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Female Mate Choice and the Emergence of Male Coercion

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Abstract

When females choose mates, males may respond in several ways: by allowing an evaluation by the female and investing substantially in subsequent reproduction (here, type 1); by allowing evaluation but withholding investment following mating (type 2); or by preventing evaluation and attempting to coerce the female to mate (type 3). In this modeling analysis, we examine the conditions under which these strategies, individually or in combination, are expected to persist in the population primarily using the criterion of evolutionary stability. We also consider the roles of female resistance, social policing, and extra-pair paternity in influencing these outcomes. Using six focal systems taken from primates, fish, birds, and insects, we derived parameters for a game-theoretical model to determine the expected evolutionary stable frequencies or unstable combinations of the male strategies based on system-specific parameter magnitudes. In chimpanzees, guppies, Japanese water striders, and scorpionflies, males making the highest investment in each reproductive event were the sole persisting type; in mallard ducks, an evolutionarily stable mixture of types 1 and 3 prevailed; and in humans, a stable mixture of types 1 and 2 persisted. In accord with the infrequency of consistent coercion across taxa, our results suggest that coercion may often be evolutionarily unstable and available only opportunistically as the strategy of last resort.

Key words: Comparative analysis, ESS, game theory, mating systems, rape, sexual conflict

Significance Statement

Our game theory model examined mate choice in six species of primates, fish birds, and insects to identify patterns predicted to persist from an evolutionary perspective. We found that differences in ecological, physiological and behavioral characteristics resulted in the persistence of individual or multiple male mating strategies generally consistent with observations in nature. In particular, coercive males could persist in a population when fertilization rates and reproductive outcomes were similar to those of less forceful males.

Introduction

Many mating systems across animal species in nature feature female mate choice, including choice exerted before mating (e.g. leks [Hoglund and Alatalo 1995] and female physical or social dominance [Clutton-Brock et al. 1988, 2006]) and after mating (e.g. selective sperm sequestering [Eberhard 1996] and some forms of last male precedence [Boorman and Parker 1976; Eady and Tubman 1996]). But coercive male mating is also found in many of these systems. Male coercion is common though not ubiquitous in systems with pre-mating female choice (Palmer 1989; Clutton-Brock and Parker 1995), often with effects detrimental to the female (Rowe et al. 1994; Crudgington and Siva-Jothy 2000; Stutt and Siva-Jothy 2001; Blanckenhorn 2002) and sometimes to the chance of successful reproduction from the mating (Warner et al. 1995; Dunn et al. 1999). Coercion can take the form of forced copulation, harassment, and intimidation (Clutton-Brock and Parker 1995). In some systems, male coercion may be opportunistic, expressed in individual encounters (McKinney et al. 1983; Mitani 1985; Emlen and Wrege 1986; Smuts and Smuts 1993); in some harem or despotic mating systems, coercion may be more integral to the mating system (Smuts and Smuts 1993; Marlowe 2000).

Game theory provides an appropriate theoretical framework for understanding mating systems because of the inherent mix of cooperation and conflict both within and between sexes (Maynard Smith 1977; Crowley and Hart 2007; Hart et al. 2011). The key processes of female choice among available males and competition between males for access to females (Darwin 1871; Kokko and Jennions 2008) have been well documented for many systems (Andersson 1994). But studying these processes in isolation (see Kuijper et al. 2012) or without adequate attention to internal consistency (e.g. Maynard Smith 1977; see Kokko et al. 2003 and Houston et al. 2013) may oversimplify the analysis and fail to account for important patterns. Previous

theoretical approaches to sexual coercion have simulated arms races between males and females with costs to morphological armaments (Parker 1979, 1983) or have taken a human-centric perspective to understand the causal relationships for sexual violence against women (Malamuth et al. 2003; Knight and Sims-Knight 2003).

Female choosiness incurs costs (e.g. time, risk) in the necessarily imperfect evaluation of potential benefits of a possible mate (Luttbeg 1996; Roff 2015). These benefits may be direct, such as extensive paternal care, or indirect, through good genes for offspring (Kokko et al. 2003; Kuijper et al. 2012; Roff 2015). In response to female choosiness, males may (1) devote substantial time and energy to maximize reproduction if chosen, at the possible expense of other pairing opportunities; (2) invest little in each pairing but more into increasing pairing frequency; or (3) pre-empt evaluation by the female via coercive mating, thus avoiding rejection and maximizing pairing frequency, though female resistance to coercion and other factors may reduce the likelihood of mating success. The imperfect male assessment expected when females pay a cost based on the extent of assessment and the vulnerability of females to coercion make it likely that male type (2) or (3) can persist or even dominate type (1) males in some circumstances. Here we address the interaction between optimizing the precision of female choice and determining the frequencies of competing male strategies. Our premise is that the evolutionarily stable (or unstable) outcomes of this game may account for some of the strategic patterns generated by animal species in nature.

The implications of variation in time available for mating were considered in an earlier series of studies (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Parker and Simmons 1996). These analyses showed that population mean values for relative times available for mating, along with adult sex ratio, can determine sexual selection and sexual competition (see

also Fromhage and Jennions 2016). The relationship between the survival-determined adult sex ratio and the investment (e.g. time commitment)-determined operational sex ratio is also important (Kokko and Jennions 2008). Our model incorporates these features and uses them to evaluate three key male strategies when choosy females can at least sometimes discriminate among them.

Studies of female choice to date have emphasized male ornaments (Scribner et al. 1989; Pradhan and van Schaik 2009) and their mating signals or displays (Reid et al. 2004; Mowles and Ord 2012). Though weapons used in male-male competition are sometimes used to coerce females, particularly in mammals, females may avoid using weapons as indicators of male quality because of this coercion potential (Pradhan and Van Schaik 2009). Females avoid coercion by avoiding exposure to coercive males and by directly resisting mating (Arnqvist 1992; Kokko 2005); but some males have specialized structures to facilitate coercion (Pradhan and van Schaik 2009), and in some cases females could benefit indirectly from mating with forceful males if forcefulness is heritable (Thornhill 1980b; Kokko 2005), though we do not expect these indirect benefits to recoup the direct costs of coercion (Cameron et al. 2003) and thus do not include them in this model. When evaluated by a female, males may display repeatedly to improve their chances of mating even when such signals are costly, according to a modeling study (Mowles and Ord 2012). Models have also shown that males may honestly advertise a commitment to parental care, depending on details of the ecological and social context (Kokko 1998; Alonzo 2012; Kokko et al. 2016), so females may gain valuable information by investing in assessment (Luttbeg 2004).

Our main goals in this study are to understand (1) the basic mating game between choosy females and males that differ in reproductive investment per offspring; (2) the circumstances in

this context that allow for the persistence of a coercive male mating strategy; and (3) the resemblance between patterns generated by the model, when parameterized for certain natural systems, to those observed in nature. The systems in the comparative part of our study are six species that include primates, fish, birds, and insects, chosen for taxonomic diversity and reasonable fit to the model's assumptions. We address ways that our approach may be extended to incorporate other potentially important features and species in future work.

The Model

Overview

The basic conceptual framework of the model, depicting a continuous-time mating and reproduction game between choosy females and three types of male strategies, is presented in Fig. 1. Given differences in time commitment to reproduction by males and females, in reproductive success with each male type, and in the effectiveness of discrimination, we solve the game by determining the evolutionarily stable frequencies of the male types (as opposed to traits) to be expected in the population and the optimal discrimination time. The complete mathematical derivation of the model is available in Online Resource 1, the MATLAB® program may be found on the corresponding author's website, and the required parameters are listed in Table 1. Here we summarize the logic underpinning the derivation.

In the model, available males, which collectively constitute the male pool, wait until randomly selected for evaluation by unpaired, reproductively active females. Males join the pool when they are not otherwise occupied with a female. Females prefer the male type that commits more time or other resources to the liaison and maximizes reproductive success (i.e. type 1). (We generally refer to the committed resource as time but allow in some case studies that follow for physical resources to substitute for time.) With only male types 1 and 2 present, where type 2

commits less time to the liaison, with generally less reproductive success as a result, the female may spend discrimination time t_d to improve her ability to discern the type of male she has encountered and decide whether to pair with him. Male courtship costs are included as the time spent under female discrimination, though some competition costs are included as reduced reproductive lifetimes. The female's ability to discriminate between types 1 and 2 is assumed to increase with the time spent discriminating, but with diminishing returns (see Luttbeg 1996). We assume that she chooses discrimination time t_d to maximize her fitness F_f . Coercive males (type 3), when encountering a female, bypass discrimination and force immediate mating. When the female pairs with a type i male, there is some chance the pair will break up following reproduction, $0 < b_i \leq 1$. Expected reproduction from each liaison with type i depends on the type-specific chance of fertilization γ_i and on offspring production r_i , given fertilization.

