Sex-ratio bias induced by mutation

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A puzzle of evolution

- Human sex ratio at birth $\approx$ 107:100
- Why so many males? [Darwin (1871)]
  Only a small number of males are needed,
  as far as the population growth is concerned.

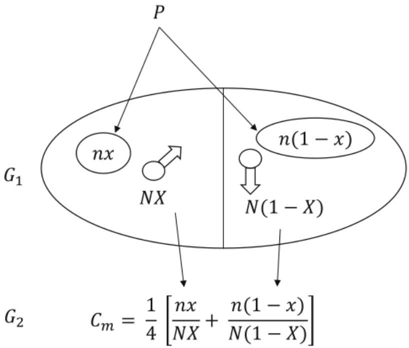
Fisher's idea

- If the sex ratio of the offspring generation is skewed toward males,

  a female-biased *mutant* $\rightarrow$ higher chance to transmit its genes

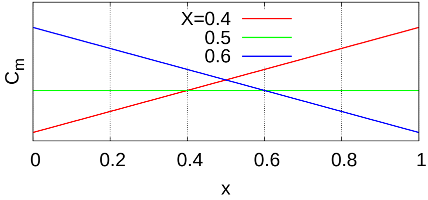
Formulation [Shaw & Mohler (1953)]

- N = population size, n = number of offspring
- X = fraction of males in the population
- x = probability for an individual to have a male offspring
- C_m = genetic contribution of the individual with x



Neutral stability of the Fisherian ratio

$$C_m = \frac{1}{4}\left[\frac{nx}{NX} + \frac{n(1-x)}{N(1-X)}\right]$$



- C_m is greater when x is biased toward the rare sex.
- Any degree of heterogeneity in x if $X = 1/2$

$$C_m \xrightarrow[X=1/2]{} \frac{1}{4}\left[\frac{nx}{N/2} + \frac{n(1-x)}{N/2}\right] = \frac{n}{2N}$$

- More detailed description?

Genetic model [Seger & Stubblefield (2002)]

- a: mutant, A: resident
- Each individual has "sex" (Male or Female) and a "gene" (a or A).
- The gene is inherited from father or mother equally probably.
- q_f (q_m) = fraction of mutant a in females (males) $\ll 1$
- x (X) = offspring sex ratio when <u>father</u> has a (A) [Gellatly (2009)].

		daughters		sons	
♂ × ♀	fraction	a	A	a	A
$a \times a$	$q_m q_f$	$\tilde{x}$		x	
$a \times A$	$q_m(1-q_f)$	$\frac{1}{2}\tilde{x}$	$\frac{1}{2}\tilde{x}$	$\frac{1}{2}x$	$\frac{1}{2}x$
$A \times a$	$(1-q_m)q_f$	$\frac{1}{2}\tilde{X}$	$\frac{1}{2}\tilde{X}$	$\frac{1}{2}X$	$\frac{1}{2}X$
$A \times A$	$(1-q_m)(1-q_f)$		$\tilde{X}$		X

$$\tilde{X} \equiv 1 - X, \qquad \tilde{x} \equiv 1 - x$$

Recurrence relation [Seger & Stubblefield (2002)]

		daughters		sons	
♂ × ♀	fraction	a	A	a	A
$a \times a$	$q_m q_f$	$\tilde{x}$		x	
$a \times A$	$q_m(1-q_f)$	$\frac{1}{2}\tilde{x}$	$\frac{1}{2}\tilde{x}$	$\frac{1}{2}x$	$\frac{1}{2}x$
$A \times a$	$(1-q_m)q_f$	$\frac{1}{2}\tilde{X}$	$\frac{1}{2}\tilde{X}$	$\frac{1}{2}X$	$\frac{1}{2}X$
$A \times A$	$(1-q_m)(1-q_f)$		$\tilde{X}$		X

- Male fraction r of the next generation

$$\begin{aligned} r &= q_m q_f x + q_m(1-q_f)\left(\tfrac{1}{2}x + \tfrac{1}{2}x\right) \\ &\quad +(1-q_m)q_f\left(\tfrac{1}{2}X + \tfrac{1}{2}X\right) + (1-q_m)(1-q_f)X \\ &= X + (x-X)q_m \end{aligned}$$

- fraction of mutant a in males of the next generation

$$q'_m = \frac{q_m q_f x + q_m(1-q_f)\frac{1}{2}x + (1-q_m)q_f\frac{1}{2}X}{r}$$

Fixed-point analysis [Seger & Stubblefield (2002)]

- Resident $= A$ with offspring sex ratio X
  Mutant $= a$ with offspring sex ratio x

$$q_f, q_m \ll 1$$

$$\begin{pmatrix} q'_m \\ q'_f \end{pmatrix} = \frac{1}{2} \begin{pmatrix} x/X & 1 \\ \tilde{x}/\tilde{X} & 1 \end{pmatrix} \begin{pmatrix} q_m \\ q_f \end{pmatrix}$$

- If resident $X = \frac{1}{2}$,
  $\Rightarrow$ the matrix has $\lambda = 1$ for any mutant x,
  $\Rightarrow$ evolutionarily stable ratio (i.e., Fisher's principle).

