

# The evolution of postpairing male mate choice

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An increasing number of empirical studies in animals have demonstrated male mate choice. However, little is known about the evolution of postpairing male choice, specifically which occurs by differential allocation of male parental care in response to female signals. We use a population genetic model to examine whether such postpairing male mate choice can evolve when males face a trade-off between parental care and extra-pair copulations (EPCs). Specifically, we assume that males allocate more effort to providing parental care when mated to preferred (signaling) females, but they are then unable to allocate additional effort to seek EPCs. We find that both male preference and female signaling can evolve in this situation, under certain conditions. First, this evolution requires a relatively large difference in parental investment between males mated to preferred versus nonpreferred females. Second, whether male choice and female signaling alleles become fixed in a population versus cycle in their frequencies depends on the additional fecundity benefits from EPCs that are gained by choosy males. Third, less costly female signals enable both signaling and choice alleles to evolve under more relaxed conditions. Our results also provide a new insight into the evolution of sexual conflict over parental care.

**KEY WORDS:** Extra-pair copulation, female sexual signal, male mate choice, parental care, postpairing.

A central focus of research on sexual selection for many years has been to determine the roles and importance of male–male competition and female mate choice in driving signal evolution (Andersson 1994). However, it has become increasingly clear that male and female sex roles can be dynamic and variable (Edward and Chapman 2011). A large number of empirical studies have documented male mate choice as being prevalent in many taxa (for reviews, see Amundsen 2000; Bonduriansky 2001; Kraaijeveld et al. 2007; Hooper and Miller 2008), resulting in several theoretical studies about the evolution of male or mutual mate choice having been published during the last decades (e.g., Ihara and Aoki 1999; Kokko and Johnstone 2002; Servedio and Lande 2006; Servedio 2007; Nakahashi 2008; Barry and Kokko 2010; South et al. 2012).

Traditionally, the mating success of males is thought to be limited by the availability of mating opportunities, that is, it is thought that the male-biased operational sex ratio (OSR) constrains the evolution of male choice (Kokko and Monaghan 2001; Kokko and Johnstone 2002). Significant benefits are required to offset the potential costs of male choice, such as through obtaining greater investment from more fecund females (Servedio and Lande 2006; Servedio 2007; Nakahashi 2008), assortative mating according to female quality (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Venner et al. 2010), and a female preference for males that court them more vigorously (South et al. 2012). In such cases, males would make their choice before pairing and copulation. However, fewer studies have examined the factors driving the evolution of postpairing male mate choice; this

may be even more common among populations than preparing mate choice (Ratikainen and Kokko 2010), because males may be able to evaluate their mates after they have been accepted, such as through certain physical contact (Edward and Chapman 2011).

One of the most direct strategies of postpairing male mate choice should be the differential allocation of parental care (Burley 1986). This behavior, which normally happens in females, has received abundant empirical support in different taxa (Sheldon 2000), but males can also adjust their parental care investment according to their mates' ornamental attractiveness (e.g., Burley 1988; Roulin 1999; Matessi et al. 2009; Mahr et al. 2012). Moreover, a number of empirical studies have suggested that some signals expressed after pairing are intended to induce higher investment of paternal care from the male parent; such signals include avian eggshell pigmentations (e.g., Moreno et al. 2005; Soler et al. 2005; Hanley and Doucet 2009; English and Montgomerie 2011), nest size (Jelínek et al. 2016), and female feather carrying in the nest (Garcia-Navas et al. 2015). These findings raise the question of why postpairing male mate choice would evolve. Specifically, because reducing parental care may entail relatively higher probabilities of breeding failure of their own nests (Møller 2000), why would males adjust their parental care investment according to female sexual signals that are expressed after pairing?

Normally, differential allocation of parental care is expected to happen when there is a trade-off between current and future reproductive fitness (Sheldon 2000). However, for many vertebrate species, males could provide significant contributions to care for offspring, while also investing energy in seeking additional extra-pair matings (Magrath and Komdeur 2003). This situation allows a trade-off between parental care and additional mating effort, during the same breeding season (e.g., Magrath and Elgar 1997; Symons et al. 2011). We propose that this trade-off, which has been somewhat overlooked (Magrath and Komdeur 2003), has the potential to influence the evolution of male mate choice for female traits. Accordingly, we suppose that males exercise mate choice by trading off parental investment with their current mate with benefits from extra-pair copulations (EPCs). That is, males may be expected to allocate more time and effort to seek EPCs after they determine postpairing that their mates are nonpreferred using physical contact or other sexual signals expressed by the females.

To our knowledge, this mechanism has not been explored or discussed theoretically or tested in the empirical studies listed above. We therefore develop a two-locus, two-allele haploid population genetic model to explore the coevolution of the phenotypes of postpairing male mate choice and a female signal. The signal only affects the parental care investment by choosy males, who carry a mate choice allele, while males without mate choice invest

without regard to the female signal. Furthermore, as a trade-off, allocating more effort to parental care by males results in lowered extra-pair fecundity, because these males put less effort into seeking EPCs. Unlike some previous studies (e.g., Servedio and Lande 2006; South et al. 2012), the costly female signaling trait is expressed after mating in our model. To avoid other selection effects, we assume that this signal does not indicate the quality of females, and therefore does not affect or predict the survivability of females before pairing. This implies that the offspring would not inherit alleles for high quality under male mate choice; our formulations could thus fall under a "null model" (sensu Prum 2010) for sexual selection under this scenario.

We find that postpairing male mate choice and costly female signals can evolve and be maintained in a population when there is a trade-off between seeking EPCs and providing parental care by the male parent. Interestingly, if the availability of EPCs for males is high enough, both male choice and female signaling traits can always be kept present through cycling, which deserves further empirical exploration. Furthermore, we find that relatively strong male preference is important for promoting the evolution of such a system. The female signaling trait does not evolve if the changes in parental care investment by males with versus without mate choice are too small. A relatively low cost to the female of expressing the signal also plays an important role in promoting signal evolution, which is consistent with some empirical evidence. Taken together, our results suggest a novel role for trade-offs in male investment in driving the evolution of a mate choice and signaling system.

## The Model

Our modeling framework is based on previous models of mutual mate choice (Servedio and Lande 2006; South et al. 2012) and male parental care (Ihara 2002; Seki et al. 2007). As in those models, we assume that generations are not overlapping and reproduction occurs between generations. The social mating system is monogamy, and thus parental care is provided only by the social mates. We assume that both males and females may engage in EPCs, which only affects paternity. All females mate and have equal mating rates. Males select their mates randomly in the population. Furthermore, we assume no variability of quality or condition (e.g., there are no "good genes"), thus concentrating on the evolution of male mate choice without other selection factors.

In our model, we assume two loci denoted by P and S. Thus, there will be four genotypes of  $P_1S_1$ ,  $P_1S_2$ ,  $P_2S_1$ , and  $P_2S_2$ . We denote their frequencies by  $x_1$ ,  $x_2$ ,  $x_3$ , and  $x_4$ , respectively. The allele frequencies of  $P_1$  and  $P_2$  are denoted by  $p_1$  and  $p_2$ . Likewise, the allele frequencies of  $S_1$  and  $S_2$  are denoted by  $s_1$  and  $s_2$ . The locus, S, which is expressed only in females, determines whether the female expresses the sexual signal preferred by males

after copulation, such as egg color, nest size, and so on;  $S_2$  females express this signal, while  $S_1$  females do not. Here, we assume that such a signal entails a direct mortality cost to the female. Because this cost is expressed after mating, and generations are not overlapping, it is manifested in the fact that nestlings will die without the female parent's care. Therefore, an  $S_2$  female with the sexual signal could only give birth to offspring and raise them successfully with a probability of  $1 - t$  relative to that for an  $S_1$  female (where  $1 \geq t \geq 0$ ). Selection on the female trait is thus manifested as fecundity selection. Alternatively, we can also think of this cost as the nest predation risk brought on by female signaling. The locus  $P$  is a preference locus that is only expressed in males, and determines the male mate choice behavior. Specifically, a  $P_1$  male shows no difference in parental care investment when he mates with an  $S_1$  or an  $S_2$  female. However, a  $P_2$  male will reduce his parental investment to  $1 - \delta_1$  when he mates with an  $S_1$  female and increase it to  $1 + \delta_2$  when he mates with an  $S_2$  female, relative to that for a  $P_1$  male.

