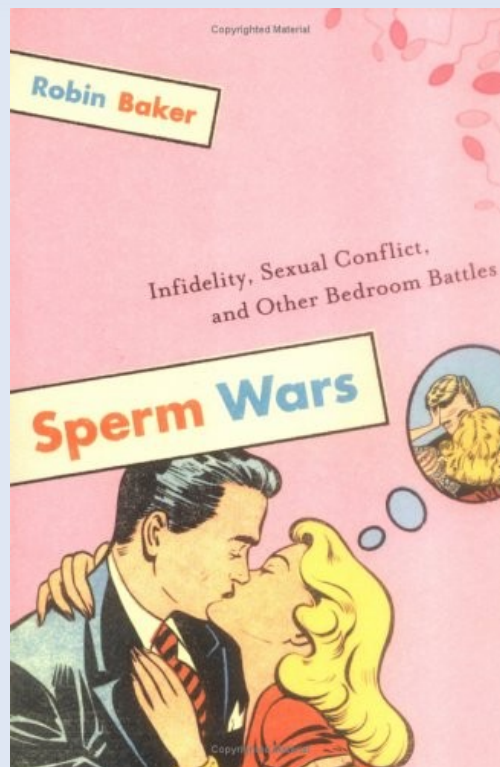


An example: Evolution under sexual conflict



Sexual conflict

- Males and females often have contrasting evolutionary interests.
- For example, females might want to remate with other males, whereas their former partners don't like this at all.
- Or females might want their partners to engage in parental care, whereas these prefer to search for more mates.
- One example of sexual conflict is **conflict over mating rate**: If copulations are harmful to females, they will prefer fewer and/or shorter copulations than males.

The bean beetle

- Male bean beetles have spiky genitalia, which serve as an "anchor" to prolong copulation.
- Long copulations increase a male's fertilization success, but cause injuries to females.
- These injuries can reduce a female's lifetime reproductive success.



More natural history

- Females kick the males during copulation. When they are prevented from doing so, copulations last longer, and females suffer more severe injuries.
- Males do not seem to gain a direct benefit from harming females (such as a delay in female remating).
- Instead, the spines seem to function as an anchor allowing males to complete sperm transfer despite the female's kicking.
- It is even possible that the kicking behavior evolved first, as a way of female mate choice.
- Further reading: Edvardsson and Tregenza, Behavioral Ecology 16: 788.

A dilemma

- Is it really possible that a behavior evolves that reduces the fitness of a male's partner (and, hence, his own)?
- Let's use a simple model to find out!
(Source: Chapter 2 of Hanna Kokko's book)

Preliminary considerations

- Simplest case: Two alleles (*a* wild-type, *A* aggressive)
- We are interested in how the frequency (x) of *A* changes over time.

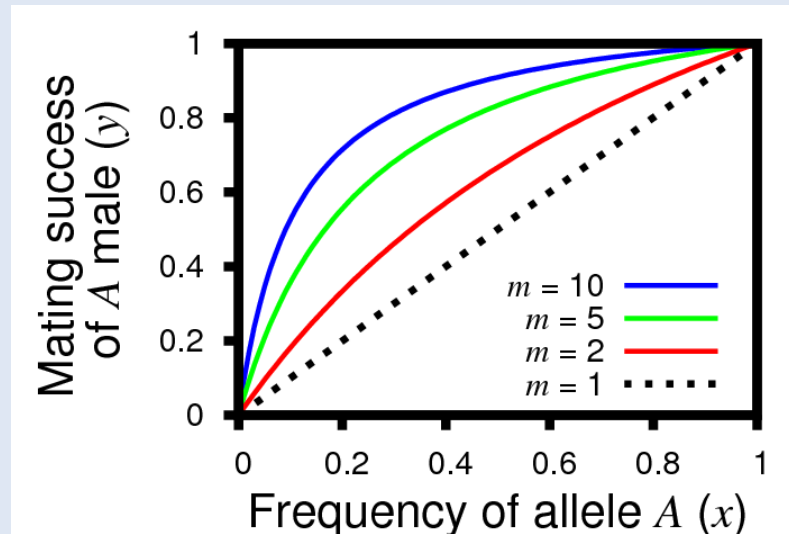
Additional simplifying assumptions:

- Discrete time
- Haploid genetics
- Random mating
- No genetic drift
- ...

Modeling the benefit of A for males

- Skip over details, just assume that, somehow, **A increases male mating success** (before selection on females)
- Let's say that the mating success of A males is m times that of a males.
- Then the proportion of A fathers (before selection on females) is

$$y = \frac{mx}{mx + (1 - x)}$$



What did we just do?

