A new theory of the evolution of polyandry as a means of inbreeding avoidance: Electronic appendices

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1 Mathematical analysis for infinite population

1.1 Model definition

We consider a dioecious, diploid species with non-overlapping generations. All females have the same fecundity R. There are L unlinked loci at which there can be two alleles A and B. We assume that the probability that an individual reaches sexual maturity is multiplied by a factor x, 1, or y for each locus which is respectively AA, AB, or BB. A alleles mutate into B alleles, and vice-versa, at a rate μ per generation.

Each female mates with a fixed number of males, and produces a brood of offspring; the phenotype determining the number m of mates is inherited by all female offspring. We assume there are alternating generations of inbreeding and outbreeding. At even generations, females choose their mates at random from the population as a whole; at odd generations, females may only mate with (randomly chosen) males from the same brood.

We assume that fecundity is high, so that broods contain large numbers of individuals. We assume, however, that the population size is kept constant by a limiting process which occurs just before the outbreeding generation. The case of a large population can therefore be simplified by considering only the average numbers of individuals of each genotype.

1.2 Recurrence relation for single locus case

We shall begin by analysing the single-locus case in detail, postponing until later a discussion of how to extend to general L. In this section we derive the equations for the general case, where all three genotypes can have different fitness, and later specialise to the two cases of interest.

Consider a particular mating unit consisting of a single mother and one or more fathers. Let a_{mat} be the probability that a maternal gamete contains an A allele, and $b_{\text{mat}} = 1 - a_{\text{mat}}$ be the probability that it contains a B allele. The corresponding probabilities for the paternal gamete are a_{pat} and $b_{\text{pat}} = 1 - a_{\text{pat}}$. The numbers ω_{AA}, ω_{AB}, and ω_{BB} of offspring[1] of, respectively, genotype AA, AB, and BB are then

$$\omega_{\text{AA}} = xRa_{\text{mat}}a_{\text{pat}} \quad (1)$$

$$\omega_{\text{AB}} = R(a_{\text{mat}}b_{\text{pat}} + b_{\text{mat}}a_{\text{pat}}) \quad (2)$$

$$\omega_{\text{BB}} = yRb_{\text{mat}}b_{\text{pat}}. \quad (3)$$

Equations (1–3) can be applied at any generation, but the gamete frequencies a and b will depend on the mating units, which differ at odd and even generations.

Even generations: At even generations, the female takes m randomly chosen mates from the whole population. We denote the *even generation mating unit* by $u = (j_0, j_1, k_0, k_1)$, where j_0 and j_1 denote the number of mothers in the mating unit of genotype AA or AB, and k_0 and k_1 denote the number of fathers of genotype AA or AB (the number of mothers and fathers of genotype BB being therefore $j_2 = 1 - j_0 - j_1$ and $k_2 = m - k_0 - k_1$).

Using Mendelian genetics, and taking mutation into account, the probability a maternal gamete contains an A allele is

$$a^{(0)}_{\text{mat}}(j_0, j_1) = (1 - \mu)(j_0 + \frac{j_1}{2}) + \mu(1 - j_0 - \frac{j_1}{2}), \quad (4)$$

where the superscript $^{(0)}$ denotes the fact that it is donated by a parent from the '0'th generation. Now consider the paternal gamete. In the absence of mutation, the probabilty that it contains an A allele would be $\frac{m_0}{m} + \frac{m_1}{2m}$. Taking mutation into

[1] '**O**mega' stands for '**O**ffspring'.

