

With Few Males, Mutations Arising in Males Fix More Readily, Yet the Neutral Average Ignores the Sex Ratio

— counting male and female copies separately, a neutral mutation fixes with one over four times the number of its own sex, the average stays one over $2N$, and favourable mutations fall below the effective-size formula — the separator is whether one looks at the sex in which a mutation arose or at the population average — [Paper 994]

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September 2026

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Abstract

Dominance divides the fixation of favourable mutations in diploids, and additive ones come near half the haploid value (Paper 982). Different numbers of males and females (the sex ratio) were not included there. For a diploid population of 40 males and females in total, this paper solves exactly a transition matrix counting mutant copies in males and in females separately, and compares how the fixation probability differs for a mutation arising in a male or a female with the effective-size formula. No new theorem or law is claimed. First, under neutrality, a mutation in the rarer sex fixes more readily: a mutation in a male agreed with $1/(4 \text{ times the number of males})$ and in a female with $1/(4 \text{ times the number of females})$ within 10^{-10} ; with 2 males and 38 females these were **0.125000** and **0.006579** (Section 2). Second, the neutral average does not depend on the sex ratio: the average weighted by the numbers of males and females in which mutations arise was $1/(2N) = 0.012500$ for all four sex ratios (Section 2). Third, favourable mutations arising in males also fix far more readily: with advantage 0.05 and 2 males to 38 females, a mutation in a male fixed with **0.212137** and in a female with **0.012209**, a ratio of **17.375044** (19 under neutrality) (Section 3). Fourth, the average for favourable mutations is further below the effective-size formula: the average over the diffusion formula with effective size was **0.970541** at 20:20 and **0.921808** at 2:38, smaller with fewer males; relative to the equal sex ratio, 2:38 gave **0.240347** exactly against **0.253053** by the formula (Section 3). Fifth, the separator is whether one looks at the sex in which a mutation arose or at the population average: a single copy weighs more in the rarer sex, and under neutrality that weight was exactly the fixation probability. Looking only at the average, the sex ratio vanished under neutrality and departed from the effective-size formula for favourable mutations (Section 4). **Keywords:** sex ratio, effective population size, fixation probability, diploid, transition matrix, population genetics.

Scope of this paper (scope note): No new theorem or law is claimed: that unequal numbers of males and females give an effective size of 4 times males times females over their sum, that a neutral mutation's fixation probability equals the share of copies it represents, and that each sex contributes half the genes of the next generation, are known in population genetics. No real values are claimed: 40 individuals in total, male to female numbers 20:20, 10:30, 5:35 and 2:38, and a per-copy advantage of 0.05 are model values and correspond to no animal. The model is not extended: one autosomal locus, with the same advantage applied to the copy frequency in each sex and offspring frequency the mean of the two sexes. Sex chromosomes, sex determination, sex-specific advantages and overlapping generations are not included. Mechanisms are not separated: the departure of the average from the effective-size formula for favourable mutations is not split into the error of the diffusion approximation and the effect of the sex ratio. Relation to earlier papers: Paper 982, in its scope note, did not extend the model, taking randomly mating diploids with non-overlapping generations and leaving out inbreeding, sex ratio, overlapping generations, linkage between genes and the mechanism of dominance; this paper sits in the seat of sex ratio (no earlier occupant; the inbreeding seat was taken by Paper 984). Paper 982 showed that dominance divides the fixation of favourable mutations in diploids, and that the diffusion formula exceeds the exact transition-matrix solution. Here, again by transition matrix, different numbers of males and females are added. Paper 984 showed that inbreeding lifts recessive fixation most. Here not inbreeding but imbalance in the numbers of the sexes is counted. What is added: finding exactly the fixation probabilities of mutations in males and in females for four sex ratios, confirming agreement with $1/(4 \text{ times the number of that sex})$ under neutrality, confirming that the weighted average does not depend on sex ratio under neutrality, comparing the average for favourable mutations with the effective-size formula, and placing the separator on "which sex, or the average".

1. Notation and the Question

Model: at one autosomal locus of a diploid population with N_m males and N_f females ($N_m + N_f = 40$), let x of the $2N_m$ male copies and y of the $2N_f$ female copies be mutant. Selection with per-copy advantage s takes each sex's frequency p to $p(1+s)/(1+ps)$, the offspring frequency is the mean $\bar{p}$ of the two sexes, and the next generation's $2N_m$ male and $2N_f$ female copies are drawn independently from binomials with $\bar{p}$. The transition matrix over states (x, y) (row sums off by at most 5.1×10^{-14}) was solved for the probability that all copies become mutant, starting with one mutant copy in a male or in a female.

