The significant role of post-pairing male behavior on the evolution of male preferences and female traits

Nan Lyu\textsuperscript{1,2}, D. Justin Yeh\textsuperscript{3}, Huw Lloyd\textsuperscript{4} & Yue-Hua Sun\textsuperscript{2}

Existing sexual selection theory postulates that a sufficiently large variation in female fecundity or other direct benefits are fundamental for generating male mate choice. In this study, we suggest that, in addition to pre-pairing preferences, choosy males can also have different post-pairing behaviors, a factor which has been comparatively overlooked by previous studies. We found that both male preferences and female traits could evolve much more easily than previously expected when the choosy males that paired with unpreferred females would allocate more efforts to seeking additional post-pairing mating opportunities. Furthermore, a costly female trait could evolve when there was a trade-off between seeking additional mating and paternal care investment within social pair for choosy males. Finally, a costly male preference and a costly female trait might still evolve and reach a stable polymorphic state in the population, which might give rise to a high variability in male choice and female traits in nature. We suggest that male mate choice may be even more common than expected, which needs to be verified empirically.
In sexually reproducing species, sex roles have traditionally been labeled as female choice and male competition\(^1\). Male mate choice first drew attention from research on species with reversed sex roles in courtship and mate choice\(^3\) whereby males evolve a strategy of providing the majority of parental care investment instead of females\(^4\). An increasing number of empirical studies have shown, however, that male mate choice also exists in species with traditional sex roles\(^5,6\). Theoretically, male preferences are selected against due to the high level of competition over attractive females\(^7\)–\(^9\), with a sufficiently large variation in female fecundity and/or quality (i.e., female viability) necessary to overcome the competitive cost and generate male preferences with traditional sex roles\(^7\)–\(^9,10\). The current evolutionary theory, therefore, suggests that the conditions required for the evolution of male mate choice are much more constrained than those for the evolution of female choice\(^8\).

Very few studies have examined the possibility of male preferences driving the evolution of costly female traits\(^11\). Additionally, it has been proposed that direct fitness benefits associated with female traits (e.g., high fecundity or quality) may be essential for the evolution of female traits in nature\(^12\)–\(^16\). For example, males may show preferences for females with a large body size, which should be highly correlated with increased female fecundity\(^17\). Other empirical studies have suggested that signaling traits such as plumage coloration in birds\(^18,19\), coloration in fish\(^20\), or sexual swellings in primates\(^21\) that are related to male choice may directly indicate female quality. It is noteworthy that, in contrast to the ubiquitous female choice for male traits, there are very few empirical examples of male preferences for female traits, which we suggest may be related to the conventional mindset that a female trait can only evolve when it is correlated with fecundity or quality. In this study, we explore how the male preferences and female traits may evolve without such a limitation.

In previous sexual selection models, male mate choice has been widely assumed to take effect during the pre-pairing period, i.e., choosy males exhibit divergent mating tendencies for females with or without the preferred signaling traits\(^9\). In this case, although choosy males are more likely to mate with their preferred females, not everyone succeeds due to male–male competition\(^7\). Furthermore, the general assumption in those models has been that choosy males would show no difference in post-pairing behavior regardless of when they mate with preferred or unpreferred females. We suggest that this assumption is an unnecessarily restrictive condition applied to previous models. In many animals (e.g., in birds and mammals) the reproductive stage of the life cycle does not end at copulation as males still need to ensure their own sperm fertilizes the eggs and perhaps provide paternal care in order to acquire fitness\(^22\). However, males may be cuckolded during the post-pairing period, resulting in multiple paternity\(^23\)–\(^25\). Thus, males may face a post-pairing trade-off between seeking additional mating and investment in breeding within social pair, including mate guarding\(^26\), providing incubation feeding\(^27\), vigilance\(^28\), and different forms of paternal care\(^22\). Some empirical studies have indicated that males within a population may vary extensively in additional mating efforts\(^29\), or even have the flexibility to take the initiative to vary their effort allocation between additional mating and reproduction within social pair\(^30\). This mechanism of post-pairing male choice-generating sexual selection for female traits has comparatively seldom been studied\(^31\) or considered by theoretical models that explore the evolution of male mate choice (but see refs. \(^15,32\)).

