

## Female Mate Choice and the Emergence of Male Coercion

Behavioral Ecology and Sociobiology

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### Online Resource 1. Derivation, Algebraic Relationships, and Proofs

#### Female Mate Choice

We assume that all females have identical characteristics but may choose between two main categories of males. These are type 1, generally devoting a substantial amount of time  $t_1$  to reproductive success ( $0 < t_1 \leq t_f$ , where  $t_f$  is the reproductive time spent by a fertilized female) and resulting in reproductive payoff for the pair of  $r_1$  when the female is successfully fertilized; and type 2, generally devoting less time  $t_2$  to reproductive success than type 1 ( $0 < t_2 \leq t_1$ ) and typically resulting in lower reproductive payoff  $r_2$  for the pair following successful fertilization ( $r_2 \leq r_1$ ).

Females can devote time  $t_d$  to evaluating a male drawn randomly from the male pool; she successfully identifies his type with probability  $d(t_d)$ . This discrimination is conducted with

diminishing returns following the exponential function  $d(t_d) = 1 - e^{-Dt_d}$ , with  $D$  the exponential rate constant in units of 1/time. Let  $m_i$  be the chance that the female pairs with a male of type  $i$  encountered in the male pool. Here, pairing implies mating and a commitment of time  $t_i$  to support reproduction. We set  $m_i = dc_i + (1-d)c_0$ , where  $c_i$  is the chance that type  $i$  is chosen for pairing if successfully categorized by the female, and  $c_0$  is the chance an individual of an undiscriminated type is chosen for pairing.

Let  $b_i$  be the chance that the pair involving a type  $i$  male breaks up after reproduction; then  $1 - b_i$  is the probability of pair fidelity, the chance that the pairing is maintained through the next reproductive cycle. Then the expected number of reproductive cycles before break-up is  $\sum_{j=0}^{\infty} (1 - b_i)^j = 1/b_i$ , and the number of reproductive cycles beyond the first in a sequence is  $1/b_i - 1 = (1-b_i)/b_i$ . Let  $t_n$  be the time following reproduction that a female is temporarily infertile regardless of receptivity to mating (e.g. the time not in estrus for mammals). Let  $\gamma_i$  be the chance of fertilization and subsequent reproduction of a female pairing with a type  $i$  male. Then a male that pairs only once (or for the last time) with a female expects to invest time  $\gamma_i t_i$  in reproduction (i.e. time  $t_i$  if the mating results in fertilization but zero time otherwise), and a male remaining with a female for additional reproductive cycles invests  $\gamma_i t_f + t_n$  time in each cycle before the last (i.e. the same time as the female). This means that a male evaluated by a female leaves the male pool for expected time  $T_i = t_d + m_i \gamma_i t_i + m_i (\gamma_i t_f + t_n) (1 - b_i) / b_i$ . Males remain unselected in the male pool for time  $\tau$ .

Let  $f_i$  be the fraction of all males *in the population* that are type  $i$ , and let  $p_i$  be the fraction of males *in the male pool* that are type  $i$ . Then with types 1 and 2 present, it follows that

$$p_1 = \frac{f_1 \tau_{12} / (\tau_{12} + T_1)}{f_1 \tau_{12} / (\tau_{12} + T_1) + f_2 \tau_{12} / (\tau_{12} + T_2)} = \frac{f_1 (\tau_{12} + T_2)}{f_1 (\tau_{12} + T_2) + f_2 (\tau_{12} + T_1)}, \text{ and } p_2 = 1 - p_1.$$

There are  $n_m$  males and  $n_f$  females in the population and thus a population sex ratio  $\sigma = n_m/n_f$ . Let  $\sigma_0$  be the sex ratio at maturation, and let  $\lambda_f$  and  $\lambda_i$  be the reproductively active lifetime of an individual female or type- $i$  male. Then

$$\sigma = \sigma_0 \frac{\sum_{j=1}^k \lambda_j f_j}{\lambda_f}$$

with  $k$  male types in the population. With males types 1 and 2 in the population, the number of males in the pool is then

$$P = \frac{n_m f_1 \tau_{12}}{\tau_{12} + T_1} + \frac{n_m f_2 \tau_{12}}{\tau_{12} + T_2}.$$

Let  $\varepsilon$  be the expected time between visits to the male pool by a particular female. Then some female is expected to arrive at the pool after every interval of  $\varepsilon/n_f$ . A male in the pool has a probability  $1/P$  of being selected when a female arrives. This means the expected number of arrivals until he is picked is  $\sum_{j=0}^{\infty} (1 - 1/P)^j = P$ . The expected total time the male waits to be picked in a pool containing male types 1 and 2 is then  $\tau_{12} = P\varepsilon/n_f$ . Thus

$$\tau_{12} = \left( \frac{f_1 \tau_{12}}{\tau_{12} + T_1} + \frac{f_2 \tau_{12}}{\tau_{12} + T_2} \right) \varepsilon \sigma.$$

Rearranging then yields

$$\varepsilon = \frac{(\tau_{12} + T_1)(\tau_{12} + T_2)}{\sigma(f_1 T_2 + f_2 T_1 + \tau_{12})}.$$

The time a female commits to each pairing with a type  $i$  male is

$$\theta_i = [\gamma_i t_f + t_n]/b_i.$$

We assume that the female always commits at least one reproductive cycle to a type 1 or type 2 male she pairs with even without successful fertilization, and thus  $\theta_i \geq t_n$ . With only a single male type  $i$  in the population, this implies that each male expects to wait in the male pool for time

$$\tau_i = \sigma \theta_i - T_i.$$

This is the expected number of female reproductive cycles per male, less the time he expects to spend out of the male pool during that interval.