Simultaneously, we assume each  $P_1$  male will gain fixed fecundity benefits from EPCs in each generation, whereas the benefits gained by  $P_2$  males directly depend on the phenotype of their mates. As a trade-off with parental investment,  $P_2$  males will sire more and less extra-pair offspring relative to  $P_1$  males when they mate with nonpreferred (i.e.,  $S_1$ ) and preferred (i.e.,  $S_2$ ) females, respectively. Because the potential availability of EPCs for males should not be unlimited in a population, if there are increased numbers of males allocating more effort to seek EPCs, the potential success rate of each male should decline due to the competition. Therefore, the realized extra-pair fecundity benefits gained by males should be frequency dependent. We can assume that the maximum potential fecundity benefits gained from EPCs by  $x_j$  males while mating with  $x_i$  females in the population is  $C_{ij} = c + e_1 d_{c1} - e_2 d_{c2}$ , where  $e_1 = 1$  and  $e_2 = 0$  if  $j = 3$  or  $4$  (i.e., males have the allele  $P_2$ ) and  $i$  is odd (i.e., females have the allele  $S_1$ ),  $e_1 = 0$  and  $e_2 = 1$  if  $j = 3$  or  $4$  and  $i$  is even (i.e., females have the allele  $S_2$ ), and  $e_1 = 0$  and  $e_2 = 0$  otherwise. Note that  $d_{c2}$  should be smaller than  $c$  to keep  $C_{ij} > 0$ . We use this maximum value to calculate the proportion of extra-pair offspring sired by  $x_j$  males with different genotypes, that is,

$$\rho_{x_j} = \frac{x_j \sum_i x_i C_{ij}}{\sum_{ij} x_i x_j C_{ij}}, \quad (1)$$

and also assess the competitive strength for EPCs by males in the population as follows:

$$\varphi = \sum_{ij} x_i x_j C_{ij}. \quad (2)$$

We assume a life cycle that begins with random pairing. The number of surviving offspring ( $\emptyset$ ) is directly determined by

parental investment from their social parents:  $\emptyset = 1 + bm$  (Ihara 2002; Seki et al. 2007). In  $\emptyset$ , the first term (i.e., 1) represents the surviving offspring due to the care provided by the female parent, while the second term (i.e.,  $bm$ ) represents the surviving offspring due to the care provided by the male parent, respectively. Here,  $b$  represents the relative effect of male, compared to female, parental care on offspring survival, and  $m$  is the expected parental care effort of male parent.

We can first derive the male parental care effort under each mating combination of  $x_i$  female and  $x_j$  male according to our above assumptions:

$$m_{ij} = 1 - f_1 \delta_1 + f_2 \delta_2, \quad (3)$$

where  $f_1 = 1$  and  $f_2 = 0$  if  $j = 3$  or  $4$  (i.e., males have the allele  $P_2$ ) and  $i$  is odd (i.e., females have the allele  $S_1$ ),  $f_1 = 0$  and  $f_2 = 1$  if  $j = 3$  or  $4$  and  $i$  is even (i.e., females have the allele  $S_2$ ) and  $f_1 = 0$  and  $f_2 = 0$  otherwise. Subsequently, the final surviving offspring ( $\emptyset_{ij}$ ) of each mating combination is affected by the female's mortality due to expressing the signal:

$$\emptyset_{ij} = (1 + bm_{ij}) (1 - kt), \quad (4)$$

where  $k = 1$  if  $i$  is even (i.e., females have the allele  $S_2$ ), and  $k = 0$  otherwise.

Because both males and females will engage in EPCs, the above surviving offspring matrix  $\emptyset_{ij}$  should contain both within-pair and extra-pair offspring produced by  $x_i$  females. We assume that males would select their EPC mates randomly among the whole population, and therefore each female would have the same probability of mating with extra-pair mates. Based on this, we assume that each female in the population will have a proportion of  $\theta$  offspring sired by the social mate and a proportion of  $1 - \theta$  sired by extra-pair mates. The realized fecundity benefits gained from EPCs by  $x_j$  males thus should be determined by the total extra-pair offspring produced by females and the proportion of  $\rho_{x_j}$ , that is,  $\rho_{x_j} (1 - \theta) \sum_{ij} \emptyset_{ij}$ .

We can expect that the proportion  $\theta$  may be frequency-dependent in reality. On one hand, if there are increased number of males allocating more effort to seek EPCs in the population (i.e., under more severe male competition, or say larger value of  $\varphi$ ), females may produce a higher proportion of extra-pair offspring because of the more frequent EPC attempts by males (Clutton-Brock and Parker 1995). On the other hand, the proportion  $\theta$  may decline when the mating pair can have higher fitness (i.e., have more surviving offspring, or say larger value of  $w = \sum_{ij} x_i x_j \emptyset_{ij}$ ), possibly because of lower levels of EPC pursuing behavior by females in the population (e.g., Pierce and Lifjeld 1998) or more intense mate guarding by males assuming females also trade-off EPCs with parental care (e.g., Wagner et al. 1996). It should always be more beneficial for males to

protect their paternity more intensively when the number of surviving offspring produced by their social mates increases. For simplicity, we first use the following arbitrary function to include both the above-mentioned effects:

$$\theta = \frac{w}{\varphi + w}. \tag{5}$$

For generality, we also relax the above assumption about the frequency-dependent function  $\theta$  by using a constant for it, which implies that each male would simply lose a fixed proportion of  $1 - \theta$  within-pair paternity. We get quite similar, but somewhat more complicated results from the more general assumption (see Supporting Information).

Male choice can result in a  $4 \times 4$  matrix  $\mathbf{F}$  of the proportion of surviving offspring between each genotype, where  $F_{ij}$  includes both within-pair ( $F_{ij}^{in}$ ) and extra-pair offspring ( $F_{ij}^{ex}$ ), that is,  $F_{ij} = F_{ij}^{in} + F_{ij}^{ex}$ , where

$$F_{ij}^{in} = \frac{x_i x_j \theta \phi_{ij}}{w}, \tag{6}$$

$$F_{ij}^{ex} = \frac{\rho_{x_j} \sum_j x_i x_j (1 - \theta) \phi_{ij}}{w}. \tag{7}$$

Following the standard equations for recombination and segregation for two loci in haploids, we can derive the recursion equations for the genotype frequencies, and then convert these into equations for the allele frequencies for  $S_2$  and  $P_2$  and linkage disequilibrium between them,  $D$ . These full equations and details of the analyses are archived in *Mathematica* files on Dryad (doi:10.5061/dryad.h422c). We calculate the equilibria analytically and determine the local stability of each equilibrium through a linear stability analysis.

## Results

### CAN MALE POSTPAIRING MATE CHOICE EVOLVE AS WITH A TRADE-OFF BETWEEN SEEKING EPCS AND PROVIDING PARENTAL CARE?

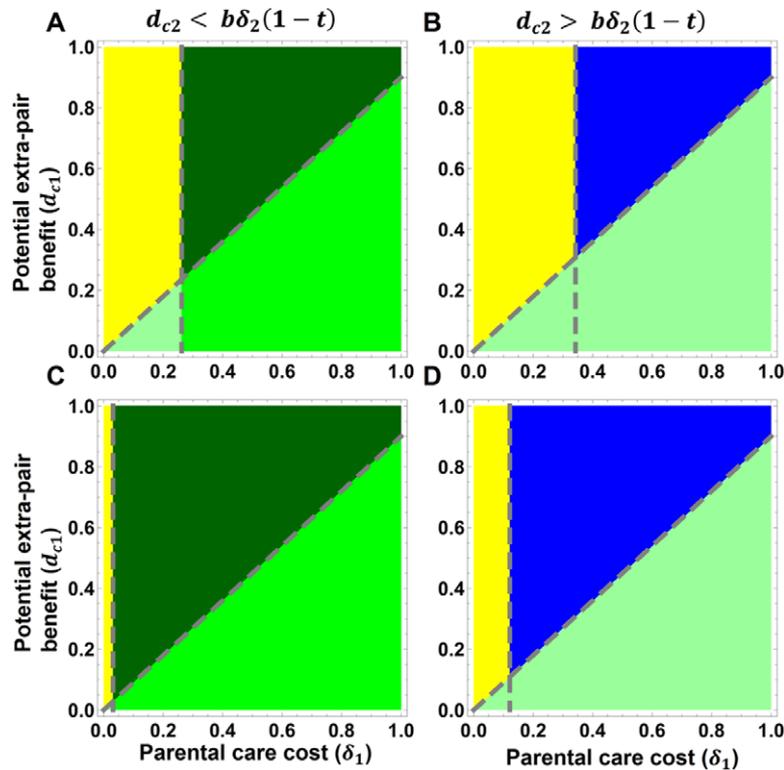
Through calculation of the equilibria of the model and the corresponding stabilities, we find that both postpairing male mate choice and female signal can evolve, given a trade-off for males between providing parental care and seeking EPCs. The equilibria are given below in the form of  $(\hat{p}, \hat{s}, \hat{D})$ , where  $\hat{p}$  and  $\hat{s}$  represent the frequency of alleles  $P_2$  and  $S_2$  at each equilibrium, and  $\hat{D}$  represents the corresponding linkage disequilibrium.