In this study, we develop population genetic models to demonstrate that male preferences and female mating signals could evolve and be much more easily maintained than previously expected if choosy males vary in both pre- and post-mating behaviors. Specifically, we assume that when choosy males form pair bonds with the preferred females, the underlying instinctive preference would drive those males to allocate greater effort to seek additional mating post-pairing. We further show that a costly female trait could evolve from direct selection originating from a post-pairing trade-off between male strategies, and that a costly male preference can still evolve to a polymorphic equilibrium. Our models represent an important extension of existing theory, which highlights the possibility of underestimating the pervasiveness of male preferences and female traits in nature due to their detection being hindered by the polymorphism. Because only a portion of males would have preferences, detecting the preference would require a larger sample size and repeated measurements in e.g., binary choice experiments, which are commonly used to detect mating preference. Similarly, as only a portion of females would express the signal in the population, a relatively limited sample size or sampling bias along with measurement or treatment may significantly affect the empirical results (e.g.,\(^33\)), although some types of signals (e.g., plumage or coloration) may be easy to detect regardless. Perhaps the biggest challenge would be when trying to detect both the signal and the preference while the nature of the signal is uncertain (e.g., some feature of a complex vocalization). Each signal would need to be repeatedly presented to multiple males.

**Results**

**Trade-off between mate guarding and seeking additional mating**. Unlike previous modeling studies on male mate choice (e.g., refs. \(^7,9\)), we include a post-pairing stage into our population genetic models that allows choosy males to have different strategies during this period. We assume that when a female chooses a male mate, reproduction occurs during which the male mate faces different post-pairing trade-offs. We first consider an intuitive trade-off between allocating effort to seeking additional mating and defending within-pair paternity (e.g., through mate guarding\(^24,34,35\) or territory defense\(^36\)). In this model, males contribute nothing but gametes to the offspring (which can be interpreted as all males contributing equally in parental care).

We assume two loci denoted P and T in our model. The first locus P determines the male preference while T determines the expression of a female signaling trait. Specifically, we assume P2 males have a preference to mate with T2 females pre-pairing. However, it does not mean that all P2 males would mate with their preferred T2 females due to the competition with other males. And if T1 females choose to mate with P2 males, the preference for T2 females might drive those P2 males to reduce their investment in breeding within social pair (e.g., reducing their effort to mate guarding or paternal care as we explored in this study), which in turn enables them to have more effort to seeking additional matings.

We consider a post-pairing life stage similar to previous models\(^7,9\). The life cycle starts by male courtship. We assume that males with the preference P2 allele are \(1 + a\) times more likely to court preferred females (T2) than unpreferred (T1) females (at a ratio of \((1 + a)/1\), respectively). All males compete for limited mating opportunities in the population depending on their courtship efforts (see Eqs. 4, 5 in “Methods”). For analytical tractability, we assume polygyny in our model to ensure all females having equal mating success, and the females choose their mate based on the male’s courtship effort. Empirical studies have indicated that polygynous species may also engage in EPCs, causing the males to face a severe risk of cuckoldry in nature (e.g.,\(^37,38\)).

After mating, a post-pairing life stage occurs, during which both males and females may engage in EPCs. We assume the
ratios of within-pair offspring produced by females of different genotypes are determined by their male mates' mate-guarding investment. Specifically, $P_1$ males (i.e., without preferences) would allocate a fixed effort to mate guarding, by which their female mates would engage in EPCs also at a fixed probability (denoted by $a$). For those females that have EPCs, we further assume that they would produce a proportion $\beta$ of extra-pair offspring. Therefore, the female mates of $P_1$ males can produce extra-pair and within-pair offspring at expected proportions of $a\beta$ and $1 - a\beta$, respectively. For analytical simplicity, we use a parameter $\theta$ (instead of $1 - a\beta$) to represent the proportion of within-pair offspring that can be fertilized by $P_1$ males, implying that their female mates would produce a proportion $1 - \theta$ of extra-pair offspring in general. For $P_2$ males, we assume they would have a variable post-pairing behavior that depends on the phenotypes of their social mates. When they mate with unpreferred $T_1$ females, $P_2$ males are prone to reduce their mate-guarding effort to seek additional matings\textsuperscript{15}, and as a result, can only fertilize a reduced proportion ($\theta$) of within-pair offspring (see Eq. 6 in “Methods”). However, they would act in a similar way to $P_1$ males when they mate with the preferred $T_2$ females.

We also assume $P_1$ males would allocate fixed effort to seek EPCs (denoted by $e$), so do $P_2$ males when they mate with the preferred $T_2$ females. For $P_2$ males that mate with unpreferred $T_1$ females, however, they can spend additional effort (e.g., longer time and/or more energy) to seek EPCs (denoted by $e + \Delta e$), because of their reduced mate guarding investment. After within-pair and extra-pair copulations, females then begin to produce offspring. We delineate the full model construction processes and the detailed model analysis in the Methods.

