How can distinct egg polymorphism be maintained in the rufescent prinia (Prinia rufescens)–plaintive cuckoo (Cacomantis merulinus) interaction—a modeling approach

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Abstract
In avian brood parasitism, both the host and the parasite are expected to develop various conflicting adaptations; hosts develop a defense against parasitism, such as an ability to recognize and reject parasitic eggs that look unlike their own, while parasites evolve egg mimicry to counter this host defense. Hosts may further evolve to generate various egg phenotypes that are not mimicked by parasites. Difference in egg phenotype critically affects the successful reproduction of hosts and parasites. Recent studies have shown that clear polymorphism in egg phenotype is observed in several host–parasite interactions, which suggests that egg polymorphism may be a more universal phenomenon than previously thought. We examined the mechanism for maintaining egg polymorphism in the rufescent prinia (Prinia rufescens) that is parasitized by the plaintive cuckoo (Cacomantis merulinus) from a theoretical viewpoint based on a mathematical model. The prinia has four distinct egg phenotypes: immaculate white, immaculate blue, white with spots, and blue with spots. Only two egg phenotypes, white with spots and blue with spots, are found in the cuckoo population. We show that the observed prinia and cuckoo phenotypes cannot be at an equilibrium and that egg polymorphism can be maintained either at stationary equilibrium or with dynamic, frequency oscillations, depending on the mutation rates of the background color and spottness. Long-term monitoring of the prinia–cuckoo interaction over a wide geographic range is needed to test the results of the model analyses.

KEYWORDS
avian brood parasitism, coevolution, egg phenotype, frequency-dependent selection, population genetics model

1 INTRODUCTION

Avian brood parasites exploit parental care of their hosts at the expense of the host’s reproductive success (Davies, 2000; Rothstein, 1990). This parasitic pressure is expected to select for host defenses to reduce the reproductive losses caused by parasitism. Host defenses, in turn, will select for counterdefenses by the parasite that defeats the host defense. Indeed, it has been established that many hosts affected by avian brood parasites have evolved a fine-tuned ability to recognize and reject parasitic eggs that look unlike their own (Davies & Brooke, 1988; Moksnes et al., 1991; Rothstein, 1975; Soler, 2014). The common cuckoo (Cuculus canorus), one of the best-studied brood parasites, has evolved sophisticated egg mimicry that prevents host recognition and egg rejection (Brooke & Davies, 1988; Davies, 2011; Honza, Moksnes, Røskaft, & Stokke, 2001; Moksnes & Røskaft, 1995).
In response to egg mimicry by the cuckoo, a host species may develop reduced intraclutch and increased interclutch variations in egg phenotype, which would require the cuckoo to mimic a particular egg phenotype in order to successfully parasitize the nest (Øien, Moksnes, & Røskaft, 1995; Stokke, Moksnes, & Røskaft, 2002; Stokke, Takasu, Moksnes, & Røskaft, 2007). Such a coevolutionary arms race might lead to polymorphism in egg phenotype (Tanaka, 2016; Yang, Li, Liang, & Møller, 2016; Yang et al., 2010).

Yang et al. (2010) demonstrated that the ashy-throated parrotbill (Paradoxornis alphonisianus), a host of the common cuckoo in South China, shows clear polymorphism in egg color with three distinct phenotypes (white, pale blue and blue eggs) that also occur in the cuckoo. The vinous-throated parrotbill (P. webbianus) in Korea also shows clear dimorphism with white or blue eggs (Kim, Yamagishi, & Won, 1995). Both parrotbill species are consistently able to recognize and reject a cuckoo egg that looks unlike their own in the clutch (Lee, Kim, & Yoo, 2005; Lee & Yoo, 2004; Yang et al., 2010) and it has been suggested that the egg color polymorphism observed in the parrotbill and the cuckoo has evolved as a result of antagonistic coevolution (Lee & Jabłoński, 2012; Yang et al., 2010).

Liang et al. (2012) studied how polymorphism with three phenotypes can be maintained in the parrotbill–cuckoo interaction using a mathematical modeling approach. They constructed a population genetics model and analyzed how the frequencies of the three egg types change with time. The model analysis suggested that polymorphism is likely maintained dynamically; the frequency of each type oscillates within a certain period and is primarily dependent on the parasitism rate.

Yang, Huang, et al. (2016) demonstrated that the plaintive cuckoo (Cacomantis merulinus) and the common tailorbird (Orthotomus sutorius) have evolved dimorphic white and blue egg phenotypes with brownish spots. The matching egg appearance between plaintive cuckoos and common tailorbirds was presumably a result of negative frequency-dependent selection, the same as in the parrotbill–cuckoo interaction (Liang et al., 2012).