The frequencies of male types in the population f_i and the fitnesses F_i associated with each male type i combine to determine average male fitness $F_m = f_1F_1 + f_2F_2 + f_3F_3$. The male type with maximal reproductive success is assumed to increase in frequency and may thereby eliminate the other types; more than one type can persist through frequency-dependence when fitnesses are equal or when outcomes are evolutionarily unstable. A persisting mixture of male types can result from competition among individuals of pure types or from an identical probabilistic mixture of strategies expressed by all males. Proofs are provided demonstrating that neither a stable mixture of all three male types nor a continuing (unstable) sequence of replacements of one male type by another is possible under our assumptions. Relative abundances of male types in the male pool p_i determine the frequency of encounter between females and each male type. When females are discriminating, the p_i will in general differ from the frequencies of mating with each type M_i .

Fitnesses are the multiplicative product of the expected rate R_i at which females and each male type produce offspring and the expected reproductive lifetime λ_i over which reproduction occurs. Social policing, in which there is some probability x that a coercer will be apprehended and removed from the male pool following a coercive event, can effectively shorten the reproductive lifetime of type 3 males, reducing the number of forced matings and potentially eliminating these males from the population, as we demonstrate. Resistance by females themselves results in reduced magnitudes of the fertilization and reproduction parameters γ_3 and r_3 , though for simplicity we assume the cost of resistance to females is negligible.

The model also accounts for extra-pair paternity (see Kokko 1999) as a proportion of the reproduction associated with a social pair including male type i that is instead attributed to a male of type j , k_{ij} . (Note that any extra-pair reproduction within type has no effect on the model's behavior.) We assume (i) that previously mated and unmated males are equally likely to achieve copulations with females and (ii) that time expenditure on extrapair copulations for both males and females is negligible compared to expenditure on reproductive success and mate assessment.

Using MATLAB® 2015b, we solved numerically for the optimal discrimination time and for the persistent male type or types, evaluating evolutionary stability based on whether a rare male of another type reached a fitness as great or greater than the otherwise optimal (fitness maximizing) male type or combination of types. In addition to results for our best-estimate default parameter magnitudes in each case (Table 2), we evaluated outcomes across plausible ranges of all key parameter values to establish the sensitivity of results to particular magnitudes. Except for unstable combinations, we determined the stable (ESS) frequencies of persisting male types i (f_i), proportions of the male types in the male pool (p_i), proportions of mates of each male type (M_i), proportion of encountered males successfully discriminated by females (d), the time

females spent discriminating (t_d), average time of males in the male pool (τ), and the fitnesses of females (F_f) and of males (F_i).

The model produces a broad array of patterns, including both evolutionarily stable and unstable combinations of male types, depending on parameter magnitudes. These include the evolutionarily stable exclusive presence of any of the three male types, any two of the male types in either evolutionarily stable or unstable combination, and all three types in an unstable mix. Single-type outcomes imply non-invasibility by either alternative type. Persistent pairs of male types result when each can invade the other member of the pair but the excluded type cannot invade the stable pair. The pair is stable if there is a mixed ESS (or evolutionarily stable state) with both frequencies strictly between 0 and 1. The pair is unstable if the two frequencies are 0 and 1, since the eliminated member of the pair can still invade the other type on its own. Though an unstable mix of all three male types is possible, we show (see Online Resource 1) that a stable mix of all three types of males is impossible, and that an unstable repetitive sequence of one male type replacing the other is also impossible for the parameter magnitudes of interest here.

Default Outcome and the Effects of Social Policing

Key parameters in our analysis, for which we typically have only rough estimates of magnitude, are the reproductive rates per fertilization by type 2 and type 3 males, r_2 and r_3 . We therefore show most of our results along an r_2 axis (or an r_3 axis in the absence of type 2) between 0 and 1 ($= r_1$); r_3 is set to some proportion of r_2 . Other parameters are held at default values (Table 1) unless otherwise indicated. At low values of r_2 and r_3 under default conditions, the outcome is pure type 1 (Fig. 2). Intermediate values result in a stable mixture of types 1 and 2, with females using discrimination to bias mating toward type 1 in the middle part of this range. When r_2 and r_3 closely approach r_1 and r_2 approaches r_3 , the outcome becomes pure type

2. Note that over this range, the mean time in the male pool increases, as females become less available for mating than the less-encumbered males via their time commitment to reproduction, with the decreasing frequency of type 1 males. The fitness of type 3 males never emerges in this example.

We equate the fertilization and reproduction parameters for types 2 and 3 (i.e. $\gamma_3 = \gamma_2 = 0.4$ and $r_3 = r_2$) and introduce substantial extra-pair paternity by type 3 on types 1 and 2 ($k_{13} = k_{23} = 0.5$), this yields pure type 3 at the default magnitude of r_2 (Fig. 3A). But by introducing a modest level of policing, in which a coercer has some non-zero probability of being permanently removed from the male pool after coercing a female, the outcome can be altered. For this example, we suppose that each type 3 individual expects to have 20 coercive mating episodes over his lifetime ($n = 20$), and that $x = 0.18$, which means that each coercion results in an 18% chance that the coercer is apprehended and prevented from further mating. This reduces the expected number of coercive matings to about 5.6, 28% of the expected number before intervention (see the light blue line and its intersection with the red dashed line in Fig. 3B). This amounts to a reduction of the reproductive lifetime of the coercer λ_3 to 28% of its default magnitude, which returns the pattern to the stable combination of types 1 and 2 exactly as in Fig.

2. Even at only an 18% apprehension rate, policing has eliminated type 3 males from the population, indicating the potential effectiveness of this response to coercive behavior.

Model Application on Focal Systems

To compare patterns generated by the model with those found in nature, we parameterized the model for animal species with internal fertilization and that show sexually coercive behavior as a potential male strategy (see Tables 1, 2, Online Resource 2), excluding species in which male strategy shifts are strongly developmentally controlled. We identified six

species for which parameters could be estimated: Japanese water striders (*Gerris elongates*), scorpionflies (*Panorpa latipennis*), guppies (*Poecilia reticulata*), mallard ducks (*Anas platyrhynchos*), chimpanzees (*Pan troglodytes schweinfurthii*), and humans (*Homo sapiens sapiens*).

We do not claim that these parameters are full and precise explanations of these species' behavior. We use these species to indicate the applications of the model and understand the emergence of sexual coercion in variety of scenarios. We explored the sensitivity of the model to each parameter and found the model generally insensitive to small parameter changes; exceptions are noted in the text. In the event of absent or ambiguous data, we varied the parameter estimates, focusing on values most consistent with current literature. For full derivation of the parameters for these species, see Online Resource 2.

Focal Systems

Male Japanese water striders engage in one of three strategies. Type 1 males are those that defend territories, call for mates, and guard their females while they lay eggs. Type 2 males are non-territorial males that only call for mates. Type 3 males are non-territorial males that engage in forced copulations. Flexibility in mating behavior is not correlated to male morphology, and strategies vary throughout the breeding season (late March to early June), with males engaging in type 1 strategies mid-season (Hayashi 1985). There is no information on the reproductive lifetimes and on fertilization rates for each mating strategies, and these parameters were explored.

There are three mating strategies for male scorpionflies. Type 1 males guard an arthropod as a nuptial gift that the female consumes while mating. If a male cannot find an arthropod, he produces and offers a salivary mass (type 2). In the absence of both an arthropod and the ability

to produce a salivary mass, type 3 males engage in forced copulations (Thornhill 1980a, b, 1981, 1982). The amount of time a female devotes to each mating (Thornhill 1982), the number of eggs per mating (Thornhill 1982), the fertilization rates (Thornhill 1980b, 1981, 1982), and reproductive lifetimes (Thornhill 1980a, 1981) vary with male strategy.

Guppies have two different male short-term mating strategies: those that display and are chosen by females to mate (type 2) and those that engage in sneak copulations when females are unreceptive (type 3) (Liley 1966), and there is no pair fidelity. Females are receptive for the first 3-5 days after giving birth, which occurs once per month, and are subsequently unreceptive until giving birth (Liley 1966; Magurran and Nowak 1991). There is no known difference in reproductive success for type 2 and type 3 males, and these parameters were explored.