We find, as expected, that all four cases of fixation of alleles at the P and S loci, (0, 0, 0), (0, 1, 0), (1, 0, 0), and (1, 1, 0) are always equilibria. To explore whether both male postpairing mate choice and the female signaling trait can evolve and be maintained in a population, we assess the stabilities of these equilibria (see Supporting Information SI1). These analyses indicate

that the equilibrium of most interest, (1, 1, 0), is locally stable when  $d_{c2} < b\delta_2(1 - t)$  and  $\delta_2 > \frac{(1+b)t - b\delta_1}{b(1-t)}$  are satisfied (see medium-green and dark green regions in Figure 1A and C, and see Supporting Information SI1). Therefore, both male choice and female signaling can fix in the population when  $P_2$  males have a relatively strong preference manifested through providing relatively high additional parental care investment after mating with  $S_2$  females (i.e., high value of  $\delta_2$ ), but only given a limited reduction in extra-pair fecundity benefits (i.e., small value of  $d_{c2}$ ). Furthermore, at the equilibrium (1, 1, 0), the  $P_1$  allele will invade if the reduction in extra-pair fecundity benefits of  $P_2$  males mating with  $S_2$  females (i.e.,  $d_{c2}$ ) is greater than the within-pair fitness increase of this pair in terms of the number of offspring (i.e.,  $b\delta_2(1 - t)$ ). Likewise, invasion of the  $S_1$  allele can occur if  $S_1$  females can produce a larger number of offspring than  $S_2$  females when mating with  $P_2$  males (i.e., which will occur when  $1 + b(1 - \delta_1) > (1 + b(1 + \delta_2))(1 - t)$  – a rearrangement of  $\delta_2 < \frac{(1+b)t - b\delta_1}{b(1-t)}$ ).

The stability of the equilibrium (0, 0, 0) is only determined by the relationship between the reduction in parental care  $b(\delta_1)$  and the additional extra-pair benefits ( $d_{c1}$ ) gained by  $P_2$  males mating with  $S_1$  females; that is, it is stable when  $d_{c1} < b\delta_1$  (the light green and medium-green regions below the oblique gray dashed line as shown in Fig. 1; see Supporting Information SI1). At this equilibrium, we can see that the allele  $S_2$  can never invade because there is always a cost to this allele (i.e.,  $t$ ) in the absence of  $P_2$  males. However, (0, 0, 0) can be invaded by the  $P_2$  allele, if the increase in extra-pair fecundity benefits (i.e.,  $d_{c1}$ ) is greater than the within-pair fitness reduction caused by reduced parental care (i.e.,  $b\delta_1$ ) by  $P_2$  males mating with  $S_1$  females (see the yellow region shown in Fig. 1). Additionally, there is a region of bistability when both the equilibria (1, 1, 0) and (0, 0, 0) are locally stable (see the medium-green area in Fig. 1A and C). In this parameter region, the equilibrium that is reached will depend upon the initial frequency of  $p_2$  and  $s_2$  (Fig. 2).

The equilibrium (0, 1, 0) is always unstable. When all males have the  $P_1$  allele, the allele  $S_1$  will invade because the signal is costly (i.e.,  $t$ ) but has no benefit. The allele  $P_2$  will also be able to invade if the increase in within-pair fitness caused by increased parental care (i.e.,  $b\delta_2(1 - t)$ ) offsets the reduction in extra-pair fecundity benefits (i.e.,  $d_{c2}$ ). At the equilibrium (1, 0, 0), the allele  $P_1$  will invade if the increase in extra-pair fecundity benefits by  $P_2$  males mating with  $S_1$  females (i.e.,  $d_{c1}$ ) is too small relative to the within-pair fitness reduction caused by reduced parental care (i.e.,  $b\delta_1$ ). The  $S_2$  allele will invade if  $S_2$  females can produce a larger number of offspring than  $S_1$  females after mating with  $P_2$  males (i.e., when  $(1 + b(1 + \delta_2))(1 - t) > 1 + b(1 - \delta_1)$ ). It can be seen that the conditions for invasion in this paragraph thus represent the flip side of the invasion criteria for the conditions (1, 1, 0) and (0, 0, 0), as described above.

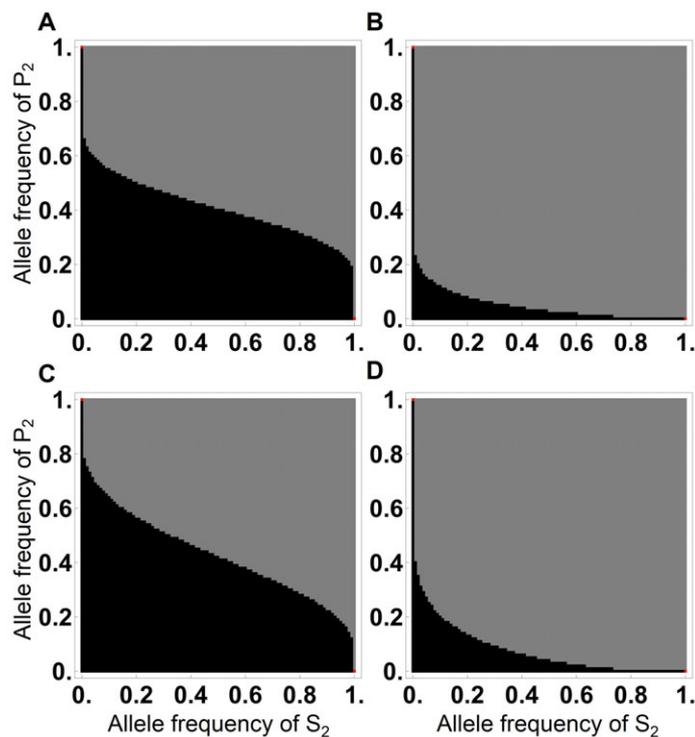


**Figure 1.** The conditions required for local stability of the four cases of fixation of alleles at the P or S loci, and the existence of an internal equilibrium. Regions indicated in light green plus the medium-green represent the conditions for the local stability of (0, 0, 0). Equilibrium (1, 0, 0) is stable in the left yellow region. The region indicated in medium-green also represents the conditions required for the local stability of (1, 1, 0) and the existence of an unstable internal equilibrium. In this region, there is bistability, such that both (1, 1, 0) and (0, 0, 0) are stable equilibria. The regions with dark green in (A) and (C) represents the conditions for only one stable equilibrium (1, 1, 0). Regions indicated in blue represent the conditions required for the existence of cycling around the internal equilibrium. The vertical dashed line shows the threshold value of  $\delta_1$  when  $\delta_2 = \frac{(1+b)t - b\delta_1}{b(1-t)}$ , the oblique dashed line is  $d_{c1} = b\delta_1$ . We set  $\delta_2 = 0.2$  to enable  $d_{c2} < b\delta_2(1 - t)$  in (A) and (C), and  $\delta_2 = 0.1$  to enable  $d_{c2} > b\delta_2(1 - t)$  in (B) and (D). The other parameters are:  $b = 0.8$ ,  $c = 1.0$ ,  $d_{c2} = 0.1$ ;  $t = 0.2$  in (A) and (B), and  $t = 0.1$  in (C) and (D).