Recently, it has been shown that the rufescent prinia (Prinia rufescens), another host of the plaintive cuckoo breeding sympatrically within the same area, has four distinct egg phenotypes: immaculate white and blue eggs without spots, and white and blue eggs with brownish spots. Only one type of eggs is found in a clutch (Yang, C., Wang, L., Zhou, B., Liang, W., Møller, AP, unpubl. data). However, the plaintive cuckoo has only two distinct egg types, either white or blue with brownish spots, that seemingly mimic host eggs (Yang, Huang, et al., 2016). Figure 1 shows these egg types observed in the rufescent prinia and the plaintive cuckoo. Although no quantitative analysis of egg color and spots has yet been done for the rufescent prinia (but see Yang, Huang, et al., 2016 for the plaintive cuckoo and the common tailorbird), distinct polymorphism is obvious.

A question then arises as to how these distinct egg phenotypes can be maintained in the rufescent prinia and the plaintive cuckoo populations. Although the interaction between the rufescent prinia and the plaintive cuckoo is seemingly similar to that of the parrotbill and the common cuckoo, the former could be different from the latter in the expression of egg phenotype; the color (white/blue) and the presence/absence of spots may be controlled by independent genes. Therefore, egg phenotype can be considered a two-dimensional trait color (white/blue) and spottiness (immaculate/spots), while egg phenotype in the latter case is one-dimensional with color (white/pale blue/blue) as the only trait involved.

In this study, we aim to explore how egg polymorphism can be maintained in the interaction between the rufescent prinia and the
TABLE 1  Acceptance probabilities, A(i, j), for all combinations of egg type (i, j = 1, 2, 3, 4). Columns represent host phenotype i and rows parasite phenotype j. In general, 1 ≥ A0 ≥ A1 ≥ A2 ≥ A3 ≥ 0.

| j = 1 | i = 1 | A0 | A1 | A2 | A3 |
|-------|-------|----|----|----|----|
| j = 2 |      | A1 | A0 | A3 | A2 |
| j = 3 |      | A2 | A3 | A0 | A1 |
| j = 4 |      | A3 | A2 | A1 | A0 |

plaintive cuckoo from a theoretical viewpoint. We construct a population genetics model using the same approach as Liang et al. (2012), but with a new assumption considered for mutations of egg phenotypes. Based on the model analysis, we suggest that (1) the observed state of four egg phenotypes in the rufescent prinia and two in the plaintive cuckoo cannot be at equilibrium, and (2) the two egg types we have not yet observed in the plaintive cuckoo (immaculate white and blue) will spread if they appear due to a mutation. We also discuss the apparent absence of the two phenotypes in the plaintive cuckoo population.

2 | THE MODEL

We assume that there are four distinct egg phenotypes in both the host and the parasite population. Although only two phenotypes (white with spots and blue with spots) have been observed in the plaintive cuckoo in South China (Yang, Huang, et al., 2016), this allows the model to deal with general situations that may occur in a future evolutionary time scale. Detailed genetic mechanisms underlying the inheritance of egg phenotype largely remain unknown. However, it is likely that egg phenotype is maternally inherited by female offspring with no parental influence on phenotype (Fossay et al., 2016; Gibbs et al., 2000; Gosler, Barnett, & Reynolds, 2000). We therefore assume that egg phenotype is maternally inherited in the model. We denote each of the four phenotypes as 1 (immaculate white), 2 (immaculate blue), 3 (white with spots), and 4 (blue with spots). Let h_i and p_i be the frequency of phenotype i in the host and the parasite population, respectively (i = 1, 2, 3, 4).

We assume that a proportion P of host nests are parasitized (0 < P < 1) and that nests are parasitized randomly, independent of phenotype (Antonov et al., 2012; Yang, Takasu, Liang, & Møller, 2015; Liang, Yang, & Takasu, 2016; Yang, Wang, Liang, & Møller, 2016; Yang, Huang, et al., 2016; but see Cherry, Bennett, & Moskát, 2007; Honza, Sulc, Jelínek, Pozgayová, & Procházka, 2014). Multiple parasitism is ignored as we implicitly assume a low parasitism rate P (but see Moskát & Honza, 2002; Takasu & Moskát, 2011). Removal of a host egg by a parasite is also ignored in order to simplify the model.