Now another way to express the interval between visits to the male pool by a female is

$$\varepsilon = p_1 m_1 \theta_1 + p_2 m_2 \theta_2 + t_d = \frac{f_1(T_2 + \tau_{12})(m_1 \theta_1 + t_d) + f_2(T_1 + \tau_{12})(m_2 \theta_2 + t_d)}{f_1 T_2 + f_2 T_1 + \tau_{12}}.$$

Equating the two expressions for  $\varepsilon$  and rearranging then yields

$$\tau_{12}^2 + [T_1 + T_2 - \sigma(f_1 m_1 \theta_1 + f_2 m_2 \theta_2 + t_d)]\tau_{12} + [T_1 T_2 - \sigma(f_1 T_2(m_1 \theta_1 + t_d) + f_2 T_1(m_2 \theta_2 + t_d))] = 0,$$

solved for  $\tau_{12}$  via the quadratic formula. (There is a single solution that yields a biologically relevant non-negative result.)

The output from a successful reproductive pairing with a type  $i$  male is  $r_i$ . Female fitness  $F_f$  is the expected rate of female reproduction  $R_f$  multiplied by her expected reproductive lifetime  $\lambda_f$ .  $R_f$  is the reproductive success from a visit to the male pool by a female, divided by the expected time commitment associated with this visit. Thus

$$F_f = R_f \lambda_f = \frac{\lambda_f(p_1 m_1 \gamma_1 r_1 / b_1 + p_2 m_2 \gamma_2 r_2 / b_2)}{p_1 m_1 \theta_1 + p_2 m_2 \theta_2 + t_d}.$$

She chooses  $d(t_d)$ ,  $c_0$ ,  $c_1$ , and  $c_2$  to maximize her fitness. With  $r_1 > r_2$ ,  $c_1 = 1$  and  $c_2 = 0$ . The probability  $c_0$  of mating with an undiscriminated male must equal 1 as  $d \rightarrow 0$ ; we therefore generally set  $c_0 = 1$ , though we can let  $c_0 = (1 - d)^\omega$ , where  $\omega > 0$ , when  $c_0$  decreases with increasing  $d$ . (This generally has little effect on the results unless  $\omega \gg 1$ .) For the two male types, expected reproductive success of an individual is

$$F_1 = R_1 \lambda_1 = \frac{\lambda_1 m_1 \gamma_1 r_1 / b_1}{\tau_{12} + T_1}, \text{ and } F_2 = R_2 \lambda_2 = \frac{\lambda_2 m_2 \gamma_2 r_2 / b_2}{\tau_{12} + T_2}.$$

Suppose  $F_1 > F_2$ . Then  $f_1$  will increase until  $F_1 = F_2$  or until  $f_1 = 1$ . An analogous outcome results from  $F_2 > F_1$ . This logic holds whether types 1 and 2 are probabilistic strategies by single

individuals *or* they represent pure strategies of competing individuals. (Technically, this corresponds to the distinction between an evolutionarily stable mixed strategy and an evolutionarily stable state of the male population.)

Putting the fitness terms together, we have that male fitness  $F_m$  is

$$F_m = f_1 F_1 + f_2 F_2.$$

The joint solution for  $t_d$  and  $f_1$  (and thus  $f_2$ ) is evolutionarily stable in the absence of mutant alternative male strategies. Of course  $F_f = F_m$ , which provides a check on the results.

### Male Coercion

Consider a mutant male (type 3) that mates with any female encountered in the male pool, bypassing the evaluation process. This coercive male has the probability  $\gamma_3$  of fertilizing and producing offspring with the female, despite a very low or zero time commitment  $t_3$ , resulting in a generally low reproductive output ( $r_3 \leq r_2$ ). Because a type 3 male is assumed to mate only once (or in one brief sequence) with the female, she expends the additional non-reproductive time  $t_n$  in association with this mating only if fertilized. As a rare mutant, we assume the coercer has to wait time  $\tau_i$  to encounter a female like the other males, where  $i$  designates the stable outcome in the absence of the mutant. The fitness of mutant type 3 is then

$$F_3 = R_3 \lambda_3 = \lambda_3 \gamma_3 r_3 / \tau_i.$$

In the remainder of this section, we simplify by setting  $\sigma_0 = 1$  and  $\lambda_f = \lambda_1 = \lambda_2 = \lambda_3$  (and thus the sex ratio  $\sigma = 1$ ), the chance of undiscriminated mating  $c_0 = 1$ , and the pairing fidelity parameters  $b_1 = b_2 = 1$ , though  $\sigma \neq 1$ ,  $c_0 = c_0(d)$ , and the  $b_i < 1$  could readily be accommodated. It follows, solving the quadratic equation for  $\tau_i$ , that the coercer can invade a population of pure type 1 when

$$\frac{\lambda_3 \gamma_3 r_3}{\tau_1} > \frac{\lambda_1 \gamma_1 r_1}{\tau_1 + T_1}, \text{ where } \tau_1 = \gamma_1 (t_f - t_1) + t_n, \text{ and thus } \frac{\lambda_3 \gamma_3 r_3}{\lambda_1 \gamma_1 r_1} > \frac{\gamma_1 (t_f - t_1) + t_n}{\gamma_1 t_f + t_n}.$$

The coercer can invade a population of pure type 2 when

$$\frac{\lambda_3 \gamma_3 r_3}{\tau_2} > \frac{\lambda_2 \gamma_2 r_2}{\tau_2 + T_2}, \text{ where } \tau_2 = \gamma_2(t_f - t_2) + t_n, \text{ and thus } \frac{\lambda_3 \gamma_3 r_3}{\lambda_2 \gamma_2 r_2} > \frac{\gamma_2(t_f - t_2) + t_n}{\gamma_2 t_f + t_n}.$$