The model also has an internal equilibrium of  $(\frac{(1+b)t}{b(\delta_1 + \delta_2 - t\delta_2)}, \frac{d_{c1} - b\delta_1}{d_{c1} + d_{c2} - b(\delta_1 + \delta_2 - t\delta_2)}, D_{in}^*)$  (Fig. 1, and see Supporting Information SI1 and SI2), when  $\delta_2 > \frac{(1+b)t - b\delta_1}{b(1-t)}$  and either the following condition set is satisfied:  $d_{c1} > b\delta_1$  and  $d_{c2} > b\delta_2(1 - t)$  (i.e., blue region in Fig. 1B and D) or  $d_{c1} < b\delta_1$  and  $d_{c2} < b\delta_2(1 - t)$  (i.e., medium-green region in Fig. 1A and C), where  $D_{in}^*$  is the stable value of linkage disequilibrium (this is calculated numerically for the following analyses). Using numerical analysis to calculate the eigenvalues of the internal equilibrium under different parameter values (see Supporting Information SI3), we find that the internal equilibrium is always unstable, with eigenvalues larger than the unit. However, we find that this equilibrium will have complex eigenvalues predicting oscillatory dynamics when  $d_{c1} > b\delta_1$  and  $d_{c2} > b\delta_2(1 - t)$  are satisfied, that is, in the blue area of Figure 1B and D. Through numerical simulation, we find that the allele frequency dynamics will always develop into cycles around the internal equilibrium with parameter values located within this area (Fig. 3A and B).

Therefore, in this region of the parameter space, both loci will be kept polymorphic with oscillating frequencies in the population, which implies that under relatively strong male preference (i.e., enabling  $\delta_2 > \frac{(1+b)t - b\delta_1}{b(1-t)}$ ), new mutations for a male preference and a female signal will always be maintained after entering the population, if the change in potential extra-pair fecundity benefits (i.e.,  $d_{c1}$  and  $d_{c2}$ ) are also great. Furthermore, we find that there will always be a time lag between the two alleles' frequency dynamics, that is, the allele frequency of  $S_2$  will still increase after the allele frequency of  $P_2$  changes from increasing to decreasing, or vice versa (Fig. 3).

Extensive numerical simulations show that the amplitude of the allele frequency oscillation is smaller under lower recombination rate (Fig. 4; Fig S1). According to a magnified view of the frequency dynamics as shown in Figure S3, we find that a lower recombination rate enables the allele frequencies to cycle with a shorter period. It can be seen that the linkage disequilibrium increases and decreases more quickly under a lower recombination



**Figure 2.** Numerical results of the bistable system with different initial frequencies of  $(p_2, s_2, 0)$ , ranging from 0.0 to 1.0 with a step size of 0.01. Regions indicated in black represent the population that will achieve the equilibrium of  $(0, 0, 0)$  from the corresponding initial state. Regions indicated in gray represent the population that will achieve the equilibrium of  $(1, 1, 0)$ . There are two red dots representing the equilibria  $(1, 0, 0)$  and  $(0, 1, 0)$ . The other parameters are:  $b = 0.8, r = 0.5, c = 0.9, \delta_1 = 0.3, \delta_2 = 0.35; t = 0.1$  in (A) and (C) and  $t = 0.01$  in (B) and (D);  $d_{c1} = 0.2, d_{c2} = 0.23$  in (A) and (B), and  $d_{c1} = 0.15, d_{c2} = 0.2$  in (C) and (D).

rate, which alternately causes the allele frequencies to change from increasing to decreasing or from decreasing to increasing more quickly (Fig. S3).

We also conduct analyses using a constant for the proportion of within-pair offspring of each female (i.e.,  $\theta$ ). For this case, we give the detailed conditions required for local stability of each equilibrium under a simplified symmetric situation (i.e.,  $\delta_1 = \delta_2 = \delta$ , and  $d_{c1} = d_{c2} = d_c$ ) in the Supporting Information S11. We get quite similar qualitative results in that both male choice and female signaling traits can be maintained either at stable non-zero allele frequencies or with oscillating frequencies (Fig. S2). Additionally, although the conditions required are relatively strict, both alleles can have a stable internal equilibrium, or say, achieve a stable polymorphic state in this situation (Fig. S2A).

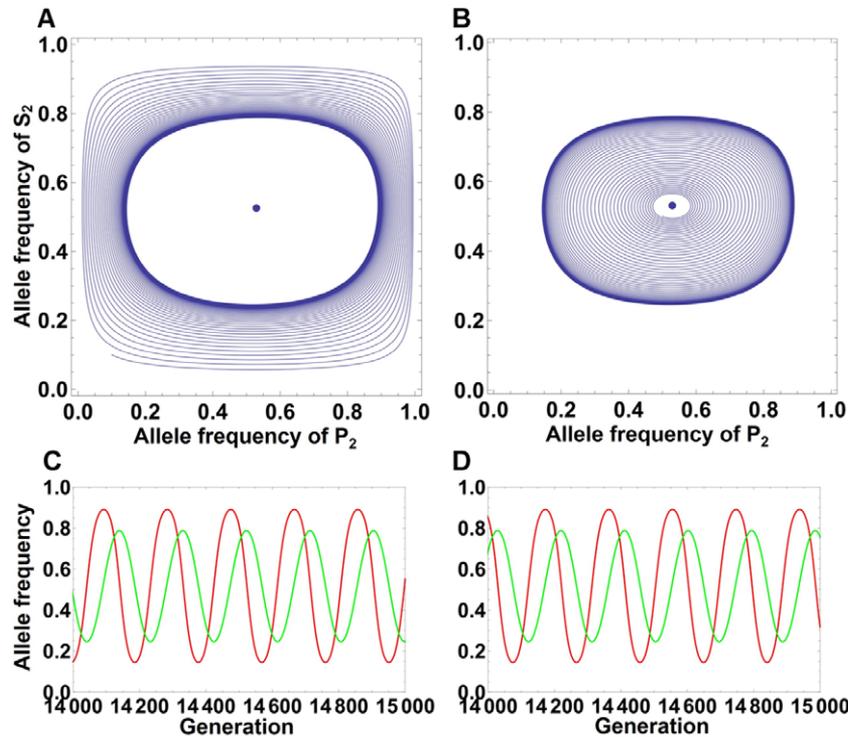
**RELATIVE IMPORTANCE OF UNEQUAL CHANGES IN MALE PARENTAL CARE AND POTENTIAL EXTRA-PAIR BENEFITS AND COSTS**

To obtain more intuition about how the outcomes of the model relate to the costs and benefits of choice behavior, we next assess the relative importance of the changes in male parental care and potential extra-pair benefits and costs when  $P_2$  males mate with  $S_1$  versus  $S_2$  females by setting  $\delta_1 = \alpha\delta_2$  and  $d_{c1} = \beta d_{c2}$ ,

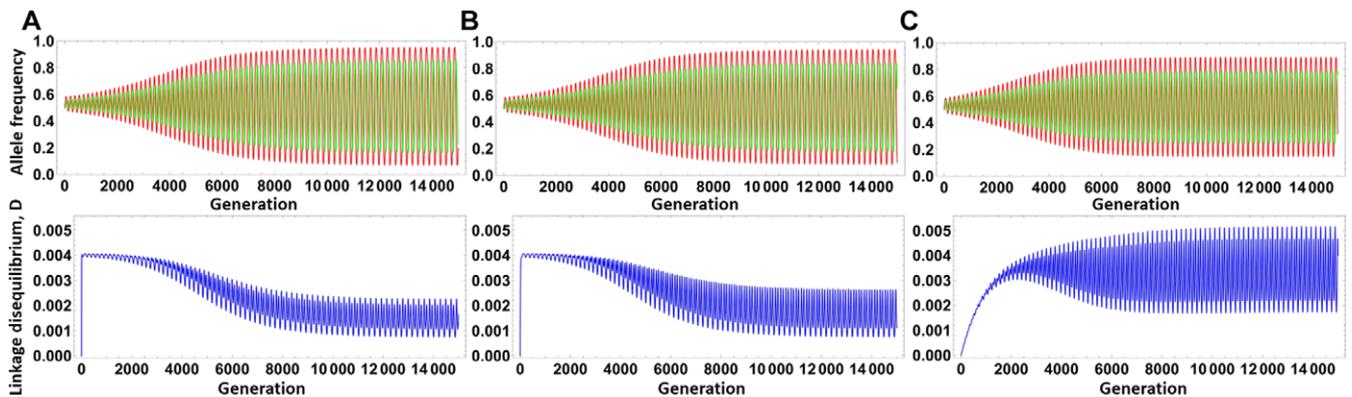
respectively. This represents  $\delta_1 > \delta_2$  and  $d_{c1} > d_{c2}$  when  $\alpha$  and  $\beta$  are larger than one, otherwise  $\delta_1 \leq \delta_2$  and  $d_{c1} \leq d_{c2}$ .