Fertilization rates vary with each strategy and predator density in the habitat (Baerends et al. 1955; Liley 1966; Pilastro et al. 2002; Magurran and Seghers 1994; Endler 1987; Rodd and Reznick 1997), and sex ratios vary with predator density (Rodd and Reznick 1997), and we explored the effect of both low and high predatory density habitats.

Chimpanzee males have three different mating strategies. Type 1 males are chosen by females as consorts, exclusively mating for an extended period while she is in estrus and providing her with resources. Type 2 males are opportunistic males that copulate with estrus females within the group. Type 3 males are possessive opportunistic males that aggressively defend estrus females from other males to mate exclusively with them for several days (Tutin 1979). Fertilization rates vary with male strategy and are estimated from the time the males spend guarding and mating with each female (Tutin 1979).

Mallard reproduction consists of long-term pairs that mate annually during the breeding season. These pairs primarily mate consensually with each other; in addition to this type 1

strategy, however, males often switch strategies and sexually coerce females mated to other males. Offspring viability (Bluhm and Gowaty 2004) and the chances of fertilization (Cunningham 2003) vary with each male strategy. Reproductive lifetimes are influenced by hunting regulations and were varied to explore this effect (Giudice 2003).

In humans, type 1 males contribute time (and other resources) to child rearing; type 2 do not contribute appreciably in this way; and type 3 males coerce females when they encounter them. Reproductive success estimates considered nuclear families, single parents, and multi-generational support (DaLeire and Kalil 2002) as well as the effects of sexual coercion on conceived offspring (see van Ee and Kleber 2013 for review). Fertilization rates are estimated according to the time committed to each male strategy, with a variety of relationships explored. Type 1 matings included established break-up rates (Kawamura 2009) and estimated conception rates (Potter and Parker 1964). Type 2 relationships included single to multiple matings incorporating female fertility variability (Wilcox et al. 1995). Type 3 fertilization rates are established empirically (Gottschall and Gottschall 2003) as are extra-pair paternity rates (Larmuseau et al. 2016). Reproductive lifetimes for type 2 and type 3 males are estimated to be progressively shorter as short-term reproductive strategies in humans are often associated with decreased reproductive lifetimes (Lalumière and Quinsey 1996; Gladden et al. 2008; Jonason et al. 2009).

Results

Japanese water striders were pure type 1 males with the default parameters for this species in the model. Unlike other water striders with coercive promiscuous mating systems (i.e. pure type 3 in the model), this species is territorial. We consider this territorial type to be type 1 via resource benefits gained (i.e. good access to suitable ovulation sites and food) by mated

females. Pure type 3 can be obtained for this species when increasing the number of extrapair fertilizations that type 3 males gain from females mated with type 1 males ($k_{13} \geq 0.34$) or when type 1 and type 3 males have equal fertilization success, parameter magnitudes that may be more consistent with other water strider species that have coercive mating systems. Changes to other parameter magnitudes had no influence.

Scorpionflies yield pure type 1 males based on the resources they provide and are similarly insensitive to the magnitudes of the other parameters. Here it is primarily the low r_3 magnitude and the shorter reproductive lifetimes of male types 2 and 3 that ensure dominance of type 1.

For guppies, in both the low and high predation regimes considered, type 2 males alone constituted the ESS; there was no type 1 to consider in this species, since all choice-based pairing is very short-term and not linked to resources. This result was insensitive to the magnitudes of r_2 , r_3 , γ_3 , and k_{23} . The male-biased adult sex ratios put other outcomes out of reach.

In mallards, in the absence of the type 2 male, there is a narrow interval of type 3 reproductive success (r_3) magnitudes with a stable mix of male types 1 and 3, including the default $r_3 = 0.74$ (Fig. 4). This result is dependent on a female-biased sex ratio ≤ 1.0 ; if instead of high female reproductive lifetimes ($\lambda_f = 1$), as estimated from data for moderately or weakly regulated duck hunting (Giudice 2003), we set $\lambda_f = 0.85$, as indicated for strictly regulated hunting (Giudice 2003), then the sex ratio becomes 1.17, and the outcome is pure type 1 males for all magnitudes of r_3 . The default magnitude $r_3 = 0.74$ results in the stable 1-3 mix for magnitudes of the extra-pair reproduction parameter for type 3 males with type-1-paired females within the range $0 \leq k_{13} \leq 0.18$, but $k_{13} > 0.18$ yields pure type 3. For $\gamma_3 < 0.27$, the ESS becomes

pure type 1. The mallard results are generally insensitive to modifications of the other parameters.

For chimpanzees, type 1 males are the ESS. This outcome was robust against substantial parameter shifts, apparently because of the long pairing interval for females with type 1 males. Obtaining the pure type 2 ESS, more consistent with the pattern in nature, requires heavy intervention such as reducing λ_3 to 0.3 (strong social policing or decreased life expectancy from higher levels of aggression) and reducing γ_1 from 0.5 to < 0.038 (presumably from intense pressure by aggressive male competitors).

For humans, default parameter magnitudes result in a stable mixture of male types 1 and 2 (Fig. 5 A-D). The results are qualitatively unchanged across a plausible range of the extra-pair reproduction parameters. The stable 1-2 mixture is the outcome for $0.09 \leq \gamma_2$, so uncertainties about the magnitude of type 2 fertilization rates (Online Resource 2) are of minor significance. The default outcome remains the stable mix of male types 1 and 2 with $\lambda_f = 0.75$ for $0.68 < \lambda_1 \leq 0.77$ (the result is pure type 2 for $0.68 \geq \lambda_1$ and pure type 1 for $\lambda_1 > 0.77$) and even with a major increase in type 3 fertilization rates (γ_3) from 0.08 to 0.4 (Fig. 5E). If type 2 pairing is very brief, comparable to type 3, then $\gamma_2 = 0.061$ (see Online Resource 2) and $t_2 = 0.5$ (as for type 3), yielding the unstable mix of types 1 and 3 at the default $r_2 = 0.9$ (Fig. 5F). Similarly, coercive types can persist in unstable mixtures in the extreme case that $\gamma_3 \geq 0.4$. Setting $r_2 > 0.99$ (i.e. nearly the same as $r_1 = 1$) shifts the ESS to pure type 2. We address $r_2 > 0.99$ and $\lambda_1 > \lambda_f$ in the Discussion. None of the other parameters have substantial effects on the patterns for humans.

Discussion

The species-specific implementations of the model are not intended as rigorous tests. Their purpose is to determine whether a simple, reproductive game among optimally choosy

females and three types of males differing in commitment to reproductive liaisons captures some of the key features and patterns found in nature. Overall, we found general agreement and gained some insight into each system, suggesting ways to follow up in future empirical or theoretical work. We summarize for each system below.

In the absence among related species of the territoriality characteristic of Japanese water striders, pairing seems unlikely, and female avoidance of males (as commonly observed in water striders—Krupa et al. 1990; Arnqvist 1992) may result in ubiquitous coercion (see the Results for this species). In nature, Japanese water strider mating behavior fluctuates based on seasonal timing. Early in the season, females mate with males displaying courtship behavior (type 2) but do not oviposit. In mid-season, males begin defending territories and courting females, which oviposit while type 1 males defend them from other males. Late in the season, coercive males begin mating opportunistically with females that are ovipositing without a male guarding them (Hayashi 1985). However, the chance of fertilization when mating at the time of oviposition is unknown. Since larger males are frequently type 1, smaller males are type 3, and medium-sized males vary their strategy throughout the breeding season (Hayashi 1985), coercive mating may have a low fertilization rate in this species, and coercion is a viable option only for males that cannot defend a territory. More exploration of this system is clearly warranted.

In scorpionflies, type 1 males should dominate the population for all realistic parameters. These results are unsurprising, as males aggressively fight for arthropod nuptial gifts (Thornhill 1980a) and resort to salivary masses or coercion only when they can provide neither of these (Thornhill 1980b). To calculate the mortality rates of the different types of males, we explored two possibilities based on two hypotheses. The first hypothesis is that coercive scorpionflies avoid the high risk of mortality associated with defending arthropods in spider webs (spiders

result in 65% of adult scorpionfly mortality) (Thornhill 1980b). The second is that coercive scorpionflies would have a higher rate of mortality because of increased male-male competition for reproductive opportunities (Thornhill 1981). We therefore ran the model twice, once with type 1 males having the lowest mortality and type 3 the highest, and again reversing type 1 and type 3 mortality rates. If type 1 scorpionfly males have the highest mortality rates, type 2 males dominate over type 1, which is not supported empirically. Evidence indicates that type 1 males are always preferred, and our results suggest that this may be, in part, due to the limited reproductive lifetime of type 3. In defending arthropods, type 1 males may be in areas where predatory spiders may attack more often. But Thornhill (1981) showed that large male scorpionflies are less likely to be killed by spiders than smaller males, so these males may be able to afford a strategy too risky for the others.