We assume that all hosts have the same ability to recognize and reject unlike eggs. Let A(i, j) represent the probability that a host with egg type i accepts a parasitic egg type j laid in the nest. It has been demonstrated that the greater the difference in egg phenotype, the lower the probability of parasite egg acceptance (Higuchi, 1998; Stokke et al., 2007; Takasu, 2003; Yang et al., 2010). We then assume that a host will accept parasite eggs according to the following rules: A(i, j) = A0 when there is no difference in egg phenotype, A1 when only color differs, A2 when only spottiness differs, and A3 when both color and spottiness differ (1 ≥ A0 ≥ A1 ≥ A2 ≥ A3 ≥ 0).

Table 1 summarizes the acceptance probabilities A(i, j) for i, j = 1, 2, 3, 4.

We also assume that each phenotype can mutate. Specifically, we assume that both the color and the spottiness mutate reciprocally; white or blue eggs change to blue or white eggs, respectively, with the probability m_c, and immaculate or spotted eggs change to spotted or immaculate eggs, respectively, with the probability m_s. No empirical data are available to estimate these mutation probabilities; however, the values would be very small and likely in the order of 10^{-4} (Bürger, Willensdorfer, & Nowak, 2006). In avian brood parasitism, both the host and the parasite have similar generation times. Thus, we assume that both the host and the parasite share the same mutation probabilities.

Using h = (h_1, h_2, h_3, h_4)^T and p = (p_1, p_2, p_3, p_4)^T as column vectors, the phenotype frequencies at the next generation h’ and p’ are given as follows:

\[
\begin{align*}
    h' &= \frac{1}{\overline{w}_h} MW_h h \\
    p' &= \frac{1}{\overline{w}_p} MW_p p
\end{align*}
\]

Here, \overline{w}_h and \overline{w}_p refer to the average fitness, \(W_h\) and \(W_p\) refer to the respective selection matrices, and \(M\) is the mutation matrix. See Appendix for the derivation.

In this model, we assume an infinitely large population, random mating, and nonoverlapping generations.

The coupled dynamics, equations (1) and (2), describe temporal changes in the frequencies h_i and p_i (i = 1, 2, 3, 4). In the next section, we analyze the frequency dynamics with a special focus on the stability of equilibria where (1) all four egg types coexist in both the host and the parasite populations, and (2) immaculate eggs are absent in the parasite population as found by Yang, Huang, et al., (2016).

3 | RESULTS

3.1 | Local stability of equilibrium

At equilibrium of equations (1) and (2) with nonzero mutations (m_c, m_s > 0), frequencies of all types have to be equal (see Appendix). By symmetry of the model, there exists a unique internal equilibrium, h* and p*, where all the four types coexist with equal frequency.

\[
h^* = \begin{pmatrix} 1 & 1 & 1 & 1 \\ 4 & 4 & 4 & 4 \end{pmatrix} \quad \text{and} \quad p^* = \begin{pmatrix} 1 & 1 & 1 & 1 \\ 4 & 4 & 4 & 4 \end{pmatrix}
\]
Local stability of an equilibrium can be checked by the magnitude of eigenvalues of the linearized dynamics around the equilibrium (Murray, 2007). A threshold exists for the mutation probability in color and spottiness, respectively, and the equilibrium (3) is locally stable when both the mutation probabilities are larger than the thresholds. Otherwise, the equilibrium is unstable and phenotype frequencies continue to oscillate with a period dependent on the acceptance probabilities $A_0$, $A_s$, $A_c$, and $A_{sc}$, the parasitism rate $P$, and the mutation probabilities $m_s$ and $m_c$. When unstable, the oscillation period $T$ is proportional to the inverse of the square root of the parasitism rate $P$ (Appendix).

Figure 2 shows typical frequency dynamics when all four types are present in both the host and the parasite populations. As the mutation probabilities are increased from zero beyond the threshold, the equilibrium (3) can be stabilized. For sufficiently small mutation probabilities, the dynamics apparently converge to a heteroclinic cycle (Seger, 1988) in which one phenotype dominates for a longer time but eventually is taken over by another phenotype (Figure 2a). When the mutation probabilities are increased but stay below the thresholds, the dynamics show a sustained but complex oscillation with various frequency modes (Figure 2b). Note that when oscillation occurs, the amplitude is larger in the parasite population than in the host population. This is because all parasite eggs are subjected to the host decision to either reject or to accept, while only a proportion $P$ of host nests are under parasitic pressure. When both the mutation probabilities are larger than the thresholds, the dynamics converge to the equilibrium (3) where all four phenotypes coexist stably with equal frequency (Figure 2c).

