



Sex roles in egg recognition and egg polymorphism in avian brood parasitism

Journal:	<i>Behavioral Ecology</i>
Manuscript ID:	Draft
Manuscript Type:	Research Article
Keywords:	avian brood parasitism, discordance, egg polymorphism, egg recognition, learning and imprinting, template-based

SCHOLARONE™
Manuscripts

View Only

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 1 **Sex roles in egg recognition and egg polymorphism in avian brood parasitism**
7

8 2 Running title: **Sex roles in egg recognition and egg polymorphism**
9

10 3
11

12 4 **Abstract**
13

14 5 Avian brood parasites impose strong selection on their hosts leading to evolution of
15 6 anti-parasite defenses like egg recognition and rejection. Discordance and
16 7 template-based cognitive mechanisms may form the base for egg recognition by hosts.
17 8 For discordance, hosts recognize eggs that constitute the minority in a clutch as alien,
18 9 while in template-based recognition hosts recognize eggs as alien when they do not
19 10 match a template that can be innate or learnt. Template-based recognition by learning
20 11 can be compromised in host species with polymorphic egg color like *Paradoxornis*
21 12 parrotbills, hosts of the common cuckoo *Cuculus canorus*, because a male that learns an
22 13 egg color in his first breeding attempt can subsequently mate with females having
23 14 different colors and therefore reject own eggs. We present a simple conceptual model to
24 15 understand how asymmetry in sex roles to care for eggs and egg polymorphism
25 16 influence the evolution of egg recognition by hosts. We derive host reproductive success
26 17 in the presence of variation in egg phenotype for both host and parasite. Our model
27 18 shows that male recognition by learning is disadvantageous unless the host has
28 19 monomorphic eggs. We suggest that inter-clutch variation in egg phenotype is key to
29 20 understanding the evolution of egg recognition and the sex involved.
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54

55 22 **Keywords:** avian brood parasitism; discordance; egg polymorphism; egg recognition;
56 23 learning and imprinting; template-based
57
58
59
60

24

Sex roles in egg recognition and egg polymorphism

1. Introduction

Avian brood parasites impose strong selection pressure on their hosts leading to evolution of anti-parasite defenses (Rothstein 1990, Davies 2000). Many hosts of brood parasites have evolved the ability to recognize and reject parasite eggs (Rothstein 1975, Davies and Brooke 1989a, b, Moksnes et al. 1991) and some hosts use multiple visual cues to reject foreign eggs (Spottiswoode and Stevens 2010). However, it remains an open question how hosts recognize and pinpoint a parasitic egg in the clutch. Two major cognitive mechanisms have been proposed; recognition by discordance and template-based recognition (Rothstein 1974, Rothstein 1978, Lotem et al. 1992, Moksnes and Røskaft 1992, Lotem 1993, Hauber et al. 2006, Moskát et al. 2010).

In recognition by discordance, hosts recognize eggs as alien whose phenotype is a minority in the clutch (Rothstein 1974). Discordance is the simplest cognitive mechanism, and it logically works as an anti-parasite defense if parasitism rate is low and if multiple parasitism is rare. Recognition by discordance has been thought unlikely (Rothstein 1974), but a recent experimental study suggests this possibility for some hosts (Moskát et al. 2010).

In template-based recognition, on the other hand, hosts know the phenotype of their own eggs and any egg that does not match a "template" is considered alien (Rothstein 1974, 1978). The template can be either innate or learnt by an imprinting-like process (Rothstein 1974, 1978, Hauber and Sherman 2001, Hauber et al. 2001). It has been demonstrated that some hosts use a learnt template; they learn and imprint on eggs of

Sex roles in egg recognition and egg polymorphism

1
2
3
4
5
6 49 their first clutch and reject eggs that do not match the learnt template in subsequent
7
8 50 breeding attempts (Rothstein 1978, Victoria 1972, Lotem et al. 1995). Recognition by
9
10 51 learning is effective if the template is formed correctly in the sense that the host has
11
12 52 imprinted on its own eggs. Although some studies have shown that there is no
13
14 53 age-specific difference in recognition ability, suggesting that no learning is involved in
15
16 54 egg recognition in some host species (Amundsen et al. 2002, Marchetti 2000, Stokke et
17
18 55 al. 2004), learning can be an important component of host defenses against parasitism in
19
20 56 other hosts (Rothstein 1974, Moskát et al. 2010, Strausberger and Rothstein 2009,
21
22 57 Shizuka and Lyon 2010).

26
27 58
28
29 59 Recognition by learning logically works for females that produce eggs and hence should
30
31 60 be able to correctly imprint on their own eggs immediately after laying. However, it
32
33 61 does not necessarily work for males that often have fewer opportunities to observe eggs
34
35 62 in their nest. Asymmetry in sex roles in producing and caring for eggs is thus likely to
36
37 63 influence the evolution of recognition by learning by restricting or even precluding the
38
39 64 male's learning ability, while recognition by discordance is not affected by such an
40
41 65 asymmetry.