Symbol	meaning
A,B	Different alleles
x	Fitness of AA homozygote relative to heterozygote
y	Fitness of BB homozygote relative to heterozygote
μ	Mutation rate (both A to B, and B to A)
R	Fecundity (same for all females)
L	Number of loci
$a_{\text{mat}}(=1-b_{\text{mat}})$	Frequency of A allele in maternal gametes
$a_{\text{pat}}(=1-b_{\text{pat}})$	Frequency of B allele in paternal gametes
$\omega_{\text{AA}}, \omega_{\text{AB}}, \omega_{\text{BB}}$	Number of offspring of genotype AA, AB, BB
m	Polyandry phenotype (number of mates)
$u=(j_0, j_1, k_0, k_1)$	Combination of genotypes in mating unit
j_0, j_1, j_2	Number of females of genotype AA, AB, BB in mating unit
k_0, k_1, k_2	Number of males of genotype AA, AB, BB in mating unit
$.^{(0)}, .^{(1)}, .^{(2)}$	Superscripts denoting generations 0, 1, and 2
$\gamma_{\text{AA}}(u), \gamma_{\text{AB}}(u), \gamma_{\text{BB}}(u)$	Number of grandoffspring of genotype AA, AB, BB from mating unit u
$\tilde{n}_{\text{AA}}, \tilde{n}_{\text{AB}}, \tilde{n}_{\text{BB}}$	Number of individuals of genotype AA, AB, BB just before population limitation event
$n_{\text{AA}}^{(i)}, n_{\text{AB}}^{(i)}, n_{\text{BB}}^{(i)}$	Number of individuals of genotype AA, AB, AB at generation $i(\in\{0,1,2\})$
N	Total population size at even generations
$\nu^{(0)}(u)$	Number of mating units of type u at generation 0
$.^*$	Superscript denoting 'mutant'
$(p_{\text{AA}}^{(i)}, p_{\text{AB}}^{(i)}, p_{\text{BB}}^{(i)})$	Relative proportion of individuals of genotype AA, AB, BB at generation i.
$W_{\text{S}}(\text{AA}), W_{\text{S}}(\text{AB}), W_{\text{S}}(\text{BB})$	Fitness of AA, AB, BB genotype on mating with a genetically identical individual
W_{O}	Fitness on outbreeding
$F(j_0, j_1, k_0, k_1)$	Generic function that depends on the mating unit
q	Frequency of A allele among gametes forming generation 1
p	Frequency of A allele at generation 1
r	Invasion rate (relative increase of mutant populatin per single generation)
δ	Inbreeding depression
κ	Fitness cost per mate
$l_{\text{AA}}, l_{\text{AB}}, l_{\text{BB}}$	Number of an individual's loci which have genotype AA, AB,BB

Table 1: Mathematical symbols used in Section 1

account, we therefore have

$$a^{(0)}_{\text{pat}}(m_0, m_1) = (1-\mu)(\frac{m_0}{m} + \frac{m_1}{2m}) + \mu(1 - \frac{m_0}{m} - \frac{m_1}{2m}) \tag{5}$$

Let $\omega^1_{\text{AA}}(u)$, $\omega^1_{\text{AB}}(u)$, $\omega^1_{\text{BB}}(u)$ denote the number of offspring of genotype AA, AB, BB from this mating unit. These can be obtained by substituting the parental gamete allele frequencies into the general equations (1–3), i.e.

$$\omega^1_{\text{AA}}(u) = xRa^{(0)}_{\text{mat}}(j_0, j_1)a^{(0)}_{\text{pat}}(m_0, m_1) \tag{6}$$

$$\omega^1_{\text{AB}}(u) = R(a^{(0)}_{\text{mat}}(j_0, j_1)b^{(0)}_{\text{pat}}(m_0, m_1) + b^{(0)}_{\text{mat}}(g_{\text{mat}})a^{(0)}_{\text{pat}}(m_0, m_1)) \tag{7}$$

$$\omega^1_{\text{BB}}(u) = yRb^{(0)}_{\text{mat}}(j_0, j_1)b^{(0)}_{\text{pat}}(m_0, m_1). \tag{8}$$

Odd generations: At odd generations, females mate randomly with males from the same brood. Assuming even numbers of males and females, there will be a total of $\frac{\omega^1_{\text{AA}}(u)+\omega^1_{\text{AB}}(u)+\omega^1_{\text{BB}}(u)}{2}$ females in a brood whose parental mating unit is u. The probability that a parental gamete is an A allele will be

$$\begin{aligned} a^1_{\text{mat}} = a^1_{\text{pat}} &= \frac{\omega^1_{\text{AA}}(u) + \frac{\omega^1_{\text{AB}}(u)}{2}}{\omega^1_{\text{AA}}(u) + \omega^1_{\text{AB}}(u) + \omega^1_{\text{BB}}(u)}(1-\mu) \\ &\quad + \frac{\omega^1_{\text{BB}}(u) + \frac{\omega^1_{\text{AB}}(u)}{2}}{\omega^1_{\text{AA}}(u) + \omega^1_{\text{AB}}(u) + \omega^1_{\text{BB}}(u)}\mu. \end{aligned} \tag{9}$$