Contrary to previous modeling outcomes that consider only a pre-pairing life stage\textsuperscript{7}, our model reveals a line of neutrally stable offspring. We delineate the full model construction processes and the detailed model analysis in the Methods.

Fig. 1 The stable internal equilibria of the two-locus models for the male preference $P_2$ and female trait $T_2$, allele frequencies when choosy males have a trade-off between mate guarding and seeking additional mating, a Effect of the relative increase in fitness gained from additional mating by $P_2$ males ($\frac{\Delta e}{e}$). The three lines in this graph represent different values of $\Delta e$. b Effect of different strengths of male preference ($a$). The parameters behind those lines satisfy $\frac{\Delta e}{e + \Delta e}$, where $\frac{\Delta e}{e}$ represents the relative increase in fitness gained from additional mating by $P_2$ males when they mate with unpreferred $T_1$ females, $\frac{\Delta e}{e}$ represents the relative loss of paternity. For both panels, $e = 0.8$, $\Delta \theta = 0.1$, and $\theta = 0.8$. We set $a = 1$ in (a) and $\Delta e = 0.7$ in (b). Where $\frac{\Delta e}{e}$ represents the relative increase in fitness gained from additional mating by $P_2$ males when they mate with unpreferred $T_1$ females, and $\frac{\Delta e}{e}$ represents the relative loss of paternity. The equilibria of this model represents a balance between the competition for preferred $T_2$ females, which selects against choosy $P_2$ males\textsuperscript{7}, and the selection for $P_2$ males due to their potential for increased extra-pair paternity from additional mating to outperform within-pair paternity loss when they mate with unpreferred $T_1$ females. Thus, an increased value of $\frac{\Delta e}{e}$ generally has a positive effect on the equilibrium frequencies of both the $P_2$ and $T_2$ alleles (Fig. 1a).

From condition (1), we can see that male preference ($a$) has no effect on determining the existence of stable polymorphic equilibria. However, a stronger male preference ($a$) can effectively hinder the evolution of male preference and female trait (i.e., resulting in lower equilibrium frequencies of $P_2$ and $T_2$, see Fig. 1b). Intuitively, when male preference ($a$) is stronger, the effect of direct negative selection on the male preference would be increased. Additionally, since choosy $P_2$ males will be less likely to mate with unpreferred $T_1$ females in this case (i.e., under a stronger male preference), it thus may lead to a much lower chance of benefitting from additional mating, further resulting in a reduced stable frequency of the male preference $P_2$ allele (Fig. 1b).

Simulations indicated that initial frequencies of the $P_2$ and $T_2$ alleles determine the evolutionary outcome in this basic model (Supplementary Fig. 1). The near vertical evolutionary trajectories mean that very little evolution occurs in the female $T_2$ trait allele because all females have the same mating success regardless of the locus T. The female trait evolves only because of the indirect selection from the genetic correlation between the female trait and the male preference\textsuperscript{8}, as we find that a positive linkage disequilibrium between the loci $P$ and $T$ arises soon (Supplementary Fig. 2). Furthermore, we numerically confirmed that the linkage disequilibrium between the two loci at the line of polymorphic equilibria is always positive. The alleles $P_2$ and $T_2$ (and $P_1$ and $T_1$) are therefore associated along this line. Two mechanisms contribute to this association. First, $P_2$ males show preferences to mate $T_2$ females pre-pairing, resulting in nonrandom mating (i.e., it would be more likely to have $P_2$ male-$T_2$ female pairs than random mating). Second, when $P_2$ males mate with unpreferred $T_1$ females, they would reduce their guarding effort to look for extra-pair mating, resulting in a portion of offspring produced by the social pair (i.e., $P_2$ male-$T_1$ female) being replaced by extra-pair paternity (which could be with $P_1$ males), while the $P_2$ males get a chance to produce extra-pair offspring with $T_2$ females through extra-pair mating. These two mechanisms thus enable $P_2$ males to have a higher probability of producing offspring with $T_2$ females than with $T_1$ females, resulting in the positive linkage disequilibrium.

