$

145

146 At equilibrium, the average reproductive success, $RS_{\text{acceptor}} = RS_{\text{rejecter}}$, we obtain the
147 parasitism rate, p^* , that balances the benefit of rejecting parasite eggs with the cost of
148 rejecting own eggs in non-parasitized nests (recognition errors) as

149

$$150 \quad p^* = \Delta F / (F - 1) / (1 - c)$$

151

152 In some species, host individuals show phenotypic plasticity in their responses against
153 parasites (based on social cues; Campobello & Sealy (2011), based on personality, Avilés &
154 Parejo (2011), based on perception of risk of parasitism, Welbergen & Davies (2009)) and
155 parasitic eggs, and hosts will more likely reject eggs if they experience additional cues other
156 than the egg itself, like for instance observing a cuckoo in the vicinity of the nest (Moksnes *et*
157 *al.*, 2000). Furthermore, the ability of individuals to reject parasitic eggs usually depends on
158 the contrast between own and foreign eggs, i.e. egg mimicry (Davies, 2000; Spottiswoode &

159 Stevens, 2010). Hence, from Eq. 1 we obtain four estimates of ΔF ; assuming that 1) all (RE1),
160 2) 50% (RE2), 3) 25% (RE3) and 4) observed % (RE4) of individuals in the population are
161 able to reject foreign eggs. The estimate RE4 is based on rejection of experimental non-
162 mimetic eggs in the specific study population (Table 1). We acknowledge that these four
163 estimates are only crude attempts to take phenotypic plasticity into account in our
164 calculations, but firstly we want to keep our calculations as simple as possible, and secondly,
165 we lacked reliable quantitative estimates of phenotypic plasticity. By calculating four
166 estimates, at least some of the phenotypic plasticity present at the individual level in specific
167 populations is taken into account.

168

169 EMPIRICAL DATA IN DISAPPEARANCE OF EGGS AND OTHER RELEVANT 170 FACTORS

171 Data on disappearance of own eggs in non-parasitized nests were retrieved from own field
172 studies in which nests were monitored throughout the egg laying and incubation periods. We
173 retrieved 1) number of host eggs lost from unparasitized host nests in the specific population;
174 2) mean clutch size in the specific population (F); and 3) rejection rate of experimentally
175 added, non-mimetic eggs within the study populations. In addition, we also retrieved 4)
176 observed parasitism rate within each population (Table 1). The number of eggs lost in each
177 population, termed “number of disappeared eggs”, was calculated as the number of eggs lost
178 from non-parasitized nests / total number of non-parasitized nests (excluding nests that were
179 naturally or experimentally parasitized). We only included nests with single host eggs lost,
180 because disappearance of more than one egg could indicate partial predation rather than actual
181 errors in recognition. Hence, in our marsh warbler *Acrocephalus palustris* population we
182 omitted cases where three out of four eggs ($N = 1$), and four out of five eggs ($N = 2$)
183 disappeared. In our corn bunting *Miliaria calandra* population we omitted cases where two

184 out of three eggs (N = 1), three out of five eggs (N = 1), and four out of five eggs (N = 1)
185 disappeared. We also omitted clutches where egg laying did not follow the “one egg per day”
186 criterion. More specifically this refers to two extraordinary cases in the chaffinch *Fringilla*
187 *coelebs* population, with an irregular egg laying sequence (Stokke *et al.*, 2002a). Furthermore,
188 loss of all eggs in the clutch was considered to be caused by predation, and such nests were
189 omitted from the calculations.

190 Nests were monitored daily from nest building until six days of incubation to allow
191 estimates of disappearance of own eggs from non-parasitized nests. Eggs were marked with
192 permanent ink in the sequence they were laid. Clutch size was estimated from completed,
193 non-parasitized clutches. Nests used to calculate recognition errors and clutch size were
194 different from those used to calculate rejection rate of experimentally added, non-mimetic
195 eggs.

196 Disappearance of eggs from non-parasitized nests were estimated in 8 study
197 populations (Table 1): (1) great reed warblers *Acrocephalus arundinaceus* in Apaj, Hungary
198 (1998-2008), (2) great reed warblers in Embalse del Hondo, Alicante, Spain (XXXX-XXXX),
199 (3) reed warblers *Acrocephalus scirpaceus* in Embalse del Hondo, Alicante, Spain (XXXX-
200 XXXX), (4) marsh warblers in Zlatia, Bulgaria (2002-2009), (5) olivaceous warblers
201 *Hippolais pallida* in Zlatia, Bulgaria (2001-2009), (6) chaffinches in Stjørdal, Norway (1999-
202 2001), (7) bramblings *Fringilla montifringilla* in Tana, Norway (2003-2004), and (8) corn
203 buntings in Zlatia, Bulgaria (2002-2009). All these species are known to be parasitized by
204 common cuckoos to various extents (Moksnes & Røskaft, 1995). Data on clutch sizes,
205 parasitism rates, and rejection rates of experimentally added, non-mimetic eggs were retrieved
206 from the literature for the same populations from which we obtained data on disappearance of
207 eggs (Moksnes *et al.*, 1991; Moksnes, Røskaft & Solli, 1994; Bártol *et al.*, 2002; Moskát &
208 Honza, 2002; Stokke *et al.*, 2002a, 2004; Antonov *et al.*, 2006a,b, 2007a,b, 2009; Hauber,

Megjegyzés [BGS1]: Csaba and Germán, Please insert years of data collection

209 Moskát & Bàn, 2006; Moskát *et al.*, 2008a,b,c, 2009; Avilés *et al.*, 2009; Vikan *et al.*, 2009,
210 2010, 2011). A few data from unpublished studies were also included; in the Spanish reed
211 warbler population (number 3 in the list above), rejection data of non-mimetic eggs refer to
212 experimentally added eggs painted pale blue.