45
46 66
47
48 67 It generally remains unclear which sex is responsible for egg recognition and rejection
49
50 68 of parasitic eggs (Davies and Brooke 1988, Sealy and Neudorf 1995, Lee et al. 2005,
51
52 69 Honza et al. 2007, Požgayová et al. 2009). However, in one study it has been
53
54 70 demonstrated that in host species where only females incubate, only females recognize
55
56 71 and reject unlike eggs while both sexes reject in species where both sexes incubate
57
58 72 (Soler et al. 2002). This finding is consistent with the idea that recognition by learning

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 73 both by females and males works as an effective defense mechanism against parasitism.
7

8 74 Recognition by learning for males, however, can be compromised if there is
9

10 75 polymorphism in egg phenotype.
11

12 76
13

14 77 *Paradoxornis* parrotbills, hosts of the common cuckoo *Cuculus canorus*, and several
15

16 78 other host species show clear polymorphism in egg color. For instance, in the
17

18 79 vinous-throated parrotbill *P. webbianus* in South Korea each female produces either
19

20 80 blue or white eggs (Lee et al. 2005, Kim et al. 1995, Lee and Yoo 2004). It is also
21

22 81 known that both sexes take part in incubation in this species (Lee et al. 2005, Jiang et al.
23

24 82 2009). The ashy-throated parrotbill *P. alphonsianus* in southern China shows three
25

26 83 distinct phenotypes, producing either white, blue or pale blue eggs (Yang et al. 2010).
27

28 84 These birds also have excellent abilities to reject foreign eggs that look dissimilar to
29

30 85 host eggs (Lee et al. 2005, Kim et al. 1995, Lee and Yoo 2004, Yang et al. 2010).
31

32 86
33

34 87 Although the detailed mechanism behind egg recognition in these parrotbill species
35

36 88 remains unknown, females may learn and imprint on the eggs they first observe and use
37

38 89 the learnt memory as a template for recognizing parasitism since each female produces
39

40 90 clutches of a constant egg phenotype throughout her life (Kim et al. 1995). However, in
41

42 91 such a polymorphic population, a male may mate with females producing different egg
43

44 92 color during his life. If a male learns that "white eggs are mine" in his first breeding, he
45

46 93 forms an inflexible image of white eggs such that subsequent matings with females
47

48 94 laying blue eggs will fail. Therefore, if recognition is based on a template that is learnt
49

50 95 by an imprinting-like process, parrotbill males should not learn their first clutch (Lee et
51

52 96 al. 2005). However, the situation is further complicated since the ashy-throated
53
54
55
56
57
58
59
60

Sex roles in egg recognition and egg polymorphism

97 parrotbill in southern China is parasitized by common cuckoos that also show egg
98 polymorphism with white, blue and pale blue eggs, each being highly mimetic to the
99 corresponding parrotbill egg color (Yang et al. 2010). It remains an open question how
100 egg polymorphism affects egg recognition by the host.

101

102 Here we develop a simple but general conceptual model that takes egg polymorphism
103 both in the host and parasite into account in an attempt to better understand the
104 mechanism by which hosts recognize parasitic eggs. We derive the average lifetime
105 reproductive success both for recognition by discordance and template-based
106 recognition by learning in the presence of variation in egg phenotype. Based on the
107 model, we discuss how egg polymorphism can affect the evolution of egg recognition
108 and how asymmetry in sex roles can influence the way by which hosts recognize and
109 reject parasite eggs.

110

111

112 **2. Methods (The model)**

113

114 We assume that each host and parasite female produces a constant type of egg
115 phenotype throughout her life (Kim et al. 1995, Collias 1993, Gosler et al. 2000,
116 Moksnes et al. 2008). Let us assume two types of egg phenotype, 1 (white) and 2 (blue),
117 for the sake of heuristically deriving the model. The number of egg types can be later
118 generalized arbitrarily as in the parrotbill and cuckoo interaction where three distinct
119 types are observed (Yang et al. 2010). We denote the frequency of host females of type
120 1 and 2 as f_{H1} and f_{H2} , respectively ($f_{H1} + f_{H2} = 1$) and that of parasite females as f_{P1} and

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 121 f_{P2} , respectively ($f_{P1} + f_{P2} = 1$).
7

8 122
9

10 123 We assume two mechanisms of recognition; 1) recognition by discordance by which
11

12 124 both host males and females recognize eggs as parasitic when the phenotype is minority
13

14 125 in the clutch; and 2) recognition by learning by which a template is learnt by an
15

16 126 imprinting-like process in the first breeding attempt. Host males learn the phenotype of
17

18 127 eggs in their nest when females complete a clutch. The template is learnt only once, and
19

20 128 males accept all eggs in their nest in the first breeding attempt. Host females learn the
21

22 129 phenotype of their eggs after laying. In later breeding attempts hosts recognize and
23

24 130 reject eggs as parasitic that do not match their learnt template. For both mechanisms, we
25

26 131 assume that hosts can always correctly reject eggs that are recognized as alien without
27

28 132 damaging other eggs in the clutch. Host males and females survive to the next breeding
29

30 133 season with a constant annual survival rate s ($0 < s < 1$), and they randomly form a new
31

32 134 pair every breeding season. Males and females are not influenced by each other when
33

34 135 rejecting an egg. No extra-pair paternity is assumed.
35

36 136
37

38 137 Let p be the probability that a host nest is parasitized either by a type 1 or 2 parasite egg.
39

40 138 We assume that parasitism rate p is sufficiently low ($p \ll 1$) so that multiple parasitism
41

