



Modeling the maintenance of egg polymorphism in avian brood parasites and their hosts

Journal:	<i>Journal of Evolutionary Biology</i>
Manuscript ID:	Draft
Manuscript Type:	Research Papers
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Liang, Wei; Hainan Normal University, College of Life Sciences Yang, Canchao; Hainan Normal University, College of Life Sciences Stokke, Bard; Norwegian University of Science and Technology, Department of Biology Antonov, Anton; Norwegian University of Science and Technology (NTNU), Biology Fossøy, Frode; Norwegian University of Science and Technology, Department of Biology VIKAN, JOHAN; Norwegian University of Science and Technology, Department of Biology Moksnes, Arne; Norwegian University of Science and Technology, Department of Biology Røskaft, Eivin; Norwegian University of Science and Technology, Department of Biology Shykoff, Jacqui; Université Paris-Sud, Laboratoire d'Ecologie, Systématique et Evolution, CNRS UPRESA 8079 Møller, Anders; Université Paris-Sud, Laboratoire d'Ecologie, Systématique et Evolution Takasu, Fugo; Nara Women's University, Information and Computer Sciences</p>
Keywords:	Birds, Host-parasite interaction, Population genetics, Simulation

1 **ARTICLE**

2

3 **Modeling the maintenance of egg polymorphism in avian brood parasites and their**
4 **hosts**

5

6 Wei Liang¹, Canchao Yang^{1,2}, Bård G. Stokke³, Anton Antonov³, Frode Fossøy³, Johan
7 R. Vikan³, Arne Moksnes³, Eivin Røskoft³, Jacqui A. Shykoff⁴, Anders P. Møller⁴ and
8 Fugo Takasu^{5*}

9

10 1 College of Life Sciences, Hainan Normal University, Haikou 571158, P. R. China

11 2 State Key Laboratory of Biocontrol, School of Life Sciences, Sun Yat-sen University,
12 Guangzhou 510275, P. R. China13 3 Department of Biology, Norwegian University of Science and Technology (NTNU),
14 NO-7491 Trondheim, Norway15 4 Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université
16 Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France17 5 Department of Information and Computer Sciences, Nara Women's University,
18 Kita-Uoya Nishimachi, Nara 630–8506, Japan

19

20 * Corresponding author

21

22 Running title: Modeling the maintenance of egg polymorphism

23 Corresponding author: Fugo Takasu

24 E-mail: takasu@ics.nara-wu.ac.jp

25 Tel & Fax: +81 742-20-3983

26 Address: Department of Information and Computer Sciences, Nara Women's University,

27 Kita-Uoya Nishimachi, Nara 630-8506, Japan

28

29

30

31

32 **Abstract (Max 150 words)**

33 In avian brood parasitism, egg phenotype plays a key role both for host and parasite
34 reproduction. Several parrotbill species of the genus *Paradoxornis* are parasitized by the
35 common cuckoo *Cuculus canorus* and clear polymorphism in egg phenotype is
36 observed. In this article, we develop a population genetics model in order to identify
37 key parameters that control maintenance of egg polymorphism. The model analyses
38 show that egg polymorphism can be maintained either statically as an equilibrium or
39 dynamically with frequency oscillations depending on the sensitivity of the host against
40 unlike eggs and how the parasite targets host nests with specific egg phenotypes. Based
41 on the model we discuss egg polymorphism observed in parrotbills and other host
42 species parasitized by the cuckoo. We suggest the possibility that frequencies of egg
43 phenotypes oscillate and we appeal for monitoring of cuckoo-host interactions over a
44 large spatiotemporal scale.

45

46 **Keywords:** Avian brood parasitism, co-evolution, egg phenotype, frequency-dependent
47 selection, oscillation, population genetics model

48 **Introduction**

49 Polymorphism in natural populations occurs as discontinuous, discrete assemblages of
50 individuals with a shared phenotype. Such polymorphism may evolve and can be
51 maintained as a consequence of frequency-dependent selection (Kettlewell, 1973;
52 Majerus, 1998; Bond, 2007). Rare mutants for novel discrete phenotypes may spread if
53 they enjoy a selective frequency-dependent advantage during interactions with any
54 selective agents. Here we focus on polymorphic phenotypes of the eggs that birds
55 produce because they can be a crucial component for successful reproduction by both
56 host and parasite in avian brood parasitism.

57

58 Accepting brood parasitism usually results in significant reduction in reproductive
59 success for the host (Rothstein, 1990; Davies, 2000). This strong parasitism pressure
60 constitutes a driving force for co-evolutionary interactions between the parasite and the
61 host where the host evolves defenses against parasitism like the ability to recognize and
62 reject parasitic eggs that look dissimilar in appearance to its own eggs (Rothstein, 1975;
63 Davies & Brooke, 1988; Moksnes et al., 1990) and the parasite evolves better egg
64 mimicry to counter the host defense (Brooke & Davies, 1988). The host may further
65 counter egg mimicry by the parasite by decreasing intra-clutch variation and increasing
66 inter-clutch variation in egg phenotype (Øien et al., 1995; Stokke et al., 2002; Stokke et
67 al., 2007).

68

69 The common cuckoo *Cuculus canorus*, one of the best studied avian brood parasites,

70 parasitizes several parrotbill species of the genus *Paradoxornis*. Kim et al. (1995)
71 showed that the vinous-throated parrotbill *P. webbianus* in Korea exhibits clear
72 dimorphism in egg color; a clutch contains either white or blue eggs. Lee & Yoo (2004)
73 and Lee et al. (2005) demonstrated that the vinous-throated parrotbill has the ability to
74 recognize and reject unlike eggs as do many other cuckoo hosts. Despite the
75 dimorphism in egg color of the parrotbill, however, only blue eggs are found in the
76 cuckoo in Korea (Kim et al., 1995; Lee & Yoo, 2004; Lee et al., 2005).

77

78 Recently, Yang et al. (2010) showed that the ashy-throated parrotbill *P. alphonisianus* in
79 southern China, a closely related species of *P. webbianus*, shows clear polymorphism in
80 egg color, with white, pale blue and blue eggs occurring, both in the parrotbill and the
81 cuckoo population. Yang et al. (2010) also demonstrated that the ashy-throated
82 parrotbill has a fine-tuned ability to recognize and reject eggs that are dissimilar beyond
83 a certain threshold. They suggested the possibility that egg polymorphism both in the
84 parrotbill and the cuckoo has evolved as a result of co-evolutionary interaction between
85 them.

86

87 Apparent absence of white cuckoo eggs in Korea should favor parrotbills that produce
88 white eggs because such "white parrotbills" can reject blue cuckoo eggs better than
89 "blue parrotbills" (Lee et al., 2005). Increase in the frequency of white parrotbills may
90 be followed by emergence of "white cuckoos" that can exploit white parrotbills more
91 efficiently than blue cuckoos. This parasitic interaction naturally raises an intriguing

92 question about the maintenance of such mutual egg dimorphism in both host and
93 parasite under frequency-dependent selection. Presence of the three egg colors both in
94 the parrotbill and the cuckoo in China also poses the same question. How can egg
95 polymorphism be maintained in both host and parasite in this co-evolutionary arms
96 race?

97

98 Egg phenotype including background color, patterns like spots, blotches and lines is
99 likely genetically determined and a female produces eggs of a constant phenotype
100 throughout her lifetime (Collias, 1993; Gosler et al., 2000; Gibbs et al., 2000; Mahler et
101 al., 2008; Moksnes et al., 2008). Several independent cases of evolution of egg
102 polymorphism (Kilner, 2006) suggest that the underlying genetic mechanisms are
103 simple and possibly only involve one or at most a few loci. A recent study on the
104 common cuckoo indicates that the genes determining egg coloration are most likely
105 found on autosomal loci, rather than the W-chromosome as previously assumed, and
106 therefore is subject to Mendelian inheritance (Fossøy et al., 2011). Also, several
107 empirical studies suggest that the background egg coloration is governed by at least two
108 autosomal loci in birds (Wei et al., 1992; Collias, 1993; Ito et al., 1993). Because egg
109 phenotype plays a key role both for the host and the parasite to successfully reproduce
110 in avian brood parasitism, frequency-dependent selection is expected to work on egg
111 phenotype to cause the egg polymorphism we observe in Korea and China.

112

113 Previous theoretical studies have demonstrated that host-parasite co-evolution can

114 promote polymorphism in the levels of host resistance and parasite virulence with their
115 levels fluctuating cyclically and that such co-evolutionary cycles are likely to occur in
116 antagonistic interactions in general (Sasaki, 2000; Tellier & Brown, 2007a; 2007b;
117 Nuismer & Thompson, 2006; Nuismer et al., 2007). Thus, the polymorphism observed
118 in the cuckoo and parrotbill interactions could be conceptually understood by these
119 previous models; egg polymorphism may be maintained with oscillating frequencies of
120 each egg phenotype. However, these models are based on simplified assumptions such
121 that hosts and parasites encounter each other completely randomly and that the trait in
122 focus is asexually inherited in haploid organisms. We consider these models too
123 simplistic to provide any quantitative and empirically testable predictions on frequency
124 changes of egg phenotypes observed in avian brood parasitism.

125

126 In order to understand how egg polymorphism can be maintained in avian brood
127 parasitism and to provide quantitative predictions that can be empirically tested, we here
128 construct a population genetics model with biologically plausible genetic and ecological
129 assumptions. Based on the model analysis, we identify key parameters that control
130 maintenance of egg polymorphism in avian brood parasitism. We suggest the possibility
131 that the parrotbill-cuckoo interactions exhibit oscillations in frequencies of distinct egg
132 colors and that egg polymorphism can be statically or dynamically maintained in the
133 host and the parasite population depending on the sensitivity of the host when
134 recognizing unlike eggs and how the parasite targets to parasitize host nests with a
135 certain egg phenotype. We discuss egg polymorphism observed in other brood parasitic

136 interactions with implications for the importance of studying the behavior by the
137 parasite when utilizing hosts with polymorphic eggs as well as the genetic mechanism
138 of egg phenotype. Finally, we emphasize that our findings have general applications
139 outside avian brood parasitism to include antagonistic interactions in general.