213

214 RESULTS

215 Disappearance of eggs from non-parasitized nests was most pronounced in great reed and reed
216 warblers (7 - 7.4%). In the remaining species, eggs disappeared in only 0 - 0.9% of the nests
217 (Table 1). Individuals in the populations included in our analyses experienced 0 to 16.7% loss
218 of own eggs in non-parasitized nests depending on how we consider rejection abilities (Table
219 1). Calculations of parasitism rates that would balance the costs of recognition errors
220 (provided that all eggs lost were due to erroneous egg rejection) show considerable variation
221 among species (Table 1, range 0 – 23.3%). Since only rejecters are assumed to erroneously
222 reject own eggs, and our estimate of recognition errors is one fixed value per population, the
223 cost of recognition errors and the corresponding balancing parasitism rate will be higher when
224 fewer individuals are classified as rejecters (Equation 1). Hence, within particular
225 populations, estimates of recognition errors and balancing parasitism rates will generally be
226 higher when considering rejection of mimetic eggs than non-mimetic eggs, since the rejection
227 rate for mimetic eggs in the population is generally lower than for non-mimetic eggs. If we
228 assume that all individuals have the ability to reject eggs (100% rejection rate), estimates of
229 both recognition errors and balancing parasitism rate can be regarded as minimum estimates.

230 The balancing parasitism rates are generally in the magnitude of 0 – 1.2%, except in
231 great reed and reed warblers where it may reach 7.7 and 23.3% respectively, depending on
232 calculation of the proportion of individuals that are able to reject parasitic eggs. In seven of
233 the eight study populations, observed parasitism rates are equal to or higher than those

234 required to balance the costs of making recognition errors, indicating that egg rejection
235 abilities should evolve and be maintained, which is in accordance with the high rejection rates
236 of non-mimetic eggs generally found in this study. Hence, recognition errors should not be
237 important as opposing selection pressure in these populations. The only exception among
238 these seven populations is the corn bunting, which experience a rather high parasitism rate but
239 still only reject non-mimetic eggs at an intermediate level. The remaining population, Spanish
240 reed warblers, experience a parasitism rate that is lower than the ones required maintaining
241 rejection behaviour with all four estimates of recognition errors (Table 1).

242

243 INSERT TABLE 1 APPROX. HERE

244

245 DISCUSSION

246 Perceptual errors may cause costs that could oppose evolution or maintenance of apparently
247 optimal adaptations like those involved in co-evolutionary arms races. Such costs may act as
248 opposing selective pressures against evolution of host defences against brood parasitism, as
249 outlined in the evolutionary equilibrium hypothesis (Rothstein, 1982a; Lotem *et al.*, 1995;
250 Davies *et al.*, 1996). Here we have shown that the magnitudes of such errors are in general
251 low across eight different host populations, even with our overestimated rates of recognition
252 errors. Furthermore, our estimates of recognition errors are comparable to those obtained from
253 other species (Marchetti, 1992, 2000; Lotem *et al.*, 1995).

254 Several European passerines regarded as suitable cuckoo hosts show strong rejection of
255 experimentally added eggs (Davies & Brooke, 1989a; Moksnes *et al.*, 1991; Moskát,
256 Szentpéteri & Barta, 2002; Honza *et al.*, 2004; Lovászi & Moskát, 2004; Procházka & Honza,
257 2004; Rutila *et al.*, 2006; Samaš *et al.*, 2011; Table 1). Such species are often characterized by
258 having a low intraclutch variation in egg appearance (Øien, Moksnes & Røskoft, 1995; Soler

259 & Møller, 1996; Stokke, Moksnes & Røskaft, 2002b), reducing the risk of making recognition
260 errors and enhancing rejection of even moderately mimetic parasitic eggs (Stokke *et al.*, 2007;
261 Moskát *et al.*, 2008a). Furthermore, several species may retain rejection behaviour in the
262 absence of parasitism over very long time periods (Underwood, Sealy & McLaren, 2004;
263 Lahti, 2006), and even after speciation events (Bolen, Rothstein & Trost, 2000; Rothstein,
264 2001; Peer & Sealy, 2004a) indicating that opposing selective pressures to egg rejection, like
265 recognition errors, are negligible in these species. Even with the existence of recognition
266 errors, rejection behaviour may be retained without apparent interspecific parasitism due to
267 several reasons. Firstly, there may be unaccounted benefits to egg rejection behaviour, such as
268 resistance to intraspecific brood parasitism, that maintain rejection behaviour and even cause
269 it to increase in frequency (Grim *et al.*, 2011, Samaš *et al.*, 2011). Secondly, interspecific
270 parasitism may still occur at a low rate without researchers being able to detect it. Hence,
271 parasitism by cuckoos laying non-mimetic eggs (i.e. from a gens with another main host) may
272 happen from time to time, but since such eggs would be ejected quickly the host population
273 appears to be non-parasitized. Such “accidental” layings are not uncommon (Čapek, 1896;
274 Chance, 1940), and the rate of which such events are occurring may be sufficient to retain
275 rejection rates as apparent from the balancing parasitism rates reported in our study. For
276 instance, Moksnes & Røskaft (1995) found 76 cuckoo eggs in chaffinches stored in European
277 museums, and out of 58,000 cases of cuckoo parasitism from Europe collected by B.G.
278 Stokke, 325 cases were recorded in chaffinch nests scattered all over Europe (unpublished
279 data). The balancing parasitism rates estimated for chaffinches and bramblings in the present
280 study are equal to zero, indicating that occasional parasitism by cuckoos is sufficient to retain
281 high rates of egg rejection. Third, the retention of egg rejection in these species may be
282 caused by immigration of rejecters from other populations that suffer high parasitism rates
283 (Soler *et al.*, 2001). Hence, there are reports of chaffinches being utilized regularly by

284 cuckoos in the European parts of Russia (Malchevsky, 1960), and bramblings are favoured
285 hosts in parts of Fennoscandia (Vikan *et al.*, 2011).