**Trade-off between paternal care investment and seeking additional mating.** Here we also consider another possible postpairing trade-off for males, which is between seeking additional mating and providing paternal care to ensure offspring survival and quality\textsuperscript{22}. In this model, we assume males of all genotypes allocate the same effort to mate guarding, and thereby females will have the same probability to be involved in EPCs. For simplicity, we assume all females produce a proportion $\theta$ of within-pair offspring and a proportion $1 - \theta$ of extra-pair offspring. For choosy $P_2$ males, we assume they will reduce their care investment in reproduction within social pair by a proportion, $\delta$, when they mate with unpreferred $T_1$ females, which translates to a reduction in fecundity. As a trade-off, they can allocate more efforts (i.e., $e + \Delta e$) to seeking additional mating (see "Methods").
This is because under a higher frequency of the P2 allele, choosy males have a trade-off between care and seeking additional mating. a) When condition (2), i.e., \( \frac{\delta}{\theta + \delta} \) is met, the model may evolve to an equilibrium point on the line of \( t_2 = 1 \) or on the line of \( t_2 = 0 \), depending on the initial frequencies. b) When \( \frac{\delta}{\theta + \delta} \) is met, it would always evolve to an equilibrium point on the line of \( t_2 = 1 \). The arrowhead curves show the evolutionary trajectories under different initial states (\( p_2 \) and \( t_2 \) are set as 0.1, 0.5, and 0.9, respectively). We set \( \Delta e = 0.1 \) in (a) and \( \Delta e = 0.8 \) in (b). For all runs, the other parameters are: \( e = 0.8, a = 1.5, \Delta \theta = 0.1, \delta = 0.1, b = 0.8 \), and \( \theta = 0.8 \).

In this case, the T2 female trait allele is more beneficial than the T1 allele due to the fecundity selection caused by male preference, i.e., T1 females (those without the trait) will suffer from a direct fitness loss when they mate with P2 males.

In this model, we find that the male preference locus always remains polymorphic when

\[
\frac{\Delta e}{e} > \frac{b \delta \theta}{(1 + b)(1 - \theta)}
\]

is met. Moreover, the T2 female trait allele always becomes fixed within the population (Fig. 2b). Similar to the condition (1) in our first model, we can see that condition (2) also examines the fitness change in P2 males when paired with T1 females. The expression on the left-hand side represents the relative increase in extra-pair fitness due to increased effort. The expression on the right-hand side represents the relative loss in within-pair fitness due to reduced parental investment. When the condition is not met, both male preference and female trait can still evolve when the initial frequencies of the P2 and T2 alleles are relatively high (Fig. 2a). In both cases, a high frequency of preference is maintained only when both the preference and the trait alleles start at relatively high frequencies, with the preference locus evolving downward for the majority of starting conditions (Fig. 2). This is because under a higher frequency of the P2 allele, choosy males not only face stronger competition pre-pairing, but also are more likely to gain a smaller amount of fitness from additional matings due to reduced paternal care investment by the social father, while their loss of within-pair fecundity remains constant. We also find that when the condition (2) is met, the frequency of the P2 allele would generally increase under a small initial value (Fig. 2b). In this case, relatively low competition for additional mating might enable choosy P2 males to gain enough fitness from EPCs to outcompete the selection on pre-pairing mate preference and the paternity loss of within-pair fecundity.

Costly female trait can evolve in some conditions. Since expressing a signaling trait is costly to females\(^9\), we investigate whether such a costly female signal can also evolve through post-pairing behavior of choosy males. Specifically, we assume T2

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**Table 1 Detailed description of each symbol used in the models.**

| Symbols | Descriptions |
|---------|--------------|
| \(a\)  | Strength of male preference |
| \(\alpha\)  | The probability of engaging in EPCs for the female mates of P1 males |
| \(\beta\)  | The proportion of extra-pair offspring produced by those females that have engaged EPCs |
| \(\theta\)  | Proportion of within-pair offspring fertilized by all P1 males, and P2 males when they mate with preferred T2 females, which is equal to \(1 - \alpha \beta \) |
| \(\Delta \theta\)  | Reduced proportion of within-pair offspring fertilized by P2 males when they mate with unpreferred T1 females |
| \(e\)  | Effort allocated to seeking EPCs by all P1 males, and P2 males when they mate with the preferred T2 females |
| \(\Delta e\)  | Additional effort allocated to seeking EPCs by P2 males when they mate with unpreferred T1 females |
| \(\delta\)  | Coefficient of the relative effect of male investment in reproduction within social pair, compared to female (i.e., 1) |
| \(m\)  | Expected care effort of male parent |
| \(s_f\)  | Viability cost for T2 females that have the trait |
| \(s_m\)  | Viability cost for P2 males that have the preference |

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**Fig. 2 The stable equilibria for the male preference P2, and female trait T2 allele frequencies when choosy males have a trade-off between care investment and seeking additional mating.**