140

141 **The model**

142 We assume sexual and diploid population both for the host and the parasite. We assume
143 three distinct egg colors, white, pale blue and blue, as observed in the parrotbill-cuckoo
144 interaction (Yang et al., 2010).

145

146 We assume the following genetics for the expression of egg phenotype. Egg color is
147 controlled by two autosomal loci. The first locus controls the presence or absence of
148 blueness with two alleles, b and B . The allele B expresses blueness and is assumed to be
149 dominant over b . The second locus controls the expression of the blueness with two
150 alleles, m and M . The allele M modifies the expression of blueness and makes eggs pale
151 blue and is assumed to be dominant over m . This diallelic two-locus assumption is
152 based on sexual inheritance of egg color observed in chickens *Gallus gallus*, village
153 weavers *Ploceus cucullatus*, and Japanese quails *Coturnix japonica* (Wei et al., 1992;
154 Collias, 1993; Ito et al., 1993). Recombination rate of the two loci is r ($0 \leq r \leq 1/2$).

155

156 As a notation, we hereafter denote egg color as 0 (white), 1/2 (pale blue) and 1 (blue).

157 Ten genotypes are possible in a population, each indexed as i and having a phenotypic

158 value as follows ($i = 1, 2, \dots, 10$). (Genotype i , its phenotype): (bm/bm , 0), (bm/bM , 0),
 159 (bM/bM , 0), (bm/Bm , 1), (bm/BM , 1/2), (bM/Bm , 1/2), (bM/BM , 1/2), (Bm/Bm , 1),
 160 (Bm/BM , 1/2), (BM/BM , 1/2). Let h_i and p_i be the frequency of genotype i in the host
 161 and the parasite population, respectively. The phenotypic frequency of egg color 0, 1/2,
 162 1, respectively, is denoted as $f_{h0} = h_1 + h_2 + h_3$, $f_{h1/2} = h_5 + h_6 + h_7 + h_9 + h_{10}$, $f_{h1} = h_4 + h_8$
 163 for the host and $f_{p0} = p_1 + p_2 + p_3$, $f_{p1/2} = p_5 + p_6 + p_7 + p_9 + p_{10}$, $f_{p1} = p_4 + p_8$ for the
 164 parasite. We assume infinitely large population, random mating, and non-overlapping
 165 generations.

166

167 We next assume the following ecological situations. Each host female builds a nest and
 168 completes a clutch of egg color determined by her genotype. Let P denote the
 169 probability that a host nest is parasitized. The probability that a nest of host female
 170 genotype i is parasitized by a parasite genotype j conditional on the nest is parasitized is
 171 assumed to be $\phi_i p_j$ where ϕ_i is the probability that a parasite targets the nest of a host
 172 genotype i . We here assumed that a host nest is parasitized once at most. Multiple
 173 parasitism is ignored in our model, which is a close approximation of reality because the
 174 probability of multiple parasitism is low in parrotbills and most other hosts (but see
 175 Moskát & Honza (2002), Takasu & Moskát (2011) for high parasitism rate that
 176 remained constant among years).

177

178 It remains unknown how a parasite decides to parasitize a host nest having a certain
 179 color of eggs in the presence of egg polymorphism in the host population. Because

180 parasites often visit host nests without laying parasitic egg presumably to check nest
 181 content (Moksnes et al., 2000), the way a parasite utilizes a host nest may not be
 182 random (Aviles et al., 2006; Cherry et al., 2007), i.e., it may be influenced by
 183 frequencies of egg phenotypes in the host population and ϕ_i might not necessarily be the
 184 same as the frequency h_i of host genotype i . Such non-random search has been
 185 demonstrated as frequency-dependent switching when birds use search images to look
 186 for prey of a particular color or pattern (Bond, 1983). In order to consider
 187 non-randomness of parasitic behavior, we assume that ϕ_i is given as follows using the
 188 host phenotype frequencies, $f_{h0}, f_{h1/2}, f_{h1}$.

189

190

$$191 \quad \phi_i = \frac{f_{h0}^n}{f_{h0}^n + f_{h1/2}^n + f_{h1}^n} \frac{h_i}{f_{h0}} \quad \text{for } i = 1, 2, 3 \text{ (host phenotype 0)}$$

192

$$193 \quad \phi_i = \frac{f_{h1/2}^n}{f_{h0}^n + f_{h1/2}^n + f_{h1}^n} \frac{h_i}{f_{h1/2}} \quad \text{for } i = 5, 6, 7, 9, 10 \text{ (host phenotype 1/2)}$$

194

$$195 \quad \phi_i = \frac{f_{h1}^n}{f_{h0}^n + f_{h1/2}^n + f_{h1}^n} \frac{h_i}{f_{h1}} \quad \text{for } i = 4, 8 \text{ (host phenotype 1)}$$

196

197

198 where the parameter n controls the propensity that the parasite is attracted to parasitize
 199 hosts having a certain egg color; the parasite utilizes hosts just randomly according to
 200 the actual frequencies ($n = 1$), the parasite is more likely to utilize a host with rare egg

201 color than would be expected by chance ($n < 1$), or the parasite is more likely to utilize
 202 a host with common egg color than would be expected by chance ($n > 1$) (Fig. 1).

203

204 [Fig. 1: How parasites parasitize host nests. Dependency on n .]

205

206 We assume that all host males and females have the same ability to recognize and reject
 207 unlike eggs and this recognition ability is innate, not learnt. The probability that a host
 208 with egg color C_H accepts parasitic egg C_P in the nest is denoted as $A(C_H, C_P)$ and it is
 209 assumed to be a decreasing function of the absolute difference in color $|C_H - C_P|$ ($C_H,$
 210 $C_P = 0, 1/2, 1$); the greater the contrast in color, the smaller the acceptance probability
 211 as has been demonstrated in many host species and modeled (Higuchi, 1998; Takasu,
 212 2003; Stokke et al., 2007; Yang et al., 2010). To simplify the notation we denote $a_0 =$
 213 $A(0, 0) = A(1/2, 1/2) = A(1, 1)$, $a_{1/2} = A(0, 1/2) = A(1/2, 0) = A(1, 1/2) = A(1/2, 1)$, $a_1 =$
 214 $A(0, 1) = A(1, 0)$ ($1 \geq a_0 \geq a_{1/2} \geq a_1 \geq 0$). A parasitized host breeding pair can produce
 215 own offspring only when it rejects parasitism successfully. Otherwise, a parasite chick
 216 fledges from the parasitized host nest. Sex ratio is fixed 1:1 and the genotype
 217 frequencies are the same in males and females both in the host and the parasite. Table 1
 218 summarizes these ecological assumptions.

219

220 [Insert Table 1 around here]

221

222 Using vector notation $\mathbf{h} = (h_1, h_2, \dots, h_{10})$ and $\mathbf{p} = (p_1, p_2, \dots, p_{10})$, the genotype

223 frequencies at the next generation \mathbf{h}' and \mathbf{p}' are given as follows

224

225

$$226 \quad \mathbf{h}' = \frac{1}{\bar{w}_H} \mathbf{T}_H \mathbf{W}_H (\mathbf{h} \otimes \mathbf{h}) \quad (1)$$

227

$$228 \quad \mathbf{p}' = \frac{1}{\bar{w}_P} \mathbf{T}_P \mathbf{W}_P (\mathbf{p} \otimes \mathbf{p}) \quad (2)$$

229

230

231 Here, \bar{w}_H and \bar{w}_P is the average fitness of the host and the parasite, respectively. \mathbf{T}_H
 232 and \mathbf{T}_P is a 10 by 10^2 transmission matrix that describes the distribution of offspring
 233 genotypes produced from a pair of two genotypes as a male and a female for the host
 234 and the parasite, respectively. \mathbf{W}_H and \mathbf{W}_P is a 10^2 by 10^2 diagonal matrix with
 235 coefficients of fitness as the reproductive success from a pair of two genotypes as a
 236 male and a female for the host and the parasite, respectively. \otimes is Kronecker product
 237 and $\mathbf{h} \otimes \mathbf{h}$ and $\mathbf{p} \otimes \mathbf{p}$ gives frequencies of mating pairs for the host and the parasite,
 238 respectively. See Appendix for the derivation.

239

240 The coupled dynamics of equation (1) and (2) describes temporal change in the
 241 genotype frequencies h_i and p_i ($i = 1, 2, \dots, 10$) and hence the phenotype frequencies f_{h0} ,
 242 $f_{h1/2}$, f_{h1} , f_{p0} , $f_{p1/2}$, f_{p1} under the genetic and ecological assumptions explained above. In
 243 the next section we analyze the frequency dynamics of egg colors, mainly focusing on

244 maintenance of egg polymorphism, firstly for asexual and secondly for sexual
 245 inheritance of egg color.

246

247 **Results**

248 *Asexual inheritance of egg color*

249 When egg color is asexually inherited to daughters, the coupled dynamics (1) and (2) is
 250 reduced to the simpler dynamics of the six phenotype frequencies f_{h0} , $f_{h1/2}$, f_{h1} , f_{p0} , $f_{p1/2}$,
 251 f_{p1} (see Appendix). When the parasite utilizes host nests randomly according to their
 252 frequencies ($n = 1$), the reduced dynamics is analytically tractable.