For all realistic parameters in guppies, males should always attempt to mate consensually using S-displays and only resort to coercion if this fails. These results are consistent with observations that males only resort to coercion in nature when females are unreceptive to S-displays (Magurran and Nowak 1991). Opportunistic coercion may thus be associated with very limited prospects for being chosen by a female and when the cost of attempted mating is low. This strong preference for type 2 males is seen in both high and low predation environments, which differ in sex ratios and the chances of each type of reproduction successfully fertilizing eggs. In both environments, the reproductive success of type 2 males would have to drop substantially for type 3 to invade; this is especially true in high predation environments, requiring a reproductive success of just over half that of low predation environments for type 3 invasion (low predation: 0.126, high predation: 0.072). Alternatively, if unchosen males could isolate and subject females to repeated gonopodial thrusts, this might raise $\gamma_3 > \gamma_2$ and allow this

coercive type to stably persist. More attention to the frequency of success of this coercive strategy and the fertilization frequency would be valuable for understanding its role here.

Unpaired mallard ducks establish pairs in the fall and generally retain the partner across many breeding seasons, though only females provide care for young. Coercive mating, which apparently accounts for most or all extra-pair mating, and extra-pair paternity itself, are well documented, with approximately 14% of offspring unrelated to the social male parent (Denk 2005). This is generally consistent with the stable combination of male types 1 and 3 found by the model. If the extra-pair coercion parameter k_{13} is raised from 0.14 to 0.18, the default becomes pure type 3, which suggests that active resistance by females may help keep the fertilization parameter γ_3 low enough to prevent a complete type 3 take-over. A female-biased sex ratio ensures that not all coercive matings must be extra-pair, because not all females will be tied up in long-term pairing, improving the competitiveness of coercers. Empirical work should address the role of resistance, the magnitude of the coercion parameter, and whether individuals pursue a consistent stable mixture of strategies.

For chimpanzees, the model finds that type 1 males in consortships should always be favored with the default parameter magnitudes, but in fact consortships are uncommon in nature. Aggressive male-male competition, not explicitly included in the model, and strict social policing could account for this discrepancy, as noted in Results. When a female chimpanzee nears estrus, she is followed by multiple males. Pairing to form consorts is solicited by males with particular females, but other males frequently intervene by keeping a potentially consorting pair from leaving the group. Consorts are initiated successfully only when the consorting male grooms the female and successfully leads her away from the group (her participation is consensual) (Tutin 1979). So while it is always beneficial for a male to engage in a consortship,

other males have an incentive to intervene and thus retain potential access to the female. This and further intervention to greatly reduce the incidence of coercion (i.e. policing) may account for the prevalence of non-coercive opportunistic mating (type 2) in nature.

For humans, the stable mixture of types 1 and 2 becomes pure type 1 if the reproductive lifetime of type 1 males more than slightly exceeds that of females, but we expect these lifetimes to coincide because of long-term pairing fidelity rather than because of physiological constraints on reproductive lifetime, which are generally less severe in males. Coercion persists if type 2 relationships last no longer than type 3 with $r_2 < r_1$. Better estimates of key parameters, the reproductive lifetimes λ , and the r values would considerably improve our confidence in the results obtained here. It has been postulated that offspring-rearing help provided by grandmothers and other members of close-knit communities (DaLeire and Kalil 2002) may remove the need for extensive male contributions of time and other resources. This would imply that $r_2 = r_1$ and thus that pure type 2 males constitute the ESS (Fig. 5 A-D). This result is consistent with an expected shift to low-commitment paternity when such male contributions are not required. In the case that type 2 males closely resemble type 3 in having only a very brief (though consensual) pairing interval, the resulting much reduced fertilization parameter $\gamma_2 = 0.061$ shifts the outcome to favor coercers in an unstable mixture with type 1 at the default r_2 magnitude. Thus when a consensual mating type focuses only on very short-term relationships, this can facilitate the persistence of coercers in the system.

General Conclusions

We have shown that a simple game-theoretic mating model based on choosy females and three male types differing in response to individual reproductive liaisons can produce persistence of all possible individual male types and combinations of types, though the combinations may be

unstable. In some circumstances, females will spend time at the expense of reproduction on discriminating between types, mating with the more desirable type and rejecting the less desirable type; but female choice and male competition often result in single male types and some stable combinations in which spending time on discrimination is non-optimal. This framework incorporates many key features of mating games in nature and encouraged us to compare model outcomes to observed natural patterns for diverse taxa that fit the assumptions relatively well.

In varying the parameters of interest, we found that relative magnitudes across male strategies of the parameters for fertilization rate given mating γ_i and reproductive success given fertilization r_i played the most prominent role in the emergence of male coercion. Varying the magnitudes of other parameters generally contributed less to the persistence of male strategies, though unbalanced sex ratios resulting from sex-specific differences in reproductive lifetime also shifted outcomes in some cases (e.g. guppies, scorpionflies). Better documented assessments of the success of alternative male mating behaviors (e.g. for guppies and Japanese water striders) and of the effectiveness of female resistance against coercion (e.g. mallards) would be particularly valuable in making more robust predictions about the emergence of male coercion.

For some species, some of the model's parameters can be found in the published literature, particularly the six focal species investigated here. In four of these six species (Japanese water striders, scorpionflies, guppies, and chimpanzees), female mate choice tends to result in evolutionarily stable male strategies of one dominant type. These outcomes are biased by females through their effect on fertilization and reproduction parameters γ_i and r_i toward high investment in reproduction by males (generally type 1, but type 2 when pairing intervals are

particularly short and type 1 is not found). In another case (humans), male types 1 and 2 form a stable mixture. The coercive male type persists in stable combination in the mallard duck system.

Coercion (type 3) is observed but relatively uncommon across taxa in nature. The model suggests one possible explanation for this: coercion may tend to be evolutionarily unstable, and that instability may be facilitated by female resistance and social policing. Usually coercion is associated with a reduced chance of fertilization (sometimes greatly reduced, though humans [Gottschall and Gottschall 2003] and some birds [D.F. Westneat, personal communication] appear to be exceptions) and commonly with a reduced reproductive success per fertilization. The potentially offsetting advantages—bypassing female mate choice, reduced investment in offspring after mating, reduced exposure to predators—have not been shown to be especially important in the systems of interest here. Coercion may tend to be the “best of a bad job”; when choice-related mating prospects are unusually bleak, this may be the best possible response, though we do not directly address this in our model (see Luttbeg 2004). (Note that the fitness of type 3 in humans is only modestly below that of types 1 and 2 at the default magnitude in Fig. 5D, perhaps keeping coercers within range when opportunities arise.) When male quality is only partially correlated with strategy and is detectable by females, a scenario not addressed in the present study, lower quality males may be the most likely to resort to coercion—despite evidence to the contrary in humans, where coercive males typically report more sexual partners than non-coercive males (Kanin 1985; Malamuth et al. 1991; Lalumière et al. 1996). While coercion could be, and in human studies often is, explained as pathological, the focus here is on evolutionary explanations and the ecological conditions that contribute to the emergence of coercion. Conclusions concerning coercion lacking an evolutionary perspective will likely be incomplete and applications of such less effective.

To the extent that coercion is heritable and a liability for males through effective resistance or policing, avoidance of mating with such males would be favorable because sons would be coercive and pay such costs (Pradhan and van Schaik 2009). However, if heritable coercion is effective at increasing the mating rate, then it should be tolerated and possibly even sought by females (Kokko 2005). Even if evolutionarily unstable, coercion might be a “spillover” consequence of maximizing mating opportunities, for which males are strongly selected (Johnson 2001; Johnson and Sih 2005). The fertilization probability γ_i may be positively related to insistence for type i males, creating a trade-off that merits investigation in future work.

We included no cost of policing in our model but note that if there is a significant cost, then a society in which coercers exist in the absence of policing may cycle between adequate and inadequate policing. As coercers appear, policing may increase to eliminate them at a cost; as coercers are eliminated, policing diminishes to reduce the cost, and coercion may reappear, and so on. Policing cycles may be detectable in human societies and perhaps some other primates.