286 On the other hand, our results also indicate that perceptual errors may be influential for
287 the evolution of egg rejection in some cases. Hence, one of our study populations experience
288 parasitism rates lower than the balancing parasitism rates. Reed warblers in Spain experience
289 a parasitism rate of 2.0%, which is slightly lower than the calculated balancing parasitism rate
290 (2.9 - 23.3%). In this population, egg rejection abilities should therefore deteriorate with time,
291 based on our current estimates of recognition errors, provided that there is no immigration of
292 rejecters from other populations, or as long as there are no large fluctuations in parasitism rate
293 among years. Several studies have focused on the influence of recognition errors in reed
294 warblers, although support for the importance of errors has been ambiguous (e.g. Davies &
295 Brooke, 1988; Davies *et al.*, 1996; Røskaft *et al.*, 2002a; Čapek *et al.*, 2010). This species
296 shows marked spatial variation in egg rejection related to parasitism pressure in the specific
297 population (Lindholm & Thomas, 2000; Stokke *et al.*, 2008), indicating that there could be
298 opposing selective pressures working against egg rejection in populations experiencing no or
299 low parasitism. Alternatively, temporal variation in parasitism (Brooke *et al.*, 1998) may also
300 lead to the same pattern with fluctuations in selective pressures depending on the current costs
301 of parasitism. Furthermore, reed warblers have substantial intraclutch variation in egg
302 appearance (Stokke *et al.*, 1999, 2002b) and are parasitized by cuckoos laying mimetic eggs
303 (Davies & Brooke, 1988), making recognition of parasitic eggs error prone. In such cases,
304 hosts may rely on conditional stimuli in perceiving the risk of parasitism (Rothstein, 1982a;
305 Davies & Brooke, 1988, 1998; Stokke *et al.*, 2005, 2007). Hence, reed warblers are more
306 likely to reject parasitic eggs when they observe a cuckoo close to the nest, indicating
307 increased risk of parasitism (Davies & Brooke, 1988; Moksnes, Røskaft & Korsnes, 1993;
308 Moksnes *et al.*, 2000). However, a recent study disclosed that the presence of a cuckoo does

309 not necessarily lead to increased risk of making recognition errors (Čapek *et al.*, 2010).
310 Careful investigations of reed warbler nests by utilizing video recordings should be
311 undertaken to determine unambiguously if disappearance of eggs is due to erroneous rejection
312 of own eggs.

313 Gene flow, not considered directly in the present study, may potentially slow down the
314 process of evolving optimally expressed traits in particular populations or lead to local mal-
315 adaptation (Nuismer, Thompson & Gomulkiewicz, 1999). Influx of rejecter or acceptor alleles
316 may therefore influence expression of egg rejection in local populations. However, this
317 critically depends on spatiotemporal variation in selection regimes (Duffy & Forde, 2009),
318 like cuckoo parasitism and costs due to recognition errors, although at present such data are
319 unavailable. Gene flow could also increase the frequency of rejecter alleles in non-parasitized
320 or weakly parasitized populations (e.g. Røskaft *et al.*, 2002b, 2006; Moskát *et al.*, 2008b),
321 thus causing errors to increase. Interestingly, there is low genetic differentiation among reed
322 warbler populations in Europe, showing evidence of extensive gene flow among populations
323 (Procházka *et al.*, 2011). The intermediate rejection of non-mimetic eggs in reed warblers and
324 possibly in corn buntings may therefore be caused by a combined effect of costs of making
325 recognition errors, gene flow and spatiotemporal variation in occurrence of parasitism
326 creating a mosaic of situations in which the opposing costs vary in relative magnitude.
327 Interestingly, the few studies available on corn buntings, indicate similar spatial variation in
328 parasitism as in reed warblers. Hence, in Italy only 1.4% (N = 208) corn bunting nests were
329 parasitized (Campobello & Sealy, 2009), which is profoundly different from the relatively
330 high parasitism rate at our Bulgarian study site.

331 It is important to acknowledge that recognition errors are probably rarer events than
332 estimated in the present study, because eggs may disappear from nests for many other reasons
333 like e.g. jostling or partial predation (e.g. Rothstein, 1982b; Lerkelund *et al.*, 1993; Moksnes

334 *et al.*, 2000; Røskaft *et al.*, 2002a). For instance, Moksnes *et al.* (2000) and Røskaft *et al.*
335 (2002a) reported that cuckoos visited and partially depredated 12% of reed warbler nests
336 without actually parasitizing them (see also Wyllie, 1975). Furthermore, cuckoos often
337 remove one or two host eggs just prior to laying their own egg (Wyllie, 1975, 1981). If the
338 host then rapidly ejects the parasitic egg, the loss of it's own egg(s) will appear to be self-
339 inflicted to the observer even when this was not actually the case. Even with daily monitoring
340 of nests such mistakes may take place.

341 In our approach, we focused only on hosts of cuckoos *Cuculus* spp. However, the same
342 argument can be used for other brood parasitic systems. One important point to consider is
343 calculations of the cost of parasitism. In the North American brown-headed cowbird
344 *Molothrus ater*, the parasite chick does not evict host chicks leading to a lower cost of
345 parasitism in most cases, but not always ($0 \leq c \leq 1$). We show that the balancing parasitism
346 rate p^* increases as c increases and hence even smaller costs due to recognition errors oppose
347 the evolution of rejection behaviour. Furthermore, even rejection costs, such as damage of
348 own eggs when trying to reject the parasitic egg, can be important for opposing egg rejection
349 in such hosts (Rohwer & Spaw, 1988; Røskaft & Moksnes, 1998) in contrast to cuckoo hosts
350 where such costs are of minor importance (Stokke *et al.*, 2005, but see Antonov *et al.*, 2009).
351 In addition, North American passerines in general have a higher intraclutch variation in egg
352 appearance than comparable species in Europe, which may increase the risk of committing
353 recognition errors (Stokke *et al.*, 2002b). However, in many cases the brown-headed cowbird
354 egg is non-mimetic, many hosts experience very high parasitism rates, and especially smaller
355 hosts also suffer high costs when raising a cowbird chick (Kilner, 2003). Therefore, lag in the
356 evolution of egg rejection (perhaps due to lack of genetic background) is still the most
357 plausible explanation for the lack of egg rejection in most hosts parasitized by cowbirds (Peer
358 & Sealy, 2004b). However, other causes than recognition errors may cause apparently sub-