3.2 Do the observed frequencies of egg phenotypes reflect a stable equilibrium?

The rufescent prinia has four egg types but only two types have been found in the plaintive cuckoo (Figure 1): immaculate white and blue eggs have not been observed in the cuckoo population (Yang, Huang, et al., 2016). For this state to be in equilibrium, the probability of a spottiness mutation has to be zero ($m_s=0$) because, otherwise, parasites with immaculate eggs exist because of mutation.

By symmetry of the model, there exists a semi-internal equilibrium where immaculate eggs are absent in the parasite population.

$$h^* = \left( \frac{1}{4} \frac{1}{4} \frac{1}{4} \frac{1}{4} \right) \quad \text{and} \quad p^* = \left( 0.25, \frac{1}{2}, \frac{1}{2} \right) \quad (4)$$

However, this equilibrium (4) exists only for a special case where the presence or absence of spots does not affect acceptance probabilities at all ($A_0 = A_s = A_c$). This special case, however, seems not to be applied to the rufescent prinia because the prinia can recognize and reject unlike eggs based on the presence or absence of spots (Yang, C., Wang, L., Zhou, B., Liang, W., Møller, AP, unpubl. data) ($A_0 > A_s$, $A_c > A_{sc}$), and thus, this state (4) cannot be an equilibrium of the dynamics (1) and (2) even when $m_s = 0$.

Figure 3 shows typical frequency dynamics when no mutation occurs in spottiness ($m_s = 0$), immaculate eggs are completely absent in the parasite population ($p_s = p_c = 0$), and the host can discriminate against the presence or absence of spottiness ($A_0 > A_s$, $A_c > A_{sc}$). In the presence of the parasite eggs with spots, the frequency of host...
eggs with spots decreases to zero and eventually the host has only immaculate eggs (both $h_3$ and $h_4$ converge to zero). When the mutation in color $m_c$ is small enough, the dynamics converge to an oscillation where hosts with immaculate eggs and parasites with spotted eggs oscillate around an equal frequency of 0.5 (Figure 3a). When the mutation in color is larger than a threshold, the dynamics converge to an equilibrium where the host and parasite each have immaculate white and blue eggs with an equal frequency of 0.5 (Figure 3b). Eventual extinction of hosts with spotted eggs in such a situation occurs irrespective of the mutation probability in color $m_c$. This is because hosts with immaculate white or blue eggs always have an advantage over hosts with white or blue eggs with spots. Therefore, the observed state of four egg types in the prinia and two egg types in the cuckoo cannot be maintained at equilibrium even if no spottness mutations occur.

### 3.3 | Can immaculate white and blue eggs spread in the parasite population?

Considering that the rufescent prinia has four egg types and is capable of recognizing and rejecting unlike eggs in terms of both color and spottness, cuckoo females producing immaculate white or blue eggs are expected to increase in frequency because they can successfully utilize the prinia nests. Figure 4 shows the increase in frequency of parasites with immaculate white and blue eggs in the presence of the spottness mutation, starting from an initial state where immaculate white and blue eggs are absent in the parasite population. Immaculate parasite eggs are produced by mutation and they steadily increase in frequency and eventually oscillate around the equilibrium (3) or converge to it depending on the size of the mutation probabilities (see Figure 2). Therefore, if spottness mutation can occur in the plaintive cuckoo, cuckoos with immaculate white or blue eggs will increase in frequency.

### 4 | DISCUSSION

Clear polymorphism in egg phenotype observed in the rufescent prinia and the plaintive cuckoo prompts us to question how these polymorphisms are maintained. We built a population genetic model for the four egg types with a two-dimensional trait including color (white or blue) and spottness (immaculate or spots) in order to answer this question. The model analysis shows the possibility that the frequency dynamics exhibit oscillation around the equilibrium where all the types are present with equal frequency and that mutation can stabilize the equilibrium. Although Liang et al. (2012) did not consider egg phenotype mutation, we reached similar conclusions to those of their study, except that we also found that mutation can stabilize the frequency dynamics.

Immaculate white and blue eggs were not found in the observed plaintive cuckoos (Yang, Huang, et al., 2016) and these phenotypes cannot be maintained at equilibrium in the presence of the four egg types of the rufescent prinia (Figure 3). However, no quantitative data are yet available to suggest any trend in the frequency change of the four egg types in the rufescent prinia population. Monitoring the prinia–cuckoo interaction over a long time scale would be worthwhile research to test such a possibility.