(Note: in these cases with a single type of male at the ESS,  $d$  and  $t_d$  are zero, because

discrimination is useless.) And the coercer can invade a stable mixture of types 1 and 2 when

$$\frac{\lambda_3 \gamma_3 r_3}{\tau_{12}} > \frac{\lambda_1 \gamma_1 r_1}{\tau_{12} + \gamma_1 t_1 + t_d}, \text{ where } \tau_{12}, \text{ the waiting time with a stable mixture of types 1 and 2, is defined}$$

as above (here with  $b_1 = b_2 = 1$ ). This inequality expresses the condition for invasibility of the

stable mixture; for this mixture,  $F_1 = F_2$ , and thus the inequality implies higher fitness for the

coercer than for types 1 and 2. Once the coercer invades, it may eliminate its competitors,

establishing a waiting time of  $\tau_3 = \gamma_3(t_f + t_n)$ , because each female either returns to the male

pool after time  $t_f + t_n$  if fertilized or immediately otherwise. Alternatively, the competitor(s) may

be able to invade a pure type 3 population. Coercers are invasible by type 1 males when

$$\frac{\lambda_3 \gamma_3 r_3}{\tau_3} < \frac{\lambda_1 \gamma_1 r_1}{\tau_3 + T_1}$$

and by type 2 males when

$$\frac{\lambda_3 \gamma_3 r_3}{\tau_3} < \frac{\lambda_2 \gamma_2 r_2}{\tau_3 + T_2}.$$

Putting these results together, mutual invasibility implies coexistence of types 1 and 3 when

$$1 + \frac{\gamma_1 t_1}{\gamma_3(t_f + t_n)} < \frac{\lambda_1 \gamma_1 r_1}{\lambda_3 \gamma_3 r_3} < 1 + \frac{\gamma_1 t_1}{\gamma_1(t_f - t_1) + t_n}$$

and coexistence of types 2 and 3 when

$$1 + \frac{\gamma_2 t_2}{\gamma_3(t_f + t_n)} < \frac{\lambda_2 \gamma_2 r_2}{\lambda_3 \gamma_3 r_3} < 1 + \frac{\gamma_2 t_2}{\gamma_2(t_f - t_2) + t_n}.$$

### Female Resistance and Policing

Female resistance to coercion is assumed to be expressed as reduced magnitudes of the fertilization probability  $\gamma_3$  and of reproductive success given fertilization  $r_3$ . The  $\gamma_3$  coefficient

may be low in part because female resistance reduces the duration or frequency of mating per coercive event. In some species, post-copulatory mechanisms may further reduce the chance of coercive fertilization. The  $r_3$  coefficient may be diminished by the lack of time or other resource commitment by the male to coercive reproduction or by damage to the female during coercion.

In some species, coercion may be restricted through social policing. In an unpoliced population with only coercive males, each male expects to obtain

$n = \frac{\lambda_3}{\tau_3 + T_3}$  matings in his reproductive lifetime. Now let  $x$  be the probability that a coercer is apprehended and prevented from further reproduction after any particular coercive mating. Then his expected number of coercive matings with policing is

$$C = \sum_{i=1}^n (1-x)^{i-1} = \sum_{i=0}^{\infty} (1-x)^i - \sum_{i=n}^{\infty} (1-x)^i = \frac{1}{x} - (1-x)^n \sum_{i=0}^{\infty} (1-x)^i = \frac{1-(1-x)^n}{x},$$

where  $x > 0$ . (As  $x$  approaches 0, the limit is found from L'Hopital's Rule:  $\lim_{x \rightarrow 0} \frac{1-(1-x)^n}{x} = n$ .)

Then type 3 can be invaded by type  $i$  when

$$C\gamma_3 r_3 < \frac{\lambda_i \gamma_i r_i}{\tau_i + T_i}.$$

$$\text{Now let } n = \frac{\lambda_3}{\tau_3 + T_3}.$$

Now type 3 can invade stable type  $i$  when

$$C\gamma_3 r_3 > \frac{\lambda_i \gamma_i r_i}{\tau_i + T_i}.$$

Because  $C$  is less than  $n$  in each case, both conditions are less favorable for type 3.

The proportion  $p_C$  of  $n$  expected to be accomplished despite policing is

$$p_C = \frac{1-(1-x)^n}{xn}.$$

We address an example of policing and its implications below.

### Extra-Pair Paternity

To this point, the description of the model has implied serial monogamy. But despite social pairing, there may be extra-pair mating and reproduction between types. Since pairing with type 2 and with type 3 males is typically brief, we restrict these cuckoldry effects to type 1 by types 2 and 3 and type 2 by type 3. Shifting paternity between types does not affect overall reproductive success (i.e.  $F_f = F_m$ ) but does alter the balance of fitnesses among male types and thus their frequencies and chance of persisting.

We include these effects in the model by transforming the fitness magnitudes for males of each type as follows:

$$F'_1 = F_1(1 - k_{12}f_2 - k_{13}f_3),$$

$$F'_2 = F_2(1 - k_{23}f_3) + k_{12}f_1F_1, \text{ and}$$

$$F'_3 = F_3 + k_{13}f_1F_1 + k_{23}f_2F_2.$$

The coefficients  $k_{ij}$  express the magnitude of the fitness increment lost by a type  $i$  male from reproduction by his mate with a type  $j$  male, per unit frequency of type  $j$ . The fitness of type 1 males is thus reduced by each of the two extra-pair coefficients for types 2 and 3 multiplied by the corresponding frequencies of the other types. The fitness of type 2 males is reduced by the type 3 coefficient multiplied by the frequency of type 3—and augmented by the type 1 coefficient multiplied by the frequency of type 1 and its fitness. The type 3 fitness is similarly augmented by the fitness increments from types 1 and 2. Note that these fitness redistributions leave total fitness unchanged, since  $F_f = F_m = f_1F'_1 + f_2F'_2 + f_3F'_3 = f_1F_1 + f_2F_2 + f_3F_3$ .

By influencing male fitness magnitudes, this extra-pair reproduction alters some of the  $\tau$  values and invasion criteria (see Online Resource 2), shifting the frequencies of male types in the population.