(a) When condition (2), i.e., \( \frac{\delta}{\theta + \delta} \) is met, the model may evolve to an equilibrium point on the line of \( t_2 = 1 \) or on the line of \( t_2 = 0 \), depending on the initial frequencies. (b) When \( \frac{\delta}{\theta + \delta} \) is met, it would always evolve to an equilibrium point on the line of \( t_2 = 1 \). The arrowhead curves show the evolutionary trajectories under different initial states (\( p_2 \) and \( t_2 \) are set as 0.1, 0.5, and 0.9, respectively). We set \( \Delta e = 0.1 \) in (a) and \( \Delta e = 0.8 \) in (b). For all runs, the other parameters are: \( e = 0.8, a = 1.5, \Delta \theta = 0.1, \delta = 0.1, b = 0.8 \), and \( \theta = 0.8 \).

**Fig. 3 The conditions required for local stability of different cases of equilibrium when males have a preference trade-off between care investment and seeking additional mating, and the female trait is costly.**

The equilibria are given in the form of \( (p_2, t_2, D) \), where \( p_2 \) and \( t_2 \) represent the frequency of the allele P2 and T2 at each equilibrium, and D represents the corresponding linkage disequilibrium. Regions indicated in blue represent the conditions for local stability of \((0, 0, O)\). Equilibrium \((1, 0, O)\) is stable in the red color region. The region indicated in yellow represents the conditions required for local stability of an equilibrium point of \( (p_2, t_2, D) \), where \( s_f < 1 - \theta \) is satisfied. The vertical black line shows the threshold value of \( \delta \) when \( s_f = 1/1 + b \).

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\( m \) represents the relative loss in within-pair fitness due to increased effort. The expression on the right-hand side represents the relative increase in extra-pair fitness due to increased effort. The expression on the left-hand side represents the relative loss in within-pair fitness due to reduced parental investment. When the condition is not met, both male preference and female trait can still evolve when the initial frequencies of the P2 and T2 alleles are relatively high (Fig. 2a). In both cases, a high frequency of preference is maintained only when both the preference and the trait alleles start at relatively high frequencies, with the preference locus evolving downward for the majority of starting conditions (Fig. 2). This is because under a higher frequency of the P2 allele, choosy males not only face stronger competition pre-pairing, but also are more likely to gain a smaller amount of fitness from additional matings due to reduced paternal care investment by the social father, while their loss of within-pair fecundity remains constant. We also find that when the condition (2) is met, the frequency of the P2 allele would generally increase under a small initial value (Fig. 2b). In this case, relatively low competition for additional mating might enable choosy P2 males to gain enough fitness from EPCs to outcompete the selection on pre-pairing mate preference and the paternity loss of within-pair fecundity.

Costly female trait can evolve in some conditions. Since expressing a signaling trait is costly to females\(^9\), we investigate whether such a costly female signal can also evolve through post-pairing behavior of choosy males. Specifically, we assume T2
females would suffer from a viability cost\textsuperscript{7}, denoted by a coefficient $s_f$. The life cycle starts with a viability selection on females (see “Methods”) and follows the same processes from the previous two models.

Firstly, the female trait allele is always lost from the population when there is a trade-off between mate guarding and seeking additional matings for choosy males (Supplementary Fig. 3). Under the trade-off between care investment within social pair and seeking additional matings, however, both male preference and the costly female trait can still be maintained polymorphically under certain parameter values. Specifically, a relatively large reduction in care investment by $P_2$ males that mate with $T_1$ females (i.e., $\delta$) and/or a low cost of female trait suffered by $T_2$ females (i.e., $s_f$) play fundamental roles in driving the evolution, i.e., requiring

$$\delta > s_f (1 + 1/b)$$

otherwise the female trait cannot evolve (Fig. 3; Supplementary Note 1). From the above condition, we can deduce that the female viability cost (i.e., $s_f$) needs to be lower than $\frac{\delta b}{1 + \theta}$, which represents the relative change of offspring produced in a single pair of $T_1$ female and $P_2$ male due to the reduction in paternal care. Under condition (3), there will always be a neutrally stable line of equilibria on $t_2 = 1$ (see Supplementary Fig. 4a), enabling the evolution of both male preference and the female trait.

