

CORRECTION



# Correction: Meiosis at three loci in autotetraploids: Probabilities of gamete modes and genotypes without and with preferential cross-over formation

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Two major corrections are required for Griswold & Asif (2023). The first correction relates to when there is preferential cross-over formation and the calculation of diallelic genotype-gamete transition probabilities. The second correction relates to calculating gamete mode probabilities with preferential cross-over formation and when the mode of action of the preferential locus is downstream and located at the middle and proximal locations.

## CALCULATION OF DIALLELIC GENOTYPE-GAMETE TRANSITION PROBABILITIES WITH PREFERENTIAL CROSS-OVER FORMATION

It was assumed in Griswold & Asif (2023) in the calculations of diallelic genotype-gamete transition probabilities (Supplementary Information [28-30, 32-34]) that given a gamete mode, the probabilities of gamete combinations arising from the mode are uniform. This is correct without preferential cross-over formation, but is not correct with preferential cross-over formation. For example, without preferential cross-over formation and for the gamete mode  $a_1b_2c_3/a_4b_4c_4$  there are  $4 \times 3 \times 2 = 24$  combinations at the level of chromosome identity, with one combination being  $a_1b_2c_2/a_3b_4c_4$ , and each combination is equally probable. With preferential cross-over formation and a tetraploid genotype  $a_1Gc_1/a_2Gc_2/a_3Gc_3/a_4Gc_4$ , the probability of the gamete combination  $a_1Gc_2/a_3Gc_4$  is different from the probability of the combination  $a_1Gc_3/a_4Gc_2$  because a GG pairing is more likely to form a crossover than a Gg pairing. Although the algorithms of Griswold & Asif (2023) accounted for different probabilities of gamete combinations, it then collapsed gamete combinations into modes of the form  $a_iGc_j/a_kGc_\ell$ , for  $i, j, k, \ell \in \{1, 2, 3, 4\}$  and  $i \neq j \neq k \neq \ell$  using Fisher's (1947) approach and notation. Supplementary Information [28-30, 32-34] then assumed a uniform probability of gamete combinations given a mode when generating diallelic genotype-gamete transition probabilities.

To account for the conditional state at the G|g locus requires shifting from collapsing gamete combinations into a single mode and instead retaining information at the level of gamete

combinations. Accordingly, in this correction the mode  $a_iGc_j/a_kGc_\ell$  is expanded into 24 gamete combinations or equivalently the set  $\{a_iGc_j/a_kGc_\ell\}$  for  $i, j, k, \ell \in \{1, 2, 3, 4\}$  and  $i \neq j \neq k \neq \ell$ . Whereas there are 37 unordered modes using Fisher's (1947) notation, there are 624 unordered gamete combinations in the revised approach. The numbered list of gamete combinations is provided for the middle case in Supplementary Information - 51C - List of gamete combinations. The same numbering applies for the proximal and distal cases and by swapping allelic ids between loci.

Although the approach of Griswold & Asif (2023) generates correct gamete mode probabilities at the level of Fisher (1947), a mode consists of gamete combinations that occur with different probabilities, such that it is not possible to directly calculate diallelic genotype-gamete probabilities from the modes reported in Griswold & Asif (2023). To do so correctly requires calculating gamete mode probabilities at the level of 624 gamete combinations and then determining which combinations give rise to a particular gamete genotype, conditioned on a diallelic parental genotype. Below are a sequence of Supplementary Information that together gives rise to a set of gamete mode probabilities and diallelic genotype-gamete transition matrices that can be used with preferential cross-over formation:

[1] Python code that calculates gamete mode probabilities at the level of gamete combinations and for each pairing arrangement during meiosis. Files are separated into whether action of the G|g locus is downstream or local and the location of the locus is distal, in the middle or proximal, as well as for scramble pairing:

[a] Supplementary Information - [4C - 9C] - A - Python Code - Gamete Mode Probabilities - Q for  $A \in \{\text{downstream, adjacent}\}$  and  $Q \in \{\text{distal, middle, proximal}\}$

[b] Supplementary Information - 22C - Python Code - Gamete Mode Probabilities - Scramble.

Within the the Python code the state of the G|g locus is entered and probabilities of all gamete combinations are calculated for all pairing arrangements. Throughout we indicate correspondence of Supplementary Information in the correction with the original paper, by adding a "C" to the number of a Supplementary file. For

example, the Supplementary Material 4C in the correction corresponds to Supplementary Material 4 in the original paper.