Testable Hypotheses and Future Directions

We have identified several avenues for building on the model in future work, including additional focus on female resistance (Kokko et al. 2003), policing, and a possible trade-off between fertilization success and male insistence that may result in coercion as a spillover strategy. Many of the ways forward would involve structuring the model around a more accurate depiction of a particular species (e.g. incorporating condition-dependence, male-male aggression into male strategies in chimpanzees, or allowing for best-of-a-bad-job opportunistic coercion in humans). More detailed information about the array of male strategies to be found in individual populations would be particularly valuable and may result in a broader array of discrete strategies or a continuous distribution along a strategy axis. Our hope is that the more general

model presented here will spark follow-up analyses that cede as little generality as possible in exchange for the deeper insights about particular species that may come from more mechanistic approaches and greater biological realism.

Our examination of focal systems has suggested testable hypotheses and other avenues for future research in understanding their mating systems. Coercion may be a viable strategy in guppies if type 3 males concentrate their reproductive efforts on the same female in an environment where she can be sequestered, thereby increasing coercive fertilization rates to surpass type 2 males. In our model, consorts are always favored in chimpanzees; we hypothesize that male-male aggression and social policing account for the dominance of short-term consensual mating, and we propose future models incorporate competition where appropriate. We predict that coercion is more frequent in Japanese water striders when habitat conditions impede a territorial male's ability to isolate and defend females, resulting in extensive extra-pair paternity (high k_{13}); more data on fertilization rates associated with the alternative strategies would be valuable in understanding this system.

Female resistance to coercion should be detectable in mallards via mechanisms to reduce fertilization success in coercive matings. Though difficult to test, we hypothesize that scorpionflies avoid extrapair copulation because, in doing so, the type 2 and 3 males would have higher reproductive success (via k_{12} or k_{13}) and potentially stabilize in the population. In human societies, we predict a positive relationship between the frequency of very brief consensual relationships (and the accompanying low fertilization rate) and coercive relationships.

By applying a game-theory approach to a wide range of model systems in which coercive strategies appear, we found that the fertilization rate and reproductive success given fertilization are the most significant predictors of sexually coercive behavior. In several species, these values

can be mediated through social policing and female reproductive decisions. A greater understanding of these values and their application may allow greater insight into the prevention of sexually coercive behavior in humans.

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Compliance with Ethical Standards

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Figure Legends

Fig. 1 Males spend time τ in the male pool before being selected by a female or before initiating coercion. Females visit the male pool, pick a random male, and, when both male types 1 and 2 (but not 3) are present, evaluate him for an optimal time t_d . If recognized, type 2 males are generally rejected, and the female picks another male for evaluation. The chance that the female encounters and reproduces with the favorable (1) or unfavorable (2) male type also depends on the respective frequencies of the types in the male pool p_i and probabilities of successful fertilization given mating γ_i . Females invest time t_f in each round of reproduction and then wait time t_n before either becoming fertilizable (and returning to the pool to choose a male) or reproducing again with the same male if the pairing persists (with probability $1-b_i$). Males invest time t_i in the mating or, if the pairing persists wait $t_f + t_n$ with the female before reproducing again. For coercive (type 3) males, $t_d = d(t_d) = 0$, $b_3 = 1$, and $t_3 \approx 0$. Females paired with a male of type i may conduct some fraction $f_j k_{ij}$ of their reproduction with type j via extra-pair mating, redistributing fitness between the two male types without influencing total fitness

Fig. 2 Default run of the model, with parameter magnitudes as in Table 1.

- A. The population is pure type 1 for low r_2 and r_3 and pure type 2 for high r_2 and r_3 . The type 3 reproduction parameter $r_3 = 0.8r_2$ along the abscissa (vertical dashed line). From approximately $r_2 = 0.27$ to 0.95 , there is a stable mix of the two types, dominated by type 1 with the help of discrimination until r_2 exceeds about 0.77 , above which there is no discrimination, and type 2 becomes more abundant. Above about $r_2 = 0.95$, the population abruptly becomes pure type 2.

- B. Here, M_1 and M_2 are the proportions of type 1 and 2 males mated by females; p_1 and p_2 are the proportions of these two types in the male pool, illustrating the discrimination bias when compared against M_1 and M_2 . The proportion of encounters in which the two types were successfully distinguished is the black line d . Within the stable mixture interval, $t_d = d(t_d) = 0$ for approximately r_2 0.27 to 0.37. But between approximately 0.37 and 0.77, $d > 0$, and female discrimination biases mating frequencies toward type 1 males.
- C. Time in the male pool is low for pure type 1 males, increases with the proportion of type 2 in a stable mixture, and is maximized for pure type 2. Discrimination times increase with r_2 and follow the pattern of d in panel B.
- D. Consistent with the other results, fitness of type 1 males is highest below about $r_2 = 0.27$; fitnesses of types 1 and 2 are equal from 0.27 to 0.95; and fitness of type 2 is highest above 0.95. Type 3 never achieves sufficient fitness to invade successfully. Female fitness and overall male fitness follow the magnitudes of the highest male types

Fig. 3 A modification of the default model and the impact of policing.

- A. Frequencies of male types vs the magnitude of reproductive success of type 2 males for the default case of Table 1, except with γ_3 increased from 0.1 to 0.4, $r_3 = r_2$, and $k_{13} = k_{23} = 0.5$. The result is pure type 1 for $r_2 \leq 0.0098$; a stable mixture of types 1 and 3 for $0.098 < r_2 \leq 0.43$; and pure type 3 for $0.43 < r_2 \leq 1$. Pure type 3 is the default outcome. This is used to consider the implications of policing for the presence and behavior of type 3 males.
- B. The proportion p_C of the expected number of lifetime coercive events that occur for different levels of policing (x) and different expected numbers of coercive events (n). The four lines correspond to $n = 5$ (green), 20 (light blue), 100 (blue), and 1000 (black). The

red dashed line marks an example magnitude of $x = 0.18$, an 18% chance that a coercer is apprehended after a coercive event. This level of policing results in reduced expected numbers of lifetime coercions per type 3 individual: 3.5 for $n = 5$, 5.5 for $n = 20$, 5.6 for $n = 100$, and 5.6 for $n = 1000$. (Note that as $n \rightarrow \infty$, the number of lifetime coercions $C \rightarrow 1/n$.) Policing not only reduces those expected numbers but can also eliminate type 3 from the population. Type 3 is eliminated, causing the pattern to revert to that of Fig. 2, for cases with $x \geq 0.18$ or $n \geq 20$

Fig. 4 Mallard ducks, with parameters as in Table 2 except that $\lambda_f = 1$. At the default magnitude of $r_3 = 0.74$, there is a stable mixture of male types 1 and 3, with about 96% type 1. The frequencies of the two types are sensitive to the magnitude of r_3 . “Default magnitudes” here are those for mallards in Table 2.

- A. Type 1 alone is the ESS below $r_3 = 0.54$. The type 1 frequency gradually and then rapidly declines for higher r_3 , reaching zero at about $r_3 = 0.78$, above which type 3 alone is the ESS.
- B. In contrast to the frequencies in panel A, the mating proportions with the two male types shift almost linearly with r_3 over the interval of the stable 1-3 mixture. Proportions of mated only diverge from proportions in pool when discrimination is successful.
- C. Time spent in the male pool is low for pure type 1, increases with r_3 for the shifting mating proportions in the interval of the stable 1-3 mixture, and then is maximal for pure type 3. There is no discrimination in the absence of type 2 males.
- D. The fitness magnitudes are consistent with the three ESS intervals: type 1, types 1 and 3, and type 3. For the mixed ESS, the green line covers the blue line

Fig. 5 Humans, with parameters as in Table 2 in panels A-D, and with altered parameters in panels E and F, produce a stable mixture of male types 1 and 2 for the default magnitude of r_2 . The default magnitude of $r_2 = 0.9$ is indicated by the vertical dashed line. The type 3 reproduction parameter $r_3 = 0.9r_2$ along the abscissa (vertical dashed line).