We denote the number of grandchildren of different genotypes from an even generation mating unit u by[2] γ_{AA}, γ_{AB}, γ_{BB}. These can then be obtained by substituting the gamete allele frequencies in Eqn. (9) into the general recurrence relations (1–3) and multiplying by the total number of females at the odd generation:

$$\gamma_{\text{AA}}(u) = xR\frac{\omega^1_{\text{AA}}(u) + \omega^1_{\text{AB}}(u) + \omega^1_{\text{BB}}(u)}{2}a^1_{\text{mat}}(u)a^1_{\text{pat}}(u) \tag{10}$$

$$\gamma_{\text{AB}}(u) = R\frac{\omega^1_{\text{AA}}(u) + \omega^1_{\text{AB}}(u) + \omega^1_{\text{BB}}(u)}{2}(a^1_{\text{mat}}(u)b^1_{\text{pat}}(u) + b^1_{\text{mat}}(u)a^1_{\text{pat}}(u)) \tag{11}$$

$$\gamma_{\text{BB}}(u) = yR\frac{\omega^1_{\text{AA}}(u) + \omega^1_{\text{AB}}(u) + \omega^1_{\text{BB}}(u)}{2}b^{(0)}_{\text{mat}}(u)b^{(0)}_{\text{pat}}(u). \tag{12}$$

The population undergoes a limitation event just before the next outbreeding event. Let $\tilde{n}_{\text{AA}}$, $\tilde{n}_{\text{AB}}$, and $\tilde{n}_{\text{BB}}$ be the total numbers of different genotypes just before the event, which are obtained by summing the contributions from all over the contributions from the contributions from all mating units. If the number of mating units of type u at the zeroth generation is $\nu^{(0)}(u)$, then we have

$$\begin{pmatrix} \tilde{n}_{\text{AA}} \\ \tilde{n}_{\text{AB}} \\ \tilde{n}_{\text{BB}} \end{pmatrix} = \sum_u \nu^{(0)}(u) \begin{pmatrix} \gamma_{\text{AA}}(u) \\ \gamma_{\text{AB}}(u) \\ \gamma_{\text{BB}}(u) \end{pmatrix}. \tag{13}$$

The population limitation event reduces the population size to N with the same mortality rate for all individuals, so the actual numbers at generation '2' will then be

$$\begin{pmatrix} n^{(2)}_{\text{AA}} \\ n^{(2)}_{\text{AB}} \\ n^{(2)}_{\text{BB}} \end{pmatrix} = \frac{N}{\tilde{n}_{\text{AA}} + \tilde{n}_{\text{AB}} + \tilde{n}_{\text{AB}}} \begin{pmatrix} \tilde{n}_{\text{AA}} \\ \tilde{n}_{\text{AB}} \\ \tilde{n}_{\text{BB}} \end{pmatrix} \tag{14}$$

1.2.1 Monomorphic population

We first consider the case where all females in the population have the same polyandry phenotype m. Let the numbers of individuals of different genotypes at the zeroth generation be $n^{(0)}_{\text{AA}}$, $n^{(0)}_{\text{AB}}$, and $n^{(0)}_{\text{BB}}$, with $n^{(0)}_{\text{AA}} + n^{(0)}_{\text{AB}} + n^{(0)}_{\text{BB}} = N$. Since there is random mating at this generation, the number mating units of type $u = (j_0, j_1, k_0, k_1)$ is multinomially distributed:

$$\nu^{(0)}(j_0, j_1, k_0, k_1) = \frac{m!}{k_0!k_1!k_2!}\frac{(n^{(0)}_{\text{AA}})^{j_0}(n^{(0)}_{\text{AB}})^{j_1}(n^{(0)}_{\text{BB}})^{j_2}}{2N}\left(\frac{n^{(0)}_{\text{AA}}}{N}\right)^{k_0}\left(\frac{n^{(0)}_{\text{AB}}}{N}\right)^{k_1}\left(\frac{n^{(0)}_{\text{BB}}}{N}\right)^{k_2} \tag{15}$$

The genotype frequencies at even generations are obtained by calculating $\nu^{(0)}$ from Equation (15) at one generation, then substituting these values into Eqn (13), where the γ_{AA}, γ_{AB}, γ_{BB} are calculated from equations (4–12). The population at the next generation is then obtained from equation (14). After repeated iterations, the system approaches an equilibrium.

