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Female resistance to sexual coercion can evolve to preserve the indirect benefits of mate choice

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Abstract

Sexual conflict over the indirect benefits of mate choice may arise when traits in one sex limit the ability of the other sex to freely choose mates but when these coercive traits are not necessarily directly harmful (i.e. forced fertilization *per se*). Although we might hypothesize that females can evolve resistance in order to retain the indirect, genetic benefits (reflected in offspring attractiveness) of mating with attractive males, up to now it has been difficult to evaluate potential underlying mechanisms. Traditional theoretical approaches do not usually conceptually distinguish between female preference for male mating display and female resistance to forced fertilization, yet sexual conflict over indirect benefits implies the simultaneous action of all of these traits. Here, we present an integrative theoretical framework that draws together concepts from both sexual selection and sexual conflict traditions, allowing for the simultaneous coevolution of displays and preferences, and of coercion and resistance. We demonstrate that it is possible for resistance to coercion to evolve in the absence of direct costs of mating to preserve the indirect benefits of mate choice. We find that resistance traits that improve the efficacy of female mating preference can evolve as long as females are able to attain some indirect benefits of mating with attractive males, even when both attractive and unattractive males can coerce. These results reveal new evolutionary outcomes that were not predicted by prior theories of indirect benefits or sexual conflict.

KEYWORDS
female preference, indirect benefits, population-genetic model, resistance, sexual conflict, sexually antagonistic coevolution, waterfowl

1 | INTRODUCTION

Sexual conflict over the indirect benefits of mate choice may be characterized by conflict arising from traits in one sex that limit the ability of the other sex to freely choose mates but which are not necessarily associated with direct harm (i.e. forced fertilization *per se*). The underlying logic is that male coercive mating behaviour should interfere with the potential indirect benefits (as realized through offspring attractiveness or quality via potential Fisherian or "good genes" effects) that females stand to gain by choosing a particular mate, and this should in turn give rise to selection for female resistance to coercion. Although this has been of interest for quite some time (Brennan & Prum, 2012; Gowaty, 1997; Gowaty & Buschhaus, 1998; Lessells, 2006; Moore & Pizzari, 2005; Parker, 1979), the mechanisms underlying the evolution of female resistance to forced fertilization, and the resulting dynamics, have been difficult to evaluate theoretically in large part due to the way that concepts of preference and resistance have been traditionally approached in the study of the evolution of female mating biases.

Preference and resistance are often considered to be "two sides of the same coin" (Kokko, 2005) because both terms are used to describe mechanisms by which a female biases mating or fertilization success towards certain males as opposed to others (Arnqvist & Rowe, 2005; Gavrilets, Arnqvist, & Friberg, 2001; Kence & Bryant, 1978; Maynard Smith, 1987). Thus, "resistance" is often considered a redundant term (Brooks & Griffith, 2010), such that the same phenomenon could be described by either "preference" or "resistance."

It follows that male mating display and coercion are also often considered to be conceptually indistinguishable (Brennan & Prum, 2012). Although a male that physically restrains a female can easily be seen as coercive, it has been argued that attractive displays can be equally coercive in a sensory bias context, particularly if it leads to harmfully high mating rates (Holland & Rice, 1998; Kokko, 2005). Further, it has also been suggested that if a male successfully coerces a female into mating, then he is "preferred" by definition (Cordero & Eberhard, 2003; Eberhard, 2002, 2005).

At the same time, the sexual conflict literature does not usually make a distinction between resistance to forced copulations to avoid direct harm and (potentially concurrent) resistance to forced fertilization itself that might mitigate only the indirect costs of coerced mating. For example, in typical sexual conflict model constructions, females may mitigate the direct harm associated with an attack by fleeing, which coincidentally eliminates the possibility of forced fertilization. Given that direct effects are generally expected to dominate indirect effects (Andrés & Morrow, 2003; Cameron, Day, & Rowe, 2003; Grafen, 1990; Iwasa, Pomiankowski, & Nee, 1991; Kirkpatrick & Barton, 1997; Kirkpatrick & Ryan, 1991), most studies of sexual conflict have therefore focused on scenarios involving the evolution of female resistance to directly harmful mating (Arnqvist & Rowe, 2005; Cameron et al., 2003; Chapman, Arnqvist, Bangham, & Rowe, 2003; Gavrilets et al., 2001; Hoyle & Gilburn, 2010; Kokko & Jennions, 2014; Rowe, Cameron, & Day, 2005). However, traits that do not stop an attack but serve to reduce the chance of forced fertilization are potentially subject to different evolutionary forces.

Up to now, it is unknown what dynamics will arise if we allow for the simultaneous expression of female preference for display and resistance to forced fertilization, along with male display and coercion. Thus, sexual conflict over indirect benefits, wherein females may evolve resistance to coercion in order to preserve the indirect benefits of mate choice for an attractive display, remains theoretically unexplored.

There are some empirical indications that treating female preference and resistance, as well as male display and coercion, as separate modalities is appropriate and could lead to a fuller understanding of the evolution of mating interactions (Brennan & Prum, 2012). Most notably, perhaps, is the example of waterfowl breeding: females in many species exercise behavioural preferences for male courtship displays, but these social choices are often subverted by violent forced copulations perpetrated by extra-pair males (McKinney, Derrickson, & Mineau, 1983). In spite of this pervasive and damaging behaviour, females are very effective (up to ~92% in Mallard, *Anas platyrhynchos*) at avoiding becoming fertilized as a result of these encounters (Evarts, 1990). In multiple lineages, females have complex vaginal structures that have co-evolved with the male phallic structures; evidence suggests that these female traits specifically function to frustrate intromission and decrease the likelihood of fertilization during forced copulation (Brennan, Clark, & Prum, 2010; Brennan et al., 2007). Evidently, in this system female preference and male mating display are distinct in modality and timing from apparent female resistance to forced fertilization and associated male coercion, but it is difficult to know how these separate phenomena may interact and evolve without an appropriate theoretical framework (Brennan & Prum, 2012).

Here, we present an integrative theoretical framework that allows for the simultaneous coevolution of displays and preferences, and of coercion and resistance. We demonstrate that it is possible for resistance to coercion to evolve in the absence of direct costs of mating to preserve the indirect benefits of mate choice. We further show, counter-intuitively, that the mechanism can function even when coercive and attractive males are not genetically distinct, and expose a previously under-appreciated role of female resistance in driving the evolution of mating interactions.

2 | THE MODEL

We developed a four-locus population-genetic model that treats female preference for a male display trait, female resistance to forced fertilization, male display and male coercive traits leading to forced fertilization as independent genetic and phenotypic traits. Although we drew some inspiration from waterfowl, the model is a general framework and is not tailored to that system's specifics.

2.1 | Genetic assumptions

For tractability, we assume a polygynous, haploid system, based largely on earlier models of sexual selection (Barton & Turelli, 1991; Kirkpatrick, 1982), expanded to incorporate four loci. All loci are autosomal, but have sex-limited expression. Females express two loci: P for mating preference and R for resistance to forced fertilization. Males express T for a display trait, and C for coercive capacity (their ability to attempt forced fertilization). Each locus has two possible alleles: T_2 males produce a display ornament whereas T_1 males do not, and C_2 males exhibit some phenotype that allows them to coerce females whereas C_1 males do not. P_2 females have a biased behavioural preference for T_2 males, whereas P_1 females mate indiscriminately with respect to the male display trait. R_2 females have some trait that lowers the fertilization success rate of coerced copulation, and R_1 females do not. If the frequencies of C_2 and R_2 are set to zero, our model equations exactly recapitulate the sexual selection model presented by Kirkpatrick (1982).

2.2 | Ecological and behavioural assumptions

We assume that the T_2 and C_2 alleles reduce male survival such that a T_2 male has a probability of (1-s_t) of surviving until the mating season relative to a T_1 male. Similarly, a C_2 male has a (1-s_c) chance of survival relative to a male with the C_1 allele. A male with both the T_2 and C_2 alleles has a survival probability of (1-s_t)(1-s_c) relative to a T_1C_1 male. As for females, the female resistance trait modelled here is analogous to a female duck's convoluted genital tract, and there is no reason to think that females with such a resistance mechanism would sustain differential direct costs to fitness from a coercive attack. Thus, viability costs due to the R_2 allele would be only in the form of the costs of developing the structure itself. Under the assumptions made in our numerical projections, we found that small costs applied to P_2 and R_2 yield qualitatively similar results to those produced when there are no costs (Figure S2); an assumption that we make of constant diversity at the T locus (see Analyses section) mimics the effects of biased mutation on the display trait, which allows costly preferences and in this case resistance to be maintained (Pomiankowski, Iwasa, & Nee, 1991). Thus, the model we present in the main text does not assume differential viability costs associated with the female-expressed P_2 and R_2 alleles, but see Appendix S1 and Figure S2 for a discussion of these effects.