Formula compared: with effective size $N_e = 4N_mN_f/(N_m + N_f)$ and initial frequency $p_0 = 1/(2N)$,

$$u = \frac{1 - e^{-4N_es p_0}}{1 - e^{-4N_es}}$$

and $u = p_0$ under neutrality. The exact solutions were averaged with weights given by the numbers of males and females in which mutations arise (N_m and N_f).

Question: with unequal numbers of males and females, how does the fixation probability differ by the sex in which a mutation arises, and how does the population average agree with the effective-size formula?

2. Neutral Mutations

Computation 2.1: fixation probability under neutrality ($s = 0$).

males : females	effective size	mutation in a male	in a female	average
20 : 20	40.0000	0.012500	0.012500	0.012500
10 : 30	30.0000	0.025000	0.008333	0.012500
5 : 35	17.5000	0.050000	0.007143	0.012500
2 : 38	7.6000	0.125000	0.006579	0.012500

For all four sex ratios, a mutation in a male agreed with $1/(4N_m)$, in a female with $1/(4N_f)$, and the average with $1/(2N)$, within 10^{-10} .

3. Favourable Mutations

Computation 3.1: fixation probability with advantage $s = 0.05$.

males : females	in a male	in a female	male over female	average	average over effective-size formula
20 : 20	0.092390	0.092390	1.000000	0.092390	0.970541
10 : 30	0.135656	0.047478	2.857251	0.069522	0.959773
5 : 35	0.159990	0.024608	6.501456	0.041531	0.940902
2 : 38	0.212137	0.012209	17.375044	0.022206	0.921808

The effective-size formula gave 0.095195, 0.072436, 0.044140 and 0.024089 from 20:20 to 2:38. Relative to the equal sex ratio, the average for 10:30, 5:35 and 2:38 was 0.752485, 0.449519 and 0.240347 exactly and 0.760927, 0.463679 and 0.253053 by the formula (exact over formula 0.988906, 0.969461 and 0.949788).

Observation 3.2

for favourable mutations, the effect of sex ratio was slightly stronger than the effective-size formula. Even at 20:20 the average was 0.970541 of the formula, which includes the error of the diffusion approximation independent of sex ratio: relative to the equal sex ratio, the exact value at 2:38 was 0.949788 of the formula. Male over female was 2.857251, 6.501456 and 17.375044 with advantage 0.05, against 3, 7 and 19 under neutrality.

4. The Separator

Observation 4.1

the separator is whether one looks at the sex in which a mutation arose or at the population average. Each sex contributes half the next generation's copies, so a single copy in the rarer sex carries more weight than one in the commoner sex: under neutrality those weights, $1/(4N_m)$ and $1/(4N_f)$, were exactly the fixation probabilities, and averaging by where mutations arise returned $1/(2N)$. For favourable mutations the average departed from the effective-size formula more with fewer males, but that departure was not split into approximation error and the effect of sex ratio.

Observation 4.2

what is not said. Sex chromosomes, sex determination, sex-specific advantages, overlapping generations, the sex ratios of real animals and the shape for larger populations are not treated. What is shown is how, in a model of 40 individuals, fixation probabilities divide by the sex in which a mutation arises and by the sex ratio.

5. Roll Call and Closing

1. a transition matrix counting male and female copies separately (Section 1): exact solution.
2. neutral mutation in one of 2 males: **0.125000** (Computation 2.1): $1/(4 \text{ times the number of males})$.
3. the neutral average stays 0.012500 (Computation 2.1): independent of sex ratio.
4. male over female for favourable mutations **17.375044** (Computation 3.1): fixes more readily in males.
5. average over effective-size formula **0.921808** (Computation 3.1): departs more with fewer males.

6. which sex, or the average (Observation 4.1): the separator; the scope note of Paper 982.

Closing: With few males, mutations arising in males fix more readily, yet the neutral average ignores the sex ratio. Solving by transition matrix with male and female copies counted separately, under neutrality a mutation in a male fixed with $1/(4 \text{ times the number of males})$ and in a female with $1/(4 \text{ times the number of females})$, 0.125000 and 0.006579 with 2 males and 38 females, while the average was 0.012500 for all four sex ratios: with advantage 0.05, male over female was 17.375044 and the average was 0.921808 of the effective-size formula. The separator is whether one looks at the sex in which a mutation arose or at the population average. Placed among the earlier papers: to the diploids Paper 982 counted without distinguishing sexes, the sex ratio Paper 982 did not include was added. To be honest: fixation probabilities by sex were set out for one model of 40 individuals. How the sex ratio divides fixation, and no further.

References

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