- A. On this frequency graph, type 1 males dominate for r_2 magnitudes below the disappearance of discrimination above 0.81, above which discrimination ceases. For r_2 magnitudes below about 0.06, pure type 1 is the ESS; there is a very short interval around $r_2 = 0.06$ with an unstable mix of types 1 and 2, which appears as a vertical spike on panels A-D; for $0.06 \leq r_2 < 0.1$, there is a stable mix of male types 1 and 2, with no discrimination; and for $0.1 \leq r_2 < 0.81$, the stable mix of types 1 and 2 persists, but with active discrimination by females in favor of type 1. For $0.81 \leq r_2 < 0.98$, including the default magnitude $r_2 = 0.9$, there is again a stable combination of types 1 and 2 without discrimination. For $r_2 > 0.98$, the ESS is pure type 2.
- B. Here, M_1 and M_2 are the proportions of males mated by females of types 1 and 2; p_1 and p_2 are the proportions of these two types in the male pool, illustrating the discrimination bias when compared against M_1 and M_2 . The proportion of encounters in which the two types were successfully discriminated is the black line d .
- C. The optimal discrimination time t_d increases with r_2 over the discrimination interval. The waiting time τ is lowest for pure type 1 and increases with the proportion of type 2.
- D. Fitnesses are consistent with the regions most clearly indicated in panel B. For $0.06 \leq r_2 < 0.98$, the red type 2 line coincides with and covers the blue type 1 line.
- E. In this case, $\gamma_3 = 0.4$ instead of the human default value $\gamma_3 = 0.08$, with all other parameters at default. Several new regions appear, but the default outcome is unchanged.

For $0 \leq r_2 \leq 0.068$, the ESS is pure type 1. Within $0.068 < r_2 \leq 0.080$, there is an unstable mixture of all three male types. For $0.080 < r_2 < 0.120$, the ESS is the stable mixture of types 1 and 2. Between $r_2 = 0.120$ and 0.792 is another unstable mix of all three male types. For $0.792 \leq r_2 \leq 0.990$ is another stable mixture of types 1 and 2 containing the default magnitude of r_2 ; for $0.990 \leq r_2 \leq 1$, pure type 2 is the ESS.

- F. With $\gamma_2 = 0.061$ and $t_2 = 0.5$ instead of the default magnitudes $\gamma_2 = 0.44$ and $t_2 = 1$, the pattern is completely altered. For $0 < r_2 \leq 0.294$, pure type 1 is the ESS; but for $0.294 < r_2 \leq 0.836$, there is an unstable mixture of types 1 and 3, dominated by type 1, indicated by the orange line at 0.9. For $0.836 < r_2 \leq 0.996$, there is still an unstable mixture of types 1 and 3, but now dominated by type 3, indicated by the orange line at 0.1 and containing the default magnitude of $r_2 = 0.9$. For $0.996 < r_2 \leq 1$, the ESS is pure type 3

Table 1 Parameters of Model

<u>Symbol</u>	<u>Definition</u>	<u>Default Magnitude and Units</u>
r_1	Reproduction from fertilization by a type 1 male	1 unit of reproduction
r_2	Reproduction from fertilization by a type 2 male	0.6 units of reproduction
r_3	Reproduction from fertilization by a type 3 male	0.48 units of reproduction
t_f	Time female spends in a reproductive event	12 time units
t_n	Time female is not in estrus per reproductive cycle	1 time unit
t_1	Time type 1 male spends in a reproductive event	12 time units
t_2	Time type 2 male spends in a reproductive event	1 time unit
t_3	Time type 3 male spends in a reproductive event	0.001 time units
b_1	Break-up probability after mating with type 1 male	0.5
b_2	Break-up probability after mating with type 2 male	1
b_3	Break-up probability after mating with type 3 male	1
D	Exponential discrimination parameter	3 (time units) ⁻¹
γ_1	Chance mating with type 1 results in fertilization	1
γ_2	Chance mating with type 2 results in fertilization	0.4
γ_3	Chance mating with type 3 results in fertilization	0.1
λ_f	Relative duration of female reproductive lifetime	1

Table 1 Parameters of Model, continued

<u>Symbol</u>	<u>Definition</u>	<u>Default Magnitude and Units</u>
λ_1	Relative duration of type 1 reproductive lifetime	1
λ_2	Relative duration of type 2 reproductive lifetime	1
λ_3	Relative duration of type 3 reproductive lifetime	1
ω	Choice function exponent for undiscriminated males	0
k_{12}	Fraction of type 1 paternity cuckolded by type 2	0
k_{13}	Fraction of type 1 paternity cuckolded by type 3	0
k_{23}	Fraction of type 2 paternity cuckolded by type 3	0

Table 2 Comparison of Six Mating Systems

Species	Mating System	Female Choice	Male Types	Altered Parameters ¹	Outcome ²
Humans <i>Homo sapiens</i>	Mutual-choice pairing with extra-pair mating	Inspection: physical and behavioral	1: Long-term investment, fidelity 2: Short-term investment 3: Negligible investment, coercion	$r_2=0.9, r_3=0.81, t_f=36,$ $t_1=36, t_3=0.5, t_n=0.8, b_1=0.06,$ $\gamma_1=0.95, \gamma_2=0.44, \gamma_3=0.08,$ $k_{12}=0.01, k_{13}=0.1, k_{23}=0.2,$ $\lambda_f=\lambda_1=0.75, \lambda_2=0.95, \lambda_3=0.9$	12
<i>Pan troglodytes</i> <i>schweinfurthii</i>	Mutual-choice pairing with extra-pair mating	Inspection: physical and behavioral	1: Consort males 2: Opportunistic males 3: Possessive males	$r_2=r_3=0.9, t_f=70, t_n=0.72, b_1=1,$ $t_1=0.3, t_2=0.001, t_3=0.075,$ $\gamma_1=0.5, \gamma_2=0.042, \gamma_3=0.13,$ $\lambda_f=0.95$	1

Table 2 Comparison of Six Mating Systems, continued

Guppies <i>Poecilia reticulata</i>	Promiscuous movement and posture signals	Inspection: posture and motion signals	1: N/A 2: Short-term mating 3: Sneak/forced mating	$r_2=1, r_3=1, t_f=0.033, t_n=0.87,$ $t_1=t_2=t_3=0, \gamma_2=0.008[L],$ $\gamma_3=0.001, b_1=1, D=4300, \lambda_1=$ $\lambda_2= \lambda_2=0.28[L], \lambda_1= \lambda_2=$ $\lambda_2=0.53[H]$	2
Japanese Water Striders <i>Gerris elongates</i>	Haphazard encounter- based polyandry	Inspection: calls and territory	1: Territorial 2: Non-territorial opportunistic 3: Non-territorial forced copulation	$r_2=1, r_3=0.95, t_f=0, t_n=10, t_1=$ $t_2=t_3=0, \gamma_1=0.9 \gamma_2=0.3, \gamma_3=0.6,$ $b_1=1, D=4300$	1
Mallard Ducks <i>Anas platyrhynchos</i>	Mutual-choice pairing, long- term fidelity	Inspection: physical and behavioral	1: Long-term partner 2: N/A 3: Forced copulation	$r_3=0.74, t_f=9, t_1=7, t_3=0,$ $t_n=1.5, \gamma_1=0.59, \gamma_3=0.37,$ $b_1=0.019, k_{13}=0.14$	13

¹ Baseline parameter magnitudes for the model are in Table 1. Only the magnitudes modified from those in Table 1 to fit the particular mating systems are indicated under "Altered Parameters". The rationale for these parameter magnitudes is in Online Resource 2.

² The persistent male type or combination of types for each system, with the default parameter magnitudes for that system, are shown in the "Outcome" column. In these cases, an ESS result with type x males only is symbolized as x ; and ESS combination of types x and y is indicated as xy ; and an unstable combination of types x and y dominated by type x is symbolized as $x.y$. (xy results when types x and y can both invade pure populations of the other, but the stable frequencies of x and y in the mixture are respectively 1 and 0.) In each case, we evaluated the sensitivity of these outcomes to key parameters while separately varying r_2 , r_3 , λ_f , γ_2 , γ_3 , t_f , and t_n , generally subject to the reasonable constraints $r_1 \geq r_2 \geq r_3$, $2 \geq \lambda_f \geq 0.5$, $\gamma_1 \geq \gamma_2$, $\gamma_1 \geq \gamma_3$, $t_f \geq t_1$, $t_f \geq t_2$, $t_f \geq t_3$, and $2 \geq t_n \geq 0$ (except Japanese water striders, which were $20 \geq t_n \geq 5$). In all cases, the outcomes were qualitatively unchanged.

