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

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Abstract

Avian brood parasites impose strong selection on their hosts leading to evolution of anti-parasite defenses like egg recognition and rejection. Discordance and template-based cognitive mechanisms may form the base for egg recognition by hosts. For discordance, hosts recognize eggs that constitute the minority in a clutch as alien, while in template-based recognition hosts recognize eggs as alien when they do not match a template that can be innate or learnt. Template-based recognition by learning can be compromised in host species with polymorphic egg color like Paradoxornis parrotbills, hosts of the common cuckoo Cuculus canorus, because a male that learns an egg color in his first breeding attempt can subsequently mate with females having different colors and therefore reject own eggs. We present a simple conceptual model to understand how asymmetry in sex roles to care for eggs and egg polymorphism influence the evolution of egg recognition by hosts. We derive host reproductive success in the presence of variation in egg phenotype for both host and parasite. Our model shows that male recognition by learning is disadvantageous unless the host has monomorphic eggs. We suggest that inter-clutch variation in egg phenotype is key to understanding the evolution of egg recognition and the sex involved.

Keywords: avian brood parasitism; discordance; egg polymorphism; egg recognition; learning and imprinting; template-based
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
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their first clutch and reject eggs that do not match the learnt template in subsequent breeding attempts (Rothstein 1978, Victoria 1972, Lotem et al. 1995). Recognition by learning is effective if the template is formed correctly in the sense that the host has imprinted on its own eggs. Although some studies have shown that there is no age-specific difference in recognition ability, suggesting that no learning is involved in egg recognition in some host species (Amundsen et al. 2002, Marchetti 2000, Stokke et al. 2004), learning can be an important component of host defenses against parasitism in other hosts (Rothstein 1974, Moskát et al. 2010, Strausberger and Rothstein 2009, Shizuka and Lyon 2010).

Recognition by learning logically works for females that produce eggs and hence should be able to correctly imprint on their own eggs immediately after laying. However, it does not necessarily work for males that often have fewer opportunities to observe eggs in their nest. Asymmetry in sex roles in producing and caring for eggs is thus likely to influence the evolution of recognition by learning by restricting or even precluding the male's learning ability, while recognition by discordance is not affected by such an asymmetry.

It generally remains unclear which sex is responsible for egg recognition and rejection of parasitic eggs (Davies and Brooke 1988, Sealy and Neudorf 1995, Lee et al. 2005, Honza et al. 2007, Požgayová et al. 2009). However, in one study it has been demonstrated that in host species where only females incubate, only females recognize and reject unlike eggs while both sexes reject in species where both sexes incubate (Soler et al. 2002). This finding is consistent with the idea that recognition by learning
both by females and males works as an effective defense mechanism against parasitism.

Recognition by learning for males, however, can be compromised if there is polymorphism in egg phenotype.

Paradoxornis parrotbills, hosts of the common cuckoo Cuculus canorus, and several other host species show clear polymorphism in egg color. For instance, in the vinous-throated parrotbill P. webbianus in South Korea each female produces either blue or white eggs (Lee et al. 2005, Kim et al. 1995, Lee and Yoo 2004). It is also known that both sexes take part in incubation in this species (Lee et al. 2005, Jiang et al. 2009). The ashy-throated parrotbill P. alphonsianus in southern China shows three distinct phenotypes, producing either white, blue or pale blue eggs (Yang et al. 2010). These birds also have excellent abilities to reject foreign eggs that look dissimilar to host eggs (Lee et al. 2005, Kim et al. 1995, Lee and Yoo 2004, Yang et al. 2010).

Although the detailed mechanism behind egg recognition in these parrotbill species remains unknown, females may learn and imprint on the eggs they first observe and use the learnt memory as a template for recognizing parasitism since each female produces clutches of a constant egg phenotype throughout her life (Kim et al. 1995). However, in such a polymorphic population, a male may mate with females producing different egg color during his life. If a male learns that "white eggs are mine" in his first breeding, he forms an inflexible image of white eggs such that subsequent matings with females laying blue eggs will fail. Therefore, if recognition is based on a template that is learnt by an imprinting-like process, parrotbill males should not learn their first clutch (Lee et al. 2005). However, the situation is further complicated since the ashy-throated
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parrotbill in southern China is parasitized by common cuckoos that also show egg polymorphism with white, blue and pale blue eggs, each being highly mimetic to the corresponding parrotbill egg color (Yang et al. 2010). It remains an open question how egg polymorphism affects egg recognition by the host.