After viability selection on males, mating occurs. All females have equal mating success (are ultimately fertilized by one male each), but males may mate multiply and vary in their relative success. Male relative mating success can be biased based on the combined effects of female mate choice, mate coercion and female resistance to coercion. First, females choose social partners based on their mate preference allele. Females with the P_2 allele are biased by a factor of (1 + *a*) towards choosing T_2 males that they encounter relative to the T_1 males they encounter in the population. P_1 females mate randomly with respect to the male T allele. Therefore, in this model females stand to gain indirect "Fisherian" (Fisher, 1930; Kirkpatrick, 1982) benefits of mate choice via sexually successful offspring. This is the simplest way to model indirect benefits, but the processes described in this model would apply equally within a "good genes" or "indicator trait" framework (Kokko, 2001; Kokko, Brooks, McNamara, & Houston, 2002)

Once females have chosen their social partners, but before fertilization, males with the coercive C_2 allele attempt to attack females and coerce them away from other males through forced fertilization, with the probability of these encounters being equal to the frequency of C_2 males in the population. During coercive attacks directed towards R_1 females, that is those females that lack the resistance allele, C_2 males have a probability of successful forced fertilization *b*. R_2 females have an effectiveness of resistance to forced fertilization γ, such that C_2 males have a chance of (1-γ)*b* of successfully forcing a fertilization. If $\gamma = 1$, then C_2 males never succeed with R_2 females. The definitions of terms are summarized in Table 1.

We define coercion in this model as activity that males employ that biases mating success, but that expressly acts independently of, and uninfluenced by, female-expressed mate preference. It is thus distinct from display, harmful mating *per se*, or "dominance" (e.g. Kokko, 2005). In our model, females may be able to resist an attempted forced fertilization, but they are unable to differentially resist males based on whether the male attempting the forced mating is an otherwise attractive (T_2) or unattractive (T_1) male (i.e. we assume the display is not visible or cannot be evaluated during coercion). This is a biologically realistic assumption that applies well to many taxa, where behavioural mating preference is based on the opportunity of the female to evaluate a complex mating display or experience an elaborate courtship.

TABLE 1 Summary of definitions of terms used in the four-locus population-genetic model

T_2 / T_1; t_1 / t_2	Allele for attractive display trait / allele for unattractive display trait, expressed by males; lowercase denotes the respective allele frequencies
C_2 / C_1; c_2 / c_1	Allele for the capacity to attempt forced fertilization (coercion) / allele for the lack of capacity to coerce, expressed by males; the respective allele frequencies
P_2 / P_1; p_2 / p_1	Allele for a biased behavioural mating preference for males with the T_2 allele by a factor (1 + a) / allele for unbiased mating, expressed by females; the respective allele frequencies
R_2 / R_1; r_2 / r_1	Allele for the capacity to resist attempted forced fertilization /allele for the lack of capacity to resist attempted forced fertilization, expressed by females; the respective allele frequencies
s_t	Viability cost to males with the T_2 allele of producing an attractive display trait
s_c	Viability cost to males with the C_2 allele associated with the capacity to coerce females
1 + *a*	Factor by which females with the P_2 allele prefer to mate with males having the T_2 allele
b	Likelihood of a male with the C_2 allele to succeed in forced fertilization of a female that lacks resistance (has the R_1 allele)
γ	Effectiveness of the capacity to resist attempted forced fertilization in females having the R_2 allele.

TABLE 2 Mating table

	Males			
Females	T_1C_1 …	T_1C_2 …	T_2C_1 …	T_2C_2 …
… P_1R_1	$y_1x'_1 - by_1x'_1c'_2$	$y_1x'_2 - by_1x'_2c'_2 + by_1x'_2$	$y_1x'_3 - by_1x'_3c'_2$	$y_1x'_4 - by_1x'_4c'_2 + by_1x'_4$
… P_1R_2	$y_2x'_1 - (1-\gamma)\,by_2x'_1c'_2$	$y_2x'_2 - (1-\gamma)\,by_2x'_2c'_2 + (1-\gamma)\,by_2x'_2$	$y_2x'_3 - (1-\gamma)\,by_2x'_3c'_2$	$y_2x'_4 - (1-\gamma)\,by_2x'_4c'_2 + (1-\gamma)\,by_2x'_4$
… P_2R_1	$\frac{y_3x'_1 - by_3x'_1c'_2}{z}$	$\frac{y_3x'_2 - by_3x'_2c'_2 + by_3x'_2z}{z}$	$\frac{(1+a)\,y_3x'_3 - b\,(1+a)\,y_3x'_3c'_2}{z}$	$\frac{(1+a)\,y_3x'_4 - b\,(1+a)\,y_3x'_4c'_2 + by_3x'_4z}{z}$
… P_2R_2	$\frac{y_4x'_1 - (1-\gamma)\,by_4x'_1c'_2}{z}$	$\frac{y_4x'_2 - (1-\gamma)\,by_4x'_2c'_2 + (1-\gamma)\,by_4x'_2z}{z}$	$\frac{(1+a)\,y_4x'_3 - (1-\gamma)\,b\,(1+a)\,y_4x'_3c'_2}{z}$	$\frac{(1+a)\,y_4x'_4 - (1-\gamma)\,b\,(1+a)\,y_4x'_4c'_2 + (1-\gamma)\,by_4x'_4z}{z}$

Frequencies of matings between males and females of each of the sixteen genotypes, where $z = x'_1 + x'_2 + (1+a)\,x'_3 + (1+a)\,x'_4$. Although the model follows every genotype frequency in males and females independently, to aid in interpretation of the table, each column here represents the sum of all male genotype frequencies after natural selection having the same alleles at the T and C loci. Since these traits are sex-limited, these groups of genotypes function identically in mating. x'_1 is the sum of all male genotype frequencies having the alleles T_1C_1 ($T_1C_1P_1R_1$, $T_1C_1P_1R_2$, $T_1C_1P_2R_1$ and $T_1C_1P_2R_2$). Similarly, x'_2 represents the sum of all male genotype frequencies having the alleles T_1C_2 and so on. The frequency of the C_2 allele within males, c'_2, is therefore equivalent to $(x'_2 + x'_4)$. The prime notation is a reminder that the genotype frequencies for males have already been adjusted by viability selection. Each row represents the sum of all female genotypes (unaffected by viability selection) that have the same alleles at the P and R loci. For example, y_1 is the sum of all female genotypes having the alleles P_1R_1 ($T_1C_1P_1R_1$, $T_1C_2P_1R_1$, $T_2C_1P_1R_1$ and $T_2C_2P_1R_1$).

The relative frequencies of matings between the various genotypes after mate choice, coercion and resistance are shown in Table 2. After matings are distributed, there is free recombination of alleles among gametes, yielding the genotype frequencies for the next generation. (The full model can be found in Data S1 and in the corresponding *Mathematica* notebook deposited in Dryad.)

With the model thus defined, we focus our analysis on the following two questions. First, we ask whether a rare female resistance (R_2) allele can invade the population via a genetic correlation (linkage disequilibrium) with the attractive male allele (T_2). We hypothesize that such indirect selection for resistance alleles will arise because R_2 females more reliably mate with T_2 males and thus reclaim the indirect benefits of mate choice that would otherwise have been lost due to coercion by C_2 males. Second, we ask how the strength of female preference (a), the effectiveness of coercion (b), and the effectiveness of resistance (γ) influence the conditions under which resistance will spread, and equilibrium frequencies.

2.3 | Analyses

We performed all analyses and numerical projections using *Mathematica* (Wolfram, 2013). First, we examined female resistance evolution and the structure of sexual conflict over indirect benefits arising from forced fertilization through a weak selection approximation of the model equations. Next, we explored dynamic outcomes of the full model via numerical projections. Lastly, we analysed the recursion equations of an informative subset of the model to further explore the conditions under which resistance would invade.