Apparent absence of immaculate white and blue eggs in the plaintive cuckoo population may be explained by very low frequencies that prevented detection in field samples given our small sample size (Yang, Huang, et al., 2016). The model analysis has shown that the oscillation period is roughly proportional to the inverse of the square root of the parasitism rate $P$. If $P$ is low, as in the case of the common cuckoo parasitism on parrotbills (4.3%, $n = 555$; Yang et al., 2010), the period could be several hundred generations (about 100 generations in Figure 2 where $p = 0.05$). We suggest that immaculate eggs might eventually appear and increase in frequency in plaintive cuckoo populations. Again, long-term monitoring is
Discerning the genetic basis of egg phenotype expression is vital in ultimately understanding how egg phenotype polymorphism is maintained. In the common cuckoo (Cuculus canorus), egg blueness is inherited asexually in female offspring from the mother (Fossey et al., 2016). To date, no genetic study has been done on the rufescent prinia and the plaintive cuckoo. Furthermore, no estimate is available for the color change (white or blue) or spottiness (absence or presence) mutation probabilities. In this paper, we have simply used an estimate of per-locus mutation rates on an order ranging from $10^{-4}$ to $10^{-5}$ (Bürger et al., 2006). Avian brood parasitism can be an ideal system because both the host and the parasite have life spans of similar length and hence evolutionary changes in egg phenotype may pace in parallel (Liang et al., 2012).

Two Prinia species exist that are closely related to the rufescent prinia in South China: the plain prinia (P. inornata) and the gray-breasted prinia (P. hodgsonii). The plain prinia lays white or blue eggs with reddish spots (Wang et al., 2016), seemingly a subset of the four egg types observed in the rufescent prinia. Egg phenotype of the gray-breasted prinia is unknown. Further comparative study to describe egg phenotype of these two and other closely related species would shed light on the genetic system of egg phenotype expression.

The plaintive cuckoo parasitizes the common tailorbird, a species that shows clear dimorphism with white and blue eggs with reddish spots (Yang, Huang et al. 2016). It could be that an apparent absence of the two egg types in the plaintive cuckoo may have resulted from a parasitic adaptation specialized for the common tailorbird. However, it remains unknown whether unique races of the plaintive cuckoo population exist, each of which is specialized on a particular host species. Empirical and theoretical studies that focus on such races are needed.

In the presence of egg polymorphism, the manner of parasitism can be a crucial determinant in the successful reproduction of the parasite. In order to ensure egg acceptance, cuckoo females should parasitize only host nests where egg phenotype matches. Although this “phenotype matching” parasitic behavior is intuitively appealing, previous empirical studies have shown conflicting results (Antonov et al., 2012; Cherry et al., 2007; Honza et al., 2014; Liang et al., 2016; Yang et al., 2015; Yang, Huang et al., 2016; Yang, Wang, Liang, Møller, 2016). In this model, we have assumed that parasites choose host nests randomly, irrespective of egg phenotype. However, nonrandom parasitism based on phenotype matching could critically affect frequency dynamics. Further study that explicitly considers nonrandom parasitism is needed.

Distinct polymorphism in egg phenotype may be a more universal phenomenon than previously expected in avian brood parasitism (Kim et al., 1995; Lee & Jabłoński, 2012; Lee & Yoo, 2004; Lee et al., 2005; Yang, Li, Liang, Møller 2016; Yang, Huang et al. 2016; Yang et al., 2010). Further study is needed, focusing on genetics and long-term monitoring, in order to fully understand how polymorphism has evolved and is maintained in avian brood parasitism.

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APPENDIX

DERIVATION OF THE MODEL

Hosts with egg type i can reproduce successfully if they are not parasitized with probability 1−P, or if they are parasitized, for example, by a parasite j with probability P pj, but successfully reject the parasitism with probability 1−Al(i, j). Thus, fitness of the host type i, wH, is given as

\[ w_H = (1 - P) + P \sum_{j=1}^{4} p_j \{1 - A(l, j)\} \]

where the second term of the right-hand side is summed over all possible parasite types.

Parasites with egg type j can reproduce only if the host accepts their eggs. Thus, fitness of the parasite type j, wP, is given as

\[ w_P = P \sum_{i=1}^{4} h_i A(l, j) \]

the sum of possible target host types.