253

254 We first look for equilibria at which the six phenotype frequencies temporarily remain
 255 unchanged, i.e., $f'_{h0} = f_{h0} = f^*_{h0}$, $f'_{h1/2} = f_{h1/2} = f^*_{h1/2}$, $f'_{h1} = f_{h1} = f^*_{h1}$, $f'_{p0} = f_{p0} = f^*_{p0}$, $f'_{p1/2} =$
 256 $f_{p1/2} = f^*_{p1/2}$, $f'_{p1} = f_{p1} = f^*_{p1}$ (* denotes equilibrium). Under the ecological assumptions
 257 that parasites randomly parasitize ($n = 1$) and that unlike eggs are more likely to be
 258 rejected ($1 \geq a_0 > a_{1/2} > a_1 \geq 0$), there exists a unique trimorphic equilibrium where all
 259 colors are present both in the host and the parasite population as

260

261

$$262 \begin{pmatrix} f^*_{h0} \\ f^*_{h1/2} \\ f^*_{h1} \end{pmatrix} = \begin{pmatrix} f^*_{p0} \\ f^*_{p1/2} \\ f^*_{p1} \end{pmatrix} = \frac{1}{3a_0 - 4a_{1/2} + a_1} \begin{pmatrix} a_0 - a_{1/2} \\ a_0 - 2a_{1/2} + a_1 \\ a_0 - a_{1/2} \end{pmatrix} \quad (4)$$

263

264

265 if and only if the condition

266

267

$$268 \quad a_0 - 2 a_{1/2} + a_1 > 0 \quad (5)$$

269

270

271 is satisfied. The condition (5) requires that the host accepts moderately mimetic eggs
272 with probability $a_{1/2}$ being less than the arithmetic average of a_0 and a_1 , which
273 biologically means that the host has high sensitivity to discriminate unlike eggs (Fig. 2).

274

275 [Insert Fig. 2 around here. Relation of the acceptance probabilities a_0 , $a_{1/2}$ and a_1]

276

277 Besides the trimorphic equilibrium (4), there are fourteen equilibria where hosts and
278 parasites are either monomorphic or dimorphic; nine equilibria where both hosts and
279 parasites are monomorphic with one of the three phenotypes, one equilibrium where
280 hosts are dimorphic with 0 and 1 and parasites are monomorphic with 1/2, one where
281 hosts are monomorphic with 1/2 and parasites are dimorphic with 0 and 1, three where
282 both hosts and parasites are dimorphic with 0 and 1/2, 0 and 1, and 1/2 and 1,
283 respectively (Fig. 3). These fourteen equilibria are possible irrespective of condition (5).

284

285 [Fig. 3: List of all possible equilibria]

286

287 Local stability of these equilibria can be analyzed by linearizing the dynamics (1) and
288 (2) (Murray, 2007). It turns out that all of the equilibria derived above are unstable and
289 that the linearized dynamics when at least two phenotypes are present both in the host
290 and the parasite population shows oscillations with a period dependent on a_0 , $a_{1/2}$, a_1
291 and P . See Appendix for derivation of these results.

292

293 Instability of equilibria where both the host and the parasite are monomorphic can be
294 readily shown as follows (see Fig. 3a). When both are monomorphic with the same
295 phenotype, rare host mutants having different phenotype can always invade the host
296 population because these have higher chance to reject parasitism and increase in
297 frequency. In the same logic, when both are monomorphic but with different phenotype,
298 rare parasite mutants having phenotype more mimetic to that of hosts can always invade
299 the parasite population because these have higher chance of parasitism acceptance and
300 increase in frequency. Therefore, monomorphic hosts and monomorphic parasites
301 cannot be maintained stably. The same logic applies to equilibria where either hosts or
302 parasites, or both, are dimorphic lacking a particular egg color (Fig. 3b, c).

303

304 Fig. 4 shows typical frequency dynamics for asexual inheritance of egg color. For
305 dimorphic hosts and dimorphic parasites with white and blue eggs (pale blue egg is
306 absent in both populations) and the parasite utilizes hosts randomly ($n = 1$), the
307 frequencies of the two phenotypes continue to oscillate. Amplitude of oscillation is
308 larger in the parasite than in the host and parasite frequencies apparently converge to a

309 heteroclinic cycle where one phenotype dominates for a longer and longer time but is
310 eventually replaced by another phenotype (Fig. 4a) (Seger, 1988). When the parasite
311 utilizes hosts with egg color in minority more than its frequency ($n < 1$), the frequency
312 dynamics can be stabilized and the two phenotypes coexist but dynamically (Fig. 4b). In
313 contrast, when the parasite utilizes hosts with egg color in majority more than the
314 frequency ($n > 1$), the dynamics is more destabilized and shows a heteroclinic cycle
315 similar to the case $n = 1$ (not shown).

316

317 For trimorphic hosts and trimorphic parasites when condition (5) is satisfied and the
318 parasite utilizes hosts randomly ($n = 1$), the frequencies of the three phenotypes exhibit
319 complex dynamics, eventually converging to a heteroclinic cycle (Fig. 4c). For n being
320 sufficiently small ($n < 1$), an equilibrium can be reached where all three phenotypes are
321 stably maintained both in the host and the parasite (Fig. 4d). When the parasite utilizes
322 hosts with egg color in majority more than the frequency ($n > 1$), the frequencies exhibit
323 complex behaviors and eventually show a heteroclinic cycle similar to the case $n = 1$
324 (not shown). When condition (5) is not met, the dynamics starting from all phenotypes
325 present converges to an equilibrium where hosts are dimorphic with white and blue and
326 parasites are monomorphic with pale blue (not shown).

327

328 [Insert Fig. 4 around here. Asexual case, $n=1$ or $n<1$, two colors or all colors present]

329

330 Fig. 5 shows the dependency of the period of oscillation in the early dynamics on the

331 parasitism rate P . The phenotype frequencies oscillate roughly with a period
332 proportional to the inverse of the square root of the parasitism rate P as predicted by
333 local stability analysis (see Appendix).

334

335 [Insert Fig. 5 around here. Dependency of the oscillation period on the parasitism rate
336 P .]

337

338 *Sexual inheritance of egg color*

339 We next focus on the case that egg color is sexually inherited, a likely case in the
340 cuckoo-parrotbill interactions. The dynamics (1) and (2) is intractable and we
341 numerically analyze the behavior.

342

343 Fig. 6 shows typical frequency dynamics for sexual inheritance of egg color. For
344 dimorphic hosts and dimorphic parasites where there are no pale blue eggs (the allele M
345 is absent) and the parasite utilizes hosts randomly ($n = 1$), the phenotypic frequencies
346 oscillate but the oscillation lasts more stably with a longer period compared with the
347 asexual case (Fig. 6a, cf. Fig. 4a). When the parasite utilizes hosts with egg color in
348 minority more than its frequency ($n < 1$), the dynamics is stabilized where both the two
349 phenotypes coexist nearly equally (Fig. 6b). In contrast, when the parasite utilizes hosts
350 with egg color in majority more than the frequency ($n > 1$), the dynamics is more
351 destabilized and shows a heteroclinic cycle similar to the asexual case $n = 1$ (not
352 shown).

353

354 For trimorphic hosts and trimorphic parasites when condition (5) is satisfied and the
355 parasite parasitizes the host randomly ($n = 1$), the frequencies of the three phenotypes
356 exhibit complex dynamics, eventually converging to a heteroclinic cycle (Fig. 6c). For n
357 being sufficiently small, a stable equilibrium can be reached where all three phenotypes
358 are stably maintained both in the host and the parasite (Fig. 6d). When condition (5) is
359 not met, the dynamics starting from all phenotypes present converges to an equilibrium
360 where hosts are dimorphic with white 0 and blue 1 and parasites are monomorphic with
361 pale blue $1/2$ (not shown).

362

363 [Insert Fig. 6 around here. Sexual case, $n=1$ or $n<1$, two colors or all colors present]

364

365 Dependency of the period of oscillation on the parasitism rate P for the sexual case is
366 shown in Fig. 5. Oscillation period is proportional to the inverse of the square root of P
367 but it is nearly two times larger than that of the asexual case.

368

369 We also investigated the effect of recombination rate of the two loci, r_H and r_P , on the
370 frequency dynamics. The dynamics are quantitatively similar unless the recombination
371 rate is nearly zero, which is consistent with linkage disequilibrium decreasing
372 exponentially whereby all genotypes are eventually created (Crow & Kimura, 1970).

373

374 **Discussion**

375 We have shown that the frequency dynamics of genotypes/phenotypes critically
376 depends on ecological factors, the sensitivity of hosts when recognizing unlike eggs
377 (acceptance probabilities a_0 , $a_{1/2}$, and a_1), and how the parasite utilizes the host
378 (parameter n).

379

380 Egg polymorphism with three phenotypes present can be maintained only when the host
381 has a high sensitivity to reject moderately mimetic eggs ($a_0 - 2a_{1/2} + a_1 > 0$). Otherwise,
382 an equilibrium is reached where the parasite shows monomorphism with the
383 intermediate pale blue color and the host showing dimorphism with two extremes of
384 white and blue.

385

386 The way the parasite targets hosts, parameter n , critically affects if polymorphism is
387 statically or dynamically maintained; only when n is sufficiently small so that hosts with
388 an egg color in minority is more parasitized, the frequency dynamics converges to a
389 stationary polymorphism. With smaller n , a negative feedback operates on the risk of a
390 host being parasitized and this contributes to stabilize the frequency dynamics.

391 Otherwise, frequencies oscillate with a period roughly proportional to the inverse square
392 root of the parasitism rate and polymorphism is dynamically maintained. In this case,
393 the amplitude of oscillation is always larger in the parasite than in the host. This is
394 because selection operates stronger in the parasite than in the host; all parasites
395 experience judgment of a host's accepting or rejecting parasitism while not all hosts are
396 parasitized. If the amplitude is large enough, a certain phenotype may be lost by chance

397 in the parasite population when the frequency becomes extremely low. This
398 demographic stochasticity has been ignored in our model but it could be significant as
399 we argue in the real system below.

400

401 These results remain qualitatively the same, irrespective of asexual or sexual inheritance
402 of egg color, although it quantitatively affects the period with which frequencies
403 oscillate; sexual inheritance results in nearly two times longer period of frequency
404 oscillation compared with asexual case.