Furthermore, when the relative fitness increase of $P_2$ is larger than $\frac{\delta b \theta}{1 + \theta (1 - \delta - \theta)}$ (and $s_f < 1 - \theta$ is met), the model may also reach a stable polymorphic equilibrium (the brown color region in Fig. 3a illustrates when the male preference and female trait are kept polymorphic in the population). In this instance, the evolutionary outcome is either an equilibrium point on the line of $t_2 = 1$, or the polymorphic equilibrium point, depending on the initial frequencies (Supplementary Fig. 4a).

We find that the linkage disequilibrium between the $P$ and $T$ loci is always positive at the polymorphic equilibrium (Supplementary Fig. 5). It thus represents that the alleles $P_2$ and $T_2$ (and $P_1$ and $T_1$) are still associated under the trade-off between male paternal care and seeking additional mating. Note that in this model, $P_2$ males would reduce their paternal care investment and seeking of additional mating, and both male preference and female trait are costly.

**Male mate choice with a viability cost can evolve.** The costs of preferences have long been known to influence evolutionary outcomes in sexual selection models whereby some extra benefit from mate choice is required to enable the evolution of a costly female choice\textsuperscript{40,41}. Here we also investigate whether male preference and female trait can still evolve when both are costly. For simplicity, we assume choosy $P_2$ males also suffer from a viability cost\textsuperscript{7}, denoted by a coefficient of $s_m$ and that viability selection for the male preference happens before sexual selection (see “Methods”). The subsequent sexual selection and reproduction processes are the same as the previous basic models.

Intriguingly, we found that the model may still have a stable polymorphic equilibrium under the post-pairing trade-off between care investment within social pair and seeking additional mating (Fig. 4). Similar to the model with costly female traits described in the previous section, a relatively large reduction in care investment and a very low cost of the female trait are essential in generating a polymorphic equilibrium, i.e., requiring $\delta > s_f (1 + 1/b)$, and $s_f < 1 - \theta$ (see Supplementary Note 2 for detailed conditions required for the stabilities of different equilibria). Furthermore, when the gain in fitness from additional mating is relatively large compared to the loss of within-pair paternity and viability costs, the polymorphic equilibrium would become the only stable point (illustrated by the brown color regions in Fig. 4a, b; and see Supplementary Note 2). When the cost of male preference ($s_m$) is also limited, satisfying $(1 - s_f)(1 - s_m) > \theta$, then polymorphic equilibrium can be achieved under a limited reduction in care ($\delta$), and also under a small increase in effort toward additional mating ($\Delta e$) (Fig. 4a, comparing to Supplementary Fig. 6), which should be biologically meaningful. Furthermore, either a higher proportion of paternity loss (i.e., under a smaller value of $\theta$) or lower costs to male preference ($s_m$) and/or female trait ($s_f$) can effectively extend the parameter range that favors a stable internal equilibrium generally (Supplementary Fig. 7). As before, we find that the linkage disequilibrium between the $P$ and $T$ loci is still positive at the polymorphic equilibrium (Supplementary Fig. 8). Numerical analyses also indicate that a weak male preference ($a$) can have a dramatically positive effect on the equilibrium frequency of the allele $T_2$ (Supplementary Fig. 8).
Discussion
Following the inclusion of male post-pairing behavior into our sexual selection model, we show that male preferences and female traits can evolve even without direct benefits for female traits, such as the higher female fecundity and/or quality\textsuperscript{11}. Furthermore, both costly male preference and costly female trait may evolve and remain polymorphic when choosy males face a trade-off between care investment within social pair and seeking additional mating\textsuperscript{22}. These findings suggest that male mate choice might be more common than expected in nature.

Cuckoldry (or indeed the existence of extra-pair offspring) plays a fundamental role in driving the evolution of male mate choice in our model. EPCs have long been detected in different animal taxa and mating systems, occurring in approximately 90\% of investigated avian species\textsuperscript{22}, and several other animal taxa, such as mammals (e.g., refs. 43–46), including humans\textsuperscript{17}. Therefore, considering post-pairing behavior in assessing the evolution of male mate choice should be relevant to a wide range of species. The commonly accepted principle of cuckoldry is that the social father loses some paternity but can also potentially gain some extra paternity by engaging in additional mating with females that are already paired\textsuperscript{48}. Whether cuckoldry is advantageous or disadvantageous to males thus depends on net yields\textsuperscript{15,32}.