359 optimal rejection rates. For instance, costs of desertion due to nest site limitation (hole
360 nesters), parasite mafia behaviour or few re-nesting opportunities may lead to acceptance of
361 parasitic eggs (e.g. Soler *et al.*, 1995; Avilés, Rutila & Møller, 2005; Hoover & Robinson,
362 2007; Krüger, 2007, 2011).

363 By using empirical data on disappearance of own eggs from non-parasitized nests, we
364 have shown that costs opposing evolution of egg rejection in hosts of avian brood parasites
365 may exist but are in general small. Importantly, our estimates are most probably overestimates
366 of true recognition errors, indicating that such costs in general are minute compared to the
367 high costs of parasitism. Recognition errors seem most likely in species with specific
368 characteristics like a high intraclutch variation in egg appearance, intermediate and variable
369 rejection rate, spatiotemporal variation in occurrence of parasitism, and parasitism by brood
370 parasites laying eggs that at least to some extent mimic host eggs, like in reed warblers and
371 perhaps corn buntings. Future studies on the importance of recognition errors should focus on
372 long-term studies of such “intermediate” rejecters at a spatiotemporal scale including several
373 populations thus taking gene flow into account, while also considering phenotypic plasticity
374 in host anti-parasite behaviour. By this approach, we should be able to obtain reliable
375 estimates of variation in recognition errors, rejection rates and parasitism rates and address the
376 importance of the various costs for the evolution of egg rejection. Finally, use of video
377 cameras (e.g. Weidinger, 2010) would disclose the proportion of eggs that are actually lost by
378 erroneous ejection of own eggs and not to other factors such as jostling or partial predation.

379 Our findings should be of importance for evaluating hypotheses set forward to explain
380 variation in expression of defences in hosts. Further research should focus on clarifying how
381 recognition errors promote selection for low intraclutch variation, an important antiparasite
382 defence in hosts of brood parasites, as host eggs with extreme appearance are expected to be
383 identified as parasitic eggs. We also suggest future research looking at how frequency of

384 recognition errors might be characteristic for specific stages of the arms race between hosts
385 and brood parasites.

386

387 ACKNOWLEDGEMENTS

388 We would like to thank Manuel Martín-Vivaldi for access to unpublished data. Tomáš Grim
389 provided constructive comments that significantly improved the ms. Permits to carry out data
390 collection were issued by Conselleria de Infraestructuras, Territorio y Medio Ambiente
391 according to the relevant Spanish national guidelines for animal research (Real Decreto
392 1201/2005, de 10 de Octubre), the Norwegian Directorate for Nature Management (permit
393 numbers 2008/1524 Art-VIID, 05/2580 ART-VI-ARES, 2007/1177 ART-VI-JAA), the Duna-
394 Ipoly National Park in Hungary, and the Ministry of Environment and Water in Bulgaria. WL
395 was funded through the National Natural Science Foundation of China (Nos. 31071938 and
396 31272328) and New Century Excellent Talents in University (NCET-10-0111). BGS and FF
397 were funded by the Research Council of Norway (218144). CY was funded through the
398 National Natural Science Foundation of China (Nos. 31101464 and 31260514). CM was
399 funded by the Hungarian National Science Fund (OTKA, No. 83217).

400

401 REFERENCES

- 402 **Anderson MG, Moskát C, Bán M, Grim T, Cassey P, Hauber ME. 2009.** Egg eviction
403 imposes a recoverable cost of virulence in chicks of a brood parasite. *PLoS ONE* **4**:
404 e7725.
- 405 **Antonov A, Stokke BG, Moksnes A, Røskaft E. 2006a.** Egg rejection in marsh warblers
406 (*Acrocephalus palustris*) heavily parasitized by common cuckoos (*Cuculus canorus*).
407 *Auk* **123**: 419-430.

408 **Antonov A, Stokke BG, Moksnes A, Røskaft E. 2006b.** Coevolutionary interactions
409 between common cuckoos and corn buntings. *Condor* **108**: 414-422.

410 **Antonov A, Stokke BG, Moksnes A, Røskaft E. 2007a.** First evidence of regular common
411 cuckoo, *Cuculus canorus*, parasitism on eastern olivaceous warblers, *Hippolais pallida*
412 *elaieica*. *Naturwissenschaften* **94**: 307-312.

413 **Antonov A, Stokke BG, Moksnes A, Røskaft E. 2007b.** Aspects of breeding ecology of the
414 eastern olivaceous warbler (*Hippolais pallida*). *Journal of Ornithology* **148**: 443-451.

415 **Antonov A, Stokke BG, Moksnes A, Røskaft E. 2009.** Evidence for egg discrimination
416 preceding failed rejection attempts in a small cuckoo host. *Biology Letters* **5**: 169-171.

417 **Avilés JM, Moskát C, Bán M, Hargitai R, Parejo D. 2009.** Common cuckoos (*Cuculus*
418 *canorus*) do not rely on indicators of parental abilities when searching for host nests:
419 the importance of host defenses. *Auk* **126**: 431-438.

420 **Avilés JM, Parejo D. 2011.** Host personalities and the evolution of behavioural adaptations
421 in brood parasitic-host systems. *Animal Behaviour* **82**: 613-618.