³ Two parameters differ as indicated for guppies between low-predation areas [L] and high-predation areas [H]

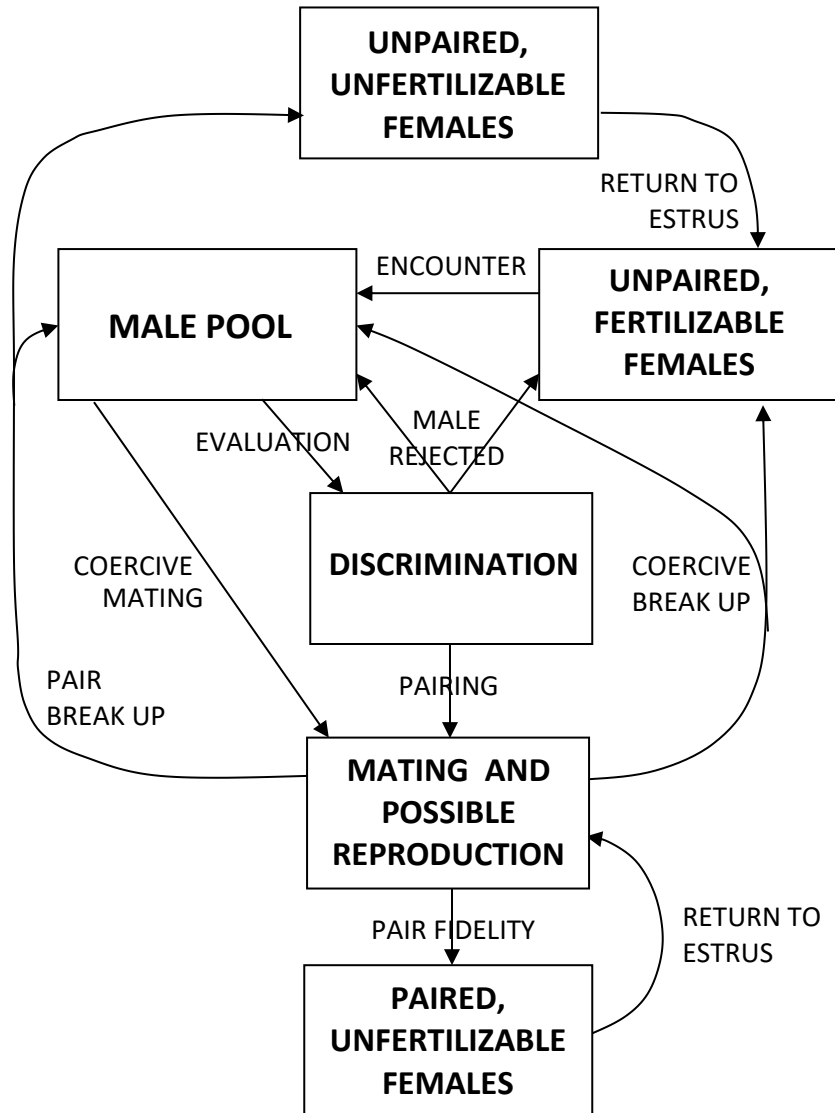


Figure 1

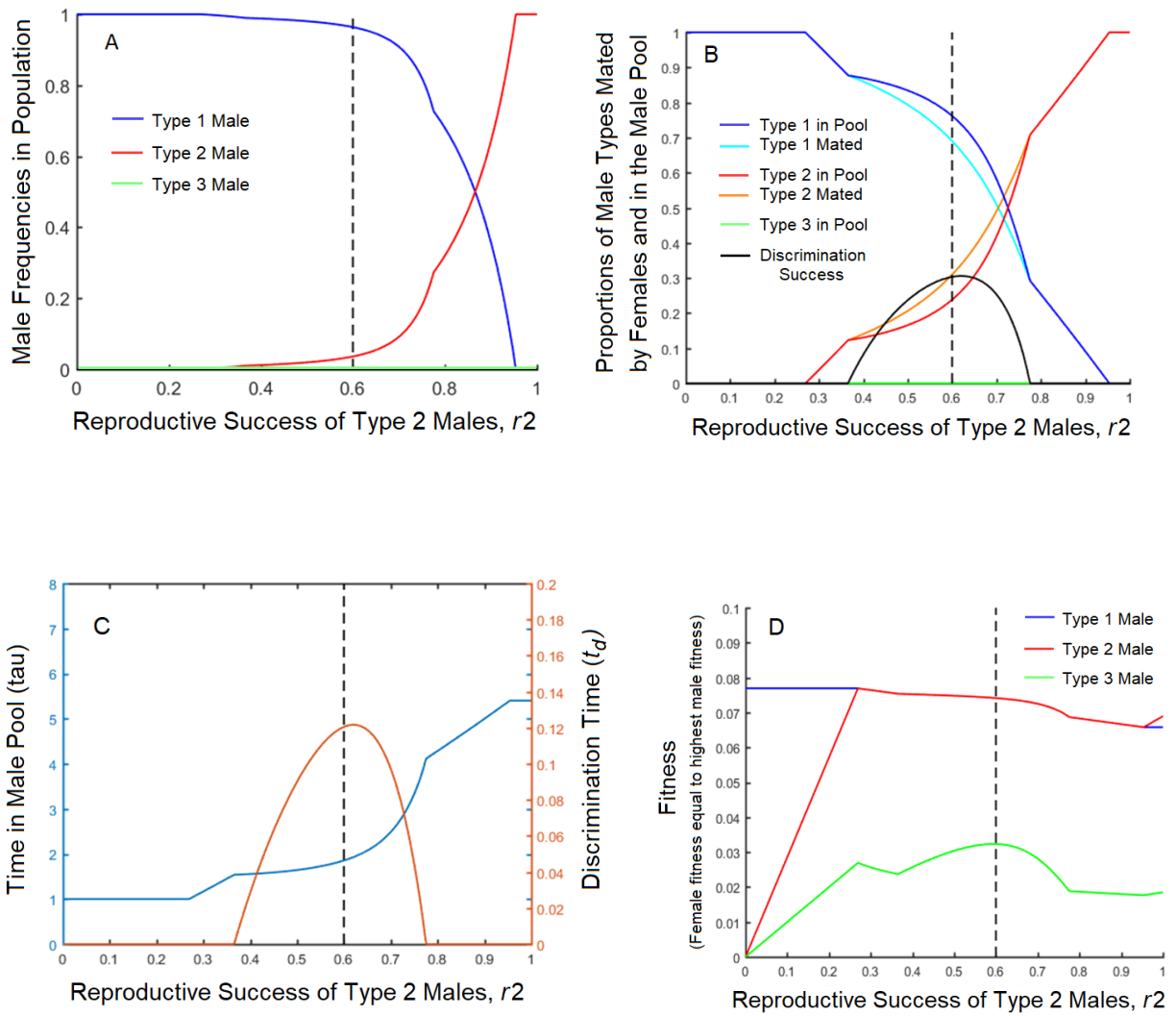


Figure 2

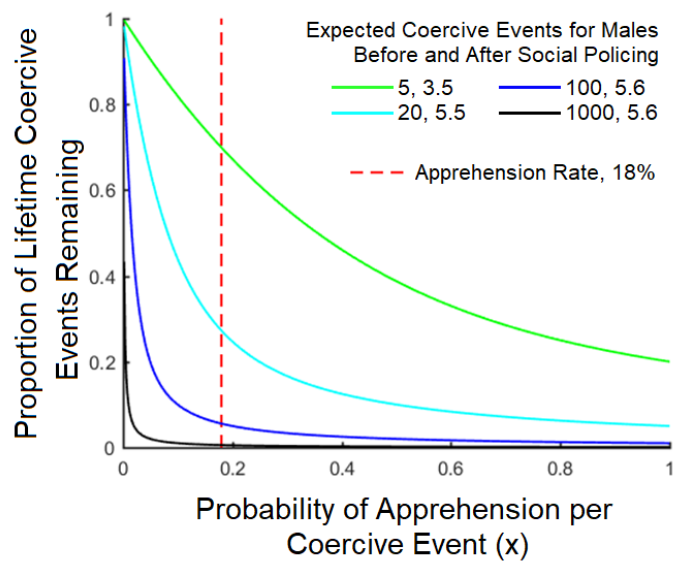
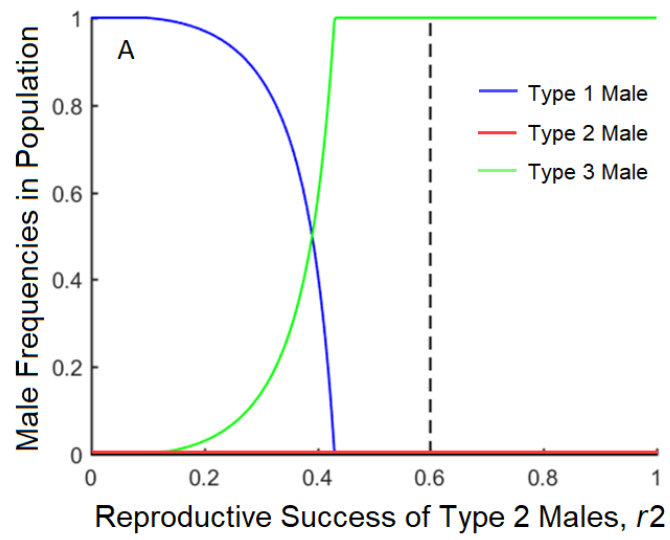