As we are primarily interested in the conflict arising from the subversion of existing mating preferences, and not the evolution of basic mating preference and ornament themselves, we assumed in our numerical projections that variation at the T locus is continuously maintained. To this end, the frequency of the T_2 allele is reset to its initial value at the end of every generation, whereas accrued linkage disequilibria are retained (Bank, Hermisson, & Kirkpatrick, 2012). This is analogous to considering a quantitative, multiallelic male display trait of constant variance. Keeping the T_2 allele from going to fixation prevents a shutdown of the dynamics of interest, allowing sexual selection to be ongoing as long as the P_2 allele persists in the population. This approximation thus allows processes, such as coevolution due to indirect selection related to forced fertilization by a random or unattractive mate, to proceed through the natural build-up of genetic associations between the loci. It produces similar qualitative effects to the more traditional assumption of biased mutation (examined explicitly in Appendix S2), including, incidentally, the effect that costly preferences can be maintained (Iwasa et al., 1991; Pomiankowski et al., 1991), but in this case, the goal is expressly to maintain variation.

We ran all numerical projections until genotype frequencies and linkage disequilibria were constant to seven decimal places. To avoid incorrect conclusions arising from slow convergence on an unstable point (which we occasionally observed), we then applied a small random perturbation and continued the projection until again constant to seven decimal places. (See Data S1 and S2 and corresponding *Mathematica* notebooks deposited in Dryad.)

For our numerical projections, we began with a population with diversity in both female preference and the male display trait (frequency 0.5 for both p_2 and t_2). To focus on scenarios that might demonstrate the potential for sexual conflict over indirect benefits, we only considered starting conditions and parameters such that in the absence of coercion and/or resistance, the female preference allele P_2 is favoured, and T_2 males have a mating advantage over T_1 males (Kirkpatrick, 1982). We then imagined that coercion and resistance enter the population at low frequencies (0.05 for both r_2 and c_2) and examined the effect of these introductions on the evolutionary outcomes. For a full summary of the parameter ranges investigated, see Figures 3 and S2.

3 | RESULTS

In the first section, we present an examination of a weak selection approximation of the model equations, followed by descriptions of the general model dynamics and equilibria, and finally an analysis of the invasion of female resistance.

3.1 | Weak selection approximation: Female resistance evolves as a result of conflict over indirect benefits

The complexity of the full model precludes a general analytical solution or stability analysis, but we can show the principal dynamics of the model by examining the leading terms of a weak selection approximation for the subset of the model in which all males have evolved the capacity to coerce, that is $c_2 = 1$. With coercion present, we can explore more closely the plausibility and the process of the evolution of female resistance driven by conflict over indirect benefits. (See full analysis in Data S3 and the corresponding *Mathematica* notebook in Dryad.)

For the approximation, we assumed weak selection (weak viability selection, small s_t and s_c, and weak sexual selection, small a), while allowing the effectiveness of coercion and resistance (the parameters b and γ, respectively) to remain at any strength. We determined the values of the linkage disequilibria, $\hat{D}$, between the T_2, P_2 and R_2 alleles at quasi-linkage equilibrium to the first order with respect to the selection parameters assumed to be weak:

$$\hat{D}_{TP} \approx \frac{1}{2} a p_1 p_2 t_1 t_2 \theta$$

$$\hat{D}_{TR} \approx \frac{1}{2} a b \gamma p_2 r_1 r_2 t_1 t_2$$

$$\hat{D}_{PR} \approx 0$$

and

$$\hat{D}_{TPR} \approx \frac{1}{6} a b \gamma p_1 p_2 r_1 r_2 t_1 t_2$$

where

$$\theta = \left(1 - b\left(1 - r_2 \gamma\right)\right)$$

Accordingly, we can approximate the expressions for Δt_2, Δp_2 and Δr_2 to the second order as follows (Note that terms containing $\hat{D}_{PR}$ do not appear because we have already substituted in the first-order approximation of zero for $\hat{D}_{PR}$. We use the first-order approximations for the linkage disequilibria because these terms are always multiplied by a parameter assumed to be small when they appear in the difference equations, thus generating appropriate second-order terms. See Data S3.):

$$\Delta t_{2\_approx} \approx \frac{1}{2} t_1 t_2 \left(a p_2 \theta - s_t\right) - \frac{1}{2} t_1 t_2 \left(s_t^2 t_2 + a^2 p_2 t_2 \theta + a s_t p_2 \theta \left(t_1 - t_2\right)\right)$$

$$\Delta p_{2\_approx} \approx \frac{1}{2} \hat{D}_{TP} \left(a p_2 \theta - s_t\right)$$

$$\Delta r_{2\_approx} \approx \frac{1}{2} \hat{D}_{TR} \left(a p_2 \theta - s_t\right)$$

The term shared by all three expressions, $\left(a p_2 \theta - s_t\right)$, represents, to the first-order, direct selection at the T locus. Therefore, we can see that both the female resistance and female preference (the R_2 and P_2 alleles) are subject solely to indirect selection, the magnitude of which is dictated by the linkage disequilibria between those respective alleles and the T_2 allele. Moreover, the evolutionary change in R_2 is driven by indirect selection on the same order of magnitude as the evolutionary change in P_2, with R_2 evolution governed by correlation between T_2 and R_2, whereas change in P_2 is governed by the correlation between T_2 and P_2 (the basis for classic Fisherian sexual selection; Kirkpatrick, 1982). This result implies that the evolution of resistance (R_2) via indirect selection in this system can be as important for the overall dynamics as the evolution of preference by sexual selection.

This result also clearly demonstrates the mechanism by which the resistant R_2 allele evolves. The R_2 allele increases because it