### Fitness Relationships



In each case,  $F_{xy}$  is the fitness of male type  $x$  in a population of type  $y$ ;  $F_{xyz}$  is the fitness of male type  $x$  in a stable combination of types  $y$  and  $z$ . Females do not discriminate between types except as indicated. The  $f_i^*$  represent evolutionarily stable frequencies of the male types in mixtures; these magnitudes are given below when discrimination is absent. In a stable mixture of types 1 and 2 when females discriminate,  $f_1^*$  and  $f_2^*$  must be determined numerically.

$$F_{11} = \lambda_1 \gamma_1 (r_1/b_1) / (\tau_1 + T_1)$$

$$F_{12} = \lambda_1 (1 - k_{12}) \gamma_1 (r_1/b_1) / (\tau_2 + T_1)$$

$$F_{13} = \lambda_1 (1 - k_{13}) \gamma_1 (r_1/b_1) / (\tau_3 + T_1)$$

$$F_{21} = \lambda_2 \gamma_2 (r_2/b_2) / (\tau_1 + T_2) + k_{12} F_{11}$$

$$F_{22} = \lambda_2 \gamma_2 (r_2/b_2) / (\tau_2 + T_2)$$

$$F_{23} = \lambda_2 (1 - k_{23}) \gamma_2 (r_2/b_2) / (\tau_3 + T_2)$$

$$F_{31} = \lambda_3 \gamma_3 r_3 / (\tau_1 + T_3) + k_{13} F_{11}$$

$$F_{32} = \lambda_3 \gamma_3 r_3 / (\tau_2 + T_3) + k_{23} F_{22}$$

$$F_{33} = \lambda_3 \gamma_3 r_3 / (\tau_3 + T_3)$$

$$F_{112} = \lambda_1 (1 - k_{12} f_2^*) \gamma_1 (r_1/b_1) / (\tau_{12} + T_1)$$

$$F_{113} = \lambda_1 (1 - k_{13} f_3^*) \gamma_1 (r_1/b_1) / (\tau_{13} + T_1)$$

$$F_{123} = \lambda_1 (1 - k_{12} f_2^* - k_{13} f_3^*) \gamma_1 (r_1/b_1) / (\tau_{23} + T_1)$$

$$F_{212} = F_{112}$$

$$F_{213} = \lambda_2 (1 - k_{23} f_3^*) \gamma_2 (r_2/b_2) / (\tau_{13} + T_2) + F_{113} k_{12} f_1^*$$

$$F_{223} = \lambda_2 (1 - k_{23} f_3^*) \gamma_2 (r_2/b_2) / (\tau_{23} + T_2)$$

$$F_{312} = \lambda_3 \gamma_3 r_3 / (\tau_{12} + T_3) + F_{112} (k_{12} f_1^* + k_{23} f_2^*)$$

$$F_{313} = F_{113}$$

$$F_{323} = F_{223}$$

Times males are out of the male pool per cycle

$$T_1 = t_d + m_1\gamma_1 t_1 + m_1(\gamma_1 t_f + t_n)(1 - b_1)/b_1$$

$$T_2 = t_d + m_2\gamma_2 t_2 + m_2(\gamma_2 t_f + t_n)(1 - b_2)/b_2$$

$$T_3 = \gamma_3 t_3$$

When females discriminate between male types 1 and 2,  $m_1 = dc_1 + (1 - d)c_0$  and  $m_2 = dc_2 + (1 - d)c_0$ ; otherwise,  $m_1 = m_2 = 1$  and  $t_d = d(t_d) = 0$ .

Time between mating with a particular male type and the female's return to the male pool

$$\theta_1 = (\gamma_1 t_f + t_n)/b_1$$

$$\theta_2 = (\gamma_2 t_f + t_n)/b_2$$

$$\theta_3 = \gamma_3(t_f + t_n)$$

Waiting times for males in the male pool (without discrimination)

$$\tau_1 = \sigma\theta_1 - T_1$$

$$\tau_2 = \sigma\theta_2 - T_2$$

$$\tau_3 = \sigma\theta_3 - T_3$$

where  $\sigma = \sigma_0 (\lambda_i / \lambda_f)$

$$\tau_{12} = \frac{T_1\gamma_2\lambda_2 r_2/b_2 - T_2\gamma_1(1 - k_{12})\lambda_1 r_1/b_1}{\gamma_1(1 - k_{12})\lambda_1 r_1/b_1 - \gamma_2\lambda_2 r_2/b_2}$$

$$\tau_{13} = \frac{T_1\gamma_3\lambda_3 r_3 - T_3\gamma_1(1 - k_{13})\lambda_1 r_1/b_1}{\gamma_1(1 - k_{13})\lambda_1 r_1/b_1 - \gamma_3\lambda_3 r_3}$$

$$\tau_{23} = \frac{T_2\gamma_3\lambda_3 r_3 - T_3\gamma_2(1 - k_{23})\lambda_2 r_2/b_2}{\lambda_2\gamma_2(1 - k_{23})r_2/b_2 - \gamma_3\lambda_3 r_3}$$

Frequencies of male types in stable mixtures (without discrimination)

Note: Only the 1-2 mixture may involve discrimination; in that case,  $f_1$  (where  $f_2 = 1-f_1$ ) and  $t_d$  are optimized numerically. In the absence of discrimination, the  $\tau_{ij}$  value can be directly calculated (above); this is substituted into the quadratic equation for  $\tau$  in the text and solved for  $f_i$ . Because the sex ratio also depends on the frequencies, the result is a quadratic equation in  $f_i$  of the form  $af_i^2 + bf_i + c = 0$ , where

$$a = (\tau_{ij}(\theta_i - \theta_j) + \theta_i T_j - \theta_j T_i)(\sigma_0/\lambda_f)(\lambda_i - \lambda_j),$$

$$b = (\tau_{ij}(\theta_i - \theta_j) + \theta_i T_j - \theta_j T_i)(\sigma_0/\lambda_f)\lambda_j + \theta_j(\tau_{ij} + T_i)(\sigma_0/\lambda_f)(\lambda_i - \lambda_j), \text{ and}$$

$$c = -\tau_{ij}^2 - (T_i + T_j)\tau_{ij} - T_i T_j + \theta_j(\tau_{ij} + T_i)(\sigma_0/\lambda_f)\lambda_j.$$

This is solved by the quadratic formula for the biologically relevant positive term. Then  $f_j = 1 - f_i$ .