In our models, the potential gain (and loss) are dependent on the frequencies of male preference and female trait alleles, which in turn leads to different evolutionary equilibria. On one hand, the total potential available fitness from EPCs in the population depends on the frequencies of the alleles \textit{P}_2 and \textit{T}_1, because choosy \textit{P}_2 males would either reduce mate guarding effort (resulting in an increased ratio of extra-pair offspring produced, i.e., \(1 - \theta \)) or paternal care (resulting in a smaller number of survival extra-pair offspring, i.e., \(1 + b(1 - \theta)\)). Alternatively, female ornaments have also been explained as a genetically correlated by-product of sexual selection on males\textsuperscript{39,50}. For instance, ornaments in female birds generally share the basic features of male ornaments in the same species, which may indicate a common genetic basis\textsuperscript{51}. In this case, our modeling results highlight the possibility that males may easily evolve the preferences for these by-products, allowing females to overcome the costs for expressing the ornament traits instead of evolving towards sex-specific expression. This seems to suggest that the mating preferences of the two sexes may target the same ornament\textsuperscript{52}, and that mutual mate choice may be present in sexually monomorphic species, which is not where researchers typically look for sexual selection. In reality, this pattern of subtle female ornamentation may have escaped our attention historically\textsuperscript{51}, leading to a further underestimation of the pervasiveness of male preferences in driving the evolution of costly female traits.

The evolution of male preferences may be constrained by different costs\textsuperscript{5}, such as the predation risk during mate searching and assessment, the inaccurate assessment of potential mates\textsuperscript{10}, and a low probability of future matings\textsuperscript{53}. In their sexual selection model, Servedio and Lande\textsuperscript{60} indicated that a viability cost to choosy males would accelerate the loss of the allele for male preference or prevent its spread when choosy males court more. Our results, however, reveal that both a costly male preference and costly female trait could evolve to a polymorphic equilibrium in the population (Supplementary Fig. 4b). We note that some empirical studies did find that both the abundance of female morphs and male preference varies among different populations (e.g.,\textsuperscript{54}). This is consistent with our model prediction because different populations might evolve into various polymorphic equilibria. Further empirical investigation is required to verify how widespread this possibility may be.

It is noteworthy that our model hinges on the assumption that the pre-pairing male mate choice and the post-pairing guarding behavior or the paternal care investment are determined by the same locus. While it seems reasonable to us that when a male is paired with a preferred female, he would be more likely to seek out other mating opportunities. Several recent empirical studies on birds have found that supergenes can determine the reproductive morphs or behavioral phenotypes associated with mating, e.g., in ruff (\textit{Philomachus pugnax})\textsuperscript{35,36} and white-throated sparrow (\textit{Zonotrichia albicollis})\textsuperscript{37,58}. We recommend further study focusing specifically on whether the pre-pairing choice and the post-pairing strategies are determined by the same locus, as well as theoretical studies on whether a linkage between the pre- and post-pairing behavior can evolve. Also worthy noting is that we have conservatively assumed that females cannot receive benefits from EPCs in our models according to some recent studies (e.g.,\textsuperscript{59,60}); however, if there are additional benefits for females\textsuperscript{42}, it should further promote the evolution of male preferences and female traits in our model framework.

Our results extend the current understanding of the direction of sexual selection and suggests the possibility that male preferences and female traits are more widespread in nature, only awaiting to be tested empirically. It has been suggested that in many animals cuckoldry may be an important source of selection pressure on behaviors or morphologies in both sexes\textsuperscript{15,32}, thus the mechanism proposed by our models may be relevant in many species. We suggest that understanding the evolutionary consequences of the effect of cuckoldry deserves more attention. Finally, we note that our models are framed focusing on male choice; the evolutionary dynamics of mutual mate choice considering both pre- and post-pairing behavior remains to be explored, as male and female mate choice may behave very differently in determining the evolutionary results\textsuperscript{67}. 
proportion of total surviving offspring between each genotype is therefore a female signaling trait. One locus $P$ determines a male preference, while the other, $T$, determines another preference. Simple male preferences are 0.5 between the two loci (i.e., free recombination). Recursion equations and numerical analyses of all model versions can be archived on Zenodo, https://doi.org/10.5281/zenodo.5717486. 

### Methods

#### Basic models.

We constructed a haploid two-locus population genetic model with non-overlapping generations to assess the evolution of male mate choice and a female signaling trait. One locus $P$ determines a male preference, while the other, $T$, determines another preference. Simple male preferences are 0.5 between the two loci (i.e., free recombination). Recursion equations and numerical analyses of all model versions can be archived on Zenodo, https://doi.org/10.5281/zenodo.5717486. 