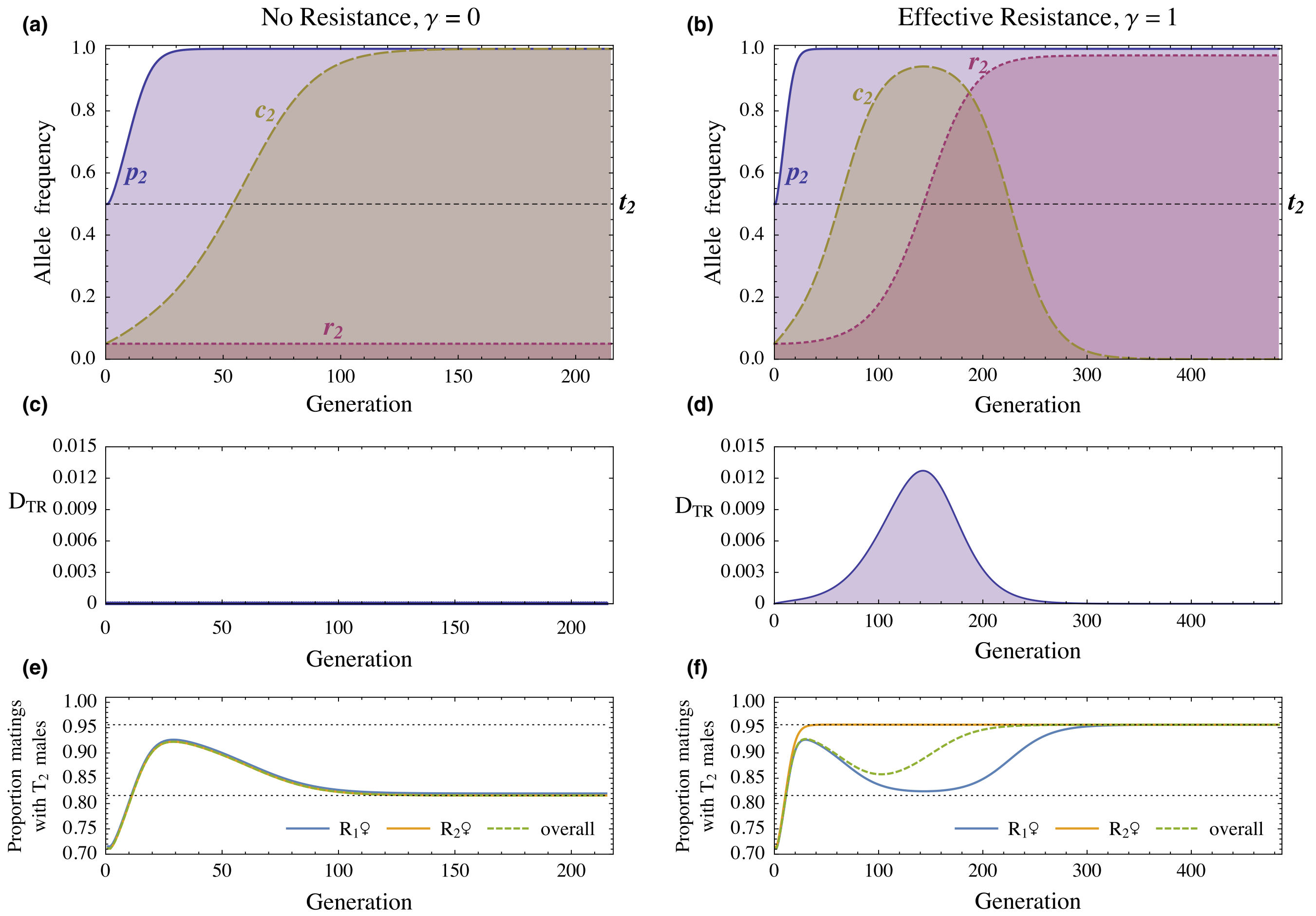

FIGURE 1 Example of numerical projections for allele frequencies (a and b), the covariance between the T_2 (attractive male display) and R_2 (female resistance) alleles, D_{TR} (c and d), the proportion of matings that are with T_2 males for nonresistant (R_1) females, for resistant (R_2) females and for matings overall (e and f), for the cases of no female resistance to forced fertilization (left panels a, c, e) and fully effective female resistance (right panels b, d, f). In both cases, initial allele frequencies are $T_2 = 0.5$, $P_2 = 0.5$, $R_2 = 0.05$ and $C_2 = 0.05$; $s_t = s_c = 0.1$, $b = 0.29$ and $a = 23$. The frequency of the allele for male attractiveness (t_2; the black dotted line in a and b) remains constant because of our assumption of maintained diversity at the T locus. Note that the number of generations to equilibrium is different for the two cases. Proportion of matings with T_2 males was calculated each generation before recombination and mutation. The upper and lower black dotted boundary lines in panels E and F represent the equilibrium proportion of matings with T_2 males for the system with free mate choice (a projection with no coercion) and restricted mate choice (a projection with coercion and no resistance), respectively. The three lines in E overlap because females do not differ in their ability to resist coercion. See Figure S3 for graphs of the remaining two-way linkages not shown here

correlates positively with the attractive T_2 allele, revealing its role in allowing females with the R_2 allele to resist coercion and more reliably retain the indirect genetic benefits of mating with T_2 males as compared to females with the R_1 allele.

At least in this scenario, resistance evolution is not correlated with a specific preference allele (the linkage disequilibrium between the P_2 and R_2 alleles, $\widehat{D}_{PR}$ is very small and negligible), and the three-way linkage ($\widehat{D}_{TPR}$, the extra association not accounted for by the pairwise linkages) does not appear in any of the second-order allele frequency expressions.

The salient θ term describes the effects of coercion and resistance on the efficacy of sexual selection by mate choice (ap_2): sexual selection is diminished by b but recovered by the effect of resistant females (r_2) and γ. Thus, in the expression for Δt_{2_approx}, we can see that for a given value of the effectiveness of coercion (b), Δt_2 will be more positive with higher frequencies of the resistant allele and the effectiveness of resistance (r_2 and γ, respectively). It is also clear that if $b = 0$, we return to basic sexual selection as modelled by Kirkpatrick (1982).

Turning to the expression for Δp_{2_approx}, we can see that r_2 and γ also play a key role in the evolution of female preference, not only due to their effect on the efficacy of sexual selection on the male attractive display trait (T_2) via the $(ap_2\theta - s_t)$ term, but also directly by increasing the magnitude of the linkage disequilibrium $\widehat{D}_{TP}$ in the face of large values of b (note the presence of θ in the expression for $\widehat{D}_{TP}$). This points plainly to the role of the R_2 allele in bolstering the efficacy of female preference.

Looking now to the expressions for Δr_{2_approx} and $\widehat{D}_{TR}$, R_2 will only evolve whether all of γ, a, p_2, b are nonzero. In other words, resistance evolution requires that the R_2 allele has any effectiveness to resist forced fertilization, female preference for display is acting, and there is successful coercion occurring in the population as a result of the proliferation of the C_2 allele.

3.2 | Numerical projections

The numerical projections of the full model (without the assumption that $c_2 = 1$) in Figure 1 demonstrate the process of the evolution of female resistance to forced fertilization by indirect selection. In the first case (Figure 1a), female resistance is completely ineffective ($\gamma = 0$), so the R_2 allele is equivalent to the nonresistant R_1 allele.

At the outset, coercion (C_2) increases and ultimately fixes in the population because coercive males gain a direct mating advantage over C_1 males (Table 2). Although attractive T_2 males are still able to retain relatively more mates, female choice is significantly subverted by coercion (Figure 1e). Females all evolve to have a preference for T_2 males (P_2 becomes fixed), but once C_2 is fixed, they are in practice often forced to mate contrary to their preference at equilibrium (Figure 1e). The sexual conflict over indirect benefits arising in this scenario would be masked in traditional theoretical formulations of the evolution of mating behaviour, since there is generally no distinction drawn between male display and coercion traits; coercion and display simply add together to dictate which males are most "attractive" (Cordero & Eberhard, 2003; Eberhard, 2002, 2005).

However, if we consider the same scenario but this time allow for an R_2 allele that is effective at resisting forced fertilization (i.e. a positive value for γ), we see that the evolution of resistance can generate an entirely different outcome (Figure 1b). As coercion begins eroding the advantage of attractive T_2 males, females with the R_2 allele can resist coercion and retain the indirect benefits of mating with T_2 males. They are more likely to mate with T_2 males than nonresistant R_1 females (Figure 1f), and therefore, R_2 becomes positively correlated with the T_2 allele, in contrast to zero correlation arising in the first case where resistance is completely ineffective (i.e. positive vs. zero linkage disequilibrium; Figure 1d,c). Resistant females have offspring that are more attractive as well as resistant to coercion, and in this case wherein γ is large, R_2 rises to the point that it is no longer advantageous for males to coerce (given the cost) and females are able to choose mates freely (Figure 1b,f).

3.3 | Evolutionary equilibria and the role of female resistance

We can learn more about the mechanism behind the evolution of resistance to forced fertilization and its implications for the system at equilibrium by looking at the final allele frequencies of a range of numerical projections. Using the same starting frequencies and values for a, s_t and s_c (Figure 1) but varying the values for the key parameters: b (the effectiveness of coercion) and γ (the effectiveness of resistance), we find that the equilibrium outcomes fall into four domains, defined by the equilibrium frequencies for P_2, C_2 and R_2 (Figure 2). We have summarized the equilibrium outcome domains of the full range of parameter values we investigated in Figure 3.

3.3.1 | Domain I: Free female choice in the absence of coercion

Domain I represents conditions where females' ability to choose preferred mates based on their behavioural preference is fully realized because coercion (the C_2 allele) fails to become established ($p_2 = 1$, $c_2 = 0$). In projections where resistance is ineffective ($\gamma = 0$), this domain is restricted to scenarios where coercion is not effective enough to increase the success of either T_1 or T_2 males, given the cost, s_c, of having the C_2 allele (Figure 2a). The C_2 allele is eliminated from the population and preference (P_2) fixes due to correlation with the display-derived mating advantage of T_2 males.

In instances where we allow R_2 females to effectively resist ($\gamma > 0$), the parameter space for the effectiveness of coercion, b, over which Domain I arises is greatly expanded to include much higher values of b that, without resistance, would otherwise have favoured the fixation of the C_2 allele (Figure 2b,c). In these cases involving larger b, coercion is initially favoured and c_2 begins to increase over time, which produces conflict over the indirect benefits of mate choice. The R_2 allele increases concurrently because resistant R_2 females are able to retain the indirect benefits of unhindered mating with an attractive T_2 male. As R_2 proliferates, it acts to reduce coercion's overall effectiveness in the population. Ultimately, just as in the example in Figure 1b, the increase in R_2 brings the system back to a state consistent with Domain I where coercion is no longer sufficiently effective to increase the success of either T_1 or T_2 males given its cost, and thus c_2 diminishes to zero at equilibrium.

Note that in Domain I, the frequency of the resistance allele, r_2, is often less than 1 at equilibrium. This clearly demonstrates the R_2 allele's specific role in mitigating conflict over the indirect benefits of mate choice arising from forced fertilization. When there is no coercion (because the coercive allele is lost), there is no longer selection to resist and r_2 ceases to evolve.

3.3.2 | Domain II: Resistance ineffective; restricted freedom of female choice due to coercion

Domain II represents conditions where females maintain a preference for attractive T_2 males, but that preference is largely circumvented by coercion against which they have no mechanism of resistance ($p_2 = 1$, $c_2 = 1$, and r_2 fails to increase; Figure 2a). This outcome is demonstrated in Figure 1(a,e): Females with the P_2 allele for preference are able to achieve some indirect benefits of mating with T_2 males, but choice based on the P_2 allele is restricted since a sizeable portion of the matings are forcibly redistributed by coercion.