42 139 can be ignored as observed in many cuckoo-host interactions (Davies and Brooke 1989b,
43

44 140 Brooke and Davies 1987, Davies et al. 1996, Brooke et al. 1998) (see Moskát and
45

46 141 Honza (2002), Takasu and Moskát (2011) for high parasitism rate that remained
47

48 142 constant among years). Predation risk is assumed to be the same for all nests
49

50 143 irrespective of egg type. In the absence of parasitism, the host obtains reproductive
51

52 144 success b if all own eggs fledge successfully.
53
54
55
56
57
58
59
60

Sex roles in egg recognition and egg polymorphism

145

146

147 *Case 1: Recognition by discordance*

148

149 Recognition by discordance makes the host always able to recognize and reject

150 parasitism when there is at most one parasite egg in the clutch with a phenotype that

151 differs from that of own eggs. Thus the average reproductive success of the host in a

152 breeding attempt, when the host adopts discordance, is calculated as

153

$$R = b\{f_{H1}(1-p) + f_{H2}(1-p) + f_{H1}Pf_{P2} + f_{H2}Pf_{P1}\}$$

$$= b(1-p) + bp(f_{H1}f_{P2} + f_{H2}f_{P1})$$

155

156 Asymmetry in the sex role to care for eggs does not matter for reproductive success.

157 Lifetime reproductive success of the host $R_{\text{discordance}}$ is then given as follows by

158 multiplying survival probability summed over breeding attempts

159

$$R_{\text{discordance}} = R + sR + s^2R + s^3R + \dots = \frac{R}{1-s}$$

161

162

163 *Case 2: Recognition by learning*

164

165 Females can always correctly learn and imprint on the phenotype of own eggs

166 immediately after laying. This learning by imprinting, however, can negatively affect

Sex roles in egg recognition and egg polymorphism

167 males in later breeding attempts because 1) males may mate with females having
 168 different egg types and reject own eggs, and 2) males may by chance learn and imprint
 169 on the phenotype of parasitic eggs.

170

171 Let q be the probability that the male is the first to observe the parasite egg in the clutch
 172 ($0 \leq q \leq 1$). The probability q will depend on the amount of time the male spends at the
 173 nest relative to the female. In bi-parental hosts where both males and female care for
 174 eggs, q will be large, but q will be low in hosts of female uni-parental care.

175

176 A host male, in any breeding attempt, faces one of six cases labeled $C(i, j)$ shown in
 177 Table 1 where i denotes the type of own eggs of the male ($i = 1$ or 2) and j is the type of
 178 cuckoo egg ($j = 0, 1, 2$) where 0 refers to no parasitism. From Table 1, we below derive
 179 host reproductive success at the t -th breeding attempt R_t ($t = 1, 2, 3, \dots$).

180

181 In the first breeding attempt ($t = 1$), males just learn the egg phenotype in the clutch and
 182 do not reject any egg. Thus, a male's reproductive success in the first breeding attempt
 183 R_1 depends totally on the female, and it is given by summing over four cases $C(1, 0)$,
 184 $C(1, 2)$, $C(2, 0)$, $C(2, 1)$ in Table 1 to yield

185

$$186 \quad R_1 = b \{ f_{H1}(1-p) + f_{H2}(1-p) + f_{H1}p f_{P2} + f_{H2}p f_{P1} \}$$

$$187 \quad = b(1-p) + bp(f_{H1}f_{P2} + f_{H2}f_{P1})$$

188

189 which is identical to the reproductive success for recognition by discordance R ($R_1 = R$).

Sex roles in egg recognition and egg polymorphism

1
2
3
4
5
6 190 In later breeding attempts ($t = 2, 3, \dots$), males recognize eggs as alien when they do not
7
8 191 match the learnt template, e.g., a male that mated with a female of type 1, but was
9
10 192 parasitized by a cuckoo of type 2 in the first breeding attempt (the case $C(1, 2)$), has
11
12 193 learnt both type 1 and 2 as his own with probability q , and this male can achieve
13
14 194 reproductive success by mating with females of both type 1 and 2 in later breeding
15
16 195 attempts unless the nest is parasitized by a parasitic egg with the same phenotype (cases
17
18 196 $C(1, 0)$, $C(1, 2)$, $C(2, 0)$, $C(2, 1)$).

197

198 Thus, a male, conditional on it having learnt type 1 as its own in the first breeding
199 attempt, obtains reproductive success R^1 in later breeding attempts by summing cases
200 $C(1, 0)$ and $C(1, 2)$ to

201

$$202 \quad R^1 = b \{ f_{H1}(1 - p) + f_{H1} p f_{P2} \}$$

203

204 Similarly, a male, conditional on it having learnt both type 1 and 2 in the first breeding
205 attempt, obtains reproductive success R^{1+2} by summing over cases $C(1, 0)$, $C(1, 2)$, $C(2,$
206 $0)$, $C(2, 1)$ to

207

$$208 \quad R^{1+2} = b \{ f_{H1}(1 - p) + f_{H1} p f_{P2} + f_{H2}(1 - p) + f_{H2} p f_{P1} \}$$

209

210 And a male, conditional on it having learnt type 2, obtains

211

$$212 \quad R^2 = b \{ f_{H2}(1 - p) + f_{H2} p f_{P1} \}$$

213

Sex roles in egg recognition and egg polymorphism

214 by summing over cases $C(2, 0)$ and $C(2, 1)$.