Figure 3

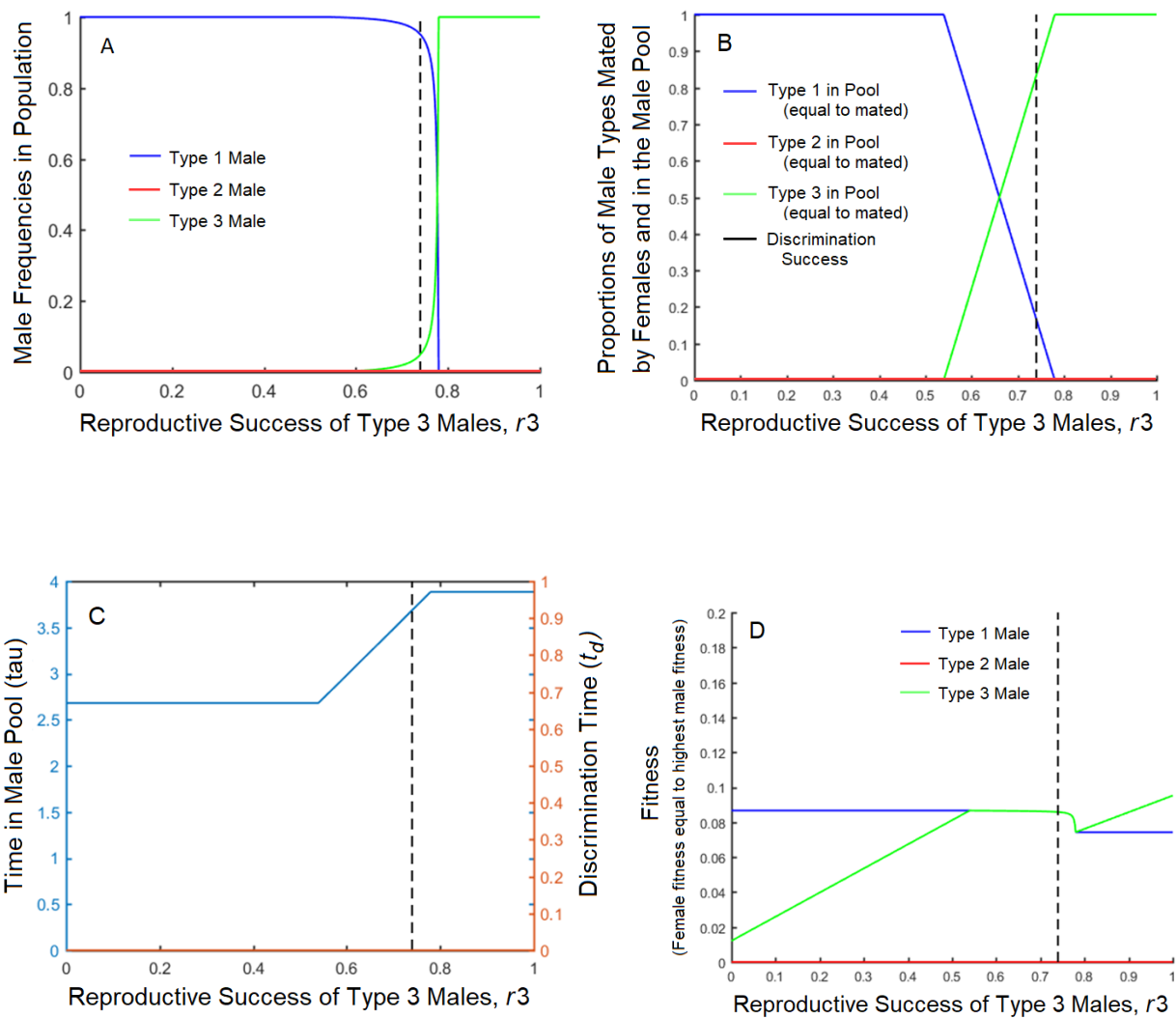


Figure 4

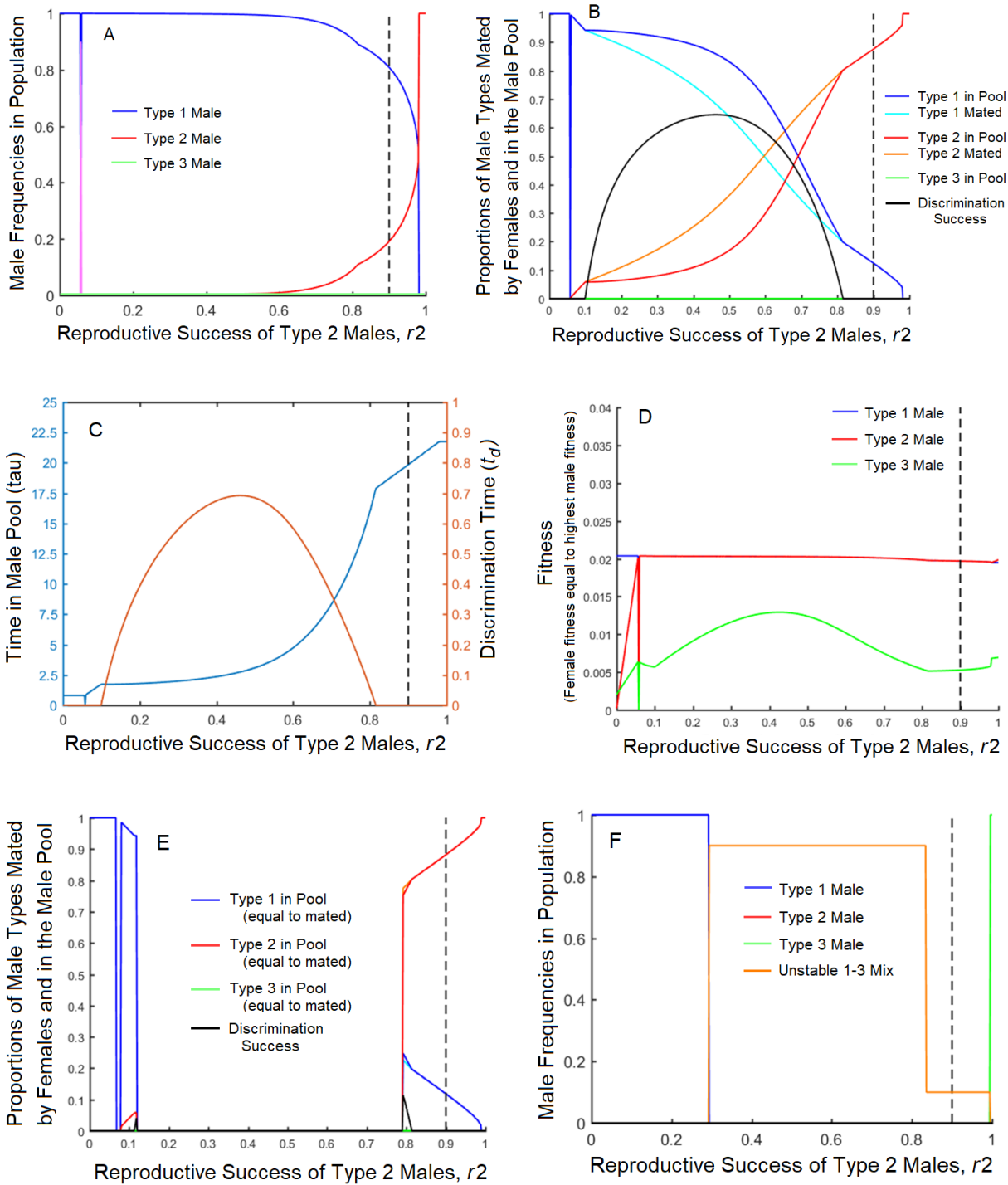


Figure 5