As the projections indicate, and as we demonstrate in more detail analytically in Appendix S3, a Domain II outcome is only possible when the effectiveness of resistance, γ, is zero. When $\gamma > 0$, there will always be selection for R_2 to increase whenever coercion exists

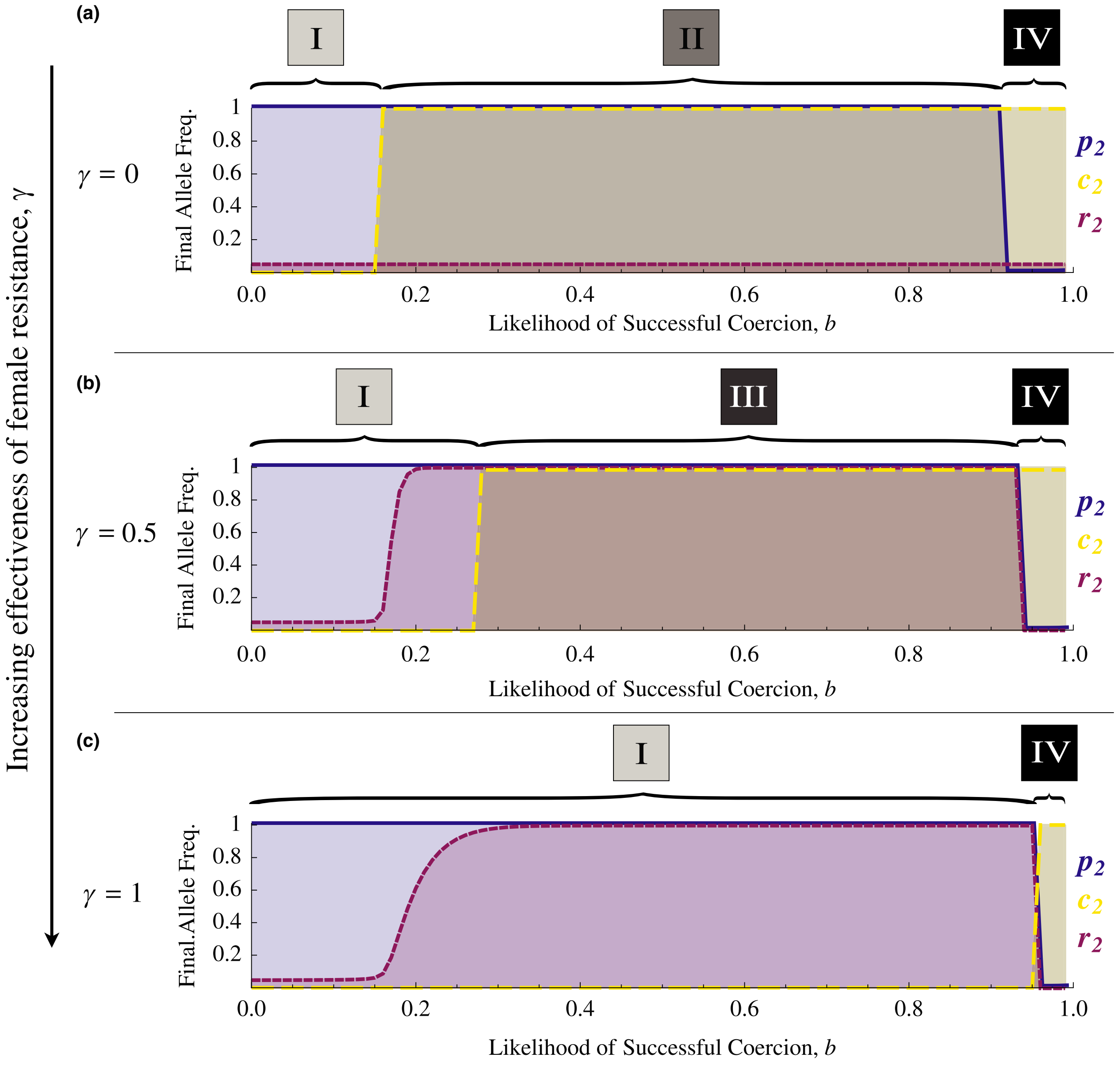

FIGURE 2 Equilibrium allele frequencies for numerical projections across values of the *b* parameter (from 0 to 1, in increments of 0.02), and for select values of increasing γ. Each vertical slice along the x-axis of each graph represents, for a particular value of *b*, the final allele frequencies for the preference (P_2), coercion (C_2) and resistance (R_2) alleles from a numerical projection of the model like the ones shown in Figure 1 (again, $s_t = s_c = 0.1$ and $a = 23$). Shaded boxes above the graphs are meant to aid in interpretation of the outcome domains: I is free female choice in the absence of male coercion; II is female preference restricted by male coercion; III is extensive reclamation of the efficacy of female preference through resistance, though coercion remains; IV is the absence of female preference and the domination of the mating system by male coercion

and the P_2 allele is favoured, indicating the presence of conflict over the indirect benefits of mate choice.

3.3.3 | Domain III: Extensive reclamation of the efficacy of female preference through resistance, though coercion remains

Domain III represents equilibrium conditions of largely, but incompletely, reclaimed freedom of female choice. Although coercion remains fixed, narrowing the gap in relative mating success between T_1 and T_2 males, females with behavioural preference for T_2 males also resist coercion, mitigating the loss of indirect benefits to the fullest extent that they can ($c_2 = 1$, $p_2 = 1$ and $r_2 = 1$). This is made possible when there is effective resistance ($\gamma > 0$; Figure 2b,c). Unlike scenarios in Domain I in which we allow $\gamma > 0$ and resistance entirely overcomes the effect of coercion, in Domain III, *b* is large enough (coercion effective enough) that all males ultimately evolve the capacity to coerce at equilibrium in spite of the effect of female resistance (and the cost of coercion, s_c).

The presence of functional resistance ($\gamma > 0$) differentiates Domain III from coercion-dominated Domain II. The R_2 allele invades because

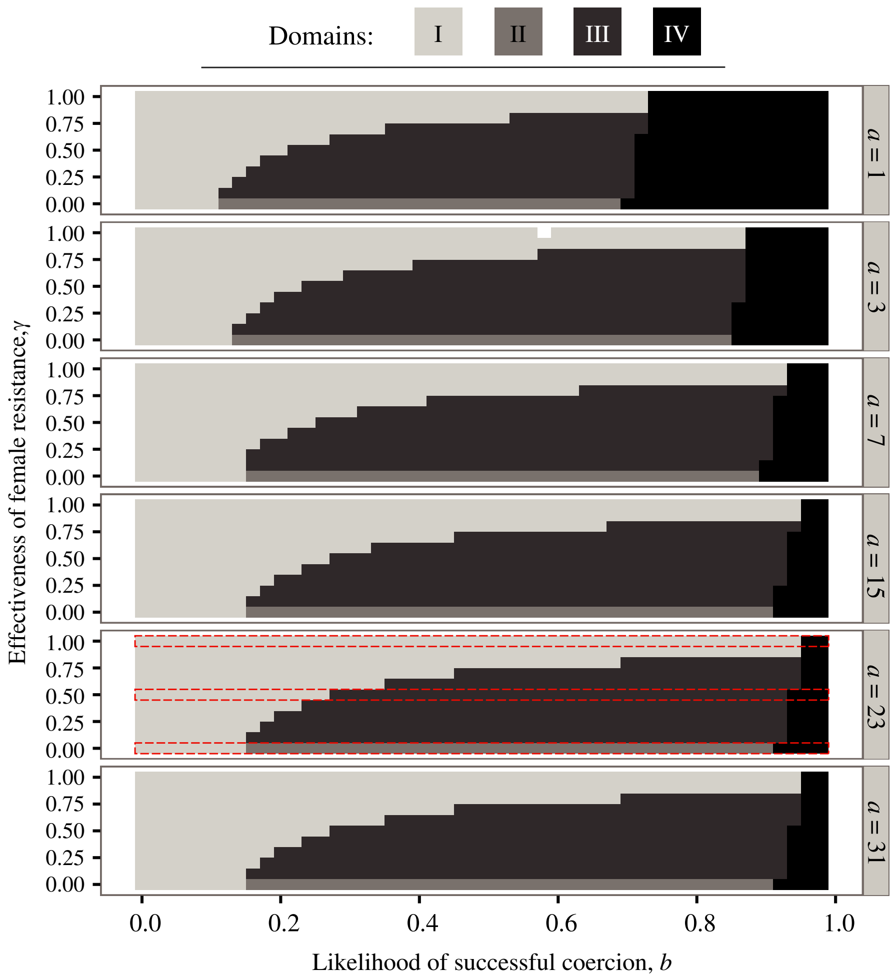

FIGURE 3 Summary of evolutionary outcome domains for numerical projections of the model across values for the parameters *a* (from the set {1, 3, 7, 15, 23, 31}), *b* (from 0 to 1, in increments of 0.02) and γ (from 0 to 1, in increments of 0.1). For all projections, initial allele frequencies are $T_2 = 0.5$, $P_2 = 0.5$, $R_2 = 0.05$ and $C_2 = 0.05$, and $s_t = s_c = 0.1$. Values for *a* for each set of projections are indicated down the right side of each panel. The red dotted rectangles indicate the three sets of results presented in detail in Figure 2. The missing tile (white space at $a = 3$, $\gamma = 1$, $b = 0.58$) is a single instance where the numerical projection went "out-of-bounds." Refer to Appendix S1 for details

females are getting their preferred male less often than they would if coercion were absent; resistance fixes in the population, mitigating the loss of indirect benefits caused by coercion and maximizing the efficacy of females' mating preferences. Domain III therefore demonstrates that in the case where females are observed to "prefer" to mate with males that are simultaneously attractive and coercive (have both the T_2 and C_2 alleles), there is indeed conflict over indirect benefits that drives the evolution of female resistance to forced fertilization.