405

406 We assumed that the acceptance probabilities $A(C_H, C_P)$ are a decreasing function of the
407 difference in color $|C_H - C_P|$ ($C_H, C_P = 0, 1/2, 1$), and that these can be represented by
408 three parameters, $a_0, a_{1/2}$, and a_1 ($1 \geq a_0 \geq a_{1/2} \geq a_1 \geq 0$), i.e., the dynamical system (1)
409 and (2) is structurally symmetric. We have carried out numerical analyses where each of
410 the acceptance probabilities $A(C_H, C_P)$ is randomly perturbed around $a_0, a_{1/2}, a_1$ with a
411 certain range to incorporate asymmetry and found that all the results remain
412 qualitatively similar. Thus, we conclude that our results are robust and not artifacts
413 caused by the symmetry of the model structure.

414

415 We assumed diallelic two-locus genetics where both the blue allele B and the modifier
416 allele M are dominant. We confirmed that modification of this genetic assumption of
417 dominance does not change the results greatly. Simple genetics as we assumed might be
418 justified by independent evolution of polymorphism in egg color in avian brood

419 parasitism (Kilner, 2006). Further empirical study to elucidate detailed genetic
420 mechanisms underlying egg phenotype expression is certainly needed.

421

422 The importance of host sensitivity against unlike egg has been suggested in theoretical
423 studies where egg phenotype is assumed to be a continuous trait which is asexually
424 inherited; the higher the host sensitivity to discriminate unlike eggs, the more discrete
425 egg phenotypes can coexist both in the host and the parasite population (Takasu, 2003;
426 2005). We have obtained qualitatively the same result in our model. Our results also
427 corroborate previous theoretical studies that co-evolutionary dynamics of adaptive traits
428 in antagonistic interactions between prey/host and predator/parasite tend to exhibit
429 oscillation in the level of adaptive traits of hosts and prey (resistance to parasitism or
430 predation) and parasites and predators (virulence or attack rate) (Seger, 1988; Gavrilets
431 & Hastings, 1998; Gandon, 2002; Nuismer et al., 2005; Nuismer & Thompson, 2006;
432 Kopp & Gavrilets, 2006; Tellier & Brown, 2007a; 2007b). In these previous models,
433 however, simpler assumptions like haploid populations, asexual inheritance of
434 phenotypes and random encounters of antagonistic organisms ($n = 1$ in our model) are
435 assumed. Random encounters that many of the previous models have assumed may be
436 justified for micro-parasites like viruses that passively contact with target hosts. In
437 contrast, avian brood parasites do not necessarily parasitize hosts randomly (Avilés et
438 al., 2006; Cherry et al., 2007) as complex cognitive mechanisms may be involved in
439 search for target hosts (Bond, 1983). We have shown that relaxing the random encounter
440 rule results in the novel finding that polymorphism can be statically maintained if a

441 rarer host egg phenotype attracts more parasites. The way the parasite utilizes hosts is
442 likely to evolve although it has not been considered in our model. We stress the need for
443 theoretical study that focuses on the evolution of parasite behaviors coupled with the
444 evolution of egg polymorphism.

445

446 The vinous-throated parrotbill in Korea shows dimorphism in egg color as white and
447 blue and the ratio of white to blue varies from 0.21:0.79 to 40:60, while only blue
448 cuckoo eggs are found (Kim et al., 1995; Lee & Yoo, 2004). The two egg colors may
449 coexist either statically or dynamically depending on how the cuckoo parasitizes the
450 dimorphic parrotbill as our model has shown. Frequency of the cuckoo parasitism in
451 blue or white parrotbills paralleled the egg-color ratio of the parrotbill population (Lee
452 et al., 2005). This implies that the cuckoo parasitizes the parrotbill in Korea just
453 randomly. In this case, we expect frequency oscillation with the period in the order of a
454 few hundred generations because 5.3% of nests (10 out of 190) were found parasitized
455 in Korea (Lee et al., 2005), and actual parasitism rate would be higher as unlike cuckoo
456 egg had been rejected before detection (Fig. 5). Then, the apparent absence of white
457 cuckoo eggs in Korea may have occurred by chance; cuckoos producing white eggs
458 were once too small in frequency and they were lost by chance. We speculate that white
459 cuckoos, if emerging by some reason like immigration from other area, are likely to
460 increase in frequency and frequency oscillation may last. Studying the way the cuckoo
461 selects host nests is needed together with long-term monitoring of egg color frequencies
462 in Korea.

463

464 The ashy-throated parrotbill in southern China shows polymorphism in egg color, white,
465 pale blue, and blue, as well as in the cuckoo population. The ratio of white:pale
466 blue:blue is 0.564:0.014:0.422 in the parrotbill, while it is 0.417:0.125:0.453 in the
467 cuckoo (Yang et al., 2010). The parrotbill in southern China recognizes and rejects
468 unlike eggs sensitively (Yang et al., 2010), and it is likely that condition (5) is satisfied,
469 so that all the three colors can be maintained either statically or dynamically. Temporal
470 variation in the three egg colors does not clearly show a trend of oscillation in
471 frequencies over the past 10 years (Yang et al., 2010). Most likely, 10 years monitoring
472 is too short to detect frequency changes because 4.3% of the parrotbill nests (24 out of
473 555) were found to be parasitized (Yang et al., 2010) and this gives an oscillation period
474 in the order of a few hundred generations (Fig. 5). We suggest that the frequencies will
475 likely change in the next several decades if the cuckoo in China parasitizes the parrotbill
476 nearly randomly, irrespective of parrotbill egg color. Further long-term monitoring and
477 behavioral study about the way the cuckoo parasitizes the parrotbill is needed.

478

479 Discrete polymorphism in egg phenotype is rare but in avian brood parasitism, and egg
480 polymorphism has likely evolved through co-evolutionary interactions between brood
481 parasites and their hosts (Kilner, 2006). The common cuckoo as a species produces eggs
482 with a variety of phenotypes but the cuckoo as a whole consists of several independent
483 host races, each of which is specialized on a particular host species by producing eggs
484 mimetic to those of the host (Moksnes & Røskaft, 1995; Davies, 2000). A similar

485 system is found in the Red-chested cuckoo *Cuculus solitarius* which has three distinct
486 egg phenotypes as chocolate/coffee brown, green-blue with red/brown spots, and coffee
487 with brown freckling (Kuiper & Cherry, 2002; Honza et al., 2005). Egg polymorphism
488 in avian brood parasitism like the cuckoo and the parrotbill interaction (Kim et al.,
489 1995; Lee & Yoo, 2004; Lee et al., 2005; Yang et al., 2010) constitutes an ideal system
490 for studying how polymorphism can be maintained in a co-evolutionary context
491 (Rothstein, 1990). It is ideal also because the time scale of the life cycle for the parasite
492 and the host is nearly equal in avian brood parasitism so that evolution of novel egg
493 phenotypes would proceed at equal pace in the two parties. Although empirical data on
494 phenotypic frequencies and their temporal changes are too limited to draw any
495 conclusion, we suggest the possibility that egg polymorphism in avian brood parasitism
496 is dynamically maintained with temporarily varying phenotypic frequencies.

497

498 In this model we assumed that both the host and the parasite populations are closed in
499 the sense that there is no gene flow to and from the outside. Extending our model to
500 consider spatial structure enables us to study a "metapopulation" genetics in which we
501 might expect a geographical gradient in phenotypic frequencies (Thompson, 2005). The
502 absence of white cuckoos in Korea and the presence of the three egg colors in southern
503 China may be continuously linked at a larger spatial scale. We may further observe
504 temporally and spatially fluctuating phenotypic frequencies where egg polymorphism is
505 dynamically maintained. Study focused at a larger spatial scale is certainly needed in
506 order to better understand how egg polymorphism is maintained spatially and to

507 demonstrate co-evolution in action in avian brood parasitism, which will certainly
508 contribute to enrich our general understanding of co-evolution in antagonistic
509 interactions.
510

511 **Acknowledgements**

512 This work was supported by Program for New Century Excellent Talents in University
513 (NCET-10-0111) to LW, National Natural Science Foundation of China (No. 31071938)
514 to LW, BGS and AA, and by Centre for Advanced Study at the Norwegian Academy of
515 Science and Letters (CAS) as a part of the project "Coevolutionary interactions and
516 adaptations in a metapopulation context". We thank the Forestry Department of
517 Guizhou Province and Kuankuoshui National Nature Reserve for support and
518 permission to carry out this study, and Y. Cai, J. Q. Wu, X. L. Guo, X. Xu, N. Wang and
519 L. W. Wang for assistance with the field work.

520

521

522 **Appendix**523 *Derivation of the model*

524 In general, the frequency of genotype i in the next generation, x_i' , is given as follows

525

526

$$527 \quad x_i' = \sum_{j,k=1}^N T(i \leftarrow j, k) w_j x_j x_k / \bar{w} \quad (i = 1, 2, \dots, N) \quad (\text{A1})$$

528

529

530 where N is the number of genotypes ($N = 10$ in our model), $T(i \leftarrow j, k)$ is the transition

531 probability that a breeding pair of genotype j as female and k as male produces offspring

532 of genotype i , w_j is the fitness as the reproductive success of the breeding pair in which

533 the female has genotype j (males do not lay eggs and the male k does not influence the

534 reproductive success in our model), and \bar{w} is the average fitness defined by

535

536

$$537 \quad \bar{w} = \sum_{j=1}^N w_j x_j$$

538

539

540 to normalize the genotype frequencies x_i' ($i = 1, 2, \dots, 10$) to sum up to 1. In vector and

541 matrix notation, equation (A1) is written as equation (1) and (2) by replacing x_i with h_i

542 and p_i for the host and the parasite, respectively.