[2] IPython notebooks that compile gamete mode probabilities at the level of gamete combinations across arrangements from [1] for each genotype at the  $G||g$  locus:

[a] Supplementary Information - [10C - 15C] - A - Python Notebook - Compile Gamete Mode Probabilities - Q - X for  $A \in \{\text{downstream, adjacent}\}$ ,  $Q \in \{\text{distal, middle, proximal}\}$  and  $X \in \{4G0g, 3G1g, 2G2g, 3G1G1g\}$

[b] Supplementary Information - 23C - Python Notebook - Compile Gamete Mode Probabilities - Scramble - X for  $X \in \{4G0g, 3G1g, 2G2g, 3G1G1g\}$ .

Here,  $4G0g$ ,  $3G1g$ ,  $2G2g$  and  $3G1G1g$  correspond to genotypes  $GGGg$ ,  $GGGg$ ,  $GGg$  and  $GGGg\&\&g$  at the preference locus.

[3] Algebraic expressions for gamete mode probabilities at the level of gamete combinations from [2] are presented in the text files

[a] Supplementary Information - [16C - 21C] - A - Gamete Mode Probabilities - Q - X for  $A \in \{\text{downstream, adjacent}\}$ ,  $Q \in \{\text{distal, middle, proximal}\}$  and  $X \in \{4G0g, 3G1g, 2G2g, 3G1G1g\}$

[b] Supplementary Information - 24C - Gamete Mode Probabilities - Scramble - X for  $X \in \{4G0g, 3G1g, 2G2g, 3G1G1g\}$ .

[4] IPython notebooks that generate diallelic genotype-gamete transition matrices separately for each location and genotype at the  $G||g$  locus:

[a] Supplementary Information - [28C - 30C] - Python Notebook - Preferential cross-over formation genotype-gamete transitions - Q - X for  $Q \in \{\text{distal, middle, proximal}\}$  and  $X \in \{4G0g, 3G1g, 2G2g\}$

The notebooks output transition probabilities in the form of sums of terms using the notation  $p(a, b)$ , where  $a$  is the number of  $G$  alleles in the parental genotype and  $b$  is a gamete mode combination that gives rise to a gamete genotype from a parental genotype. The  $3G1G1g$  case is not included because this will require additional consideration, accounting for mutation during meiosis.

[5] Text files of probabilities from [4]:

[a] Supplementary Information - [32C - 34C] - Preferential cross-over formation - Genotype-gamete transition matrix - Q - X

for  $Q \in \{\text{distal, middle, proximal}\}$  and  $X \in \{4G0g, 3G1g, 2G2g\}$

#### GAMETE MODE PROBABILITIES WITH DOWNSTREAM PREFERENTIAL CROSS-OVER FORMATION AT THE MIDDLE AND DISTAL LOCATIONS

A repeated coding error was found involving the use of parenthesis and compound or/and statements in functions  $\text{biv}_D$ ,

**Table 1.** Mean estimates of the probability of a synaptic partner switch (upper) and  $p_{pref}$  (lower), as well as standard deviations (in parentheses) across 100 replicates.

Sample size	Location of $G  g$ locus				Distal	Middle	Middle (local)	Proximal
	Distal	Middle	Middle (local)	Proximal				
$GGGg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.01, p_{pref} = 0.95$					$GGGg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.01, p_{pref} = 0.50$			
5000	0.01 (0.004)	0.01 (0.003)	0.01 (0.004)	0.01 (0.002)	0.01 (0.002)	0.01 (0.002)	0.01 (0.003)	0.01 (0.002)
	0.95 (0.005)	0.95 (0.005)	0.95 (0.004)	0.91 (0.25)	0.50 (0.008)	0.50 (0.01)	0.50 (0.007)	0.54 (0.44)
50000	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)
	0.95 (0.001)	0.95 (0.001)	0.95 (0.001)	0.95 (0.05)	0.50 (0.003)	0.50 (0.004)	0.50 (0.003)	0.46 (0.27)
$GGGg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.25, p_{pref} = 0.95$					$GGGg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.25, p_{pref} = 0.50$			
5000	0.25 (0.01)	0.25 (0.009)	0.25 (0.01)	0.25 (0.009)	0.25 (0.02)	0.25 (0.01)	0.25 (0.01)	0.25 (0.01)
	0.95 (0.008)	0.95 (0.006)	0.95 (0.009)	0.95 (0.03)	0.50 (0.02)	0.50 (0.02)	0.50 (0.009)	0.49 (0.15)
50000	0.25 (0.004)	0.25 (0.003)	0.25 (0.004)	0.25 (0.003)	0.25 (0.004)	0.25 (0.003)	0.25 (0.004)	0.25 (0.003)
	0.95 (0.002)	0.95 (0.002)	0.95 (0.002)	0.95 (0.01)	0.50 (0.004)	0.50 (0.005)	0.50 (0.004)	0.50 (0.04)
$GGgg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.01, p_{pref} = 0.95$					$GGgg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.01, p_{pref} = 0.50$			
5000	0.01 (0.003)	0.01 (0.005)	0.01 (0.003)	0.01 (0.009)	0.008 (0.009)	0.01 (0.009)	0.01 (0.007)	0.01 (0.008)
	0.95 (0.003)	0.95 (0.004)	0.95 (0.003)	0*	0.50 (0.008)	0.50 (0.01)	0.50 (0.008)	0.01 (0.10)
50000	0.01 (0.001)	0.01 (0.001)	0.01 (0.001)	0.01 (0.003)	0.01 (0.004)	0.01 (0.003)	0.01 (0.003)	0.01 (0.003)
	0.95 (0.001)	0.95 (0.001)	0.95 (0.001)	0*	0.50 (0.003)	0.50 (0.004)	0.50 (0.003)	0*
$GGgg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.25, p_{pref} = 0.95$					$GGgg$ parent: $p_{cp} = p_{pm} = p_{md} = 0.25, p_{pref} = 0.50$			
5000	0.25 (0.01)	0.25 (0.01)	0.25 (0.01)	0.25 (0.01)	0.25 (0.02)	0.25 (0.01)	0.25 (0.01)	0.25 (0.01)
	0.95 (0.006)	0.95 (0.006)	0.95 (0.005)	0.86 (0.20)	0.50 (0.02)	0.50 (0.01)	0.50 (0.01)	0.42 (0.34)
50000	0.25 (0.002)	0.25 (0.004)	0.25 (0.003)	0.25 (0.003)	0.25 (0.005)	0.25 (0.004)	0.25 (0.004)	0.25 (0.004)
	0.95 (0.001)	0.95 (0.002)	0.95 (0.002)	0.93 (0.06)	0.50 (0.005)	0.50 (0.004)	0.50 (0.003)	0.46 (0.19)