3.3.4 | Domain IV: Female mate preference lost following the evolution of male coercion

Domain IV is defined by equilibrium outcomes in which the female preference for attractive T_2 males is evolutionarily lost ($p_2 = 0$). Here, coercion is sufficiently effective (*b* sufficiently large) to decrease the relative mating success of T_2 males such that the cost of having the T_2 allele (s_t) is no longer compensated for by the sexual selection advantage conferred by female preference. Past this threshold, there are actually indirect costs to females associated with preferring T_2 males since T_2 males have lower overall fitness than T_1 males (Figure 4b,c). Thus, females evolve to lose all mating preferences (P_2) at equilibrium (Figure 4a).

As the effectiveness of resistance (γ) increases, Domain IV becomes more restricted in parameter space (Figure 2), but within Domain IV, R_2 fails to evolve. Coercion only produces conflict over the indirect benefits of mate choice if it acts to circumvent female preference, and in Domain IV, coercion is sufficiently effective to make preference disfavoured. Resistant R_2 females mate more reliably with attractive T_2 males, but in Domain IV, this is not enough to rescue the indirect benefits of preference (Figure 4c). The possibility for sexual conflict over indirect benefits is eliminated, and resistance is lost (Figure 4a). The Domain IV outcome can be thought of as conceptually similar to the evolution of *de facto* preference for coercive males demonstrated by some previous models (Eberhard, 2002; Kokko, 2005).

3.4 | Invasion of the allele for resistance to forced fertilization

Eigenvalue analysis is inconclusive (the leading eigenvalue equals one) for this model, which precludes drawing conclusions from traditional invasion analyses. However, we can gain further insights from the scenario in which all females have a behavioural preference for mating with T_2 males, but all males use coercion as part of

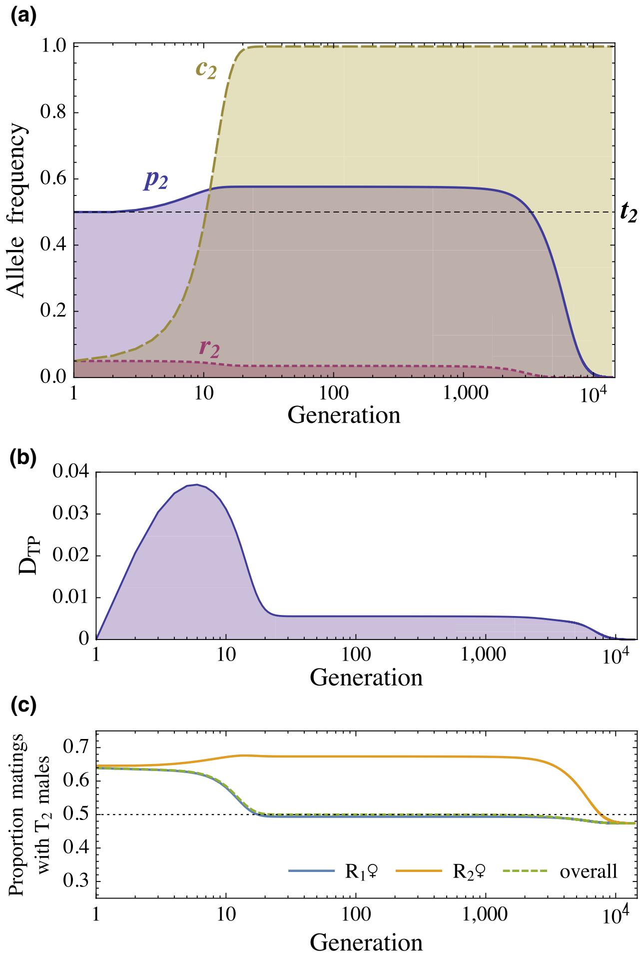

FIGURE 4 Example of a Domain IV outcome. Here, we show a numerical projection for allele frequencies (a) and the associated correlation between the T_2 (male attractive display) and P_2 (female preference) alleles, D_{TP} (b). We also show the proportion of matings with T_2 males for nonresistant (R_1) females, for resistant (R_2) females, and for matings overall (c). Male coercion (C_2) fixes quickly, whereas female preference is ultimately lost, but slowly. To show both processes, we have displayed generation time on a logarithmic scale. Initial allele frequencies are $T_2 = 0.5$, $P_2 = 0.5$, $R_2 = 0.05$ and $C_2 = 0.05$; $s_t = s_c = 0.1$, $a = 4$, $b = 0.9$ and $\gamma = 1$. Again, the frequency of t_2 remains constant because of our assumption of maintained diversity at the T locus. The black dotted line in panel C represents the 0.5 threshold at which T_1 and T_2 males have equal fitness and females mate randomly with respect to attractiveness. See Figure S4 for graphs of the remaining two-way linkages not shown here

their strategy for getting mates (c_2 and p_2 are equal to one; Domain II above). Dispensing with the assumption of constant frequency at the T locus employed in our numerical projections, we can identify conditions where coercion acts to decrease the relative mating success of T_2 males such that, given the viability selection on the T_2 allele, there will be a stable mixed equilibrium at the T locus in the absence of female resistance (Appendix S3). Simultaneously accounting for the effects of display and coercion in this way reveals sexual conflict over indirect benefits that would be unappreciated in theoretical formulations where coercion is considered indistinguishable from display. Indeed, it can be shown analytically that female resistance (the R_2 allele) will always invade in such a scenario (Appendix S3).

Essentially, coercion interferes with the efficacy of female preference. Before R_2 invades, coercion has the effect of diminishing the force of sexual selection on the male display trait, and thus, coercion restrains the T_2 allele from rising to fixation. The invasion of the R_2 allele allows females to avoid forced fertilization and reclaim indirect genetic benefits of mating with popular T_2 males. As long as females with a mating preference are able to attain some indirect benefits of mating with attractive males in the face of coercion, there will always be selection for alleles that improve females' ability to realize their preference.

3.5 | Coercive and attractive males need not be distinct

It has been hypothesized that in order for female resistance to forced fertilization to evolve, coercive males must be distinct from attractive males (Brennan & Prum, 2012). Brennan and Prum (2012) reasoned that if attractive males also act coercively, it would erase the indirect benefits to females gained by resisting forced fertilization. However, this prediction is not correct; the evolution of female resistance does not require attractive and coercive males to be completely distinct individuals.

In our model, any male with the C_2 allele has the capacity to coerce, independent of its allele at the T locus. In numerical projections, we have seen that the C_2 allele will often be fixed at equilibrium, yet in these scenarios often there is also selection favouring the evolution of female resistance.

Coercion generally diminishes the force of sexual selection by reducing the variation in mating success between male genotypes caused by female preference. As expected, because both attractive and unattractive males have the opportunity to coerce, coercion perpetrated by attractive males has the effect of bolstering mating success for T_2 males and maintaining the indirect benefits to females of preferring attractive males.

However, attractive males are also subject to the loss of mates via coercion perpetrated by unattractive males, such that they will never fully reclaim (through their own coercive behaviour) their original proportion of mates garnered through display. Thus, the inefficiency produced by coercion remains, and we find that the evolution of general resistance to forced fertilization will always be favoured in order to improve females' ability to fully realize their mating preferences (provided that the effectiveness of coercion is not sufficient to produce a Domain IV outcome).