#### Proof that a stable mix of all three male types is impossible

For clarity, we consider the case with all  $k$ 's = 0,  $\sigma_0 = 1$ ; all  $\lambda$ 's equal.

A stable mix of all three male types requires that each type could invade a stable mix of the other two. So we need  $F_{312} > F_{112}$ ,  $F_{123} > F_{223}$ , and  $F_{213} > F_{113}$ . From the last two of those relationships, we have that

$$\gamma_1(r_1/b_1)(\tau_{23} + T_2) > \gamma_2(r_2/b_2)(\tau_{23} + T_1),$$

$$\text{and } \gamma_2(r_2/b_2)(\tau_{13} + T_1) > \gamma_1(r_1/b_1)(\tau_{13} + T_2).$$

Now substituting for  $\tau_{23}$  and  $\tau_{13}$  and simplifying, the two inequalities respectively yield

$$\gamma_1(r_1/b_1)T_2 > \gamma_2(r_2/b_2)T_1,$$

and  $\gamma_2(r_2/b_2)T_1 > \gamma_1(r_1/b_1)T_2$ , a direct contradiction. Thus the three criteria cannot be simultaneously satisfied, and a stable mix of all three male types is impossible. Note that this contradiction implies that the successful invasion of a stable mix of types 2 and 3 by type 1 and the successful invasion of a stable mix of types 1 and 3 by type 2 are jointly impossible. Neither

of these stable mixes involves female discrimination, and so the altered susceptibility to invasion when females discriminate is irrelevant to this main conclusion.

Proof that a repeating sequence of the three male types is impossible

As in the previous proof, we consider the case with all  $k$ 's = 0,  $\sigma_0 = 1$ ; all  $\lambda$ 's equal.

A repeating sequence might go from dominance by type 1 to dominance by type 2 to type 3 to type 1 and so on (here called sequential replacement), or it might go from type 3 to type 2 to type 1 to type 3 and so on (here called counter-sequential replacement). We show the proof that sequential replacement is impossible; the other proof proceeds in an analogous manner and thus will not be included here.

Type 1 is unidirectionally replaced by type 2 if  $F_{21} > F_{11}$  and  $F_{22} > F_{12}$ ; type 2 is then replaced in like manner by type 3 if  $F_{32} > F_{22}$  and  $F_{33} > F_{23}$ ; and type 3 is replaced by type 1 if  $F_{13} > F_{33}$  and  $F_{11} > F_{31}$ .

Rearranging inequality  $F_{11} > F_{31}$  yields  $\frac{\tau_1}{\tau_1 + T_1} > \frac{\lambda_3 \gamma_3 r_3}{\lambda_1 \gamma_1 r_1 / b_1}$ . Now we rearrange relationships  $F_{33} > F_{23}$  and  $F_{21} > F_{11}$  so that the  $\lambda \gamma r / b$  terms, one divided by the other, are on the greater-than side of the inequality in each case. In multiplying the greater-than sides together and then the less-than sides together, the inequality must still hold, yielding  $\frac{\lambda_3 \gamma_3 r_3}{\lambda_1 \gamma_1 r_1 / b_1} > \frac{\tau_3 (\tau_1 + T_2)}{(\tau_3 + T_2)(\tau_1 + T_1)}$ . It follows that  $\frac{\tau_1}{\tau_1 + T_1} > \frac{\tau_3 (\tau_1 + T_2)}{(\tau_3 + T_2)(\tau_1 + T_1)}$ . Cross-multiplying and simplifying then results in  $\tau_1 > \tau_3$ .

$F_{13} > F_{33}$  implies that  $\frac{\tau_3}{\tau_3 + T_1} > \frac{\lambda_3 \gamma_3 r_3}{\lambda_1 \gamma_1 r_1 / b_1}$ . Now again using the result derived from  $F_{33} > F_{23}$  and

$F_{21} > F_{11}$ , we have  $\frac{\tau_3}{\tau_3 + T_1} > \frac{\tau_3 (\tau_1 + T_2)}{(\tau_3 + T_2)(\tau_1 + T_1)}$ . In this case, rearrangement yields  $\tau_3 (T_1 - T_2) >$

$\tau_1 (T_1 - T_2)$ . We are only interested in cases with  $T_1 \geq T_2$ , since  $\gamma_1 > \gamma_2$ ,  $t_1 > t_2$ , and  $b_1 \leq b_2$ ; and

with discrimination,  $m_1 > m_2$ . This means that either  $\tau_3 > \tau_1$  or  $\tau_3 = \tau_1$  (based on  $\lim_{T_1 \rightarrow T_2} \left( \frac{\tau_3}{\tau_1} \right) = 1$ ),

which directly contradicts the result above. We conclude from this (and the analogous counter-sequential result not shown) that a repeating sequence of the three male types is impossible.

## Online Resource 2. Finding Parameter Magnitudes for the Six Systems

### Japanese Water Striders

Most male water striders engage exclusively in forced copulation, but Japanese water striders are an exception. 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 the strategies chosen vary throughout the season (late March to early June), with type 1 strategies emerging mid-season (Hayashi 1985). We estimate  $r_1 = r_2 = 1$  and  $r_3 = 0.95$  to account for the usurpation of female choice and effects of mating with a non-chosen male.

The time females spend in reproduction is estimated from the average copulation time plus oviposition time ( $t_f = 0.00045$ ). Type 1 males guard mates for as long as females oviposit ( $t_1 = t_f$ ), and type 2 males do not guard at all ( $t_2 = 0.0001$ ). Type 3 males guard only sometimes and are known to leave before the female has finished ( $t_3 = 0.00022$ ). The mating season lasts approximately 2 months ( $t_n = 10$ ), and there is no pairing fidelity ( $b_i = 1$ ) (Hayashi 1985). There is no information on the sex ratios of Japanese water striders, so we estimate equal  $\lambda_i$  values; but since water striders are known to have fluctuating sex ratios throughout the breeding season (Vepsäläinen and Savolainen 1995), we explore the effect of this.