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

2. Methods (The model)

We assume that each host and parasite female produces a constant type of egg phenotype throughout her life (Kim et al. 1995, Collias 1993, Gosler et al. 2000, Moksnes et al. 2008). Let us assume two types of egg phenotype, 1 (white) and 2 (blue), for the sake of heuristically deriving the model. The number of egg types can be later generalized arbitrarily as in the parrotbill and cuckoo interaction where three distinct types are observed (Yang et al. 2010). We denote the frequency of host females of type 1 and 2 as $f_{H1}$ and $f_{H2}$, respectively ($f_{H1} + f_{H2} = 1$) and that of parasite females as $f_{P1}$ and...
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\[ f_{P2}, \text{ respectively } (f_{P1} + f_{P2} = 1). \]

We assume two mechanisms of recognition; 1) recognition by discordance by which both host males and females recognize eggs as parasitic when the phenotype is minority in the clutch; and 2) recognition by learning by which a template is learnt by an imprinting-like process in the first breeding attempt. Host males learn the phenotype of eggs in their nest when females complete a clutch. The template is learnt only once, and males accept all eggs in their nest in the first breeding attempt. Host females learn the phenotype of their eggs after laying. In later breeding attempts hosts recognize and reject eggs as parasitic that do not match their learnt template. For both mechanisms, we assume that hosts can always correctly reject eggs that are recognized as alien without damaging other eggs in the clutch. Host males and females survive to the next breeding season with a constant annual survival rate \( s \) \((0 < s < 1)\), and they randomly form a new pair every breeding season. Males and females are not influenced by each other when rejecting an egg. No extra-pair paternity is assumed.

Let \( p \) be the probability that a host nest is parasitized either by a type 1 or 2 parasite egg. We assume that parasitism rate \( p \) is sufficiently low \((p << 1)\) so that multiple parasitism can be ignored as observed in many cuckoo-host interactions (Davies and Brooke 1989b, Brooke and Davies 1987, Davies et al. 1996, Brooke et al. 1998) (see Moskát and Honza (2002), Takasu and Moskát (2011) for high parasitism rate that remained constant among years). Predation risk is assumed to be the same for all nests irrespective of egg type. In the absence of parasitism, the host obtains reproductive success \( b \) if all own eggs fledge successfully.
Case 1: Recognition by discordance

Recognition by discordance makes the host always able to recognize and reject parasitism when there is at most one parasite egg in the clutch with a phenotype that differs from that of own eggs. Thus the average reproductive success of the host in a breeding attempt, when the host adopts discordance, is calculated as

\[ R = b \left\{ f_{H1}(1 - p) + f_{H2}(1 - p) + f_{H1}pf_{P2} + f_{H2}pf_{P1} \right\} \]

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

Asymmetry in the sex role to care for eggs does not matter for reproductive success. Lifetime reproductive success of the host \( R_{\text{discordance}} \) is then given as follows by multiplying survival probability summed over breeding attempts

\[ R_{\text{discordance}} = R + sR + s^2R + s^3R + ... = \frac{R}{1 - s} \]

Case 2: Recognition by learning

Females can always correctly learn and imprint on the phenotype of own eggs immediately after laying. This learning by imprinting, however, can negatively affect
males in later breeding attempts because 1) males may mate with females having
different egg types and reject own eggs, and 2) males may by chance learn and imprint
on the phenotype of parasitic eggs.

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

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

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

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

which is identical to the reproductive success for recognition by discordance $R$ ($R_1 = R$).
In later breeding attempts ($t = 2, 3, ...$), males recognize eggs as alien when they do not match the learnt template, e.g., a male that mated with a female of type 1, but was parasitized by a cuckoo of type 2 in the first breeding attempt (the case $C(1, 2)$), has learnt both type 1 and 2 as his own with probability $q$, and this male can achieve reproductive success by mating with females of both type 1 and 2 in later breeding attempts unless the nest is parasitized by a parasitic egg with the same phenotype (cases $C(1, 0), C(1, 2), C(2, 0), C(2, 1)$).

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

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

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

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

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

$$R^2 = b \{ f_{H2}(1 - p) + f_{H2} p f_{P1} \}$$
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by summing over cases \( C(2, 0) \) and \( C(2, 1) \).