422 **Avilés JM, Rutila J, Møller AP. 2005.** Should the redstart *Phoenicurus phoenicurus* accept
423 or reject cuckoo *Cuculus canorus* eggs? *Behavioral Ecology and Sociobiology* **58**:
424 608-617.

425 **Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T. 2002.** Responses of great reed
426 warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a
427 cuckoo *Cuculus canorus* dummy and egg mimicry. *Journal of Avian Biology* **33**: 420-
428 425.

429 **Begum S, Moksnes A, Røskaft E, Stokke BG. 2011.** Interactions between the Asian koel
430 (*Eudynamys scolopacea*) and its hosts. *Behaviour* **148**: 325-340.

431 **Bolen GM, Rothstein SI, Trost CH. 2000.** Egg recognition in yellow-billed and black-billed
432 magpies in the absence of interspecific parasitism: implications for parasite-host
433 coevolution. *Condor* **102**: 432-438.

434 **Brooke M de L, Davies NB. 1988.** Egg mimicry by cuckoos *Cuculus canorus* in relation to
435 discrimination by hosts. *Nature* **335**: 630-632.

436 **Brooke M de L, Davies NB, Noble DG. 1998.** Rapid decline of host defences in response to
437 reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing
438 world. *Proceedings of the Royal Society of London, Series B* **265**: 1277-1282.

439 **Campobello D, Sealy SG. 2009.** Avian brood parasitism in a Mediterranean region: hosts and
440 habitat preferences of common cuckoos *Cuculus canorus*. *Bird Study* **56**: 389-400.

441 **Campobello D, Sealy SG. 2011.** Use of social over personal information enhances nest
442 defense against avian brood parasitism. *Behavioral Ecology* **22**: 422-428.

443 **Čapek V. 1896.** Beiträge zur Fortpflanzungsgeschichte des Kuckucks. *Ornithologisches*
444 *Jahrbuch* **7**: 41-72, 102-117, 146-157, 165-183.

445 **Čapek M, Požgayová M, Procházka P, Honza M. 2010.** Repeated presentations of the
446 common cuckoo increase nest defense by the Eurasian reed warbler but do not induce
447 it to make recognition errors. *Condor* **112**: 763-769.

448 **Chance EP. 1940.** *The truth about the cuckoo*. London: Country Life.

449 **Davies NB. 2000.** *Cuckoos, cowbirds and other cheats*. London: T & AD Poyser.

450 **Davies NB, Brooke M de L. 1988.** Cuckoos versus reed warblers: adaptations and
451 counteradaptations. *Animal Behaviour* **36**: 262-284.

452 **Davies NB, Brooke M de L. 1989a.** An experimental study of co-evolution between the
453 cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal*
454 *Ecology* **58**: 207-224.

455 **Davies NB, Brooke M de L. 1989b.** An experimental study of co-evolution between the
456 cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination
457 and general discussion. *Journal of Animal Ecology* **58**: 225-236.

458 **Davies NB, Brooke M de L. 1998.** Studies in coevolution. In: Rothstein SI, Robinson SK,
459 eds. *Parasitic birds and their hosts; studies in coevolution*. New York: Oxford
460 University Press, 59-79.

461 **Davies NB, Brooke M de L, Kacelnik A. 1996.** Recognition errors and probability of
462 parasitism determine whether reed warblers should accept or reject mimetic cuckoo
463 eggs. *Proceedings of the Royal Society of London, Series B* **263**: 925-931.

464 **Duffy MA, Forde SE. 2009.** Ecological feedbacks and the evolution of resistance. *Journal of*
465 *Animal Ecology* **78**: 1106-1112.

466 **Grim T, Rutila J, Cassey P, Hauber ME. 2009.** The cost of virulence: an experimental
467 study of egg eviction by brood parasitic chicks. *Behavioral Ecology* **20**: 1138-1146.

468 **Grim T, Samaš P, Moskát C, Kleven O, Honza M, Moksnes A, Røskaft E, Stokke BG.**
469 **2011.** Constraints on host choice: why do parasitic birds rarely exploit some common
470 potential hosts? *Journal of Animal Ecology* **80**: 508-518.

471 **Hauber ME, Moskát C, Bán M. 2006.** Experimental shift in hosts' acceptance threshold of
472 inaccurate-mimic brood parasite eggs. *Biology Letters* **2**: 177-180.

473 **Honza M, Procházka P, Stokke BG, Moksnes A, Røskaft E, Čapek M Jr, Mrlík V. 2004.**
474 Are blackcaps current winners in the evolutionary struggle against the common
475 cuckoo? *Journal of Ethology* **22**: 175-180.

476 **Hoover JP, Robinson SK. 2007.** Retaliatory mafia behavior by a parasitic cowbird favors
477 host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences of*
478 *the United States of America* **104**: 4479-4483.

479 **Kilner RM. 2003.** How selfish is a cowbird nestling? *Animal Behaviour* **66**: 569-576.

480 **Krüger O. 2007.** Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints.
481 *Philosophical Transactions of the Royal Society B, Biological Sciences* **362**: 1873-
482 1886.

483 **Krüger O. 2011.** Brood parasitism selects for no defence in a cuckoo host. *Proceedings of the*
484 *Royal Society of London, Series B* **278**: 2777-2783.

485 **Lahti DC. 2005.** Evolution of bird eggs in the absence of cuckoo parasitism. *Proceedings of*
486 *the National Academy of Sciences of the United States of America* **102**: 18057-18062.

487 **Lahti DC. 2006.** Persistence of egg recognition in the absence of cuckoo brood parasitism:
488 pattern and mechanism. *Evolution* **60**: 157-168.