As the reduction in parental care given to  $S_1$  females ( $\delta_1$ ), increases with all else constant, there is a bigger and bigger region where  $P_2$  and  $S_2$  cannot invade (light green, moving right Fig. 5A and B). As the extra care given to  $S_2$  female ( $\delta_2$ ) increases (moving left on the figures), the model may enter a region where the only stable equilibrium occurs when the alleles  $P_2$  and  $S_2$  are fixed (dark green, Fig. 5B), that is,  $(1, 1, 0)$ . This region also appears when  $P_2$  males mated to  $S_1$  females get a large number of EPCs (i.e., under a high value of  $d_{c1}$ , Fig. 5C and D). So when either type of benefit ( $d_{c1}$  or  $\delta_2$ ) is very high, we obtain this region of fixation of  $P_2$  and  $S_2$ , and when in contrast, either type of cost in the model ( $d_{c2}$  or  $\delta_1$ ) is very high, the alleles  $P_1$  and  $S_1$  are more likely to be fixed.

This way of parameterizing the model makes it clear that obtaining  $(1, 1, 0)$  as the only stable equilibrium requires a relatively small parental care cost/benefit ratio, that is,  $\alpha$  (Fig. 5B) or relatively high potential extra-pair benefit/cost ratio, that is,  $\beta$  (Fig. 5C and D). Also, the fixation of both the  $P_2$  and  $S_2$  alleles can be the only equilibrium especially when the mortality cost of female signaling,  $t$ , is relatively small (Fig. 5B and D vs. A and C).



**Figure 3.** Frequency dynamics of two alleles under different initial frequencies when the internal equilibrium exists. Simulations are ran for a total of 15,000 generations. The initial state is set to (0.1, 0.1, 0) in (A) and (C), and (0.5, 0.5, 0) in (B) and (D). The points shown in (A) and (B) are the corresponding internal equilibrium of the model. (C, D) The frequency dynamics of the alleles  $P_2$  (red curve) and  $S_2$  (green curve) during the last 1000 generations of (A) and (B), respectively. The other parameters are:  $b = 0.8$ ,  $t = 0.1$ ,  $c = 0.9$ ,  $d_{c1} = 0.8$ ,  $d_{c2} = 0.75$ ,  $r = 0.001$ , and  $\delta_1 = 0.2$ ,  $\delta_2 = 0.25$ .



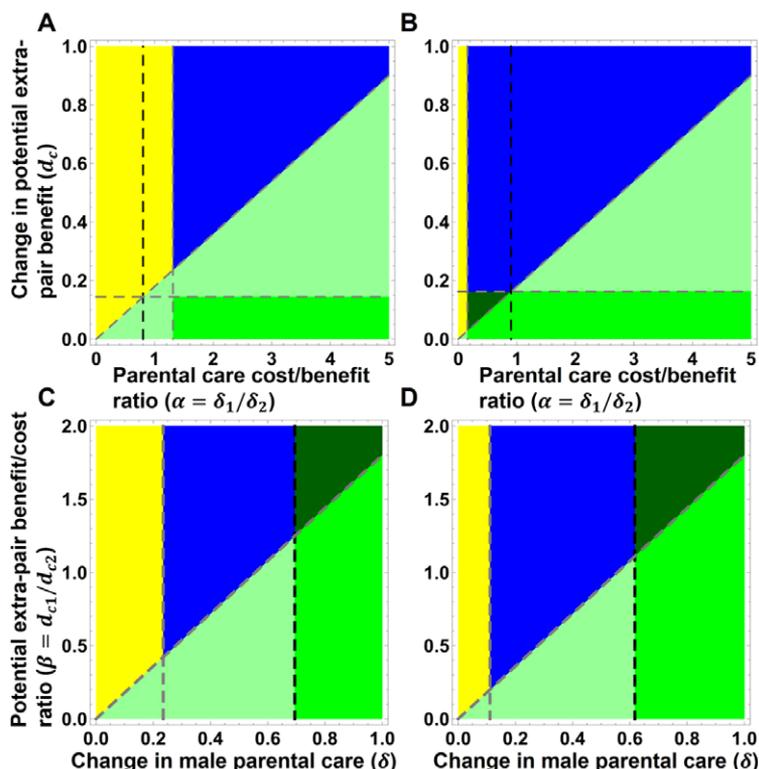
**Figure 4.** Frequency dynamics of two alleles and linkage disequilibrium under different recombination rates when the internal equilibrium exists. The red curve in the above figures represents the frequency of  $P_2$  and the green curve the frequency of  $S_2$ . The initial state is set to (0.5, 0.5, 0). (A)  $r = 0.5$ , (B)  $r = 0.1$ , and (C)  $r = 0.001$ . The other parameters are the same as in Figure 3.

Additionally, if the parental care cost of  $P_2$  males mating with  $S_1$  females ( $\delta_1$ ) is equal to zero, the population can only evolve to the fixation of the  $P_2$  allele (with only the  $S_1$  allele present) provided the potential benefit in EPCs gained by males in these matings  $d_{c1}$  is positive (along the y axis in Fig. 5A and B). If, in contrast, there are no available additional extra-pair benefits (i.e.,  $d_{c1} = 0$ , along the x axis in Fig. 5C and D), the population can still achieve the fixation of both  $P_2$  and  $S_2$  alleles under a quite

high value of increase in parental care from these matings ( $\delta_2$ ), provided that  $d_{c2} < b\delta_2(1 - t)$  is satisfied and  $P_2$  and  $S_2$  start at a relatively high frequency.

### LESS COSTLY FEMALE SIGNALS CAN FACILITATE THE EVOLUTION OF POSTPAIRING MALE MATE CHOICE

For those two occasions shown above when both traits can evolve simultaneously, that is, the existence of oscillations around the



**Figure 5.** Representative figures of the relative importance of unequal changes in male parental care (i.e.,  $\delta_1$  and  $\delta_2$ ) and potential extra-pair benefits and costs (i.e.,  $d_{c1}$  and  $d_{c2}$ ). In (A) and (B), we set  $d_{c1} = d_{c2} = d_c$  and  $\delta_1 = \alpha\delta_2$  to assess the relative effect of the reduction ( $\delta_1$ , when  $P_2$  males mate with  $S_1$  females) versus increase ( $\delta_2$ , when  $P_2$  males mate with  $S_2$  females) in parental care. In (C) and (D), we set  $\delta_1 = \delta_2 = \delta$  and  $d_{c1} = \beta d_{c2}$  to assess the relative effect of the increase ( $d_{c1}$ , when  $P_2$  males mate with  $S_1$  females) versus reduction ( $d_{c2}$ , when  $P_2$  males mate with  $S_2$  females) in extra-pair mating benefits. The color definitions for local stabilities are generally the same as in Figure 1. The regions with dark green in (B–D) represents the conditions for only one stable equilibrium of (1, 1, 0). In (A) and (B), the oblique dashed line is  $d_c = b\delta_1$ , the horizontal gray dashed line is  $d_c = b\delta_2(1 - t)$ , the vertical black dashed line shows  $\alpha = 1 - t$ , and the gray dashed line represents the corresponding value of  $\alpha$  when  $\delta_2 = \frac{(1+b)t - b\delta_1}{b(1-t)}$ . In (C) and (D), the oblique dashed line shows  $d_{c1} = b\delta$ , the vertical black dashed line shows  $d_{c2} = b\delta(1 - t)$  and the gray one represents  $\delta = \frac{(1+b)t}{b(2-t)}$ . We set  $\delta_2 = 0.2$  in (A) and (B) and  $d_{c2} = 0.5$  in (C) and (D) for illustration. The other parameters are:  $b = 0.9$ ,  $c = 1.0$ ,  $t = 0.2$  in (A) and (C), and  $t = 0.1$  in (B) and (D).

internal equilibrium and the stable equilibrium (1, 1, 0), we find that the cost of female signal, that is, the value of  $t$ , plays a significant role in facilitating the evolution of both male mate choice and female signaling. Specifically, the condition of  $\delta_2 > \frac{(1+b)t - b\delta_1}{b(1-t)}$  is essential for both situations, and moreover, the local stability of the equilibrium of (1, 1, 0) also requires the condition of  $d_{c2} < b\delta_2(1 - t)$  (see Supporting Information S11). Note that decreasing the value of  $t$  can effectively extend the regions indicated by both of these inequalities (Figs. 1B and 5B and D). Furthermore, numerical simulations reveal that the population will evolve to (1, 1, 0) under larger regions of the initial states with a smaller value of  $t$  (Fig. 2B and D).