543

544 We here describe the details of fitness matrices \mathbf{W}_H , \mathbf{W}_P and the transmission matrices545 \mathbf{T}_H , \mathbf{T}_P .

546

547 Fitness matrix for the host \mathbf{W}_H is given as follows using parasitism rate P

548

549

550
$$\mathbf{W}_H = (1 - P)\mathbf{I} + P\tilde{\mathbf{W}}$$

551

552

553 where the first term in the r.h.s. is reproductive success when not parasitized and the

554 second term is that when parasitized. Here \mathbf{I} is the 10^2 by 10^2 identity matrix with 1555 along diagonal elements and 0 elsewhere. $\tilde{\mathbf{W}}$ consists of ten 10 by 10 diagonal556 matrices \mathbf{W}_i defined as

557

558

559
$$\tilde{\mathbf{W}} = \begin{pmatrix} \tilde{\mathbf{W}}_1 & 0 & L & 0 \\ 0 & \tilde{\mathbf{W}}_2 & 0 & 0 \\ M & 0 & O & 0 \\ 0 & 0 & 0 & \tilde{\mathbf{W}}_{10} \end{pmatrix}, \quad \tilde{\mathbf{W}}_i = \begin{pmatrix} w_i & 0 & L & 0 \\ 0 & w_i & 0 & 0 \\ M & 0 & O & 0 \\ 0 & 0 & 0 & w_i \end{pmatrix}$$

560

561

562 where w_i is host reproductive success from host female genotype i ($i = 1, 2, \dots, 10$). For

563 the host to successfully reproduce, parasitism has to be rejected. Thus, from Table 1, w_i
 564 is obtained as products of the probability of being parasitized by a parasite j and the
 565 probability of rejecting the parasitism

566

567

$$568 \quad w_i = \sum_{j=1}^{10} \{1 - A(C_H(i), C_P(j))\} p_j \phi_i \frac{1}{h_i}$$

569

570

571 where $C_H(i)$ and $C_P(i)$ refers to the egg color of genotype i of the host and the parasite,
 572 respectively. We have assumed that the probability that a host genotype i is parasitized
 573 is given by ϕ_i in which the parameter n controls the way the parasite searches host nests.
 574 Thus we have to divide the term by h_i to derive fitness (when $n = 1$, $\phi_i = x_i$)

575

576 For the parasite to successfully reproduce, parasitism has to be accepted. Thus the
 577 fitness matrix for the parasite \mathbf{W}_P is given as equally as above but the element w_i is
 578 replaced with

579

580

$$581 \quad w_i = \sum_{j=1}^{10} A(C_H(j), C_P(i)) \phi_j$$

582

583

584 as products of the probability of parasitism to host genotype j and the probability of the
 585 parasitism being accepted, summed over all possible host genotypes.

586

587 Transmission matrix \mathbf{T} consists of ten 10 by 10 square matrices \mathbf{T}_i ($i = 1, 2, \dots, 10$)
 588 arranged horizontally

589

590

$$591 \quad \mathbf{T} = (\mathbf{T}_1 \quad \mathbf{T}_2 \quad \dots \quad \mathbf{T}_{10})$$

592

593

594 The j -th column of \mathbf{T}_i represents the frequencies of offspring genotypes produced by a
 595 breeding pair (the female is genotype i and the male is j) and the column sum amounts
 596 to 1 ($j = 1, 2, \dots, 10$). E.g.,

597

598

$$599 \quad \mathbf{T}_1 = \begin{pmatrix} 1 & 1/2 & 0 & 1/2 & (1-r)/2 & r/2 & 0 & 0 & 0 & 0 \\ 0 & 1/2 & 1 & 0 & r/2 & (1-r)/2 & 1/2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1/2 & r/2 & (1-r)/2 & 0 & 1 & 1/2 & 0 \\ 0 & 0 & 0 & 0 & (1-r)/2 & r/2 & 1/2 & 0 & 1/2 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

600

601

602 using recombination rate r of the two loci. In the same way, \mathbf{T}_2 through \mathbf{T}_{10} are obtained.603 The host and the parasite have a recombination rate r_H and r_P , respectively.

604

605 *Asexual inheritance*

606 Asexual inheritance of egg phenotypes (no male contribution to offspring egg color) can

607 be implemented by setting the matrix \mathbf{T}_i to have 0 in all elements except the i th row608 being 1 ($i = 1, 2, \dots, 10$).

609

610

611

$$\mathbf{T}_i = \begin{pmatrix} 0 & 0 & L & 0 \\ \mathbf{M} & & & \\ 1 & 1 & L & 1 \\ 0 & 0 & L & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

612

613

614 This applies both to the host and the parasite. In asexual inheritance, the frequency

615 dynamics of 10 genotypes in the host and the parasite populations (20 genotypes in

616 total) can be reduced to the frequency dynamics of six phenotypes, $\mathbf{h} = (f_{h0}, f_{h1/2}, f_{h1})$, \mathbf{p} 617 $= (f_{p0}, f_{p1/2}, f_{p1})$.

618

619

620 ***Local stability***

621 Local stability of an equilibrium can be studied by examining eigenvalues of the
622 linearized dynamics around the equilibrium.

623

624 For the equilibrium (4) when condition (5) is met and all three colors are present, we
625 have two zero and four complex eigenvalues

626

627

$$628 \quad \lambda_1 = \lambda_2 = 0$$

629

$$630 \quad \lambda_{3,4} = 1 \pm (a_0 - a_{1/2})(a_0 - a_1)\beta i$$

631

$$632 \quad \lambda_{5,6} = 1 \pm (a_0 - a_{1/2})(a_0 - 2a_{1/2} + a_1)\beta i$$

633

634

635 where

636

637

$$638 \quad \beta = \sqrt{\frac{P}{(a_0^2 - 2a_{1/2}^2 + a_0a_1)\{3a_0 - 4a_{1/2} + a_1 - P(a_0^2 - 2a_{1/2}^2 + a_0a_1)\}}}$$

639

640

641 is a positive real value when the condition (5) is satisfied and the parasitism rate P is
 642 small enough. The absolute value of the four complex eigenvalues is always larger than
 643 unity and the equilibrium (4) is unstable; once perturbed the six frequencies oscillate
 644 approximately with periods

645

646

$$647 \quad T_1 = \frac{2\pi}{\tan^{-1}(a_0 - a_{1/2})(a_0 - a_1)\beta} \propto \frac{1}{\sqrt{P}}$$

648

649 and

650

$$651 \quad T_2 = \frac{2\pi}{\tan^{-1}(a_0 - a_{1/2})(a_0 - 2a_{1/2} + a_1)\beta} \propto \frac{1}{\sqrt{P}},$$

652

653

654 both of which are proportional to the inverse of square root of parasitism rate P . A
 655 shorter period will dominate actual frequency oscillation.

656

657

658 **Literature cited**

- 659 Avilés, J.M., Stokke, B.G., Moksnes, A., Røskoft, E., Åsmul, M. & A.P. Møller. 2006.
660 Rapid increase in cuckoo egg matching in a recently parasitized reed warbler population.
661 Journal of Evolutionary Biology 19:1901-1910.
662
- 663 Bond, A.B. 2007. The evolution of color polymorphism: crypticity, searching images,
664 and apostatic selection. Annual Review of Ecology, Evolution and Systematics
665 38:489-514.
666
- 667 Bond, A.B. 1983. Visual search and selection of natural stimuli in the pigeon: the
668 attention threshold hypothesis. Journal of Experimental Psychology: Animal Behavior
669 Processes 9:292-306.
670
- 671 Brooke, M. de L. & Davies, N.B. 1988. Egg mimicry by cuckoos *Cuculus canorus* in
672 relation to discrimination by hosts. Nature 335:630-632.
673
- 674 Cherry, M.I., Bennett, A.T.D. & Moskát, C. 2007. Do cuckoos choose nests of great
675 reed warblers on the basis of host egg appearance?. Journal of Evolutionary Biology
676 20:1218-1222.
677
- 678 Collias, E.C. 1993. Inheritance of egg-color polymorphism in the village weaver
679 (*Ploceus cucullatus*). Auk 110:683-692.

680

681 Crow, J.F. & Kimura, M. 1970. Introduction to Population Genetics Theory. Harper &
682 Row Publishers, New York, New York.

683

684 Davies, N.B. 2000. Cuckoos, cowbirds and other cheats. Poyser, London.

685

686 Davies, N.B. & Brooke, M. de L. 1988. Cuckoos versus reed warblers. Adaptations and
687 counter-adaptations. *Animal Behaviour* 36:262-284.

688

689 Fossøy, F., Antonov, A., Moksnes, A., Røskaft, E, Vikan, J.R., Møller, A.P., Shykoff, J.A.
690 & Stokke, B.G. 2011. Genetic differentiation among sympatric cuckoo host races: males
691 matter. *Proceedings of the Royal Society B: Biological Sciences* 278:1639-1645.

692

693 Gandon, S. 2002. Local adaptation and the geometry of host-parasite coevolution.
694 *Ecology Letters* 5:246-256.

695

696 Gavrilets, S. & Hastings, A. 1998. Coevolutionary chase in two-species systems with
697 applications to mimicry. *Journal of Theoretical Biology* 191:415-427.

698

699 Gibbs, H.L., Sorenson, M.D., Marchetti, K., Brooke, M. de L., Davies, N.B. &
700 Nakamura, H.. 2000. Genetic evidence for female host-specific races of the common
701 cuckoo. *Nature* 407:183-186.

702

703 Gosler, A.G., Barnett, P.R. & Reynolds, S.J. 2000. Inheritance and variation in eggshell
704 patterning in the great tit *Parus major*. Proceedings of the Royal Society B: Biological
705 Sciences 267:2469-2473.

706

707 Higuchi, H. 1998. Host use and egg color of Japanese cuckoos. In Parasitic birds and
708 their hosts: Studies in coevolution (Rothstein, S.I. & Robinson, S.K., eds), pp. 80–93.
709 Oxford University Press, Oxford, U. K.