489 **Lerkelund HE, Moksnes A, Røskaft E, Ringsby TH. 1993.** An experimental test of optimal
490 clutch size of the fieldfare; with a discussion on why brood parasites remove eggs
491 when they parasitize a host species. *Ornis Scandinavica* **24**: 95-102.

492 **Lindholm AK, Thomas RJ. 2000.** Differences between populations of reed warblers in
493 defences against brood parasitism. *Behaviour* **137**: 25-42.

494 **Lotem A, Nakamura H. 1998.** Evolutionary equilibria in avian brood parasitism. In:
495 Rothstein SI, Robinson SK, eds. *Parasitic birds and their hosts; studies in*
496 *coevolution*. New York: Oxford University Press, 223-235.

497 **Lotem A, Nakamura H, Zahavi A. 1995.** Constraints on egg discrimination and cuckoo-host
498 co-evolution. *Animal Behaviour* **49**: 1185-1209.

499 **Lovász P, Moskát C. 2004.** Break-down of arms race between the red-backed shrike (*Lanius*
500 *collurio*) and common cuckoo (*Cuculus canorus*). *Behaviour* **141**: 245-262.

501 **Malchevsky AS. 1960.** On the biological races of the common cuckoo, *Cuculus canorus* L in
502 the territory of the European part of the USSR. *Proceedings of the International*
503 *Ornithological Congress* **12**: 464-470.

504 **Marchetti K. 1992.** Costs to host defence and the persistence of parasitic cuckoos.
505 *Proceedings of the Royal Society of London, Series B* **248**: 41-45.

506 **Marchetti K. 2000.** Egg rejection in a passerine bird: size does matter. *Animal Behaviour* **59**:
507 877-883.

508 **Martín-Gálvez D, Soler JJ, Martínez JG, Krupa AP, Richard M, Soler M, Møller AP,**
509 **Burke T. 2006.** A quantitative trait locus for recognition of foreign eggs in the host of
510 a brood parasite. *Journal of Evolutionary Biology* **19**: 543-550.

511 **Moksnes A, Røskaft E. 1995.** Egg-morphs and host preference in the common cuckoo
512 (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum
513 collections. *Journal of Zoology* **236**: 625-648.

514 **Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC. 1991.**
515 Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies.
516 *Behaviour* **116**: 64-89.

517 **Moksnes A, Røskaft E, Greger Hagen L, Honza M, Mørk C, Olsen PH. 2000.** Common
518 cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus*
519 nests. *Ibis* **142**: 247-258.

520 **Moksnes A, Røskaft E, Korsnes L. 1993.** Rejection of cuckoo (*Cuculus canorus*) eggs by
521 meadow pipits (*Anthus pratensis*). *Behavioral Ecology* **4**: 120-127.

522 **Moksnes A, Røskaft E, Solli MM. 1994.** Documenting puncture ejection of parasitic eggs by
523 chaffinches *Fringilla coelebs* and blackcaps *Sylvia atricapilla*. *Fauna norvegica,*
524 *Series C* **17**: 115-118.

525 **Moskát C, Avilés JM, Bán M, Hargitai R, Zölei A. 2008a.** Experimental support for the use
526 of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behavioral Ecology*
527 *and Sociobiology* **62**: 1885-1890.

528 **Moskát C, Hansson B, Barabás L, Bártol I, Karcza Z. 2008b.** Common cuckoo *Cuculus*
529 *canorus* parasitism, antiparasite defence and gene flow in closely located populations
530 of great reed warblers *Acrocephalus arundinaceus*. *Journal of Avian Biology* **39**: 663-
531 671.

532 **Moskát C, Hauber ME, Avilés JM, Bán M, Hargitai R, Honza M. 2009.** Increased host
533 tolerance of multiple cuckoo eggs leads to higher fledging success of the brood
534 parasite. *Animal Behaviour* **77**: 1281-1290.

535 **Moskát C, Honza M. 2002.** European cuckoo *Cuculus canorus* parasitism and host's
536 rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus*
537 *arundinaceus* population. *Ibis* **144**: 614-622.

538 **Moskát C, Székely T, Cuthill IC, Kisbenedek T. 2008c.** Hosts' responses to parasitic eggs:
539 Which cues elicit hosts' egg discrimination? *Ethology* **114**: 186-194.

540 **Moskát C, Szentpéteri J, Barta Z. 2002.** Adaptations by great reed warblers to brood
541 parasitism: a comparison of populations in sympatry and allopatry with the common
542 cuckoo. *Behaviour* **139**: 1313-1329.

543 **Nuismer SL, Thompson JN, Gomulkiewicz R. 1999.** Gene flow and geographically
544 structured coevolution. *Proceedings of the Royal Society of London, Series B* **266**:
545 605-609.

546 **Øien IJ, Moksnes A, Røskaft E. 1995.** Evolution of variation in egg color and marking
547 pattern in European passerines: adaptations in a coevolutionary arms race with the
548 cuckoo, *Cuculus canorus*. *Behavioral Ecology* **6**: 166-174.

549 **Øien IJ, Moksnes A, Røskaft E, Honza M. 1998.** Costs of cuckoo *Cuculus canorus*
550 parasitism to reed warblers *Acrocephalus scirpaceus*. *Journal of Avian Biology* **29**:
551 209-215.

552 **Payne RB. 1967.** Interspecific communication signals in parasitic birds. *American Naturalist*
553 **101:** 363-375.

554 **Peer BD, Sealy SG. 2004a.** Fate of grackle (*Quiscalus* spp) defenses in the absence of brood
555 parasitism: implications for long-term parasite-host coevolution. *Auk* **121:** 1172-1186.

556 **Peer BD, Sealy SG. 2004b.** Correlates of egg rejection in hosts of the brown-headed cowbird.
557 *Condor* **106:** 580-599.

558 **Procházka P, Honza M. 2004.** Egg discrimination in the yellowhammer. *Condor* **106:** 405-
559 410.