- We have replaced all kinds of complicated scenarios (e.g., the effect of A on the duration of copulation) by a very simple assumption.
- This means that the model will be able to tell us whether structures that increase male success at the expense of females can evolve in principle.
- The model will tell us nothing about the mechanism by which male fitness is increased. It just assumes that such mechanisms exist.

Modeling the cost of *A* for females

- Mating with an *A* male reduces a female's fecundity.
- Females produce *B* offspring when mated to an *a* males, but $b \times B$ offspring when mated to an *A* male ($0 \leq b \leq 1$).
- Obviously, these costs also affect the fitness of the male.

Modeling the dynamics of A

- 1) Find frequencies of mating pairs.
- 2) Find number and type of offspring derived from these mating pairs.
- 3) Sum up everything and calculate how the frequency of A changes over one generation.
- 4) Repeat

Doing the book-keeping

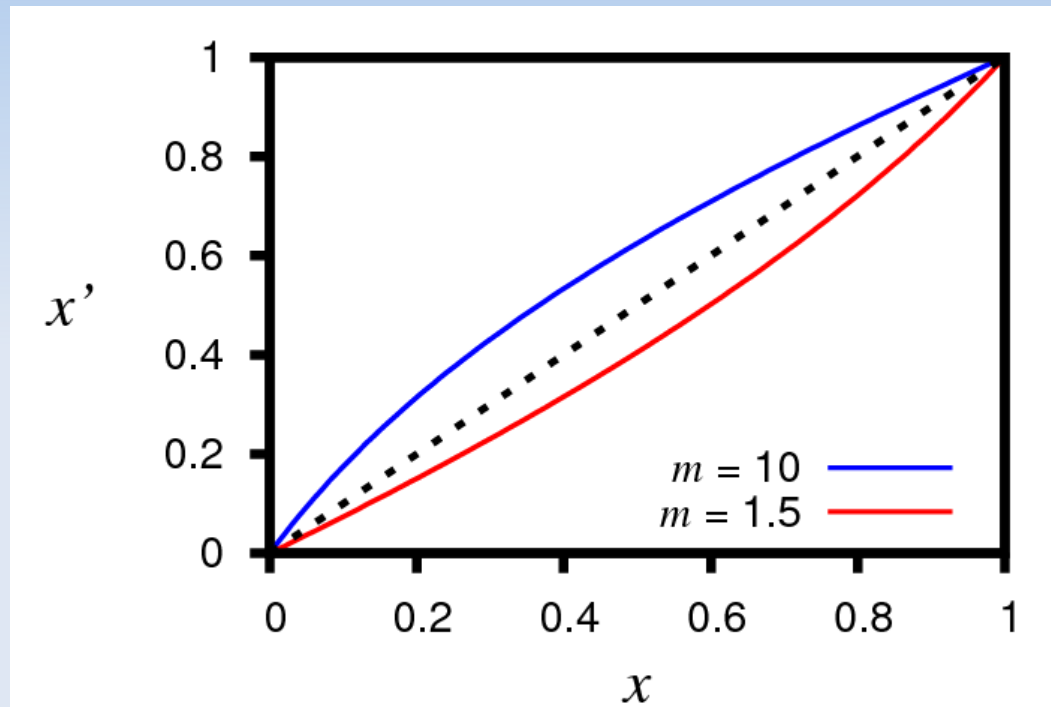
Female	Male	Frequency of mating	Numer of A offspring	Number of a offspring
A	A	$x y$	bB	0
A	a	$x (1-y)$	$B / 2$	$B / 2$
a	A	$(1-x) y$	$bB / 2$	$bB / 2$
a	a	$(1-x) (1-y)$	0	B

Remember $y = mx / (mx + 1 - x)$

Total number of A offspring	$n_A = N [xy bB + x(1-y) B/2 + (1-x)y bB/2]$
Total number of a offspring	$n_a = N [x(1-y) B/2 + (1-x)y bB/2 + (1-x)(1-y) B]$
New frequency of A	$x' = n_A / (n_A + n_a)$

N is total population size.

Numerical analysis



x' increases if m is sufficiently large.

Analytical solution

After simplification, we have

$$x' = \frac{1}{2} \frac{x + y[b - (1 - b)x]}{1 - (1 - b)y} = \frac{1}{2} \frac{x(1 - x + bm(1 + x))}{1 - (1 - bm)x}$$

The dynamics of A depend on whether x' is smaller, equal to or larger than x . We find that

- $x = 0$ and $x = 1$ are equilibria,

and that for $0 < x < 1$

- A spreads if $m > 1 / b$, and
- a spreads if $m < 1 / b$.

These results are independent of N and B .

Conclusions

- So, we have learned that structures harming females can indeed evolve, provided the benefit for the male (in terms of mating success) outweighs the cost for the female.
- OK, maybe we could have guessed that much from the outset.
- But now we can be sure.
- In general, it is not unusual that the result of a model looks trivial in hind-sight.