## Discussion

Although recent empirical studies have demonstrated the presence and extent of male mate choice in nature, little is known about

adaptive mechanisms of female signaling or how male preference for such signal evolves (Chenoweth et al. 2006). This is particularly true for postpairing male mate choice (Edward and Chapman 2011), which can directly affect female breeding success. In this study, we found that postpairing male mate choice for costly female signals can evolve when male parental care investment is high enough to substantially benefit both signaling females and choosing (investing) males, even when these males pay a direct trade-off by losing opportunities for EPCs.

Additionally, we find that these factors can interact to cause trait and preference cycling (see below). This mechanism, which is different from the previous hypothesis of differential allocation (Sheldon 2000), thus provides a new reasonable way to offset the potential cost associated with male mate choice (i.e., the lower parental care investment of males that are mated to a nonpreferred female). They also give insight to explain interesting phenomena detected in the field, such as blue eggs in birds, which have been

proposed to be related to postpairing male mate choice (Moreno and Osorno 2003). We suggest that the main conclusions of our study need to be tested empirically in the future, to further improve our understanding of postpairing male mate choice in nature.

## TWO WAYS TO GET MALE MATE CHOICE AND FEMALE SIGNALS—FIXED OR CYCLING PREFERENCES AND SIGNALS

In our model, both male mate choice and female signals can be maintained in the population either by becoming fixed or by cycling. Male and female parents each face a trade-off, which is the source of cycling in the model. For males, there is a trade-off between allocating effort to parental care and seeking additional extra-pair matings. In turn, females expressing the signal pay a fecundity cost, but they can induce social mates with the mate choice allele to provide more parental care. We demonstrate that under these assumptions both male choice and female signal can evolve and be maintained in the population by cycling. Specifically, if the increase and the decrease in extra-pair fecundity, with preferred and nonpreferred females, respectively, is high enough to offset the corresponding change in within-pair fitness in that type of pairing (i.e.,  $d_{c1} > b\delta_1$  and  $d_{c2} > b\delta_2(1 - t)$ ), new mutants for male choice and female signaling can be maintained simultaneously through periodic oscillation (Figs. 1, 3, and 4 and see Supporting Information SI). Note that in the case where females always have a constant proportion of extra-pair offspring (i.e.,  $1 - \theta$ ), although the internal equilibrium can be stable under restricted conditions, the cycling will persist under parameter values in quite large regions (Fig. S2).

The observed oscillations are a result of frequency-dependent selection involved in the trade-offs of gaining extra-pair fecundity and providing parental care by males. According to our assumptions, each mating combination will have a certain proportion of offspring sired by extra-pair fathers. Males will thus have to compete to sire a limited number of extra-pair offspring, which will cause negative frequency-dependent selection on any allele increasing extra-pair mating.

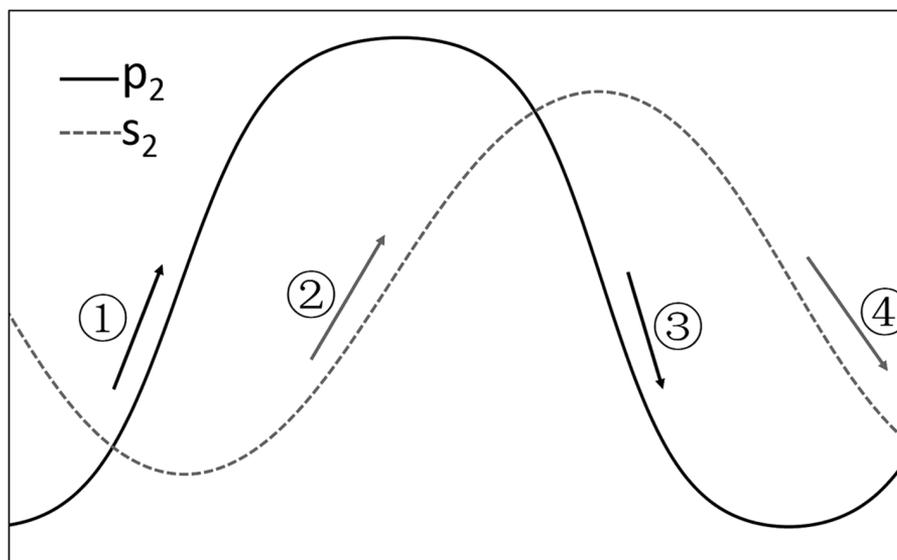
Let us take a population initially dominated by  $P_1$  and  $S_1$  alleles as an example;  $P_2$  males will have higher fitness compared to  $P_1$  males because they can gain more benefits from EPCs to overcome their fitness lost within-pair (i.e.,  $d_{c1} > b\delta_1$ , see arrow 1, Fig. 6). Then, as  $P_2$  males increase,  $S_2$  females will have increasingly higher fitness because they will receive more male parental care (i.e., from  $1 - \delta_1$  to  $1 + \delta_2$  by  $P_2$  males; arrow 2, Fig. 6). When  $P_2$  and  $S_2$  alleles increase to certain frequencies,  $P_1$  males will then increase due to their higher extra-pair fecundity benefits compared to  $P_2$  males when there is a high frequency of  $S_2$  females. In other words, the fecundity benefits that  $P_1$  males gain from EPCs will outweigh the combined effects of low EPCs but high parental care of  $P_2$  males (i.e.,  $d_{c2} > b\delta_2(1 - t)$ , see

arrow 3, Fig. 6). Finally, because the  $S_2$  allele is costly for females but cannot bring additional male parental care when  $p_1$  is too high, the  $S_2$  allele will then gradually be displaced by the  $S_1$  allele (see arrow 4, Fig. 6). Note that because there is positive linkage disequilibrium between the P and S loci (Fig. 4), increases (or decreases) in  $P_2$  will also tend to cause a modest increase (or decrease) in  $S_2$  due to this genetic association. This will contribute to the shifts in direction of the frequency changes described above (and also, as previously discussed, may contribute to the effects of tighter recombination on the period of the cycles).

Interestingly, the evolutionary pressure of increasing extra-pair fecundity drives two of the turns in this cycle. The first step described above, the increase in choosy,  $P_2$  males when the population consists of nonchoosy,  $P_1$  males and nonsignaling  $S_1$  females is due to the benefit of extra-pair matings. Likewise, when males with the choice allele and signaling females predominate, there are many opportunities for EPCs by  $P_1$  males that do not invest as much, in a population of signaling females, in parental care. The male choice allele thus both increases and is lost under different population compositions by the same selective force.

The finding of cycling can provide a possible explanation for inconsistent observations given by empirical studies. For example, sexual selection has been proposed to explain the evolution of egg color in birds, through the suggestion that males may adjust their parental care investment according to the colors of eggs produced by their mates (Moreno and Osorno 2003). Although this has been verified in several bird species, the conclusions are still controversial (Kilner 2006), and it is unclear why some studies have failed to find empirical support (e.g., Krist and Grim 2007; Honza et al. 2011; Johnsen et al. 2011). Similarly, some experimental studies found no or limited support for the ability of males to differentially allocate resources, for example in rock sparrows (*Petronia petronia*) (Pilastro et al. 2003), blue tits (*Cyanistes caeruleus*) (Limbou et al. 2013), and tree swallows (*Tachycineta bicolor*) (Berzins and Dawson 2016). We suggest that the oscillating frequencies as shown in Figures 3 and 4 may be a potential reason for those inconsistent empirical results among bird species, because male individuals with the mate choice allele may be polymorphic in a population, and more importantly, the mate choice allele may reach low frequencies during oscillations in some populations. Therefore, we suggest that future studies of male differential allocation behaviors and egg coloration should be conducted over larger spatiotemporal scales to account for this possibility.

Additionally, both the female signal and male choice alleles in our model can always fix in the population if the additional extra-pair fecundity benefits gained by  $P_2$  males after mating with  $S_1$  females is greater than the within-pair fitness reduction (i.e.,  $d_{c1} > b\delta_1$ ), the increase in within-pair fitness after mating with  $S_2$  females can offset the extra-pair fecundity benefits lost (i.e.,  $d_{c2} < b\delta_2(1 - t)$ ), and the number of offspring produced by



- ①  $p_2$  increases since  $P_2$  males have more benefits from EPCs than  $P_1$  males when there are lots of  $S_1$  females;
- ②  $s_2$  increases since  $S_2$  females receive more parental care when there are lots of  $P_2$  males, enough to outweigh the fecundity cost of signaling  $S_2$  females;
- ③  $p_2$  decreases since  $P_1$  males have more benefits from EPCs than do  $P_2$  males when there are lots of  $S_2$  females in this parameter range, the increase in  $P_2$  fitness due to parental care does not compensate;
- ④  $s_2$  decreases since  $S_2$  females are expressing the costly signal with little benefits when there are not enough  $P_2$  males.