There is no information on chances of fertilization for each type of mating strategy; however, water striders are believed to have sperm competition favoring the most recent sperm (displacing up to 65% of the previous male's sperm) (Rubenstein 1989). Since type 2 males mate

first without an accompanying oviposition, we estimate a 30% chance of reproduction ( $\gamma_2 = 0.3$ ). Type 1 males mate-guard while the females oviposit, so we estimate a 90% chance of fertilization ( $\gamma_1 = 0.9$ ). As type 3 males mate when a female is unguarded, potentially displacing a previous male's sperm, we estimate a 60% chance of fertilizing ( $\gamma_3 = 0.6$ ) (Hayashi 1985). We explore a range of magnitudes for these parameters as well.

Since there is no extra-pair copulation, the magnitudes of  $k_{12}$ ,  $k_{13}$ , and  $k_{23}$  were set to zero. The discrimination coefficient  $D$  was estimated from assuming that the females are able to distinguish between type 1 and 2 males accurately approximately half the time in approximately 10 minutes ( $D = 4300$ ).

### Scorpionflies

There are three mating strategies for male scorpionflies. Type 1 males guard an arthropod as a nuptial gift that the female consumes while mating. Type 2 males produce and offers a salivary mass; this strategy is linked to inability to find or defend an arthropod. Type 3 males engage in forced copulations with females without offering any nuptial gifts, either because they could not gain access to an arthropod and could not produce a salivary mass or because they have higher reproductive success via coercion (Thornhill 1980a,b, 1981, 1982).

The  $r$ -values were chosen based on the number of eggs laid for each type of reproductive event. Females lay the most eggs with an arthropod nuptial gift; when given a salivary mass, they produce approximately two-thirds of the arthropod amount; in forced copulations, they produce approximately one-sixth of the arthropod amount (Thornhill 1982) ( $r_1 = 1$ ,  $r_2 = 0.67$ ,  $r_3 = 0.17$ ). The amount of time a female spends reproductive depends on the type of mating she received; she lays eggs much faster after a forced copulation than she does a consensual copulation (Thornhill 1982); we estimated by using the average of these ( $t_f = 0.052$ ), though we explore this

as well. Females are sexually receptive for all but the time that they are inseminated (Thornhill 1982), which is included in  $t_f$ , so we set  $t_n = 0$  to represent extended receptivity. Since egg batches seem to be fertilized by a single male, we set  $k_{12} = k_{13} = k_{23} = 0$ .

Males do not differ in copulation time (Thornhill 1982), but males defending arthropods or salivary masses spend additional time guarding the nuptial gift. We estimate the time for arthropod-guarding to be approximately 30 minutes  $t$  and for salivary-guarding to be approximately 1 hr ( $t_1 = 0.0036$ ,  $t_2 = 0.0048$ ,  $t_3 = 0.0024$ ). There is no pairing fidelity ( $b_i = 1$ ). The reproductive sex ratio is 1:1 (Thornhill 1980b), but type 2 males and type 3 males are expected to have shorter reproductive lifespans than females or type 1 males (Thornhill 1980a, 1981) ( $\lambda_f = \lambda_1 = 1$ ,  $\lambda_2 = 0.8$ ,  $\lambda_3 = 0.5$ ). However, since type 1 males tend to find their insects in spider webs, and since spiders are the primary predators of scorpionflies (Thornhill 1980b), it is possible that type 1 and 2 males have the highest mortality rates, followed by type 3 ( $\lambda_f = \lambda_3 = 1$ ,  $\lambda_1 = 0.5$ ,  $\lambda_2 = 0.8$ ). We explore this as well.

Fertilization rates for type 1 and 2 males are approximately equal ( $\gamma_1 = \gamma_2 = 1$ ) (Thornhill 1981, 1982); when forced copulations are successful, they have an insemination rate of approximately 50% (Thornhill 1980b, 1982). However, since forced copulation is achieved in only about 22% of attempts, the insemination rate becomes 11% ( $\gamma_3 = 0.11$ ) (Thornhill 1980b). We explore both of these rates. For our default, we varied  $r_2$ , with  $r_3$  being one-fourth of  $r_2$ .

Since there is no extra-pair copulation, the magnitudes of  $k_{12}$ ,  $k_{13}$ , and  $k_{23}$  were set to zero. The discrimination coefficient  $D$  was estimated from the time females spend between mating events, estimated at one day (Thornhill 1974) ( $D = 21$ ).

## Guppies

Guppies have two different male mating strategies: those that display and are chosen by females to mate and those that engage in sneak copulations when females are unreceptive. Both are short-term matings, and we have designated them type 2 and type 3, respectively. Male reproductive behavior differs dramatically based on the level of predation they experience, so we did separate runs for low-predation environments and high-predation environments (Liley 1966).

The reproductive success per reproductive cycle for type 2 and 3 males ( $r_2$  and  $r_3$ ) were set at 1, as there is no known influence on offspring success based on reproductive strategy; however, we vary the  $r$ -values to explore this. Females devote basically their entire lives to reproduction—they are either fertile and mating, pregnant, or giving birth. Their time commitment per birth event has been estimated as 24 hours ( $t_f = 0.033$ ) (B.D. Neff, personal communication). Because females are only sexually receptive during the first 3-5 days after giving birth (once per month) (Liley 1966; Magurran and Nowak 1991), we estimate the time that a female is not sexually receptive to be the other 26 days of the month ( $t_n = 0.87$ ). Type 2 males spend approximately 5 seconds for each S-display (Luyten and Liley 1985) ( $t_2 = 0.0000014/\text{month}$ ), and type 3 males considerably less (estimated at half of  $t_2$ ).

There is no pair fidelity in guppies ( $b_i = 1$ ). The sex ratios vary depending on the population: in low-predator populations, females outnumber males almost four to one (Rodd and Reznick 1997) ( $\lambda_1 = \lambda_2 = \lambda_3 = 0.28\lambda_f$ ); in high predator, it is almost two to one (Rodd and Reznick 1997) ( $\lambda_1 = \lambda_2 = \lambda_3 = 0.53\lambda_f$ ). Time spent reproductive is approximately the same, except for the effects of predation on males, which influenced the sex ratios.