215

216 Then, the average reproductive success in the t -th breeding ($t = 2, 3, 4, \dots$), R_t , is given

217 by multiplying each conditional average with the probability that a male learns type 1

218 ($C(1, 0)$, $C(1, 1)$), both type 1 and 2 ($C(1, 2)$, $C(2, 1)$), type 2 ($C(2, 0)$, $C(2, 2)$) in the

219 first breeding attempt to yield

220

$$221 \quad R_t = f_{H1} \{ 1 - p + p f_{P2} (1 - q) + p f_{P1} \} R^1 + p q (f_{H1} f_{P2} + f_{H2} f_{P1}) R^{1+2} +$$

$$222 \quad f_{H2} (1 - p + p f_{P1} (1 - q) + p f_{P2}) R^2$$

223

224 The average lifetime reproductive success R_{learning} is then given as follows using R_t ($t =$

225 1, 2, 3, ...).

226

$$227 \quad R_{\text{learning}} = R_1 + sR_2 + s^2R_3 + s^3R_4 + \dots$$

228

229 If males do not learn and do not reject any egg as in female uni-parental host species

230 (only female learns and rejects), the reproductive success of each breeding attempt

231 depends only on female action. The average lifetime reproductive success $R_{\text{female only}}$

232 learning is then given as follows using R_1 , which is identical to $R_{\text{discovere}}$.

233

$$234 \quad R_{\text{female only learning}} = R_1 + sR_1 + s^2R_1 + s^3R_1 + \dots = \frac{R_1}{1 - s} = R_{\text{discordance}}$$

235

236

Sex roles in egg recognition and egg polymorphism

237 3. Results

238

239 Recognition by discordance and recognition by female only learning result in an
240 identical lifetime reproductive success ($R_{\text{discordance}} = R_{\text{female only learning}}$).

241

242 The difference in average lifetime reproductive success for recognition by female only
243 learning (or recognition by discordance) and that by both male and female learning, $\Delta =$

244 $R_{\text{female only learning}} - R_{\text{learning}}$, can be arranged as

245

$$\begin{aligned} \Delta &= \frac{bs}{1-s} \left\{ (1 - pf_{p1})(1 - pqf_{p1})f_{H1}(1 - f_{H1}) + (1 - pf_{p2})(1 - pqf_{p2})f_{H2}(1 - f_{H2}) \right\} \\ &= \frac{bs}{1-s} f_{H1}(1 - f_{H1}) \left[2 - (1 + q)p + p^2q \{ 1 - 2f_{p1}(1 - f_{p1}) \} \right] \end{aligned} \quad (1)$$

247

248 It can easily be shown from eq (1) that Δ is always non-negative; recognition by males'

249 learning the first clutch always results in a loss of host lifetime reproductive success (Δ

250 ≥ 0 ; $R_{\text{discordance}} = R_{\text{female only learning}} \geq R_{\text{learning}}$). It can be further shown that (1) the loss Δ

251 increases with increasing frequency of the rarer host phenotype, being proportional to

252 $f_{H1}(1 - f_{H1})$, which reflects the probability that a male will breed with a female of a

253 different type in subsequent breeding attempts and a measure of inter-clutch variation in

254 host egg phenotype. Δ is zero only when the host is monomorphic in egg phenotype; (2)

255 Δ is a decreasing function of the probabilities p and q ; (3) Δ decreases with increasing

256 frequency of the rarer parasite phenotype $f_{p1}(1 - f_{p1})$, a measure of inter-clutch variation

257 in parasite egg phenotype, but the dependency becomes disproportionately smaller as

258 the probability p becomes smaller; and (4) Δ increases as s increases.

Sex roles in egg recognition and egg polymorphism

259

260 Until now we assume two egg phenotypes in the host and the parasite population. The
 261 number of egg types can be arbitrarily generalized by elaborating Table 1, e.g., we first
 262 derive probabilities of a male learning a certain egg type in the first breeding attempt
 263 and then calculate reproductive success in later breeding attempts conditional on that
 264 the male has learnt each egg type (not shown here). With N types of egg phenotype, Δ is
 265 given as,

266

$$267 \quad \Delta = \frac{bs}{1-s} \sum_{i=1}^N (1 - pqf_{Pi})(1 - pf_{Pi})f_{Hi}(1 - f_{Hi}) \quad (2)$$

268

269 where f_{Hi} and f_{Pi} is the frequency of type i females in the host and the parasite,
 270 respectively ($i = 1, 2, \dots, N$). For this general case, the properties of Δ are qualitatively
 271 the same as the case of $N = 2$ and our conclusion remains the same.

272

273

274 4. Discussion

275

276 We have shown that recognition by discordance and recognition by female only learning
 277 result in an identical reproductive performance by the host ($R_{\text{discordance}} = R_{\text{female only learning}}$).