[2] **G**amma stands for **G**randchildren

1.2.2 Invasion by a mutant

We now consider a rare mutant with polyandry phenotype m^* in a wild type population with polyandry phenotype m. The mutant sub-population will have different genotype abundances $n^*_{\rm AA}$, $n^*_{\rm AB}$, $n^*_{\rm BB}$ from the wild type. However, provided the mutant remains rare, the mutant will give a negligible contribution to the total population, so the wild type population $n_{\rm AA}$, $n_{\rm AB}$, $n_{\rm BB}$ can be calculated by the same procedure as in Section 1.2.1, independently of $n^*_{\rm AA}$, $n^*_{\rm AB}$, $n^*_{\rm BB}$. However, the wild type population has a very strong influence on the mutant: at even generations, the random mates chosen by mutant females will overwhelmingly be from the wild type population, so the number of mutant mating units of type $u = (j_0, j_1, k_0, k_1)$ will be

$$\nu^{(0)*}(j_0,j_1,k_0,k_1) = \frac{m!}{k_0!k_1!k_2!}\frac{(n^{(0)*}_{\rm AA})^{j_0}(n^{(0)*}_{\rm AB})^{j_1}(n^{(0)*}_{\rm BB})^{j_2}}{2N}\left(\frac{n^{(0)}_{\rm AA}}{N}\right)^{k_0}\left(\frac{n^{(0)}_{\rm AB}}{N}\right)^{k_1}\left(\frac{n^{(0)}_{\rm BB}}{N}\right)^{k_2}. \quad (16)$$

The abundance of the mutant population just before the next generation will be given by

$$\begin{pmatrix}\tilde{n}^*_{\rm AA}\\ \tilde{n}^*_{\rm AB}\\ \tilde{n}^*_{\rm BB}\end{pmatrix} = \sum_u \nu^{*0}(u)\begin{pmatrix}\gamma^*_{\rm AA}(u)\\ \gamma^*_{\rm AB}(u)\\ \gamma^*_{\rm BB}(u)\end{pmatrix}, \quad (17)$$

(where the γ are calculated from Equations (4–12) using $m \to m^*$). The population limitation event reduces the (overwhelmingly wild type) total population to N, so the mortality rate is $\frac{N}{\tilde{n}_{\rm AA}+\tilde{n}_{\rm AB}+\tilde{n}_{\rm AB}}$ (the denominator being the total wild type population size before the limitation event). The mutant population at the next generation is therefore

$$\begin{pmatrix}n^{(2)*}_{\rm AA}\\ n^{(2)*}_{\rm AB}\\ n^{(2)*}_{\rm BB}\end{pmatrix} = \frac{N}{\tilde{n}_{\rm AA}+\tilde{n}_{\rm AB}+\tilde{n}_{\rm AB}}\begin{pmatrix}\tilde{n}^*_{\rm AA}\\ \tilde{n}^*_{\rm AB}\\ \tilde{n}^*_{\rm BB}\end{pmatrix}. \quad (18)$$

Note that, since $j_0+j_1+j_2 = 1$, $\nu^{(0)*}$ is linear in $(n^{(0)*}_{\rm AA}, n^{(0)*}_{\rm AB}, n^{(0)*}_{\rm BB})$, and Equations (16–18) produce a linear relationship between the abundances at the zeroth and second generations. The rate at which the mutant invades is given by the dominant eigenvalue associated with this linear relationship.