- This is not the whole story, though.

Continuous-time approximation

- ϵ = small deviation from the Fisherian sex ratio, $X = 1/2$

- If $X = \frac{1}{2} + \epsilon$,

$$\frac{dq_m}{dt} \approx c_1 q_m - c_2 q_m^2$$

  for the fraction of mutant a in males.

- $c_1 \propto \epsilon$: Restoring force vanishes as $\epsilon \to 0$ (neutral stability),
  $\therefore q_m \sim 1/t$

- The logistic equation can be solved.
  $\Longrightarrow$ Male fraction $r(t|X, x)$ at time t
  for given resident X and mutant x

Renormalizing fluctuations

- Mutants appear at rate μ with any probability of a male offspring.
  $\Rightarrow$ Average sex ratio over mutant $x \in (0,1)$

$$\bar{r}(t|X) = \int_0^1 r(t|X,x)dx$$

$\Rightarrow$ Effective population sex ratio X'
experienced by another mutant at time $t = \mu^{-1}$

$$X' = \bar{r}\left(t = \mu^{-1}|X\right)$$

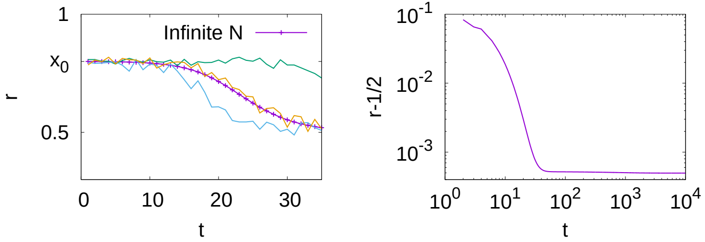
$$X \to X' \to X'' \to \ldots \to X^{(\infty)}$$

- 'Dressed' value

$$\epsilon^{(\infty)} = X^{(\infty)} - 1/2 \approx 0.36\mu - 1.46\mu^2$$

Cross-checks

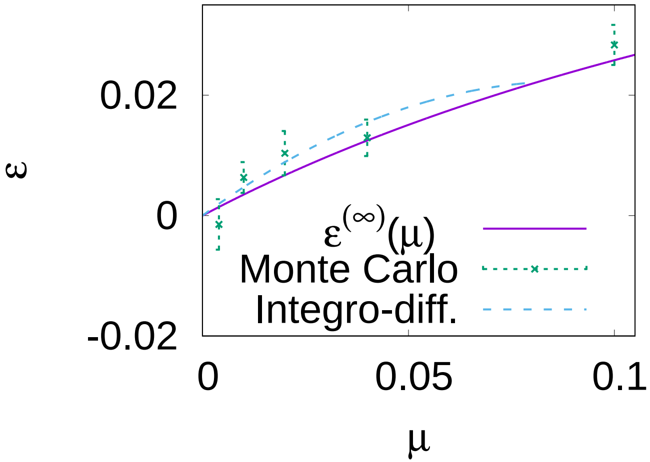
- Monte Carlo
  1. Every individual i has its own x_i $(i = 1, 2, \ldots, N)$.
  2. Choose a male(=father) and a female(=mother).
  3. An offspring's sex is determined by x_{father}, and it inherits either x_{father} or x_{mother} equally probably.
  4. Mutation $x_i \to x_i' \in (0, 1)$ occurs with probability $\mu \ll 1$.



- Integro-differential equation for distribution $(N \to \infty)$

$$\lim_{t\to\infty} r_{\text{fit}}(\mu) \approx 1/2 + 0.5\mu - 2.8\mu^2$$

Results



Summary [Phys. Rev. E 99, 022403 (2019)]

- Correction to Fisher's theory
- Infinitely slow relaxation to the Fisherian ratio
  - Perturbed by any small mutation rate μ
  - Dynamic equilibrium, not captured by fixed-point analysis
- Father effect
  - Broken symmetry between males and females
- Predictions
  - $\mu \geq 0.05$ if responsible for $107 : 100$
  - More sons if μ increases

    $\Longrightarrow$ supported by empirical data [Scherb et al. (2013)]