710

711 Honza, M., Kuiper, S.M. & Cherry, M.I. 2005. Behaviour of African turdid hosts
712 towards experimental parasitism with artificial red-chested cuckoo *Cuculus solitarius*
713 eggs. Journal of Avian Biology 36:517-522.

714

715 Ito, S., Tsudzuki, M., Komori, M. & Mizutani, M. 1993. Celadon: An eggshell color
716 mutation in Japanese quail. Journal of Heredity 84:146-147.

717

718 Kettlewell, H.B.D. 1973. The evolution of melanism. Clarendon, Oxford.

719

720 Kilner, R.M. 2006. The evolution of egg colour and patterning in birds. Biological
721 Reviews 81:383-406.

722

723 Kim, C.H., Yamagishi, S. & Won, P.O. 1995. Egg-color dimorphism and breeding

- 724 success in the crow tit (*Paradoxornis webbiana*). Auk 112:831-839.
- 725
- 726 Kopp, M. & Gavrillets, S. 2006. Multilocus genetics and the coevolution of quantitative
- 727 traits. Evolution 60:1321-1336.
- 728
- 729 Kuiper, S.M. & Cherry, M.I. 2002. Brood parasitism and egg matching in the
- 730 Red-chested Cuckoo *Cuculus solitarius* in southern Africa. Ibis 144:632-639.
- 731
- 732 Lee, J.W. & Yoo, J.C. 2004. Effect of host egg color dimorphism on interactions
- 733 between the vinous-throated parrotbill (*Paradoxornis webbianus*) and common cuckoo
- 734 (*Cuculus canorus*). Korean Journal of Biological Sciences 8:77-80.
- 735
- 736 Lee, J.W., Kim, D.W. & Yoo, J.C. 2005. Egg rejection by both male and female
- 737 vinous-throated parrotbills *Paradoxornis webbianus*. Integrative Bioscience 9:211-213.
- 738
- 739 Mahler, B., Confalonieri, V.A., Lovette, I.J. & Reboreda, J.C. 2008. Eggshell spotting in
- 740 brood parasitic shiny cowbirds (*Molothrus bonariensis*) is not linked to the female sex
- 741 chromosome. Behavioral Ecology and Sociobiology 62:1193-1199.
- 742
- 743 Majerus, M.E.N. 1998. Melanism. Oxford University Press, Oxford.
- 744
- 745 Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M. & Pedersen, H.C. 1990.

746 Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies.

747 Behaviour 116:64-89.

748

749 Moksnes, A. & Røskaft, E. 1995. Egg-morphs and host preference in the common

750 cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum

751 collections. Journal of Zoology 236:625-648.

752

753 Moksnes, A., Røskaft, E., Hagen, L.G., Honza, M., Mørk, C. & Olsen, P.H. 2000.

754 Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus*

755 *scirpaceus* nests. Ibis 142:247-258.

756

757 Moksnes, A., Røskaft, E., Rudolfson, G., Skjelseth, S., Stokke, B.G., Kleven, O., Gibbs,

758 H.L., Honza, M., Taborsky, B., Teuschl, Y., Vogl, W. & Taborsky, M. 2008. Individual

759 female common cuckoos *Cuculus canorus* lay constant egg types but egg appearance

760 cannot be used to assign eggs to females. Journal of Avian Biology 39:238-241.

761

762 Moskát, C. & Honza, M. 2002. European Cuckoo *Cuculus canorus* parasitism and

763 host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus*

764 *arundinaceus* population. Ibis 144:614-622.

765

766 Murray, J.D. 2007. Mathematical biology: I. An introduction, 3rd edn. Springer, Berlin.

767

- 768 Nuismer, S.L., Doebeli, M. & Browning, D. 2005. The coevolutionary dynamics of
769 antagonistic interactions mediated by quantitative traits with evolving variances.
770 *Evolution* 59:2073-2082.
771
- 772 Nuismer, S.L. & Thompson, J.N. 2006. Coevolutionary alternation in antagonistic
773 interactions. *Evolution* 60:2207-2217.
774
- 775 Nuismer, S.L., Ridenhour, B.J. & Oswald, B.P. 2007. Antagonistic coevolution
776 mediated by phenotypic differences between quantitative traits. *Evolution*
777 61:1823-1834.
778
- 779 Øien, I.J., Moksnes, A. & Røskaft, E. 1995. Evolution of variation in egg color and
780 marking pattern in European passerines: adaptations in a coevolutionary arms race with
781 the Cuckoo *Cuculus canorus*. *Behavioral Ecology* 6:166-174.
782
- 783 Rothstein, S.I. 1975. Evolutionary rates and host defenses against avian brood
784 parasitism. *American Naturalist* 109:161-176.
785
- 786 Rothstein, S.I. 1990. A model system for co-evolution: avian brood parasitism. *Annual*
787 *Review of Ecology and Systematics* 21:481-508.
788
- 789 Sasaki, A. 2000. Host-parasite coevolution in a multilocus gene-for-gene system.

790 Proceedings of the Royal Society B: Biological Sciences 267:2183-2188.

791

792 Seger, J. 1988. Dynamics of some simple host-parasite models with more than two
793 genotypes in each species. Philosophical Transaction of the Royal Society B: Biological
794 Sciences 319:541-555.

795

796 Stokke, G.B., Moksnes, A. & Røskaft, E. 2002. Obligate brood parasites as selective
797 agents for evolution of egg appearance in passerine birds. Evolution 56:199-205.

798

799 Stokke, G.B., Takasu, F., Moksnes, A. & Røskaft, E. 2007. The importance of clutch
800 characteristics and learning for antiparasite adaptations in hosts of avian brood parasites.
801 Evolution 61:2212-2228.

802

803 Takasu, F. 2003. Co-evolutionary dynamics of egg appearance in avian brood parasitism.
804 Evolutionary Ecology Research 5:345-362.

805

806 Takasu, F. 2005. A theoretical consideration on co-evolutionary interactions between
807 avian brood parasites and their hosts. Ornithological Science 4:65-72.

808

809 Takasu, F. & Moskát, C. 2011. Modeling the consequence of increased host tolerance
810 toward avian brood parasitism. Population Ecology 53:187-192.

811

812 Tellier, A. & Brown, J.K.M. 2007a. Stability of genetic polymorphism in host-parasite
813 interactions. *Proceedings of the Royal Society B: Biological Sciences* 274:809-817.

814

815 Tellier, A. & Brown, J.K.M. 2007b. Polymorphism in multilocus host-parasite
816 coevolutionary interactions. *Genetics* 177:1777-1790.

817

818 Thompson, J.N. 2005. *The geographic mosaic of coevolution*. University of Chicago
819 Press, Chicago.

820

821 Yang, C., Liang, W., Cai, Y., Shi, S., Takasu, F., Møller, A.P., Antonov, A., Fossøy, F.,
822 Moksnes, A., Røskft, E. & Stokke, B.G. 2010. Coevolution in action: disruptive
823 selection on egg colour in an avian brood parasite and its host. *PLoS ONE* 5(5): e10816.

824 doi:10.1371/journal.pone.0010816.

825

826 Wei, R., Bitgood, J.J. & Dentine, M.R. 1992. Inheritance of tinted eggshell colors in
827 white-shell stocks. *Poultry Science* 71:406-418.

828

829

836 **Figure legends**

837 Fig. 1

838 The way the parasite targets to parasitize a host nest. The inner disk represents host
839 phenotypic frequency of the three colors, 0, 1/2 and 1, each being 16.7%, 33.3% and
840 50.0% (1/6, 2/6, 3/6), respectively, as an example. The outer disk represents relative
841 frequencies of host nests being actually parasitized, $\phi_1 + \phi_2 + \phi_3$, $\phi_5 + \phi_6 + \phi_7 + \phi_9 + \phi_{10}$,
842 and $\phi_4 + \phi_8$. If parasites randomly search for host nests to parasitize ($n = 1$), the relative
843 frequencies become identical to the actual frequencies of the three colors (Left). If
844 parasites utilize hosts with an egg color in minority more than actual frequencies ($n < 1$),
845 hosts with color 0 is more likely parasitized (Middle). If parasites utilize hosts with an
846 egg color in majority more than actual frequencies ($n > 1$), hosts with color 1 are more
847 likely parasitized (Right).

848

849 Fig. 2

850 The acceptance probabilities of parasitic eggs by the host, a_0 , $a_{1/2}$, and a_1 , plotted
851 against the difference in egg color. The host does not tolerate moderately mimetic eggs
852 (thick lines) and host sensitivity is high ($a_0 - 2a_{1/2} + a_1 > 0$). The host tolerates the
853 moderately mimetic eggs (gray lines) and sensitivity is low ($a_0 - 2a_{1/2} + a_1 < 0$). The
854 unique trimorphic equilibrium (4) is possible if and only if the condition (5), $a_0 - 2a_{1/2} +$
855 $a_1 > 0$, is satisfied.

856

857

858 Fig. 3

859 Possible equilibria of the frequency dynamics of (1) and (2) when egg color is asexually
 860 inherited and the parasite parasitizes randomly ($n = 1$). The horizontal axis represents
 861 egg color of the host and the parasite. The vertical axis represents frequency (scale is
 862 arbitrary except for monomorphic equilibria). a) Both the host and the parasite are
 863 monomorphic in egg color. b) The host is dimorphic with 0 and 1 and the parasite
 864 monomorphic with 1/2. Or the host is monomorphic with 1/2 and the parasite dimorphic
 865 with 0 and 1. c) Both the host and the parasite are dimorphic. d) All colors are present
 866 both in the host and the parasite. This trimorphic equilibrium is possible if and only if
 867 condition (5) is satisfied.