How extremely stupid not to have thought of that.
(T. H. Huxley about natural selection)

A different model: intralocus sexual conflict

- So far, a cost has been paid by females mating with *A* males.
- Now, assume instead that the cost is paid by females carrying the *A* allele (irrespective of whom they mate with).
- That is, the allele *A* is beneficial in males, but deleterious in females.
- This model will turn out to be slightly more interesting than the previous one.

The new model

Female	Male	Frequency of mating	Numer of A offspring	Number of a offspring
A	A	$x y$	bB	0
A	a	$x (1-y)$	$bB / 2$	$bB / 2$
a	A	$(1-x) y$	$B / 2$	$B / 2$
a	a	$(1-x) (1-y)$	0	B

Remember $y = mx / (mx + 1 - x)$

Total number of A offspring	$n_A = N [xy bB + x(1-y) bB/2 + (1-x)y B/2]$
Total number of a offspring	$n_a = N [x(1-y) bB/2 + (1-x)y B/2 + (1-x)(1-y) B]$
New frequency of A	$x' = n_A / (n_A + n_a)$

N is total population size.

Solving the new model

With intralocus sexual conflict, we get

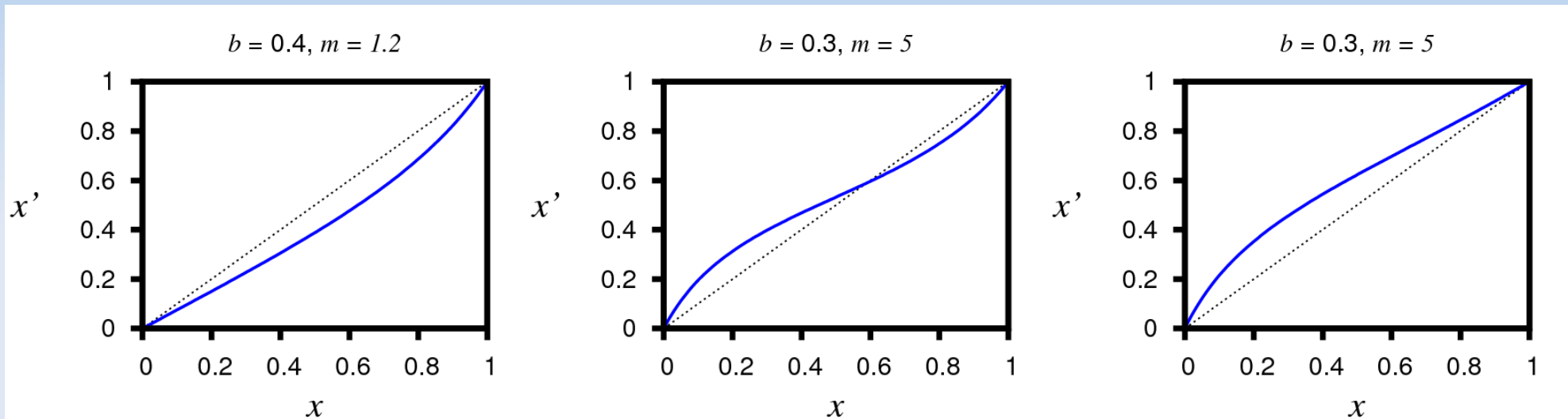
$$x' = \frac{x}{2} \frac{(b+m)(1-x) + 2bmx}{(1-(1-b)x)(1-(1-m)x)}$$

This model has an internal equilibrium at

$$x = \frac{2-b-m}{2(1-b)(1-m)}$$

in addition to the trivial equilibria at $x = 0$ and $x = 1$.

Numerical analysis



Each of the three equilibria can be stable.

Analysis

- Conditions for existence of intermediate equilibrium
 - $b \leq 1/2$ and $m + b > 2$, or
 - $b > 1/2$ and $2-b < m < b / (2b-1)$
- Intermediate equilibrium is stable if the first derivative of x at the equilibrium value is less than 1.
- A simpler way is to look at the derivative at $x = 0$:
 $dx' / dx (x=0) = (m + b) / 2$
- Therefore, if the intermediate equilibrium exists, it is stable.
- $x = 0$ is stable is $m + b < 2$.
- $x = 1$ is stable if $m + b > 2$ but the intermediate equilibrium does not exist.

Conclusions

- Intralocus sexual conflict leads to fundamentally different dynamics.
- In particular, there is a possibility for a protective polymorphism.
- The intermediate equilibrium is maintained, because the *A* allele is beneficial if it is rare, but (net) deleterious if it is common.
- Currently, I don't have a good intuitive explanation for this finding.
- Further reading: Kokko and Brooks 2003, *Ann. Zool. Fennici* 40: 207.