278 This is because we have assumed that parasitism rate is sufficiently low that multiple
 279 parasitism can be ignored (a parasite egg is always a phenotypic outlier in the clutch
 280 unless it is perfectly mimetic to the host eggs), and that females can always learn the
 281 phenotype of their own eggs correctly after laying. However, if there is considerable

1 Sex roles in egg recognition and egg polymorphism

2
3
4
5
6 282 intra-clutch variation in egg phenotype, which was ignored in our model, recognition by
7
8 283 discordance will be disadvantageous because hosts may reject some of their own eggs
9
10 284 even in the absence of parasitism. Recognition by female only learning, on the other
11
12 285 hand, is not influenced by such intra-clutch variation.

13
14
15 286

16
17 287 We have also shown that males' learning the first clutch always results in a loss of host
18
19 288 lifetime reproductive success in the presence of egg polymorphism ($\Delta = R_{\text{female only learning}}$
20
21 $- R_{\text{learning}} > 0$); males should not learn which egg phenotype to reject based on his
22
23 289 experience with his first clutch unless the host is monomorphic in egg phenotype. The
24
25 290 loss Δ becomes smaller as parasitism rate p increases, as the probability that the male is
26
27 291 the first to observe parasite egg q increases, and as inter-clutch variation in parasite egg
28
29 292 phenotype increases. This counter intuitive result can be explained as follows. The
30
31 293 larger the three parameters, the more likely the male is to wrongly learn non-mimetic
32
33 294 cuckoo egg and own eggs in the clutch. This mis-imprinting by males, however,
34
35 295 contributes to increase the probability of successful breeding with females producing
36
37 296 different egg phenotypes in later breeding attempts; males, by mis-imprinting, become
38
39 297 more tolerant to different egg phenotypes in the population.
40
41 298
42
43
44
45

46 299

47
48
49 300 We did not explicitly model recognition by an innate template where hosts know the
50
51 301 phenotype of own eggs at hatching. Such an innate template would be unlikely to
52
53 302 evolve in the presence of egg polymorphism because there would need to be a perfect
54
55 303 genetic correlation between egg phenotype (which color of eggs a female produces) and
56
57 304 the innate template (which color does a female or a male genetically recognize as
58
59 305 her/his own color). Even in this case, however, average lifetime reproductive success of
60

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 306 the host can be derived, which turns out to be equal to $R_{\text{discordance}}$ and $R_{\text{female only learning}}$
7
8 307 because the host can reproduce successfully only when the nest is parasitized by a
9
10 308 parasite egg whose phenotype is different from that of host eggs.
11

12 309

13
14
15 310 Timing of learning egg phenotype is important. In our model, host females learn egg
16
17 311 phenotype immediately after egg laying while host males learn after clutch completion;
18
19 312 females are better placed than males to learn egg phenotype. However, if females delay
20
21 313 learning until the clutch is completed as observed in some host species (Lotem et al.
22
23 314 1992, 1995), they can learn a non-mimetic parasitic egg phenotype as their own and
24
25 315 accept parasitism in later breeding attempts. The delayed learning by females likely
26
27 316 results in a reduced lifetime success both of $R_{\text{female only learning}}$ and R_{learning} but the
28
29 317 asymmetry in sex roles to care for eggs will remain important, i.e., Δ remains positive
30
31 318 and males should not learn egg phenotype in the presence of egg polymorphism.
32
33 319 Explicit modeling of the effect of the timing of learning is needed.
34
35 320

36
37
38
39
40
41 321 In our model, we focused on heterospecific brood parasitism where hosts and parasites
42
43 322 belong to different species. In conspecific brood parasitism where host individuals can
44
45 323 behave as parasites, lifetime reproductive success is composed of two factors, one from
46
47 324 behaving as a host (rearing own eggs) and another as a parasite and our model cannot be
48
49 325 applied to such a system (Lyon 2003). We also assumed that frequencies of each egg
50
51 326 type remain constant in the population. However, these frequencies may change over
52
53 327 time (Yang et al. 2010). Further studies including conspecific parasitism and frequency
54
55 328 dynamics incorporated into the models are needed.
56
57
58
59

60 329

Sex roles in egg recognition and egg polymorphism

1
2
3
4
5
6 330 It has been shown that both males and females of the vinous-throated parrotbill reject
7
8 331 non-mimetic model eggs (Lee et al. 2005). However, in that study, a male's past
9
10 332 breeding partner was unknown, and males that rejected unlike eggs could have learnt a
11
12 333 different phenotype in their first breeding attempt. Parrotbill males incubate (Lee et al.
13
14 334 2005), and males could potentially learn their eggs as demonstrated for bi-parental host
15
16 335 species (Soler et al. 2002). The probability that a male detects a parasitism event before
17
18 336 the female does, q , would therefore be high and this reduces the reproductive loss by
19
20 337 male recognition through learning. Experiments manipulating the first mate are
21
22 338 necessary for clarifying how and when males learn the phenotype of their mate's eggs.
23
24 339
25
26
27
28
29 340 Birds are sensitive to ultraviolet range to which humans are blind (Bennett and Cuthill
30
31 341 1994, Cherry and Bennett 2001). To bird eyes, egg polymorphism may be common and
32
33 342 such hidden polymorphism can crucially affect the way hosts recognize parasitism as
34
35 343 our model has shown. It has been suggested that egg polymorphism most likely has
36
37 344 evolved through co-evolutionary interactions between brood parasites and their hosts
38
39 345 (Kilner 2006). Under parasitism, the host first evolves an ability to recognize and reject
40
41 346 unlike eggs either by discordance or learnt template, and the parasite in turn evolves
42
43 347 better egg mimicry. To counter parasite egg mimicry, the host may further evolve
44
45 348 smaller intra-clutch and larger inter-clutch variation in egg phenotype (Stokke et al.
46
47 349 2002, 2007), and egg polymorphism may evolve both in the host and the parasite (Yang
48
49 350 et al. 2010). Evolution of egg polymorphism, however, makes host recognition by
50
51 351 learning their first clutch by males more disadvantageous as our model has shown,
52
53 352 while recognition by discordance and by female only learning is unaffected. If the
54
55 353 ability to learn to recognize foreign eggs is expressed in both sexes by genetic
56
57
58
59
60