Little is known about the chance of conceiving an offspring per reproductive event, but we estimated this based on the odds of each type of sexual event releasing sperm (Baerends et al.



1955; Liley 1966;), the amount of sperm that each type successfully delivers (Pilastro et al. 2002), the estimated number of events a female encounters each month (Magurran and Seghers 1994), which varies based on predator status (Endler 1987), and on the number of males in each population, which also varies based on predator status (Rodd and Reznick 1997). Estimates for low predator populations are 0.0082 for S-display and 0.0013 for sneak attempts. For high predator populations, they are 0.014 and 0.0011, respectively.

Since there is no extra-pair copulation, the magnitudes of  $k_{12}$ ,  $k_{13}$ , and  $k_{23}$  were set to zero. The discrimination coefficient  $D$  was estimated from assuming that the male evaluation process lasts approximately 10 minutes of observing the sigmoid display (Liley 1966; Magurran and Nowak 1991) ( $D = 4300$ ).

### Mallard Ducks

Mallard reproduction consists of long-term pairs that mate primarily consensually with each other; in addition to this type 1 strategy, however, males often switch strategies and sexually coerce females mated to other males. We are primarily interested in sexual coercion outside of mated pairs, though our fertilization calculation of type 1 males includes the negative influence of this secondary strategy.

Offspring viability is significantly lower when females are coerced to mate with their non-primary partner (Bluhm and Gowaty 2004) ( $r_1 = 1$ ,  $r_3 = 0.739$ ). Females spend approximately 9 months in reproduction, from courtship to offspring maturing to flight ( $t_f = 9$ ); type 1 males invest the same amount of time up until hatching ( $t_1 = 7$ ) (Drilling et al. 2002). Type 3 males invest very little in reproduction ( $t_3 = 0.0002$ ). The probability of breakup in type 1 relationships is very low ( $b_1 = 0.019$ ), while coercion results in immediate breakup ( $b = 1$ ). The primary sex ratio is presumed to be 1 (Giudice 2003, but see Denk 2005).

Reproductive lifetimes are similar for adult males and females, and we set  $\lambda_f = \lambda_1 = \lambda_2 = \lambda_3 = 1$ . Hunting may help maintain the equal sex ratio in some populations; severely restricted hunting may result in a male-biased sex ratio (Giudice 2003).

The empirically-established chance of a type 1 mating fertilizing an egg  $\gamma_1 = 0.59$ , and for type 3  $\gamma_3 = 0.37$  (Cunningham 2003). The rate of extra-pair paternity in mallards is approximately 14% (Denk 2005), and since all EPCs are coerced in mallards, this becomes the fraction of potential type 1 offspring instead fathered by type 3 males ( $k_{13} = 0.14$ ;  $k_{12} = k_{23} = 0$ ).

As pairs usually take approximately one month to form at the beginning of courtship in the fall (Drilling et al. 2002), we estimated the time for a female to distinguish types 1 and 3 males with a probability of 50% to be about 1 week ( $D = 3$ ).

### Chimpanzees

Chimpanzee males have three different mating strategies. Type 1 males are chosen by females as consorts, spending an extended period of time mating exclusively with each other while she is in estrus and providing her with resources. Type 2 males are opportunistic males that copulate with females in estrus within the group. Type 3 males are possessive opportunistic males that aggressively defend estrus females from other males in order to mate exclusively with them (Tutin 1979). We set  $r_1 = 1$  and  $r_2 = r_3 = 0.9$ , as there was little evidence for differences in reproductive success for types 2 and 3.

The birth interval, composed of mating, pregnancy, and rearing, is 70 months ( $t_f = 70$ ). Type 1 males engage in approximately 10-day consorts with females ( $t_1 = 0.3$ ). Type 2 males are opportunistic and invest very little time in reproduction ( $t_2 = 0.001$ , approximately 1 hour). Type 3 males prevent the female from mating with other males while she is fertile, approximately 2-3 days ( $t_3 = 0.075$ ) (Tutin 1979), and females spend approximately 26 days out of their 36-day

cycle not in estrus ( $t_n = 0.72$ ) (Graham 1979). There is no pairing fidelity (the  $b_i = 1$ ), and the sex ratios are approximately equal. Females tend to be reproductive for slightly less time than the males ( $\lambda_f = 0.95$  and  $\lambda_1 = \lambda_2 = \lambda_3 = 1$ ) (Tutin 1979).

Approximately half of all consorts result in pregnancy ( $\gamma_1 = 0.5$ ) (Tutin 1979). In opportunistic mating, a female mates with approximately 12 males (Tutin 1979), so we estimate the chances of one of those males fertilizing an egg to be  $1/12$  ( $\gamma_2 = 0.042$ ). Since type 3 males spend approximately one quarter of the time that type 1 males spend per reproductive event (Tutin 1979), we estimate their chances of fertilization to be approximately one quarter that of type 1 ( $\gamma_3 = 0.13$ ).

Since there is no extra-pair copulation, the magnitudes of  $k_{12}$ ,  $k_{13}$ , and  $k_{23}$  were set to zero. As chimpanzee females regularly mate with males from outside of the group (Tutin 1979), it is reasonable to assume a female should be able to discern between the type 1 and 2 males with a probability of 50% in approximately 1 week ( $D = 3$ ).