#### Post-pairing trade-off between mate guarding and seeking additional mating.

During post-pairing stage, we firstly considered a trade-off between mate guarding (i.e., protecting within-pair paternity) and seeking additional mating for males. In this model, the proportions of within-pair offspring produced by females of genotype $i$ that mate with males of genotype $j$ (denoted by $\theta_{ij}$) are determined by male guarding investment, thus

$$\theta_{ij} = \theta - k \Delta \theta,$$

where $k = 1$ if $j = 3$ or 4 and $i$ is odd, otherwise $k = 0$ (see in the main text). Correspondingly, the efforts for seeking EPCs by males of genotype $j$ that mate with females of genotype $i$ are $e_{ij} = e + kAe$, where $k = 1$ if $j = 3$ or 4 and $i$ is odd, otherwise $k = 0$. We assume the fecundity benefits gained from EPCs by males of different genotypes are directly determined by their effort on seeking EPCs. Thus, the proportions of extra-pair offspring sired by males of different genotypes in the population are

$$\rho_{ij} = \frac{\sum F_{ij}}{\sum F_{ij}},$$

where $\phi_{ij}$ represents the number of surviving offspring produced by a single pair in which the male has the $i$ genotype and the female has the $j$ genotype. Note that $\phi_{ij}$ is the same for all mated pairs in this model, and thus is set to a unit (i.e., 1). The proportion of total surviving offspring between each genotype is therefore $O_1 = O_{1i} + O_{1j}$. Recombination and segregation follow mating (both within-pair and extra-pair) for two loci in haploids. Recombination ratios are assumed for simplicity to be $0.5$ between the two loci (i.e., free recombination). Recursion equations were used to compute the allele frequencies of $P$ and $T$, and the linkage disequilibria between the loci $P$ and $T$ in the next generation. Details of the recursion equations and numerical analyses of all model versions can be archived in Mathematica files on Zenodo (https://doi.org/10.5281/zenodo.5717486).

Another trade-off between paternal care and seeking additional mating. In our second post-pairing trade-off scenario for choosy males, the trade-off occurs between seeking additional mating and providing paternal care to the breeding within social pair. For analytical simplicity, we assume each female produces a proportion $\theta$ of within-pair offspring and a proportion $1 - \theta$ of extra-pair offspring. During offspring production in this model, we assume the number of surviving offspring ($\phi_{ij}$) produced by females of genotype $i$ with males of genotype $j$ is directly determined by the investment from the social parents: $\phi_{ij} = 1 + b \Delta \phi$. In this equation, 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., $b \Delta \phi$) represents the surviving offspring due to the care provided by the male parent. We can treat $b$ as a coefficient of the relative effect of male investment in reproduction within social pair, compared to female, and $\Delta \phi$ is the expected effect of male parental care.

#### Costly female trait.

In the above models, the female trait is assumed to be costly. For our next model, we would like to know whether male preferences and female traits can still evolve when such traits confer a cost to female viability. Specifically, we assume that $T_2$ females that have a trait would suffer from a viability cost (denoted by a coefficient of $e_i > 0$). Therefore, we have four updated genotype frequencies for females denoted as $x_i$ (i ranges from 1 to 4):

$$x_i = \frac{1}{1 - e_i b_{T2}},$$

where $b_{T2} = 1$ when $i$ is even, and $b_{T2} = 0$ otherwise; $x_i$ represents the allele frequency of the female trait. The viability selection happens before sexual selection and all other processes like sexual selection, recombination, and segregation are the same as our previous basic models. The two trade-offs described in the above two subsections are both considered here.

#### Costly male mate choice.

In order to investigate the effect of a cost of male preference in our model, we assume that choosy $P_2$ males would also suffer from a viability cost (denoted by a selection coefficient of $x_{P2} > 0$) during their searching for or evaluating the mates. Then, the frequency of each male genotype before sexual selection would be

$$x_i = \frac{1}{1 - e_i b_{P2}},$$

where $b_{P2} = 1$ if $j = 3$ or 4 (i.e., males have the $P_2$ allele), otherwise $b_{P2} = 0$. The sexual selection, recombination, and segregation processes are the same as our basic models. As we have found that the male trade-off between mate guarding and seeking additional mating cannot give rise to the evolution of both male choice and costly female traits (see Supplementary Fig. 3), we only considered the trade-off between paternal care and seeking additional mating in this model.

#### Reporting summary.

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

### Data availability

All material required to replicate this study is available in Zenodo, https://doi.org/10.5281/zenodo.5717486. 

### Code availability

The Mathematica code to replicate the analyses and figures has been deposited in Zenodo, https://doi.org/10.5281/zenodo.5717486. 

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