The average fitness of the host and the parasite is then given as

\[ \bar{w}_H = \sum_{i=1}^{4} h_i w_H \quad \text{and} \quad \bar{w}_P = \sum_{j=1}^{4} p_j w_P, \]

respectively.

Frequencies after host recognition against unlike eggs, h* and p*, are given as follows:

\[ h^* = \frac{1}{\bar{w}_H} \bar{w}_H h \quad \text{and} \quad p^* = \frac{1}{\bar{w}_P} \bar{w}_P p \]

in matrix and vector notation where \( \bar{W}_H \) and \( \bar{W}_P \) are the selection matrices of the host and the parasite, respectively, which are given as follows:

\[
\bar{W}_H = \begin{pmatrix}
w_{H1} & 0 & 0 & 0 \\
0 & w_{H2} & 0 & 0 \\
0 & 0 & w_{H3} & 0 \\
0 & 0 & 0 & w_{H4}
\end{pmatrix}
\quad \text{and} \quad
\bar{W}_P = \begin{pmatrix}
w_{P1} & 0 & 0 & 0 \\
0 & w_{P2} & 0 & 0 \\
0 & 0 & w_{P3} & 0 \\
0 & 0 & 0 & w_{P4}
\end{pmatrix}
\]

Mutations of the color (white or blue) and the spottiness (absence or presence) can be represented by a transition matrix \( M \) whose (i, j) element denotes the probability that a type j mutates to type i (i, j = 1, 2, 3, 4).

\[
M = \begin{pmatrix}
1 - m_s - m_c & m_c & m_s & 0 \\
m_s & 1 - m_s - m_c & 0 & m_c \\
m_c & 0 & 1 - m_s - m_c & m_s \\
0 & m_s & m_c & 1 - m_s - m_c
\end{pmatrix}
\]

where double mutations in both color and spottiness are assumed to be negligible.

Frequencies after mutation are then given as \( M h^* \) and \( M p^* \) using the mutation matrix for the host and the parasite, respectively. This results in equations (1) and (2).

POSSIBLE EQUILIBRIA

Without mutations (\( m_s = m_c = 0 \)), equilibria \( h^* \) and \( p^* \) can be derived by solving the following equations:

\[ h^* = \frac{1}{\bar{w}_H} \bar{W}_H h^* \quad \text{and} \quad p^* = \frac{1}{\bar{w}_P} \bar{W}_P p^*. \]

For \( h^* \) and \( p^* \) to be in equilibrium of (1) and (2) when mutations occur (\( m_s, m_c > 0 \)), the following equations have to be satisfied:

\[ h^* = M h^* \quad \text{and} \quad p^* = M p^* \]

Solving these equations results in \( h^* \) and \( p^* \) having equal frequency for all four types.

LOCAL STABILITY ANALYSIS

Linearizing the dynamics (1) and (2) around the equilibrium (3) results in a community matrix that has two zero and six complex eigenvalues.

\[ \lambda_1 = \lambda_2 = 0 \]

\[ \lambda_{3,4} = (1 - 2m_s) \left\{1 + i(\Delta_0 - \Delta_1 + \Delta_2 + \Delta_3)\beta\right\} \]

\[ \lambda_{5,6} = (1 - 2m_c) \left\{1 + i(\Delta_0 + \Delta_1 - \Delta_2 - \Delta_3)\beta\right\} \]

\[ \lambda_{7,8} = (1 - 2m_s - 2m_c) \left\{1 + i(\Delta_0 - \Delta_1 - \Delta_2 + \Delta_3)\beta\right\} \]

where

\[ \beta = \sqrt{\frac{p}{\left[\Delta_0 + \Delta_1 + \Delta_2 + \Delta_3\right] - 4p(\Delta_0 + \Delta_1 + \Delta_2 + \Delta_3)}} \]

is a positive real value. The absolute value of the six complex eigenvalues can be less than unity when mutation probabilities \( m_s \) and \( m_c \) are larger than thresholds \( m_s^* \) and \( m_c^* \), respectively. These threshold values can be obtained as maximum solutions of \( |\beta_{3,4}| = 1, |\beta_{5,6}| = 1, \) and \( |\beta_{7,8}| = 1 \). When \( m_s \) and \( m_c \) are less than thresholds \( m_s^* \) and \( m_c^* \), respectively, all of the six complex eigenvalues are less than unity in absolute value and the equilibrium (3) is locally stable. Otherwise, it is unstable. The imaginary part \( \omega \) of these complex eigenvalues determines the oscillation period \( T \) when perturbed around the equilibrium as \( T = \frac{2\pi}{\omega} \).