Then, the average reproductive success in the \( t \)-th breeding \((t = 2, 3, 4, \ldots)\), \( R_t \), is given by multiplying each conditional average with the probability that a male learns type 1 \((C(1, 0), C(1, 1))\), both type 1 and 2 \((C(1, 2), C(2, 1))\), type 2 \((C(2, 0), C(2, 2))\) in the first breeding attempt to yield

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

The average lifetime reproductive success \( R_{\text{learning}} \) is then given as follows using \( R_t \) \((t = 1, 2, 3, \ldots)\).

\[
R_{\text{learning}} = R_1 + s R_2 + s^2 R_3 + s^3 R_4 + \ldots
\]

If males do not learn and do not reject any egg as in female uni-parental host species (only female learns and rejects), the reproductive success of each breeding attempt depends only on female action. The average lifetime reproductive success \( R_{\text{female only learning}} \) is then given as follows using \( R_1 \), which is identical to \( R_{\text{discoverer}} \).

\[
R_{\text{female only learning}} = R_1 + s R_1 + s^2 R_1 + s^3 R_1 + \ldots = \frac{R_1}{1-s} = R_{\text{discordance}}
\]
3. Results

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

The difference in average lifetime reproductive success for recognition by female only learning (or recognition by discordance) and that by both male and female learning, $\Delta = R_{\text{female only learning}} - R_{\text{learning}}$, can be arranged as

$$
\Delta = \frac{bs}{1-s} \left\{ (1 - pf_{p1})(1 - pqf_{p1}) f_{H1}(1 - f_{H1}) + (1 - pf_{p2})(1 - pqf_{p2}) f_{H2}(1 - f_{H2}) \right\}
$$

$$
= \frac{bs}{1-s} f_{H1}(1 - f_{H1}) \left[ 2 - (1 + q)p + p^2 q \left( 1 - 2f_{p1}(1 - f_{p1}) \right) \right] \tag{1}
$$

It can easily be shown from eq (1) that $\Delta$ is always non-negative; recognition by males' learning the first clutch always results in a loss of host lifetime reproductive success ($\Delta \geq 0$; $R_{\text{discordance}} = R_{\text{female only learning}} \geq R_{\text{learning}}$). It can be further shown that (1) the loss $\Delta$ increases with increasing frequency of the rarer host phenotype, being proportional to $f_{H1}(1 - f_{H1})$, which reflects the probability that a male will breed with a female of a different type in subsequent breeding attempts and a measure of inter-clutch variation in host egg phenotype. $\Delta$ is zero only when the host is monomorphic in egg phenotype; (2) $\Delta$ is a decreasing function of the probabilities $p$ and $q$; (3) $\Delta$ decreases with increasing frequency of the rarer parasite phenotype $f_{p1}(1 - f_{p1})$, a measure of inter-clutch variation in parasite egg phenotype, but the dependency becomes disproportionately smaller as the probability $p$ becomes smaller; and (4) $\Delta$ increases as $s$ increases.
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Until now we assume two egg phenotypes in the host and the parasite population. The number of egg types can be arbitrarily generalized by elaborating Table 1, e.g., we first derive probabilities of a male learning a certain egg type in the first breeding attempt and then calculate reproductive success in later breeding attempts conditional on that the male has learnt each egg type (not shown here). With $N$ types of egg phenotype, $\Delta$ is given as,

$$\Delta = \frac{bs}{1-s} \sum_{i=1}^{N} (1-pqf_p)(1-pf_p)f_m(l-f_m)$$

(2)

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

4. Discussion

We have shown that recognition by discordance and recognition by female only learning result in an identical reproductive performance by the host ($R_{\text{discordance}} = R_{\text{female only learning}}$). This is because we have assumed that parasitism rate is sufficiently low that multiple parasitism can be ignored (a parasite egg is always a phenotypic outlier in the clutch unless it is perfectly mimetic to the host eggs), and that females can always learn the phenotype of their own eggs correctly after laying. However, if there is considerable
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intra-clutch variation in egg phenotype, which was ignored in our model, recognition by discordance will be disadvantageous because hosts may reject some of their own eggs even in the absence of parasitism. Recognition by female only learning, on the other hand, is not influenced by such intra-clutch variation.

We have also shown that males' learning the first clutch always results in a loss of host lifetime reproductive success in the presence of egg polymorphism ($\Delta = R_{\text{female only learning}} - R_{\text{learning}} > 0$); males should not learn which egg phenotype to reject based on his experience with his first clutch unless the host is monomorphic in egg phenotype. The loss $\Delta$ becomes smaller as parasitism rate $p$ increases, as the probability that the male is the first to observe parasite egg $q$ increases, and as inter-clutch variation in parasite egg phenotype increases. This counter intuitive result can be explained as follows. The larger the three parameters, the more likely the male is to wrongly learn non-mimetic cuckoo egg and own eggs in the clutch. This mis-imprinting by males, however, contributes to increase the probability of successful breeding with females producing different egg phenotypes in later breeding attempts; males, by mis-imprinting, become more tolerant to different egg phenotypes in the population.