560 **Procházka P, Stokke BG, Jensen H, Fainová D, Bellinvia E, Fossøy F, Vikan JR, Bryja,**
561 **J, Soler M. 2011.** Low genetic differentiation among reed warbler *Acrocephalus*
562 *scirpaceus* populations across Europe. *Journal of Avian Biology* **42:** 103-113.

563 **Rohwer S, Spaw CD. 1988.** Evolutionary lag versus bill-size constraints: a comparative
564 study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology* **2:** 27-36.

565 **Røskaft E, Moksnes A. 1998.** Coevolution between brood parasites and their hosts; an
566 optimality theory approach. In: Rothstein SI, Robinson SK, eds. *Parasitic birds and*
567 *their hosts; studies in coevolution*. New York: Oxford University Press, 236-254.

568 **Røskaft E, Moksnes A, Meilvang D, Bicík V, Jemelíková J, Honza M. 2002a.** No evidence
569 for recognition errors in *Acrocephalus* warblers. *Journal of Avian Biology* **33:** 31-38.

570 **Røskaft E, Moksnes A, Stokke BG, Moskát C, Honza M. 2002b.** The spatial habitat
571 structure of host populations explains the pattern of rejection behavior in hosts and
572 parasitic adaptations in cuckoos. *Behavioral Ecology* **13:** 163-168.

573 **Røskaft E, Takasu F, Moksnes A, Stokke BG. 2006.** Importance of spatial habitat structure
574 on establishment of host defenses against brood parasitism. *Behavioral Ecology* **17:**
575 700-708.

576 **Rothstein SI. 1982a.** Mechanisms of avian egg recognition: Which egg parameters elicit
577 responses by rejecter species? *Behavioral Ecology and Sociobiology* **11**: 229-239.

578 **Rothstein SI. 1982b.** Successes and failures in avian egg and nestling recognition with
579 comments on the utility of optimality reasoning. *American Zoologist* **22**: 547-560.

580 **Rothstein SI. 2001.** Relic behaviours, coevolution and the retention versus loss of host
581 defences after episodes of avian brood parasitism. *Animal Behaviour* **61**: 95-107.

582 **Ruttila J, Jokimäki J, Avilés JM, Kuisanlahti-Jokimäki M-L. 2006.** Responses of
583 parasitized and unparasitized common redstart (*Phoenicurus phoenicurus*) populations
584 against artificial cuckoo parasitism. *Auk* **123**: 259-265.

585 **Ruttila J, Latja R, Koskela K. 2002.** The common cuckoo *Cuculus canorus* and its cavity
586 nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system?
587 *Journal of Avian Biology* **33**: 414-419.

588 **Samaš P, Hauber ME, Cassey P, Grim T. 2011.** Repeatability of foreign egg rejection:
589 testing the assumptions of co-evolutionary theory. *Ethology* **117**: 606-619.

590 **Soler JJ, Martínez JG, Soler M, Møller AP. 1999.** Genetic and geographic variation in
591 rejection behavior of cuckoo eggs by European magpie populations: an experimental
592 test of rejecter-gene flow. *Evolution* **53**: 947-956.

593 **Soler JJ, Martínez JG, Soler M, Møller AP. 2001.** Coevolutionary interactions in a host-
594 parasite system. *Ecology Letters* **4**: 470-476.

595 **Soler JJ, Møller AP. 1996.** A comparative analysis of the evolution of variation in
596 appearance of eggs of European passerines in relation to brood parasitism. *Behavioral*
597 *Ecology* **7**: 89-94.

598 **Soler M, Martín-Vivaldi M, Fernández-Morante J. 2012.** Conditional response by hosts to
599 parasitic eggs: the extreme case of the rufous-tailed scrub robin. *Animal Behaviour* **84**:
600 421-426.

601 **Soler M, Soler JJ, Martinez JG, Møller AP. 1995.** Magpie host manipulation by great
602 spotted cuckoos: evidence for an avian mafia? *Evolution* **49**: 770-775.

603 **Spottiswoode CN, Koorevaar J. 2012.** A stab in the dark: chick killing by brood parasitic
604 honeyguides. *Biology Letters* **8**: 241-244.

605 **Spottiswoode CN, Stevens M. 2010.** Visual modeling shows that avian host parents use
606 multiple visual cues in rejecting parasitic eggs. *Proceedings of the National Academy
607 of Sciences of the United States of America* **107**: 8672-8676.

608 **Starling M, Heinsohn R, Cockburn A, Langmore NE. 2006.** Cryptic genes revealed in
609 pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. *Proceedings of
610 the Royal Society of London, Series B* **273**: 1929-1934.

611 **Stoddard MC, Stevens M. 2010.** Pattern mimicry of host eggs by the common cuckoo, as
612 seen through a bird's eye. *Proceedings of the Royal Society of London, Series B* **277**:
613 1387-1393.

614 **Stoddard MC, Stevens M. 2011.** Avian vision and the evolution of egg color mimicry in the
615 common cuckoo. *Evolution* **65**: 2004-2013.

616 **Stokke BG, Hafstad I, Rudolfson G, Moksnes A, Møller AP, Røskaft E, Soler M. 2008.**
617 Predictors of resistance to brood parasitism within and among reed warbler
618 populations. *Behavioral Ecology* **19**: 612-620.

619 **Stokke BG, Honza M, Moksnes A, Røskaft E, Rudolfson G. 2002a.** Costs associated with
620 recognition and rejection of parasitic eggs in two European passerines. *Behaviour* **139**:
621 629-644.

622 **Stokke BG, Moksnes A, Røskaft E. 2002b.** Obligate brood parasites as selective agents for
623 evolution of egg appearance in passerine birds. *Evolution* **56**: 199-205.

624 **Stokke BG, Moksnes A, Røskaft E. 2005.** The enigma of imperfect adaptations in hosts of
625 avian brood parasites. *Ornithological Science* **4**: 17-29.