Estimates of parameters are based on parental genotypes  $GGGg$  or  $GGgg$  and for proximal, middle and distal locations of the  $G||g$  locus. Unless noted, the action of the  $G||g$  locus is downstream toward the centromere, except for an examination of performance when the  $G||g$  locus is in the middle and acts locally. For a given parental genotype either 5000 or 50,000 gametes are produced. True values for the probability of a synaptic partner switch were 0.01 or 0.25 and for  $p_{pref}$  was 0.95 or 0.50.

\*Estimates at lower bound of 0.

quad\_A\_D, quad\_B\_D, and quad\_C\_D (Supplementary Information 5 & 6 from the original paper). This error has been corrected in Supplementary Information files 5C & 6C (above).

Because of this coding error, the gamete mode probabilities at the level of Fisher's (1947) notation in Supplementary Information - [17, 18] - A - Python Notebook - Compile Gamete Mode Probabilities - Q for  $A \in \{\text{downstream}, \text{adjacent}\}$ ,  $Q \in \{\text{distal}, \text{middle}, \text{proximal}\}$  are incorrect and the user is directed to Supplementary Information - 17C & 18C.

#### AFFECTED RESULTS REPORTED IN MAIN TEXT

[1] Due to the or/and coding error, equations 4, 7 and 9 have been corrected and full expressions are calculated and presented for

[a] Eq. 4 in Supplementary Information - 12C - Downstream - Python Notebook - Compile Gamete Mode Probabilities - Proximal - 2G2g

[b] Eq. 7 in Supplementary Information - 11C - Downstream - Python Notebook - Compile Gamete Mode Probabilities - Middle - 2G2g

[c] Eq. 9 in Supplementary Information - 11C - Downstream - Python Notebook - Compile Gamete Mode Probabilities - Middle - 2G2g.

[2] Furthermore, the dash-dot and long-dash/short-dash lines in Figure 6 were potentially affected by the coding error, but for the parameter values plotted, the corrected plots are very similar to the paper and presented in Supplementary Information - 11C & 12C.

[3] Lastly, Table 1 assumed gamete combinations were uniform given a mode when calculating diallelic genotype-gamete transition probabilities, as well as included results from the or/and coding error. A corrected Table 1 is presented below. The original paper noted poor estimates of preferential cross-over formation when the location of the preferential locus was in the middle and proximal. With the correction poor estimates occur when the preferential locus is proximal, but not when the locus is in the middle. Preferential cross-over formation when the locus is proximal may have only a weak effect on gamete mode probabilities for the context and parameter values examined, such that its estimate is poor. Better performance when the locus is in the middle and in the correction reflects the correction to Supplementary Information 33. Without the correction there was leakage to gametes formed when alleles at the G||g locus mismatched during chromosome pairing.

We sincerely apologize for the errors that required correction.

#### ADDITIONAL INFORMATION

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41437-024-00686-1>.

#### REFERENCES

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