We did not explicitly model recognition by an innate template where hosts know the phenotype of own eggs at hatching. Such an innate template would be unlikely to evolve in the presence of egg polymorphism because there would need to be a perfect genetic correlation between egg phenotype (which color of eggs a female produces) and the innate template (which color does a female or a male genetically recognize as her/his own color). Even in this case, however, average lifetime reproductive success of
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the host can be derived, which turns out to be equal to $R_{\text{discordance}}$ and $R_{\text{female only learning}}$ because the host can reproduce successfully only when the nest is parasitized by a parasite egg whose phenotype is different from that of host eggs.

Timing of learning egg phenotype is important. In our model, host females learn egg phenotype immediately after egg laying while host males learn after clutch completion; females are better placed than males to learn egg phenotype. However, if females delay learning until the clutch is completed as observed in some host species (Lotem et al. 1992, 1995), they can learn a non-mimetic parasitic egg phenotype as their own and accept parasitism in later breeding attempts. The delayed learning by females likely results in a reduced lifetime success both of $R_{\text{female only learning}}$ and $R_{\text{learning}}$ but the asymmetry in sex roles to care for eggs will remain important, i.e., $\Delta$ remains positive and males should not learn egg phenotype in the presence of egg polymorphism. Explicit modeling of the effect of the timing of learning is needed.

In our model, we focused on heterospecific brood parasitism where hosts and parasites belong to different species. In conspecific brood parasitism where host individuals can behave as parasites, lifetime reproductive success is composed of two factors, one from behaving as a host (rearing own eggs) and another as a parasite and our model cannot be applied to such a system (Lyon 2003). We also assumed that frequencies of each egg type remain constant in the population. However, these frequencies may change over time (Yang et al. 2010). Further studies including conspecific parasitism and frequency dynamics incorporated into the models are needed.
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It has been shown that both males and females of the vinous-throated parrotbill reject non-mimetic model eggs (Lee et al. 2005). However, in that study, a male's past breeding partner was unknown, and males that rejected unlike eggs could have learnt a different phenotype in their first breeding attempt. Parrotbill males incubate (Lee et al. 2005), and males could potentially learn their eggs as demonstrated for bi-parental host species (Soler et al. 2002). The probability that a male detects a parasitism event before the female does, $q$, would therefore be high and this reduces the reproductive loss by male recognition through learning. Experiments manipulating the first mate are necessary for clarifying how and when males learn the phenotype of their mate's eggs.

Birds are sensitive to ultraviolet range to which humans are blind (Bennett and Cuthill 1994, Cherry and Bennett 2001). To bird eyes, egg polymorphism may be common and such hidden polymorphism can crucially affect the way hosts recognize parasitism as our model has shown. It has been suggested that egg polymorphism most likely has evolved through co-evolutionary interactions between brood parasites and their hosts (Kilner 2006). Under parasitism, the host first evolves an ability to recognize and reject unlike eggs either by discordance or learnt template, and the parasite in turn evolves better egg mimicry. To counter parasite egg mimicry, the host may further evolve smaller intra-clutch and larger inter-clutch variation in egg phenotype (Stokke et al. 2002, 2007), and egg polymorphism may evolve both in the host and the parasite (Yang et al. 2010). Evolution of egg polymorphism, however, makes host recognition by learning their first clutch by males more disadvantageous as our model has shown, while recognition by discordance and by female only learning is unaffected. If the ability to learn to recognize foreign eggs is expressed in both sexes by genetic
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correlation, reproductive loss by male learning could be an inevitable side effect of learning to recognize parasitism in bi-parental host species. In this case, hosts might evolve to mate assortatively so that correct matching of learnt template to egg phenotype is guaranteed. Such a conflict does not occur in host species where only females incubate and males do not take part in care of eggs and in host species where hosts recognize foreign eggs by discordance. We suggest that the cognitive mechanism that hosts use to recognize parasitic egg can be a crucial component that determines subsequent coevolutionary interactions of the host and the parasite.

Little attention has been paid to sex roles in the way that hosts recognize brood parasitism in relation to variation in egg phenotype. We suggest that inter-clutch variation is a key to understanding the evolution of egg recognition and which sex is responsible for which action. Further field experiments and cognitive behavioral studies are clearly needed.
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### Tables and legends

#### Table 1

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<td>$C(1, 0), C(1, 2)$</td>
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<td>$\varphi 1 + (1)$</td>
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#### Table 1 legend

Six possible cases that a male can face and the reproductive consequences in later breeding attempts. In the second column, $\varphi 1$ and $\varphi 2$ refers to a host female of egg type 1 and 2, and, (1) and (2) refers to a cuckoo egg of type egg 1 and 2, respectively. See text for further explanations.