### Humans

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. For default values, we set  $r_1 = 1$ . In unigenerational families, raising a child without paternal support can have serious negative effects of offspring success ( $r_2 = 0.9$ ); however, humans evolved in extended family kin groups with extensive grandparent support, and children in these multigenerational families with only one mother have shown to have success at least equal to those from families with only one parent (DaLeire and Kalil 2002). We therefore consider  $r_2 = 1$  as well. We set  $r_3 = 0.90r_2$  to incorporate the physical, emotional, psychological, and social effects on children conceived from rape (see van Ee and Kleber 2013 for review). The

time the female spends in reproduction is estimated based on time to conceive. This includes the typical within-pair time to conception (approximately 10-12 months for 95% of couples; Potter and Parker 1964), the duration of pregnancy, and the duration of lactation (which varies culturally but averages around 1-1.5 years; Jones 1986; Jakobsen et al. 1996), resulting in an interbirth interval of approximately 3 years ( $t_f = t_1 = 36$ ).

We assume that type 2 males engaging in short-term reproductive strategies spend approximately 1 month in each relationship ( $t_2 = 1$ ), with type 3 males spending approximately 2 weeks in a relationship to take into account varying coercive strategies (date rape, kidnapping, stalking, etc.) ( $t_3 = 0.5$ ). We suggest that type 1 males have a 94% chance of remaining in a long-term relationship after conceiving a child ( $b_1 = 0.06$ —based on data from Kawamura 2009), whereas all other types breakup immediately after the reproductive event ( $b_2 = b_3 = 1$ ). Women have a reproductive lifetime approximately 75% that of men (Carlier and Steeno 1984; Paulson et al. 2001; te Velde and Pearson 2002; Vincent et al. 2002; Anderson et al. 2003) ( $\lambda_f = 0.75$ ). But type 1 males have high pair fidelity and generally tend to match the reproductive lifetime of their mates. So we set  $\lambda_1 = \lambda_f = 0.75$  but explore variation in operational sex ratio.

Males who engage in a short-term reproductive strategy are prone to risky and criminal behavior and may thus depart early from the population either by decreased lifespan or incarceration (Lalumière and Quinsey 1996; Gladden et al. 2008; Jonason et al. 2009). We therefore estimate the reproductive lifetime of type 2 males to be slightly less than the physiological relative maximum of 1 ( $\lambda_2 = 0.95$ ), with an even lower reproductive lifetime of type 3 males ( $\lambda_3 = 0.9$ ).

We estimated  $\gamma_1 = 0.95$ , as 95% of couples conceive within 10-12 months (Potter and Parker 1964). We estimated the odds of conceiving for other males based on female fertility at

different points in their cycle. Women have no chance of conceiving outside an approximate 6-day window leading up to ovulation, with probability of conception during that 6-day window varying from 0.1 to 0.33 (Wilcox et al. 1995). Type 2 fertilization rates depend on the type of relationship. For the default, we address the effect of a “new, short-lived relationship” (six episodes of intercourse over two weeks, including the week of high fertility,  $\gamma_2 = 0.44$ ). We also consider a “one-night stand” outside the week of menstruation ( $\gamma_2 = 0.061$ ) and a “weekend fling” scenario (intercourse three times during the week of high fertility,  $\gamma_2 = 0.516$ ). For type 3 males, evidence suggests that the per-incident pregnancy rate is approximately 0.08, which is higher than the random chance of fertilization, suggesting that type 3 males may be able to selectively choose women in the fertile phase of their cycle by detecting subtle cues of fertility and fecundity (Gottschall and Gottschall 2003) ( $\gamma_3 = 0.08$ ).

We estimated  $k_{12}$  from the proportion of human births resulting from extra-pair paternity (Larmuseau et al. 2016). The magnitudes of  $k_{13}$  and  $k_{23}$  were set to 0.2 and 0.3, respectively, as rough guesses. We assume that if coercers were to become abundant in the population, a substantial proportion of births would result from coercion, despite protection that might be afforded by pairing with a type 1 or type 2 male. The level of protection would presumably be less with a type 2 male than with type 1. That these numbers are only guesses becomes important in the context of our results showing that if  $k_{13}$  is a substantial over-estimate, then the expected outcome for humans becomes a stable mix of types 1 and 2. Improved estimates of these extra-pair paternity parameters is a high priority for future work with this model and more sophisticated successors.

The discrimination coefficient  $D$  was estimated from assuming that an evaluation process lasting about one week should enable the female to distinguish types 1 and 2 males with a

probability of 50% ( $D = 3$ ). The out-of-estrus interval  $t_n$  was set at 0.8 of a month (time unit), corresponding to the infertile proportion of the monthly cycle.

Online Resource 3. Brief explanation of the MATLAB® computer program DatingGame used to obtain the main results

After the descriptive heading in the program listing is a list of parameters that can be modified to produce different runs. Each run generates four figures in the format of text Figures 2, 4, and 5. The correspondence between the parameters in text Table 1 and those in the code is obvious with a few exceptions:  $D$  in the text is `del` in the code;  $\lambda$  parameters in the text are `lam` parameters in the code;  $\gamma$  parameters in the text are `gam` parameters in the code;  $\omega$  in the text is `om` in the code;  $\sigma$  in the supplement derivation is `sigp` in the code; and `half` and `mult` in the code are parameters that apply when the  $d(t_d)$  function is sigmoid rather than hyperbolic, a case not addressed either in the manuscript or the supplement.

Just below the parameter list in the code are three lines marked `***modify***`. The four output graphs are plotted against an abscissa that runs from `xmin` to `xmax` and has a default magnitude of `xdef`. Below the vectors initialized with zeros is a line marked `*****parameter being varied on x axis*****`. This indicates that in the default run this parameter is  $r_2$ . In the line immediately after, the magnitude of  $r_3$  is linked to that of  $r_2$  by the multiplier `R23`. This can be commented out when  $r_3$  is to remain fixed. When the run is based on varying  $r_3$  alone, both previous lines would be commented out and the comment symbol `%` would be removed from `r3 = x(i)`. Obviously  $r_1$  could be varied in this way instead, or some other parameter of interest. Details of the graphics formatting can be altered in the final lines of code. The precision of the

hill-climbing algorithms to find fitnesses and  $t_d$  is fixed in the code at 0.00001 (1e-5 in MATLAB), which seems to provide plenty of precision, but this could easily be adjusted.

Any problems implementing this program should be referred to the authors.