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 354 correlation, reproductive loss by male learning could be an inevitable side effect of
7
8 355 learning to recognize parasitism in bi-parental host species. In this case, hosts might
9
10 356 evolve to mate assortatively so that correct matching of learnt template to egg
11
12 357 phenotype is guaranteed. Such a conflict does not occur in host species where only
13
14 358 females incubate and males do not take part in care of eggs and in host species where
15
16 359 hosts recognize foreign eggs by discordance. We suggest that the cognitive mechanism
17
18 360 that hosts use to recognize parasitic egg can be a crucial component that determines
19
20 361 subsequent coevolutionary interactions of the host and the parasite.
21
22
23
24
25

26 362

27 363 Little attention has been paid to sex roles in the way that hosts recognize brood
28
29 364 parasitism in relation to variation in egg phenotype. We suggest that inter-clutch
30
31 365 variation is a key to understanding the evolution of egg recognition and which sex is
32
33 366 responsible for which action. Further field experiments and cognitive behavioral studies
34
35 367 are clearly needed.
36
37
38

39 368

40 369
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1 Sex roles in egg recognition and egg polymorphism
2
3
4

5
6 370 **References**

7
8 371 Amundsen, T., Brobakken, P.T., Moksnes, A., Røskoft, E. 2002. Rejection of common
9
10 372 cuckoo *Cuculus canorus* eggs in relation to female age in the bluethroat *Luscinia*
11
12 373 *svecica*. J. Avian Biol. 33:366-370.

13
14 374

15
16
17 375 Benett, A.T.D, Cuthill, I.C. 1994. Ultraviolet vision in birds: what is its function? Vis.
18
19 376 Res. 34:1471-1478.

20
21 377

22
23
24 378 Brooke, M. de L., Davies, N.B. 1987. Recent changes in host usage by cuckoos *Cuculus*
25
26 379 *canorus* in Britain. J. Anim. Ecol. 56, 873-883.

27
28 380

29
30
31 381 Brooke, M. de L., Davies, N.B., Noble, D.G. 1998. Rapid decline of host defenses in
32
33 382 response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a
34
35 383 changing world. Proc. R. Soc. Lond. B 265:1277-1282.

36
37 384

38
39
40 385 Cherry, M.I., Bennett, A.T.D. 2001. Egg colour matching in an African cuckoo, as
41
42 386 revealed by ultraviolet-visible reflectance spectrophotometry. Proc. R. Soc. Lond. B
43
44 387 268:565-571.

45
46 388

47
48
49 389 Collias, E.C. 1993. Inheritance of egg-color polymorphism in the village weaver
50
51 390 (*Ploceus cucullatus*). Auk 110:683-692.

52
53 391

54
55
56 392 Davies, N.B. 2000. Cuckoos, cowbirds and other cheats. London: Poyser.

57
58 393
59
60

1 Sex roles in egg recognition and egg polymorphism
2
3
4
5

6 394 Davies, N.B., Brooke, M. de L. 1988. Cuckoos versus reed warblers. Adaptations and
7
8 395 counter-adaptations. Anim. Behav. 36:262-284.
9

10 396

11
12 397 Davies, N.B., Brooke, M. de L. 1989a. An experimental study of co-evolution between
13
14 398 the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. Anim. Ecol.
15
16 399 58:207-224.
17
18

19 400

20
21
22 401 Davies, N.B., Brooke, M. de L. 1989b. An experimental study of co-evolution between
23
24 402 the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination
25
26 403 and general discussion. J. Anim. Ecol. 58:225-236.
27
28

29 404

30
31 405 Davies, N.B., Brooke, M. de L., Kacelnik, A. 1996. Recognition errors and probability
32
33 406 of parasitism determine whether reed warblers should accept or reject mimetic cuckoo
34
35 407 eggs. Proc. R. Soc. Lond. B 263:925-931.
36
37

38 408

39
40
41 409 Gosler, A.G., Barnett, P.R., James Reynolds, S. 2000. Inheritance and variation in
42
43 410 eggshell patterning in the great tit *Parus major*. Proc. R. Soc. Lond. B 267:2469-2473.
44
45

46 411

47
48 412 Hauber, M.E., Sherman, P.W. 2001. Self-referent phenotype matching: theoretical
49
50 413 considerations and empirical evidence. Trends Neurosci. 24(10):609-616.
51
52