1.2.3 Inbreeding depression at odd generations

Because of the alternation between in- and outbreeding, the genotype abundances at odd generations will be different from those at even generations, even in equilibrium. We are interested in the inbreeding depression measured at odd generations, because this is the point at which polyandry at even generations influences the level of inbreeding.

Let $(p^{(1)}_{\rm AA}, p^{(1)}_{\rm AB}, p^{(1)}_{\rm BB}) = \frac{1}{n^{(1)}_{\rm AA}+n^{(1)}_{\rm AB}+n^{(1)}_{\rm BB}}(n^{(1)}_{\rm AA}, n^{(1)}_{\rm AB}, n^{(1)}_{\rm BB})$ be the fraction of individuals which of genotypes AA, AB, BB. If an individual breeds with one that is genetically identical, the number of offspring will be $W_{\rm S}({\rm G})$ for genotype G, where

$$W_{\rm S}({\rm AA}) = R[x(1-\mu)^2 + 2\mu(1-\mu) + y\mu^2] \quad (19)$$

$$W_{\rm S}({\rm AB}) = R\frac{x+2+y}{4} \quad (20)$$

$$W_{\rm S}({\rm BB}) = R[x\mu^2 + 2\mu(1-\mu) + y(1-\mu)^2]. \quad (21)$$

The average fitness on selfing will then be

$$E(W_{\rm S}) = W_{\rm S}({\rm AA})p^{(1)}_{\rm AA} + W_{\rm S}({\rm AB})p^{(1)}_{\rm AB} + W_{\rm S}({\rm BB})p^{(1)}_{\rm BB} \quad (22)$$

Meanwhile, the average mean fitness on outbreeding will be $W_{\rm O}$, where

$$\begin{aligned} E(W_{\rm O}) &= x[(1-\mu)p^{(1)}_{\rm AA} + \frac{p^{(1)}_{\rm AB}}{2} + \mu p^{(1)}_{\rm BB}]^2 \\ &\quad +2[p^{(1)}_{\rm AA}(1-\mu) + \frac{p^{(1)}_{\rm AB}}{2} + \mu p^{(1)}_{\rm BB}][\mu p^{(1)}_{\rm AA} + \frac{p^{(1)}_{\rm AB}}{2} + (1-\mu)p^{(1)}_{\rm BB}] \\ &\quad +y[\mu p^{(1)}_{\rm AA} + \frac{p^{(1)}_{\rm AB}}{2} + (1-\mu)p^{(1)}_{\rm BB}]^2 \\ &= 1-(1-x)[(1-\mu)p^{(1)}_{\rm AA} + \frac{p^{(1)}_{\rm AB}}{2} + \mu p^{(1)}_{\rm BB}]^2 - (1-y)[\mu p^{(1)}_{\rm AA} + \frac{p^{(1)}_{\rm AB}}{2} + (1-\mu)p^{(1)}_{\rm BB}]^2 \end{aligned} \quad (23)$$

u	(0,0,0,0)	(1,0,0,0)	(0,1,0,0)	(0,0,1,0)	(0,0,0,1)
$a^{(0)}_{\rm mat}$	μ	1	$\frac{1}{2}$	0	0
$a^{(0)}_{\rm pat}$	μ	0	0	$\frac{1}{m}$	$\frac{1}{2m}$
$\omega^1_{\rm AA}$	0	0	0	0	0
$\omega^1_{\rm AB}$	$2R\mu$	R	$\frac{R}{2}$	$\frac{R}{m}$	$\frac{R}{2m}$
$\omega^1_{\rm BB}$	$R(1-2\mu)$	0	$\frac{R}{2}$	$\frac{R(m-1)}{m}$	$\frac{R(2m-1)}{2m}$
$a^1_{\rm mat}$	2μ	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2m}$	$\frac{1}{4m}$
$\gamma_{\rm AA}$	0	$\frac{xR^2}{8}$	$\frac{xR^2}{32}$	$\frac{xR^2}{8m^2}$	$\frac{xR^2}{32m^2}$
$\gamma_{\rm AB}$	$2R^2\mu$	$\frac{R^2}{4}$	$\frac{3R^2}{16}$	$\frac{R^2(2m-1)}{4m^2}$	$\frac{R^2(4m-1)}{16m^2}$
$\gamma_{\rm BB}$	$\frac{R^2}{2}(1-4\mu)$	$\frac{R^2}{8}$	$\frac{9R^2}{32}$	$\frac{R^2(2m-1)^2}{8m^2}$	$\frac{R^2(4m-1)^2}{32m^2}$

Table 2: Expansion for small μ of various quantities, for different even generation mating units $u = (j_0, j_1, k_0, k_1)$. Truncated to order μ for $u = (0,0,0,0)$, and order 1 for other mating units.