3.5.1 | Resistance to attractive coercers

It has been further suggested that if attractive males were in fact superior at coercion compared to unattractive males, then there would never be conflict over indirect benefits since the interests of females and males would be aligned, with the effect of coercive behaviour by T_2 males simply adding to the effect of their attractive display (Getty, 1999; Kokko, 2005; Kokko, Brooks, Jennions, & Morley, 2003).

Although it would be possible for attractive T_2 males to obtain a net benefit from coercion if they were better at coercion than unattractive T_1 males, we can now see that conflict over indirect benefits will only be eliminated if the gains made by T_2 males through coercion alone are so large that they confer relatively greater mating success than would be conferred through display alone. There is a significant portion of parameter space wherein the matings lost by T_2 males due to coercion perpetrated by T_1 males are not completely made up for, even if T_2 males are superior coercers. Thus, in such cases there would continue to be selection favouring a resistance allele that allows females to mate with T_2 males in a proportion nearer to their actual preference.

We can show this analytically using the same, simpler model subset applied in our invasion analysis for R_2, where we set c_2 and p_2 equal to 1. This time, we identify specific values of the effectiveness of coercion, b: b_1 for T_1 males and b_2 for T_2 males. Now we will define a coefficient ε, the factor by which T_2 males are the superior coercers, so that $\varepsilon b_1 = b_2$, where $1 \leq \varepsilon \leq 1/b_1$ and $0 \leq b_2 \leq 1$. Analysis of the newly parameterized model equations reveals that R_2 will always invade if $(a + 1) > \varepsilon$ (Appendix S4).

This result has a very straightforward interpretation: for coercion to confer indirect benefits to attractive T_2 males such that conflict over indirect effects is eliminated and resistance does not evolve, the coefficient of superior coercion, ε, must be greater than the attractiveness coefficient $(1 + a)$. Indeed, when $1 < (a + 1) < \varepsilon$, the intermediate equilibrium for T_2 in the absence of R_2 becomes unstable, since past this threshold the effects of coercion and sexual selection are no longer in opposition. In other words, it is not enough for T_2 males to simply be the superior coercers. The benefit T_2 males get from coercing must be absolutely greater than what they would get from display alone. Otherwise, female resistance will always be favoured.

Significantly, for empiricists, this indicates that the presence of individuals that concurrently engage in, and gain success from, both display-oriented and coercive behaviours in a system by no means precludes the possibility of ongoing conflict over indirect benefits or the presence of selection for resistance to coercive acts such as forced fertilization.

4 | DISCUSSION

By modelling female preference and resistance, and male display and coercion as independent, simultaneously evolving traits, our new integrative framework demonstrates a clear and plausible mechanism for the evolution of female resistance to forced fertilization in the absence of direct harm to females via sexual conflict over indirect benefits. Coercion circumvents female mating preferences, causing females to mate (on average) with less attractive males than they would otherwise prefer. In this model, resistance evolves because females that resist forced fertilizations are better able to retain the indirect genetic benefits of mating with their preferred male.

Our model further reveals a previously unappreciated potential role for sexual conflict over indirect benefits in generating evolutionary outcomes that would have been difficult, if not impossible, to describe using traditional formulations. Rather evolving *de facto* preferences for coercive males (Kokko, 2005) or losing their mating preferences entirely (Rosenthal & Servedio, 1999; Rowe et al., 2005), females can evolve new resistance traits and mechanisms that allow them to maintain the effectiveness of mate choice. Indeed, the evolution of resistance to mitigate sexual conflict over indirect benefits can often prevent male coercion from becoming established under conditions where coercion would have otherwise evolved (Domain I; Figure 2). Resistance only fails to evolve in a very narrow band of parameter space representing very (perhaps unrealistically) high effectiveness of male coercion (Domain IV; Figure 2).

Selection for resistance will always exist when: (1) females are unable to mate with preferred males at a frequency that matches what they would obtain in the absence of coercion and (2) attractive males retain a sufficient mating advantage to overcome the viability cost of display. The evolution of resistance either results in increased effectiveness of females' preference (Domain III) or a shift in male behaviour to abandon coercion (Domain I with effective resistance ($\gamma > 0$)).

Our framework also allowed us to explicitly examine some previous verbal predictions about sexual conflict over indirect benefits and the evolution of resistance to forced fertilization. We have shown that, contrary to Brennan and Prum (2012), attractive and coercive males need not be genetically distinct in order to produce sexual conflict over indirect benefits. Our invasion analyses further reveal, contrary to previous suppositions (Getty, 1999; Kokko, 2005; Kokko et al., 2003), that female resistance will always evolve (given the conditions in the previous paragraph) even in cases where attractive males are superior coercers, as long as the mating success attractive males garner through coercion is not greater than the mating success they would have achieved through their attractive display.

Lastly, our model employs specific concepts of coercion and resistance in the context of sexual conflict over indirect benefits that will be useful from a theoretical perspective as well as for future empirical studies. Up to now, when the term "resistance" has been applied in the sexual conflict literature, it has largely meant a change in female behaviour or morphology that acts to mitigate direct costs associated with mating, either by reducing mating rate or by reducing the direct costs of mating (e.g. Rice & Holland, 1999). By treating preference and resistance as independent female traits, our model highlights an additional and distinct kind of resistance: specifically, female traits that evolve to mitigate the loss of indirect benefits arising from male traits that circumvent female choice. Similarly, coercion as treated here is distinct from display, "dominance" or "persuasion" (Eberhard, 2002; Kokko, 2005) because it only is meaningful (and only produces sexual conflict) in the context of the circumvention of an existing preference.

Our model also draws a distinction between coercion that may produce direct harm to females and the aspect of coercion that only acts to circumvent female mate choice. As we have shown, a coercive trait can be any trait that serves to circumvent an existing mating preference, giving rise to conflict over the loss of potential indirect benefits. This specific form of coercion may be concurrent with direct costs of mating to females, but not necessarily. Consider a scenario where coercive mating is directly harmful, and females evolve traditional resistance in the form of fleeing from their attackers. We do not necessarily expect females to be perfectly successful at avoiding attacks, even if all females evolve to attempt to flee. Among those females that are coerced, we predict that there will still be potential selection for a copulatory or post-copulatory resistance mechanism that allows them to retain the indirect benefits of mating with a preferred male, giving rise to dynamics that we have explored in this paper. Under our framework, this would be a five-locus model (including female resistance by fleeing), and as such, we have not undertaken such an analysis here, but exploring the intersection between traditional sexual conflict scenarios involving direct harm and our model of conflict arising from forced fertilization is a clear next step.

Taken all together, it is clear that whenever there is mate choice, there will nearly always be selection for coercion. Unattractive males will always be under pressure to circumvent female preference (using some means besides display) in order to increase their relative mating success. It is also evident that because coercion can include any mechanism that produces sexual conflict over indirect benefits, it is not limited only to obvious behaviours such as harmful physical restraint. Coercion and sexual conflict over indirect benefits are therefore likely ubiquitous, and can take many previously unexplored and less obvious forms. For example, although infanticide may be directly harmful to female fecundity, it also concurrently interferes with females' ability to have offspring sired by a particular male. Thus, infanticide may also be fruitfully examined as conflict over indirect benefits. Indeed, "friendships" between females and subordinate males have been suggested as an evolved response to mitigate infanticide in baboons, and such behaviour would easily fit the definition of a "resistance" trait in our framework (Palombit, 2009, 2014; Prum, 2017; Smuts, 1985). Competitive behaviour among males may also be construed as coercion that gives rise to sexual conflict if the effect of male–male aggressive interactions biases female matings in a direction contrary to their mating preferences (Prum, 2017). This could be a significant, yet unexplored factor in the evolution of systems where males have the opportunity to directly interfere with each other as well as with females, such as lek-breeding or harem-based systems.

There are also likely many well-studied empirical systems that bear all the hallmarks of sexual conflict over indirect benefits that been overlooked because we lacked the appropriate theoretical framework. These would include breeding systems, like waterfowl, that plausibly involve distinct, concurrent processes of male display and coercion, female preference and resistance. For example, *Calopteryx* damselflies (Odonata: Calopterygidae) have a system of male courtship display and female evaluation, but matings and subsequent oviposition are often interrupted and these choices subverted by forced mating from interloping males (Córdoba-Aguilar, 2002; Waage, 1979). Significantly, this scenario is also coupled with complex, co-evolved genital morphologies, with males apparently able to eject sperm from competing males and females coevolving genital traits to resist such attempts (Córdoba-Aguilar, 2005).