626 **Stokke BG, Moksnes A, Røskaft E, Rudolfson G, Honza M. 1999.** Rejection of artificial
627 cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed
628 warblers (*Acrocephalus scirpaceus*). *Proceedings of the Royal Society of London,*
629 *Series B* **266**: 1483-1488.

630 **Stokke BG, Rudolfson G, Moksnes A, Røskaft E. 2004.** Rejection of conspecific eggs in
631 chaffinches: the effect of age and clutch characteristics. *Ethology* **110**: 459-470.

632 **Stokke BG, Takasu F, Moksnes A, Røskaft E. 2007.** The importance of clutch
633 characteristics and learning for antiparasite adaptations in hosts of avian brood
634 parasites. *Evolution* **61**: 2212-2228.

635 **Takasu F. 1998.** Why do all host species not show defense against avian brood parasitism:
636 evolutionary lag or equilibrium? *American Naturalist* **151**: 193-205.

637 **Underwood TJ, Sealy SG, McLaren CM. 2004.** Experiments on egg discrimination in two
638 North American corvids: further evidence for retention of egg ejection. *Canadian*
639 *Journal of Zoology* **82**: 1399-1407.

640 **Vikan JR, Stokke BG, Fossøy F, Jackson C, Huhta E, Rutila J, Moksnes A, Røskaft E.**
641 **2009.** Fixed rejection responses to single and multiple experimental parasitism in two
642 *Fringilla* hosts of the common cuckoo. *Ethology* **115**: 840-850.

643 **Vikan JR, Fossøy F, Huhta E, Moksnes A, Røskaft E, Stokke BG. 2011.** Outcomes of
644 brood parasite-host interactions mediated by egg matching: common cuckoos
645 *Cuculus canorus* versus *Fringilla* finches. *PLoS ONE* **6**: e19288.

646 **Vikan JR, Stokke BG, Rutila J, Huhta E, Moksnes A, Røskaft E. 2010.** Evolution of
647 defences against cuckoo (*Cuculus canorus*) parasitism in bramblings (*Fringilla*
648 *montifringilla*): A comparison of four populations in Fennoscandia. *Evolutionary*
649 *Ecology* **24**: 1141-1157.

- 650 **Weidinger K. 2010.** Foraging behaviour of nest predators at open-cup nests of woodland
651 passerines. *Journal of Ornithology* **151**: 729-735.
- 652 **Welbergen JA, Davies NB. 2009.** Strategic variation in mobbing as a front line of defense
653 against brood parasitism. *Current Biology* **19**: 235-240.
- 654 **Wyllie I. 1975.** Study of cuckoos and reed warblers. *British Birds* **68**: 369-378.
- 655 **Wyllie I. 1981.** *The cuckoo*. London: Batsford.
- 656

Table 1. Data used to calculate the balancing parasitism rate (%) required for opposing maximum estimates of costs due to recognition errors. The frequency of recognition errors is estimated as the proportion of own eggs lost out of all eggs laid ($(\Delta F/F) \cdot 100$) in non-parasitized nests assuming that 1) all (RE1), 50% (RE2), 3) 25% (RE3) of the individuals are capable of rejecting eggs. As a fourth estimate (RE4) we also consider the proportion of individuals in the population that are able to reject experimental non-mimetic eggs (see Equation 1 for calculation). *Individuals that recognized and pecked foreign eggs. **Rejection rate of non-mimetic eggs in Hungarian population used. Numbers in brackets refer to number of nests. See Methods for more details.

Species	Locality	Number of disappeared eggs	RE1 (%)	RE2 (%)	RE3 (%)	RE4 (%)	Parasitism rate (%)	Rejection rate, RE4 (%)	Clutch size	Balancing parasitism, RE1	Balancing parasitism, RE2	Balancing parasitism, RE3	Balancing parasitism, RE4
<i>Acrocephalus arundinaceus</i>	Hungary	4 (54)	1.53 (54)	3.07 (54)	6.13 (54)	1.61 (54)	59.4 (546)	95.2 (58)	4.83 (137)	1.9	3.9	7.7	2.0
<i>A. arundinaceus</i>	Spain	6 (86)	1.50 (86)	3.01 (86)	6.01 (86)	1.58(86)**	12.1 (116)	NA	4.64 (59)	1.9	3.8	7.7	2.0**
<i>A. scirpaceus</i>	Spain	17 (229)	2.09 (229)	4.18 (229)	8.36 (229)	16.73 (229)	2.0 (402)	12.5 (16)	3.55 (273)	2.9	5.8	11.6	23.3
<i>A. palustris</i>	Bulgaria	1 (157)	0.14 (157)	0.27 (157)	0.54 (157)	0.15 (157)	28.3 (532)	88.2 (17)	4.68 (159)	0.2	0.3	0.7	0.2
<i>Hippolais pallida</i>	Bulgaria	1 (113)	0.23 (113)	0.46 (113)	0.92 (113)	0.25 (113)	26.6 (128)	91.3 (23)*	3.85 (113)	0.3	0.6	1.2	0.3
<i>Fringilla coelebs</i>	Norway	0 (38)	0.00 (38)	0.00 (38)	0.00 (38)	0.00 (38)	0.0 (220)	87.0 (152)	4.75 (92)	0.0	0.0	0.0	0.0
<i>F. montifringilla</i>	Norway	0 (57)	0.00 (57)	0.00 (57)	0.00 (57)	0.00 (57)	0.0 (250)	78.4 (37)	6.02 (189)	0.0	0.0	0.0	0.0
<i>Miliaria calandra</i>	Bulgaria	1 (118)	0.17 (118)	0.34 (118)	0.69 (118)	0.30 (118)	14.6 (356)	56.5 (108)	4.93 (119)	0.2	0.4	0.9	0.4