53 414

54
55 415 Hauber, M.E., Russo, S.A., Sherman, P.W. 2001. A password for species recognition in
56
57 416 a brood-parasitic bird. Proc. R. Soc. Lond. B 268:1041-1048.
58
59

60 417

Sex roles in egg recognition and egg polymorphism

- 1
2
3
4
5
6 418 Hauber, M.E., Moskát, C., Bán, M. 2006. Experimental shift in hosts' acceptance
7
8 419 threshold of inaccurate-mimic brood parasite eggs. *Biol. Lett.* 2:177-180.
9
10 420
11
12 421 Honza, M., Požgayová, M., Procházka, P., Tkadlec, E. 2007 Consistency in egg
13
14 422 rejection behaviour: responses to repeated brood parasitism in the blackcap (*Sylvia*
15
16 423 *atricapilla*). *Ethology* 113:344-351.
17
18
19 424
20
21
22 425 Jiang, Y., Sun, Y.H., Lu, N., Bi, Z. 2009. Breeding biology of the Grey-hooded
23
24 426 parrotbill (*Paradoxornis zappeyi*) at Wawushan, Sichuan, China. *Wilson J. Ornithol.*
25
26 427 121:800-803.
27
28
29 428
30
31
32 429 Kilner, R.M. 2006. The evolution of egg colour and patterning in birds. *Biol. Rev.*
33
34 430 81:383-406.
35
36 431
37
38
39 432 Kim, C.H., Yamagishi, S., Won, P.O. 1995. Egg-color dimorphism and breeding success
40
41 433 in the crow tit (*Paradoxornis webbiana*). *Auk* 112:831-839.
42
43 434
44
45
46 435 Lee, J.W., Yoo, J.C. 2004. Effect of host egg color dimorphism on interactions between
47
48 436 the vinous-throated parrotbill (*Paradoxornis webbianus*) and common cuckoo (*Cuculus*
49
50 437 *canorus*). *Korean J. Biol. Sci.* 8:77-80.
51
52
53 438
54
55
56 439 Lee, J.W., Kim, D.W., Yoo, J.C. 2005. Egg rejection by both male and female
57
58 440 vinous-throated parrotbills *Paradoxornis webbianus*. *Integrative Biosci.* 9:211-213.
59
60 441

1 Sex roles in egg recognition and egg polymorphism
2
3
4

5 442 Lotem, A. 1993. Learning to recognize nestlings is maladaptive for cuckoo *Cuculus*
6 443 *canorus* hosts. *Nature* 362:743-744.
7
8
9

10 444

11 445 Lotem, A., Nakamura, H., Zahavi, A. 1992. Rejection of cuckoo eggs in relation to host
12 446 age: a possible evolutionary equilibrium. *Behav. Ecol.*, 3:128-132.
13
14
15
16

17 447

18 448 Lotem, A., Nakamura, H., Zahavi, A. 1995. Constrains on egg discrimination and
19 449 cuckoo-host co-evolution. *Anim. Behav.* 49:1185-1209.
20
21
22
23

24 450

25 451 Lyon, B.E. 2003. Egg recognition and counting reduce costs of avian conspecific brood
26 452 parasitism. *Nature* 422:495-499.
27
28
29
30

31 453

32 454 Marchetti, K. 2000. Egg rejection in a passerine bird: size does matter. *Anim. Behav.*
33 455 59:877-883.
34
35
36
37

38 456

39 457 Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M., Pedersen, H.C. 1991.
40 458 Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies.
41
42
43
44

45 459 *Behaviour* 116:64-89.
46
47
48

49 460

50 461 Moksnes, A., Røskaft, E. 1992. Responses of some rare cuckoo hosts to mimetic model
51 462 cuckoo eggs and to foreign conspecific eggs. *Ornis Scand.* 23:17-23.
52
53
54

55 463

56 464 Moksnes, A., Røskaft, E., Rudolfsen, G., Skjelseth, S., Stokke, B.G., Kleven, O., Gibbs,
57 465 H.L., Monza, M., Taborsky, B., Teuschl, Y., Vogl, W., Taborsky, M. 2008. Individual
58
59
60

1 Sex roles in egg recognition and egg polymorphism

2
3
4
5
6 466 female common cuckoos *Cuculus canorus* lay constant egg types but egg appearance
7
8 467 cannot be used to assign eggs to females. J. Avian Biol. 39:238-241.

9
10 468

11
12 469 Moskát, C., Honza, M. 2002. European Cuckoo *Cuculus canorus* parasitism and host's
13
14
15 470 rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus*
16
17 471 *arundinaceus* population. Ibis 144:614-622.

18
19
20 472

21
22 473 Moskát, C., Bán, M., Székely, T., Komdeur, J., Lucassen, R.W.G., van Boheemen, L.A.,
23
24 474 Hauber, M.E. 2010. Discordancy or template-based recognition? Dissecting the
25
26
27 475 cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. J. Exp.
28
29 476 Biol. 213:1976-1983.

30
31 477

32
33
34 478 Požgayová, M., Procházka, P., Honza, M. 2009. Sex-specific defence behaviour against
35
36 479 brood parasitism in a host with female-only incubation. Behav. Proc. 81:34-38.

37
38
39 480

40
41 481 Rothstein, S.I. 1974. Mechanisms of avian egg recognition: possible learned and innate
42
43 482 factors. Auk 91:796-807.