Yellow dung fly females (*Scathophaga stercoraria;* Diptera: Scathophagidae) must visit dung to oviposit, where there they encounter incessant coercive attacks from multiple competitive, territory-holding males (Sigurjonsdottir & Parker, 1981). Smaller males seek matings with females away from dung, and it has been suggested that females may behaviourally prefer these less violent males (Gress et al., 2015). Intriguingly, there is also evidence that female dung flies may exercise "cryptic choice" among males outside the context of copulation through sperm storage and selective insemination (Ward, 2000). Beyond observations of morphology and behaviour that is likely associated with sexual conflict over indirect benefits, future studies may employ pedigree analysis or experimental manipulations to disentangle the direct and indirect fitness effects of coercion and their relationships to female resistance traits.

Our finding that ongoing conflict over indirect benefits can exist when both attractive and unattractive males may coerce (even when attractive males are the superior coercers) is also significant for empiricists as it implies that sexual conflict may be playing an important role in many systems where no one would have thought to look for it before. Finally, our model suggests that resistance to coercion that circumvents preference will contribute to the strength of sexual selection due to mate choice, with important implications for the expected rate of sexual ornament elaboration within populations, and the diversity of ornaments among lineages.

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REFERENCES

Andrés, J. A., & Morrow, E. H. (2003). The origin of interlocus sexual conflict: is sex-linkage important? *Journal of Evolutionary Biology*, *16*, 219–223.

Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton, NJ: Princeton University Press.

Bank, C., Hermisson, J., & Kirkpatrick, M. (2012). Can reinforcement complete speciation? *Evolution*, *66*, 229–239.

Barton, N., & Turelli, M. (1991). Natural and sexual selection on many loci. *Genetics*, *127*, 229–255.

Brennan, P. L. R., Clark, C. J., & Prum, R. O. (2010). Explosive eversion and functional morphology of the duck penis supports sexual conflict in waterfowl genitalia. *Proceedings of the Royal Society B*, *277*, 1309–1314.

Brennan, P. L. R., & Prum, R. O. (2012). The limits of sexual conflict in the narrow sense: new insights from waterfowl biology. *Philosophical Transactions of the Royal Society B*, *367*, 2324–2338.

Brennan, P. L. R., Prum, R. O., McCracken, K. G., Sorenson, M. D., Wilson, R. E., & Birkhead, T. R. (2007). Coevolution of male and female genital morphology in waterfowl. *PLoS ONE*, *2*, e418.

Brooks, R. C., & Griffith, S. C. (2010). Mate choice. In D. F. Westneat & C. W. Fox (Eds.), *Evolutionary behavioral ecology* (pp. 416–433). Oxford, UK: Oxford University Press.

Cameron, E., Day, T., & Rowe, L. (2003). Sexual conflict and indirect benefits. *Journal of Evolutionary Biology*, *16*, 1055–1060.

Chapman, T., Arnqvist, G., Bangham, J., & Rowe, L. (2003). Sexual conflict. *Tree*, *18*, 41–47.

Cordero, C., & Eberhard, W. (2003). Female choice of sexually antagonistic male adaptations: a critical review of some current research. *Journal of Evolutionary Biology*, *16*, 1–6.

Córdoba-Aguilar, A. (2002). Wing pigmentation in territorial male damselflies, *Calopteryx haemorrhoidalis*: a possible relation to sexual selection. *Animal Behavior*, *63*, 759–766.

Córdoba-Aguilar, A. (2005). Possible coevolution of male and female genital form and function in a calopterygid damselfly. *Journal of Evolutionary Biology*, *18*, 132–137.

Eberhard, W. G. (2002). The function of female resistance behavior: intromission by coercion vs. female cooperation in sepsid flies Diptera. *Revista de Biologica Tropical*, *50*, 485–505.

Eberhard, W. G. (2005). Evolutionary conflicts of interest: are female sexual decisions different? *American Naturalist*, *165*, S19–S25.

Evarts, S. (1990). *Male reproductive strategies in a wild population of Mallards (*Anas platyrhynchos*)*. Minneapolis, MN: University of Minnesota. PhD

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford,UK: Clarendon Press.

Gavrilets, S., Arnqvist, G., & Friberg, U. (2001). The evolution of female mate choice by sexual conflict. *Proceedings of the Royal Society B*, *268*, 531–539.

Getty, T. (1999). Chase-away sexual selection as noisy reliable signaling. *Evolution*, *53*, 299–302.

Gowaty, P. A. (1997). Sexual dialectics, sexual selection, and variation in reproductive behavior. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology* (pp. 351–384). New York, NY: Chapman & Hall.

Gowaty, P. A., & Buschhaus, N. (1998). Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy. *American Zoology*, *38*, 207–225.

Grafen, A. (1990). Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology*, *144*, 473–516.

Gress, B. E., Starmer, W. T., Virgen, M. A., Agu, A., Attila, K. A., Bazluke, E. E., … Hui, B. M. (2015). Stepping off the pasture: evidence of widespread alternative male mating tactics in the yellow dung fly. *Behaviour*, *153*, 143–157.

Holland, B., & Rice, W. R. (1998). Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution*, *52*, 1–7.

Hoyle, A., & Gilburn, A. S. (2010). Sexually antagonistic co-evolution: a model and an empirical test. *Journal of Evolutionary Biology*, *23*, 166–174.

Iwasa, Y., Pomiankowski, A., & Nee, S. (1991). The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution*, *45*, 1431–1442.

Kence, A., & Bryant, E. H. (1978). A model of mating behavior in flies. *American Naturalist*, *112*, 1047–1062.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution*, *82*, 1–12.

Kirkpatrick, M., & Barton, N. (1997). The strength of indirect selection on female mating preferences. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 1282–1286.

Kirkpatrick, M., & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature*, *350*, 33–38.

Kokko, H. (2001). Fisherian and "good genes" benefits of mate choice: how (not) to distinguish between them. *Ecology Letters*, *4*, 322–326.

Kokko, H. (2005). Treat 'em mean keep 'em -sometimes keen: evolution of female preferences for dominant and coercive males. *Evolutionary Ecology*, *19*, 123–135.

Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B*, *270*, 653–664.

Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society B*, *269*, 1331–1340.

Kokko, H., & Jennions, M. D. (2014). The relationship between sexual selection and sexual conflict. In W. R. Rice & S. Gavrilets (Eds.), *The genetics and biology of sexual conflict* (pp. 23–36). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Lessells, C. M. (2006). The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B*, *361*, 301–317.

Maynard Smith, J. (1987). Sexual selection: a classification of models. In J. W. Bradbury & M. B. Andersson (Eds.), *Sexual selection: Testing the alternatives* (pp. 9–20). Chichester, UK: Wiley.

McKinney, F., Derrickson, S. R., & Mineau, P. (1983). Forced copulation in waterfowl. *Behavior*, *86*, 250–294.

Moore, A. J., & Pizzari, T. (2005). Quantitative genetic models of sexual conflict based on interacting phenotypes. *American Naturalist*, *165*, S88–S97.

Palombit, R. A. (2009). "Friendship" with males": a female counterstrategy to infanticide in chacma baboons of the Okavango Delta. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females* (pp. 377–409). Cambridge, MA: Harvard University Press.

Palombit, R. A. (2014). Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. In W. R. Rice & S. Gavrilets (Eds.), *The genetics and biology of sexual conflict* (pp. 199–228). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Parker, G. A. (1979). Sexual selection and sexual conflict. In M. S. Blum & N. A. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 123–166). New York, NY: Academic Press.

Pomiankowski, A., Iwasa, Y., & Nee, S. (1991). The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution*, *45*, 1422–1430.

Prum, R. O. (2017). *The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the animal world—and us*. New York, NY: Doubleday.

Rice, W. R., & Holland, B. (1999). Reply to comments on the chase-away model of sexual selection. *Evolution*, *53*, 302–306.

Rosenthal, G. G., & Servedio, M. R. (1999). Chase-away sexual selection: resistance to "resistance". *Evolution*, *53*, 296–299.

Rowe, L., Cameron, E., & Day, T. (2005). Escalation, retreat, and female indifference as alternative outcomes of sexually antagonistic coevolution. *American Naturalist*, *165*, S5–S18.
Sigurjonsdottir, H., & Parker, G. (1981). Dung fly struggles: evidence for assessment strategy. *Behavioral Ecology and Sociobiology*, *8*, 219–230.
Smuts, B. (1985). *Sex and friendship in baboons*. New York, NY: Aldine.
Waage, J. K. (1979). Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behavioral Ecology and Sociobiology*, *6*, 147–154.
Ward, P. I. (2000). Cryptic female choice in the yellow dung fly *Scathophaga stercoraria* (L.). *Evolution*, *54*, 1680–1686.
Wolfram, S. (2013). *Mathematica*. Champaign, IL: Wolfram Research.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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