868

869 Fig. 4

870 Frequency dynamics of the three phenotypes of the host and the parasite when egg color
 871 is asexually inherited. Black curve represents frequency of white 0, gray curve for blue
 872 1 and dotted curve for pale blue 1/2. a) Pale blue eggs (1/2) are absent both in the host
 873 and the parasite. Parasites search for host nests randomly ($n = 1$). b) Same as a) but
 874 parasites utilize host nests with an egg color in minority more often than its frequency
 875 ($n = 0.5$). c) All colors are present and parasites search for host nests randomly ($n = 1$).
 876 d) Same as c) but parasites are attracted to hosts with an egg color in minority ($n = 0.5$).
 877 Initial frequencies of the three color in the host and the parasite (f_{h0} , $f_{h1/2}$, f_{h1} , f_{p0} , $f_{p1/2}$,
 878 f_{p1}) are set equal to those observed in Yang et al. (2010), (313/547, 0, 234/547, 10/21, 0,
 879 11/21) for a) and b), (313/555, 8/555, 234/555, 10/24, 3/24, 11/24) for c) and d),

880 respectively. Parameters used in common are $a_0 = 0.8$, $a_{1/2} = 0.3$, $a_1 = 0.1$ and $P = 0.05$
881 based on Yang et al. (2010).

882

883 Fig. 5

884 Dependency of oscillation period T on the parasitism rate P . Dot and rectangle shows
885 period T for asexual and sexual inheritance, respectively. Dotted and thick curve
886 represents least-square fit of the inverse of square root of the parasitism rate P ; $20.0/\sqrt{P}$
887 (asexual) and $41.9/\sqrt{P}$ (sexual). Oscillation period T was calculated by Fourier analysis
888 from time series of the phenotypic frequencies where pale blue was absent and parasites
889 utilize hosts randomly ($n = 1$). For asexual inheritance, time series data in the early 300
890 generations were used to avoid the effect caused by heteroclinic cycle.

891

892 Fig. 6

893 Frequency dynamics of the three phenotypes of the host and the parasite when egg color
894 is sexually inherited. Black curve represents frequency of white 0, gray curve for blue 1
895 and dotted curve for pale blue 1/2. a) Pale blue eggs (1/2) are absent both in the host and
896 the parasite (the allele M is absent). Parasites search for host nests randomly ($n = 1$). b)
897 Same as a) but parasites utilize host nests with an egg color in minority more often than
898 its frequency ($n = 0.5$). c) All colors are present and parasites search for host nests
899 randomly ($n = 1$). d) Same as c) but parasites are attracted to hosts with an egg color in
900 minority ($n = 0.5$). Note that the dynamics (1) and (2) are calculated up to 4,000
901 generations for c) and d). Initial frequencies of ten genotypes in the host and the parasite

902 are set equal to the Hardy-Weinberg equilibrium whose phenotypic frequencies match
903 those observed in Yang et al. (2010), $(f_{h0}, f_{h1/2}, f_{h1}, f_{p0}, f_{p1/2}, f_{p1}) = (313/547, 0, 234/547,$
904 $10/21, 0, 11/21)$ for a) and b), $(313/555, 8/555, 234/555, 10/24, 3/24, 11/24)$ for c) and
905 d), respectively. Parameters used in common are $a_0 = 0.8$, $a_{1/2} = 0.3$, $a_1 = 0.1$, $P = 0.05$
906 and recombination rate $r_H = r_P = 0.5$ (the two loci are not linked).