44
45
46 483

47
48 484 Rothstein, S.I. 1975. Evolutionary rates and host defenses against avian brood
49
50 485 parasitism. Am. Nat. 109:161-176.

51
52
53 486

54
55 487 Rothstein, S.I. 1978. Mechanisms of avian egg recognition: additional evidence for
56
57 488 learned components. Anim. Behav. 26:671-677.

58
59
60 489

1 Sex roles in egg recognition and egg polymorphism
2
3
4

5 490 Rothstein, S.I. 1990. A model system for co-evolution: avian brood parasitism. *Ann.*
6
7
8 491 *Rev. Ecol. Syst.* 21:481-508.
9

10 492
11
12 493 Sealy, S.G., Neudorf, D.L. 1995. Male northern orioles eject cowbird eggs: implications
13
14 494 for the evolution of rejection behavior. *Condor* 97:369-375.
15
16
17 495

18
19 496 Shizuka, D., Lyon, B.E. 2010. Coots use hatch order to learn to recognize and reject
20
21 497 conspecific brood parasitic chicks. *Nature* 463:223-226.
22
23
24 498

25
26 499 Soler, M., Martín-Vivaldi, M., Pérez-Contreras, T. 2002. Identification of the sex
27
28 500 responsible for recognition and the method of ejection of parasitic eggs in some
29
30 501 potential common cuckoo hosts. *Ethology* 108:1093-1101.
31
32
33 502

34
35 503 Spottiswoode, G.N., Stevens M. 2010. Visual modeling shows that avian host parents
36
37 504 use multiple visual cues in rejecting parasitic eggs. *PNAS* 107:8672-8676.
38
39
40 505

41
42 506 Stokke, B.G., Moksnes, A., Røskaft, E. 2002. Obligate brood parasites as selective
43
44 507 agents for evolution of egg appearance in passerine birds. *Evolution* 56:199-205.
45
46
47 508

48
49 509 Stokke, B.G., Rudolfsen, G., Moksnes, A., Røskaft, E. 2004. Rejection of conspecific
50
51 510 eggs in chaffinches: the effect of age and clutch characteristics. *Ethology* 110:459-470.
52
53
54 511

55
56 512 Stokke, B.G., Takasu, F., Moksnes, A., Røskaft, E. 2007. The importance of clutch
57
58 513 characteristics and learning for antiparasite adaptations in hosts of avian brood parasites.
59
60

1 Sex roles in egg recognition and egg polymorphism

2
3
4
5
6 514 Evolution 61:2212-2228.

7
8 515

9
10 516 Strausberger, B.M., Rothstein, S.I. 2009. Parasitic cowbirds may defeat host defense by
11
12 517 causing rejecters to misimprint on cowbird eggs. Behav. Ecol. 20:691-699.

13
14
15 518

16
17 519 Takasu, F., Moskát, C. 2011. Modeling the consequence of increased host tolerance
18
19 520 toward avian brood parasitism. Popul. Ecol. 53:187-192.

20
21
22 521

23
24 522 Victoria, J.K. 1972. Clutch characteristics and egg discriminative ability of the African
25
26 523 village weaverbird *Ploceus cucullatus*. Ibis 114:367-376.

27
28
29 524

30
31 525 Yang, C., Liang, W., Cai, Y., Shi, S., Takasu, F., Møller, A.P., Antonov, A., Fossøy, F.,
32
33 526 Moksnes, A., Røskaft, E., Stokke, B.G. 2010. Coevolution in action: disruptive selection

34
35 527 on egg colour in an avian brood parasite and its host. PLoS ONE 5(5): e10816.

36
37 528 doi:10.1371/journal.pone.0010816.

38
39
40
41 529

Sex roles in egg recognition and egg polymorphism

530 **Tables and legends**

531

532 Table 1

Labels	Cases	Probabilities	Egg type learnt by the male	Cases that the host obtains reproductive success <i>b</i> in later breeding attempts
$C(1, 0)$	♀1	$f_{H1}(1 - p) + f_{H1} p f_{P2} (1 - q)$	1	$C(1, 0), C(1, 2)$
$C(1, 1)$	♀1 + (1)	$f_{H1} p f_{P1}$	1	$C(1, 0), C(1, 2)$
$C(1, 2)$	♀1 + (2)	$f_{H1} p f_{P2} q$	1, 2	$C(1, 0), C(1, 2),$ $C(2, 0), C(2, 1)$
$C(2, 0)$	♀2	$f_{H2} (1 - p) + f_{H2} p f_{P1} (1 - q)$	2	$C(2, 0), C(2, 1)$
$C(2, 1)$	♀2 + (1)	$f_{H2} p f_{H1} q$	1, 2	$C(1, 0), C(1, 2),$ $C(2, 0), C(2, 1)$
$C(2, 2)$	♀2 + (2)	$f_{H2} p f_{P2}$	2	$C(2, 0), C(2, 1)$

533

534

535 Table 1 legend

536 Six possible cases that a male can face and the reproductive consequences in later

537 breeding attempts. In the second column, ♀1 and ♀2 refers to a host female of egg type

538 1 and 2, and, (1) and (2) refers to a cuckoo egg of type egg 1 and 2, respectively. See

539 text for further explanations.

540