**Figure 6.** Schematic of the allele frequency oscillations when an internal equilibrium exists in the model.

$S_1$  females is greater than that produced by  $S_2$  females that mated with  $P_2$  males (i.e.,  $\delta_2 > \frac{(1+b)t - b\delta_1}{b(1-t)}$ ). Even if the potential extra-pair fecundity benefits gained or lost by  $P_2$  males are relatively limited (i.e., with a small value of  $d_{c1}$ ), both the female signal and male choice alleles still have a chance to become fixed in the population, depending on the initial state of the allele frequencies (Figs. 1 and 2). Under a relatively high initial frequency of the  $P_2$  allele,  $P_2$  males have higher within-pair fitness than do  $P_1$  males when there are enough  $S_2$  females in the population. Although the expected extra-pair fecundity fitness of  $P_1$  males mated to  $S_2$  females is higher than that of  $P_2$  males, it cannot compensate for the lower within-pair fitness of  $P_1$  males compared to  $P_2$  males when the additional extra-pair fecundity benefits are quite limited (i.e., with small value of  $d_{c2}$ ). Due to a relatively large value of male parental care with high  $\delta_2$ ,  $S_2$  females will also have higher fitness than do  $S_1$  females in this parameter range, which can outweigh the costs of expressing the signals. Therefore, both the male choice and female signals can be fixed in the population in the parameter range shown by the medium-green and dark green color in Figures 1 and 5.

We also highlight the importance of male parental care, which deserves more empirical attention in the future. The presence of a relatively strong male preference (i.e., with large values of male parental care investment  $\delta_1$  and/or  $\delta_2$ ) is essential for the

evolution of both the female signaling and male choice alleles. This is especially true for the female signal, which will have no chance to evolve when  $\delta_2$  is smaller than  $\frac{(1+b)t - b\delta_1}{b(1-t)}$  (Fig. 1). This implies that in those species with male postpairing male mate choice, males should have relatively strong preferences with great changes in their parental care investment. Alternatively, in these cases male parental care should play a relatively important role in offspring survival, because large value of  $b$  can decrease the threshold value of  $\frac{(1+b)t - b\delta_1}{b(1-t)}$  (under a relatively small value of  $t$  when  $t - \delta_1 < 1 - t$  is satisfied), and this then extends the region of the maintenance of both male mate choice and female signals.

**SEXUAL CONFLICT OVER PARENTAL CARE**

Our modeling results give a new explanation for how sexual conflict over parental care can evolve through the feedback of sexual selection (Kokko and Jennions 2008). Generally, each parent should prefer to shift more of the costly care for the offspring onto its mate, and then conflict arises (Trivers 1972; Houston et al. 2005). It has been expected that sexually antagonistic co-evolution between traits that function to increase care by the other sex, and those that function to resist such manipulations, would resolve such conflicts (Chapman et al. 2003).

In this study, we show that postpairing male mate choice and female signals also reflect a conflict over parental care

between the sexes. Males with mate choice would prefer to decline parental care if they dislike their social mates, while females expressing the signal can attract their social mates that have mate choice to provide better parental care. The varied evolutionary outcomes provide us a new insight into the evolution of such conflict. Specifically, if the change in male parental care investment in a male's own nest is relatively small (i.e., when  $\delta_2 < \frac{(1+b)t-b\delta_1}{b(1-t)}$ ), the signaling allele  $S_2$  will have no chance of being maintained in the population, and moreover, all females will suffer from lower parental investment from their mates if the additional extra-pair fecundity benefits are great enough, because when  $d_{c1} > b\delta_1$  is satisfied, male mate choice and the loss of signal is the only equilibrium (Fig. 1B and D).

However, if the additional male investment with preferred females  $\delta_2$  and/or the reduction of male investment with nonpreferred females  $\delta_1$  increase, which enables  $\delta_2 > \frac{(1+b)t-b\delta_1}{b(1-t)}$ , both the  $P_2$  and  $S_2$  alleles can be maintained in the population. Both male mate choice and the female signal can then exist either as a certain proportion of the population, that is, oscillating around the internal equilibrium, or by fixing across the entire population, that is, achieving the equilibrium of (1, 1, 0). As shown in Figure 2, if the initial frequencies of allele  $P_2$  and  $S_2$  are large enough, the equilibrium of (1, 1, 0) is ultimately achieved in the population under some parameter values. Additionally, the male choice allele  $P_2$  and female signaling allele  $S_2$  can always become fixed in the population, as the only equilibrium, under certain conditions (see the dark green region shown in Figs. 1A and C, and 5B–D). In this situation, the conflict would be resolved in that all females would express the costly sexual signal and receive increased male parental care. In summary, relatively intense changes in parental care by  $P_2$  males can enable the spread of costly sexual signals in females, conversely attracting increased numbers of  $P_2$  males to allocate more effort to parental care.

### THE IMPORTANCE OF A LESS COSTLY SIGNAL

For many species with heavily ornamented females (e.g., Hill 1993; Amundsen and Forsgren 2001; Domb and Pagel 2001; LeBas et al. 2003), males could make their decision before copulation by assessing the quality or fecundity of the females from their size or ornamentation (Chenoweth et al. 2006). Male mate choice considered in this study occurs after copulation, which means that the signal in females assessed by males should be neither obvious nor intuitive in this case. The costs for females in these instances should be lower than the signals that occur prepairing, because such inconspicuous signals can effectively reduce the potential predation risk for females and/or for nests, and then play an important role in promoting the evolution of both choice and the signal as revealed by our model (Figs. 1, 2, and 5). Based on this, we can deduce that if the trait were to represent the inherited high quality of females (i.e., as in a “good gene” scenario),

both male choice and female signaling will evolve more easily, because the high offspring survivability brought by the inherited high quality from  $S_2$  females can compensate to some degree for the costs of the signal.

A potential example of postpairing signal by females is bird eggs that have blue-green coloration, produced by the pigment biliverdin (Kennedy and Vevers 1976). The expression of this signal should be costly for females (Siefferman et al. 2006), due to the fact that the accumulation of these chemicals in the shell gland for coloring eggs may affect the antioxidant capacity of individual females (Moreno and Osorno 2003). However, because this color signal is expressed in the eggs, the female's potential mortality risk due to the expressed sexual signal should be lower than in species with ornamented females, from the perspective of detection by predators. Nest size has also been used as a form of signal by males in the Great Reed Warbler (*Acrocephalus arundinaceus*) (Jelínek et al. 2016), and has been indicated to have no effect on nest predation or parasitism in the field (Jelínek et al. 2015). Moreover, female feather carrying in the nest has also recently been proposed to affect male investment (García-Navas et al. 2015). This type of low-cost sexual signal should therefore facilitate the evolution of postpairing male mate choice behavior and female sexual signals in those species.

### AUTHOR CONTRIBUTIONS

N.L. and Y.H.S. designed the project, N.L. and M.S. performed research, N.L., M.S., H.L. and Y.H.S. wrote the manuscript.

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### DATA ARCHIVING

The doi for our data is 10.5061/dryad.h422c.

### LITERATURE CITED

- Amundsen, T. 2000. Why are female birds ornamented? *Trends Ecol. Evol.* 15:149–155.
- Amundsen, T., and E. Forsgren. 2001. Male mate choice selects for female coloration in a fish. *Proc. Natl. Acad. Sci. U. S. A.* 98:13155–13160.
- Andersson, M.B. 1994. *Sexual selection*. Princeton Univ. Press, Princeton, NJ.
- Barry, K. L., and H. Kokko. 2010. Male mate choice: why sequential choice can make its evolution difficult. *Anim. Behav.* 80:163–169.
- Berzins L. L., and R. D. Dawson. 2016. Experimentally altered plumage brightness of female tree swallows: a test of the differential allocation hypothesis. *Behaviour* 153:525–550.
- Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.* 76:305–339.

- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* 127:415–445
- . 1988. The differential-allocation hypothesis: an experimental test. *Am. Nat.* 132:611–628.
- Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. *Trends Ecol. Evol.* 18:41–47.
- Chenoweth, S. F., P. Doughty, and H. Kokko. 2006. Can non-directional male mating preferences facilitate honest female ornamentation? *Ecol. Lett.* 9:179–184.
- Clutton-Brock, T. H., and G. A. Parker. 1995. Punishment in animal societies. *Nature* 373:209–216.
- Domb, L. G. and M. Pagel. 2001. Sexual swellings advertise female quality in wild baboons. *Nature* 410:204–206.
- Edward, D. A., and T. Chapman. 2011. The evolution and significance of male mate choice. *Trends Ecol. Evol.* 26:647–654.
- English, P. A., and R. Montgomerie. 2011. Robin's egg blue: does egg color influence male parental care? *Behav. Ecol. Sociobiol.* 65:1029–1036.
- Fawcett, T. W., and R. A. Johnstone. 2003. Mate choice in the face of costly competition. *Behav. Ecol.* 14:771–779.
- García-Navas, V., F. Valera, and M. Griggio. 2015. Nest decorations: an 'extended' female badge of status? *Anim. Behav.* 99: 95–107.
- Hårdling, R., and H. Kokko. 2005. The evolution of prudent choice. *Evol. Ecol. Res.* 7:697–715.
- Hanley, D., and S. M. Doucet. 2009. Egg coloration in ring-billed gulls (*Larus delawarensis*): a test of the sexual signaling hypothesis. *Behav. Ecol. Sociobiol.* 63:719–729.
- Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution* 47:1515–1525.
- Honza, M., M. Požgayová, P. Procházka, and M. I. Cherry. 2011. Blue-green eggshell coloration is not a sexually selected signal of female quality in an open-nesting polygynous passerine. *Naturwissenschaften* 98:493–499.
- Hooper, P. L., and G. F. Miller. 2008. Mutual mate choice can drive costly signaling even under perfect monogamy. *Adapt. Behav.* 16:53–70.
- Houston, A.I., T. Székely, and J. M. McNamara. 2005. Conflict between parents over care. *Trends Ecol. Evol.* 20:33–38.
- Ihara, Y. 2002. A model for evolution of male parental care and female multiple mating. *Am. Nat.* 160:235–244.
- Ihara, Y., and K. Aoki. 1999. Sexual selection by male choice in monogamous and polygynous human populations. *Theor. Popul. Biol.* 55:77–93.
- Jelínek, V., M. Požgayová, and M. Honza. 2015. Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the Great Reed Warbler *Acrocephalus arundinaceus*. *Ibis* 157:396–400.
- Jelínek, V., M. Požgayová, M. Honza, and P. Procházka. 2016. Nest as an extended phenotype signal of female quality in the great reed warbler. *J. Avian Biol.* 47:428–437.
- Johnsen, A., K. Vesterkjær, and T. Slagsvold. 2011. Do male Pied Flycatchers (*Ficedula hypoleuca*) adjust their feeding effort according to egg colour? *Ethology* 117:309–317.
- Kennedy, G., and H. Vevers. 1976. A survey of avian eggshell pigments. *Comp. Biochem. Phys. B* 55:117–123.
- Kilner, R. 2006. The evolution of egg colour and patterning in birds. *Biol. Rev.* 81:383–406.
- Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Bio.* 21:919–948.
- Kokko, H., and R. A. Johnstone. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. Lond. B* 357:319–330.
- Kokko, H., and P. Monaghan. 2001. Predicting the direction of sexual selection. *Ecol. Lett.* 4:159–165.
- Kraaijeveld, K., F. J. Kraaijeveld-Smit, and J. Komdeur. 2007. The evolution of mutual ornamentation. *Anim. Behav.* 74:657–677.
- Krist, M., and T. Grim. 2007. Are blue eggs a sexually selected signal of female collared flycatchers? A cross-fostering experiment. *Behav. Ecol. Sociobiol.* 61:863–876.
- LeBas, N. R., L. R. Hockham, and M. G. Ritchie. 2003. Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proc. R. Soc. B* 270:2159–2165.
- Limbou, T., A. C. Mateman, and C. M. Lessells. 2013. Opposite differential allocation by males and females of the same species. *Biol. Lett.* 9:20120835.
- Møller, A. P. 2000. Male parental care, female reproductive success, and extrapair paternity. *Behav. Ecol.* 11:161–168.
- Magrath, M. J., and M. A. Elgar. 1997. Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc. R. Soc. B* 264:1731–1736.
- Magrath, M. J., and J. Komdeur. 2003. Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18:424–430.
- Mahr, K., M. Griggio, M. Granatiero, and H. Hoi. 2012. Female attractiveness affects paternal investment: experimental evidence for male differential allocation in blue tits. *Front. Zool.* 9:14.
- Matessi, G., C. Carmagnani, M. Griggio, and A. Pilastro. 2009. Male rock sparrows differentially allocate nest defence but not food provisioning to offspring. *Behaviour* 146:209–223.
- Moreno, J., and J. L. Osorno. 2003. Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecol. Lett.* 6:803–806.
- Moreno, J., J. Morales, E. Lobato, S. Merino, G. Tomás, and J. Martínez-de la Puente. 2005. Evidence for the signaling function of egg color in the pied flycatcher *Ficedula hypoleuca*. *Behav. Ecol.* 16:931–937.
- Nakahashi, W. 2008. Quantitative genetic models of sexual selection by male choice. *Theor. Popul. Biol.* 74:167–181.
- Pierce, E. P., and J. T. Lifjeld. 1998. High paternity without paternity-assurance behavior in the Purple Sandpiper, a species with high paternal investment. *Auk* 115:602–612.
- Pilastro, A., M. Griggio, and G. Matessi. 2003. Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment? *Anim. Behav.* 66:265–271.
- Prum, R. O. 2010. The Lande–Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. *Evolution* 64:3085–3100.
- Ratikainen, I. I. and H. Kokko. 2010. Differential allocation and compensation: who deserves the silver spoon? *Behav. Ecol.* 21:195–200.
- Roulin, A. 1999. Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behav. Ecol.* 10:688–695.
- Seki, M., J. Y. Wakano, and Y. Ihara. 2007. A theoretical study on the evolution of male parental care and female multiple mating: effects of female mate choice and male care bias. *J. Theor. Biol.* 247:281–296.
- Servedio, M. R. 2007. Male versus female mate choice: sexual selection and the evolution of species recognition via reinforcement. *Evolution* 61:2772–2789.
- Servedio, M. R. and R. Lande. 2006. Population genetic models of male and mutual mate choice. *Evolution* 60:674–685.
- Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. *Trends Ecol. Evol.* 15:397–402.
- Siefferman, L., K. J. Navara, and G. E. Hill. 2006. Egg coloration is correlated with female condition in eastern bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* 59:651–656.
- Soler, J. J., J. Moreno, J. Aviles, and A. P. Moller. 2005. Blue and green egg-color intensity is associated with parental effort and mating system in passerines: the sexual selection hypothesis. *Evolution* 59:636–644.

- South, S. H., G. Arnqvist, and M. R. Servedio. 2012. Female preference for male courtship effort can drive the evolution of male mate choice. *Evolution* 66:3722–3735.
- Symons, N., P. A. Svensson, and B. B. Wong. 2011. Do male desert gobies compromise offspring care to attract additional mating opportunities? *PLoS One* 6:e20576.
- Trivers, R. 1972. Parental investment and sexual selection. Pp. 136–179 in B. Campbell, ed. *Sexual selection and the Descent of Man 1871–1971*. Aldine, Chicago.
- Venner, S., C. Bernstein, S. Dray, and M. C. Bel-Venner. 2010. Make love not war: when should less competitive males choose low-quality but defensible females? *Am. Nat.* 175:650–661.
- Wagner, R. H., M. D. Schug, and E. S. Morton. 1996. Confidence of paternity, actual paternity and parental effort by purple martins. *Anim. Behav.* 52:123–132.

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### *Supporting Information*

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Figure S1.** Examples of the evolutionary dynamics under different recombination rates when the internal equilibrium exists.

**Figure S2.** Numerical analysis results of the stabilities of internal equilibria when  $\theta$  is a constant.

**Figure S3.** Magnified frequency dynamics of the  $P_2$  and  $S_2$  alleles and linkage disequilibrium (generations ranging from 13,500 to 15,000) under different recombination rates when the internal equilibrium exists.