907

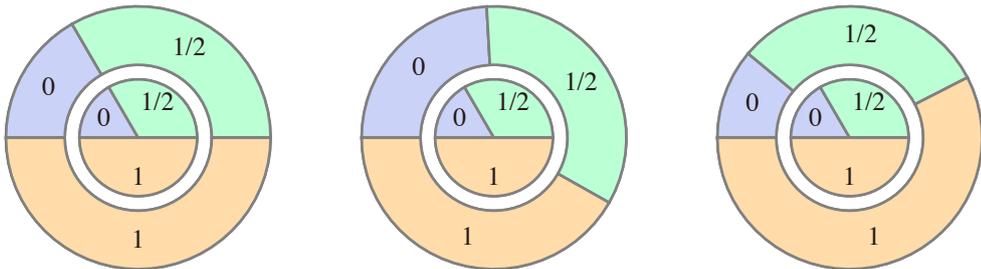


Figure 1

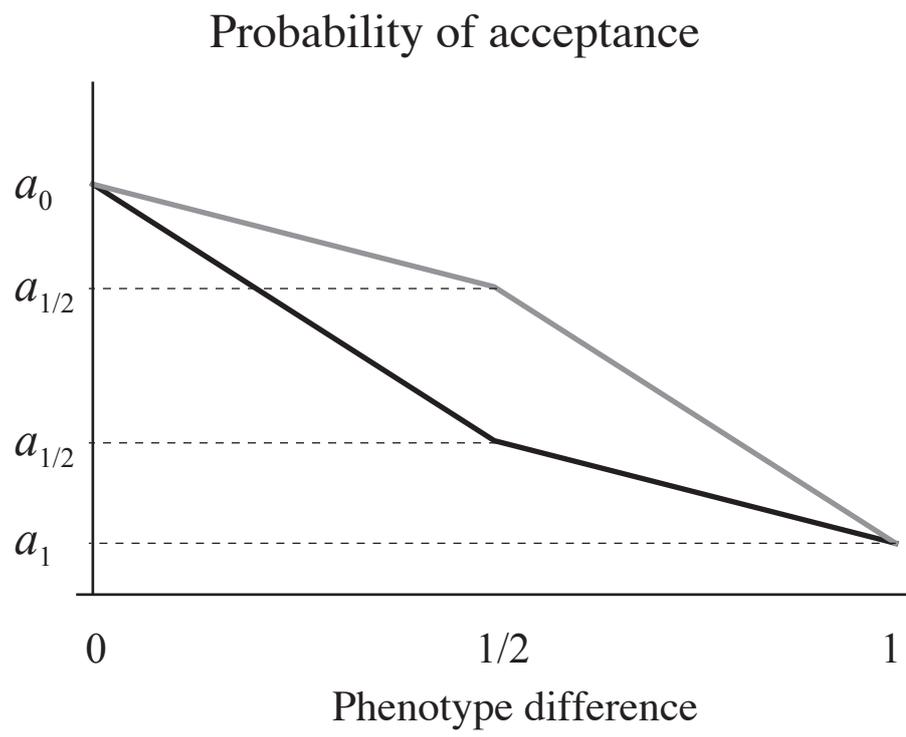


Figure 2

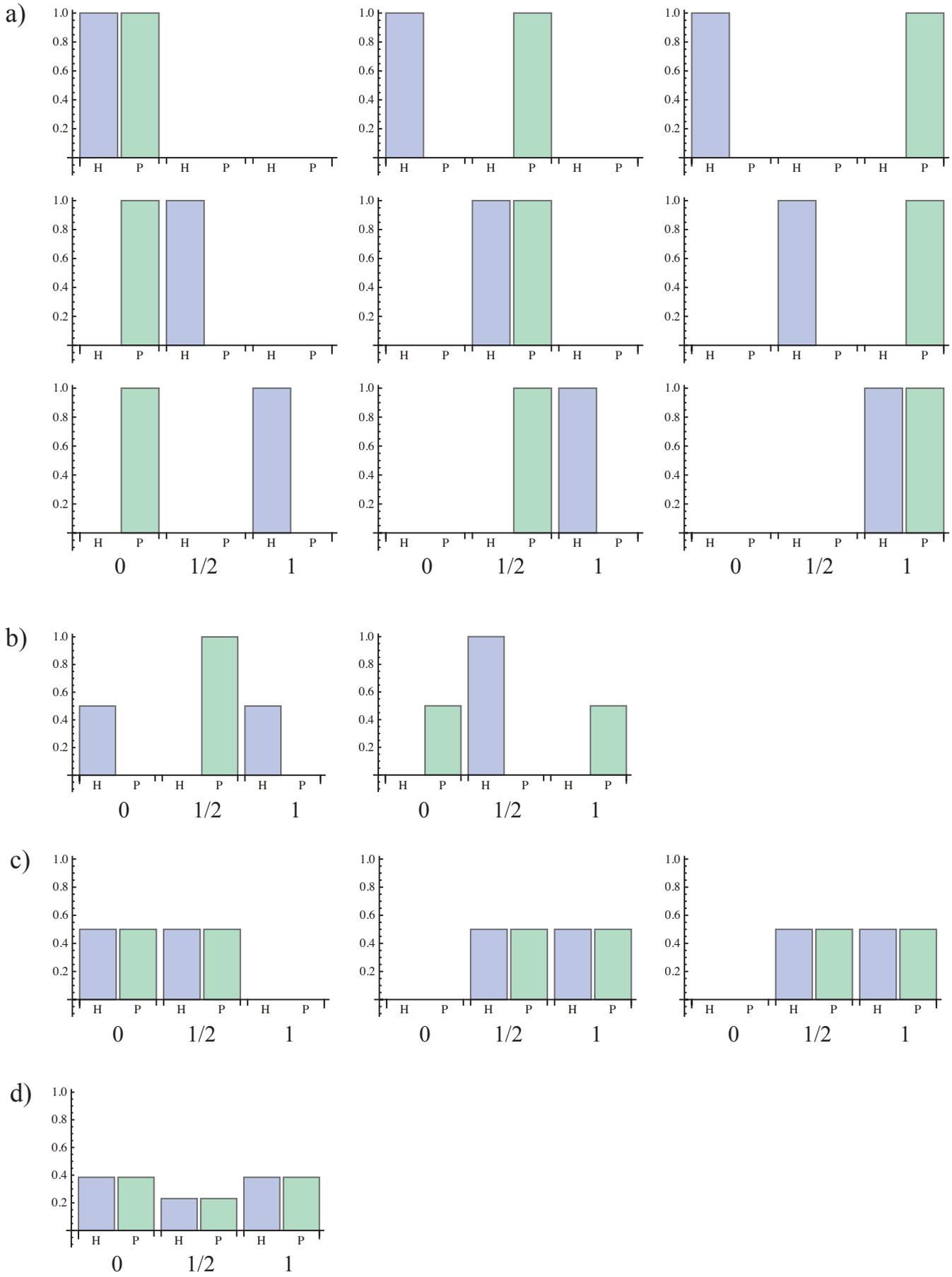


Figure 3

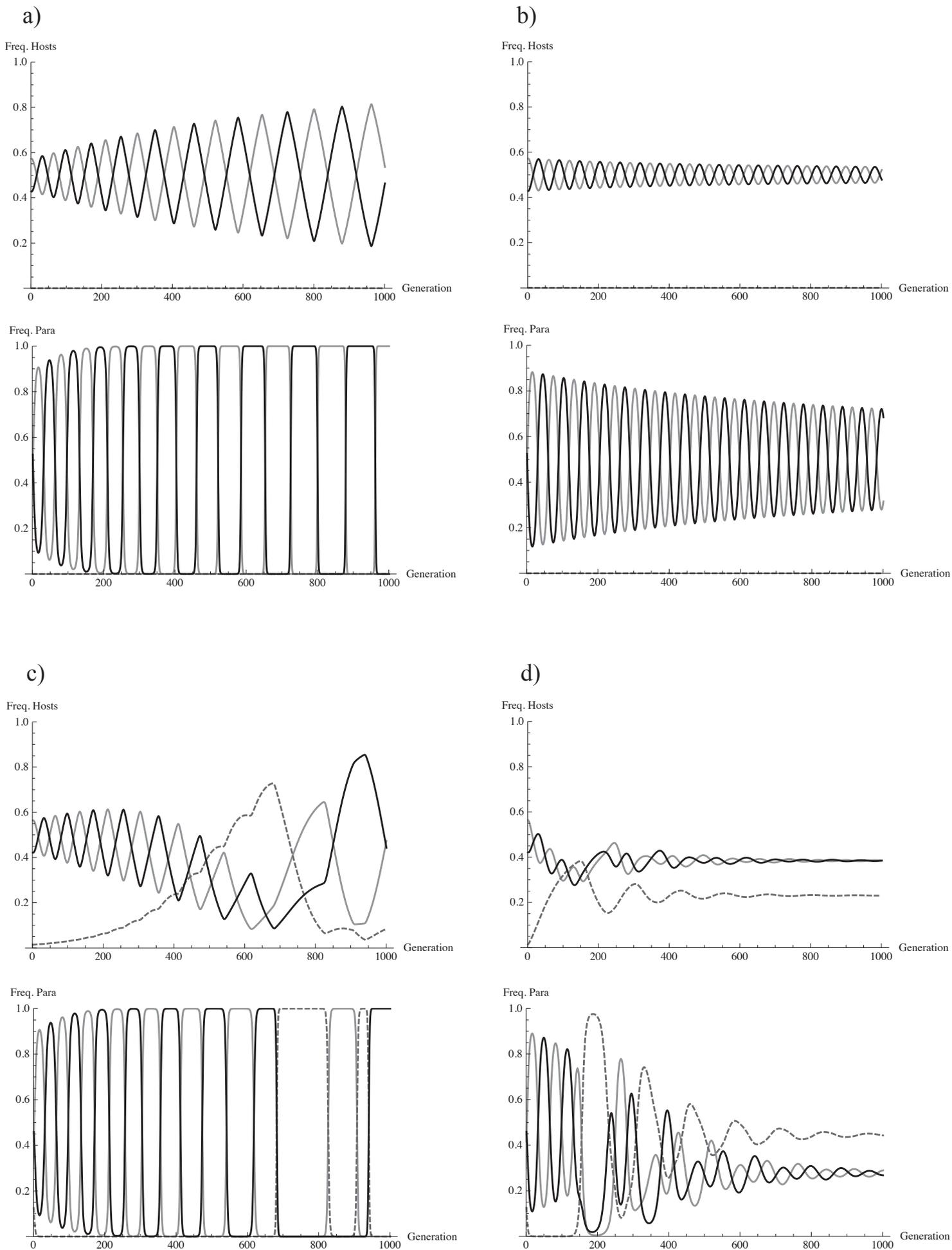


Figure 4

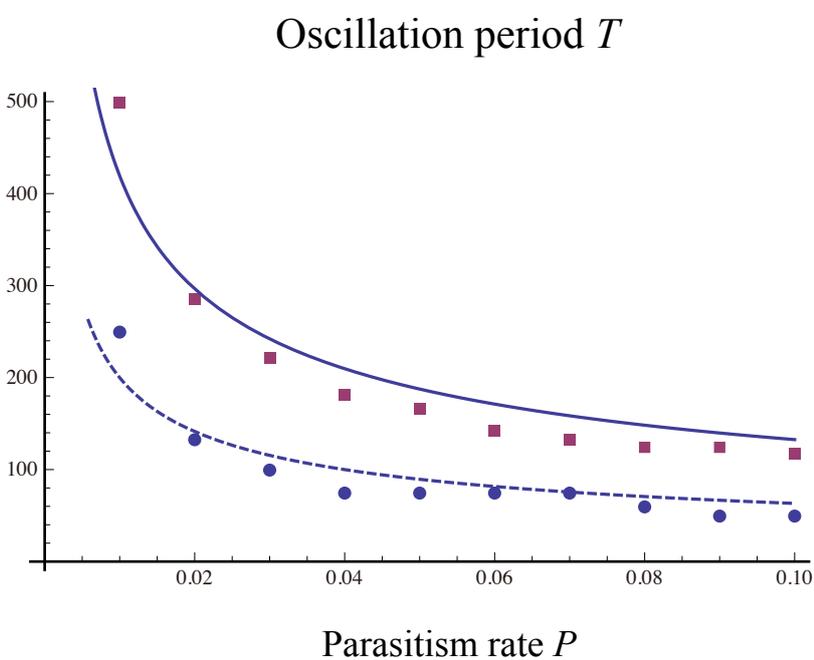


Figure 5

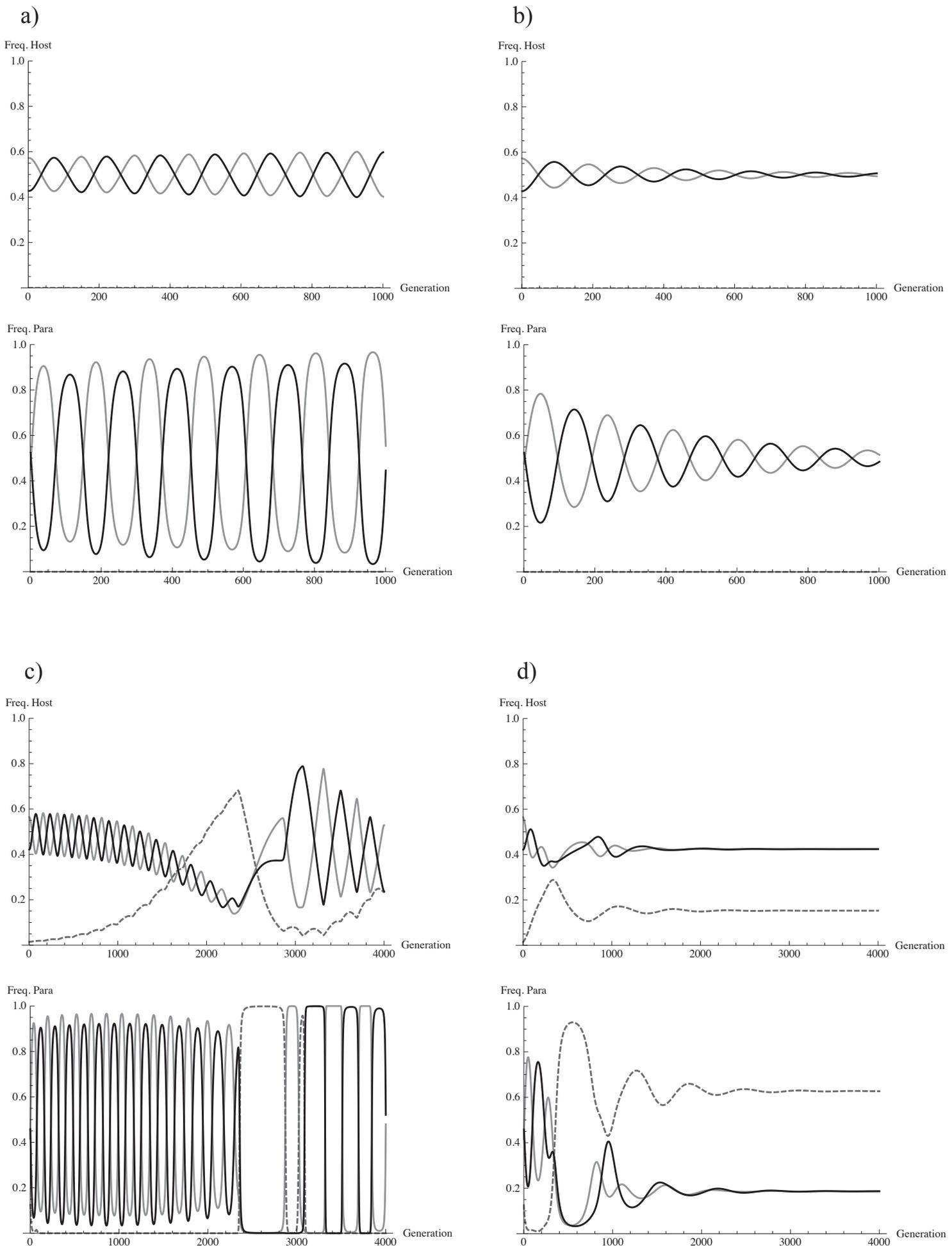


Figure 6