1.3 Recessive, deleterious trait

We first consider the recessive case $0 < x < 1$, $y = 1$. Selection will tend to purge the deleterious allele, and if the mutation rate μ is numerically small then the abundance of A will also be small. We can therefore develop a perturbation expansion to determine the properties of the system in the limit where μ is small. We first derive results for the single-locus case, then explain how to extend these to general L.

1.3.1 Rare allele expansion

The rarity of the deleterious allele can be exploited in Equations such as (15) and (16), which represent an average over even generation mating units u: the rarity of the deleterious allele determines which u's contribute to which order in μ, and hence which mating units need to be considered for a given order in perturbation theory. Let us defing genotype frequencies for the wild type $(p^{(0)}_{\rm AA}, p^{(0)}_{\rm AB}, p^{(0)}_{\rm BB}) = \frac{1}{N}(n^{(0)}_{\rm AA}, n^{(0)}_{\rm AB}, n^{(0)}_{\rm BB})$, and for the mutant $(p^{(0)*}_{\rm AA}, p^{(0)*}_{\rm AB}, p^{(0)*}_{\rm BB}) = \frac{1}{N^{(0)*}}(n^{*0}_{\rm AA}, n^{*0}_{\rm AB}, n^{*0}_{\rm BB})$, where $N^{(0)*} = n^{*0}_{\rm AA} + n^{*0}_{\rm AB} + n^{*0}_{\rm BB}$ is the population size of the mutant population at the zeroth generation. Using (16), the average of any function $F(u)$ over mutant mating units at the zeroth generation is

$$
\begin{aligned}
\sum_u \nu^{(0)*}(u) F(j_0,j_1,k_0,k_1) &= \sum_{j_0,j_1,k_0,k_1} \frac{m!}{k_0!k_1!k_2!} \frac{(p^{(0)*}_{\rm AA})^{j_0}(p^{(0)*}_{\rm AB})^{j_1}(p^{(0)*}_{\rm BB})^{j_2}}{2} \left(p^{(0)}_{\rm AA}\right)^{k_0} \left(p^{(0)}_{\rm AB}\right)^{k_1} \left(p^{(0)}_{\rm BB}\right)^{k_2} F(j_0,j_1,k_0,k_1) \\
&= \frac{N^{(0)*}}{2}\Big[\frac{p^{(0)*}_{\rm BB}}{2}\left(p^{(0)}_{\rm BB}\right)^{m^*} F(0,0,0,0) + \frac{p^{(0)*}_{\rm AA}}{2}\left(p^{(0)}_{\rm BB}\right)^{m^*} F(1,0,0,0) + \\
&\quad + \frac{p^{(0)*}_{\rm AB}}{2}\left(p^{(0)}_{\rm BB}\right)^{m^*} F(0,1,0,0) + + \frac{p^{(0)*}_{\rm BB}}{2} m^* p^{(0)}_{\rm AA}\left(p^{(0)}_{\rm BB}\right)^{m^*-1} F(0,0,1,0) + \\
&\quad + \frac{p^{(0)*}_{\rm BB}}{2} m^* p^{(0)}_{\rm AB}\left(p^{(0)}_{\rm BB}\right)^{m^*-1} F(0,0,0,1) + \ldots\Big] \\
&= \frac{N^{(0)*}}{2}\Big[\frac{F(0,0,0,0)}{2} + p^{(0)*}_{\rm AA}\frac{[F(1,0,0,0)-F(0,0,0,0)]}{2} + \\
&\quad + p^{(0)*}_{\rm AB}\frac{[F(0,1,0,0)-F(0,0,0,0)]}{2} + m^* p^{(0)}_{\rm AA}\frac{[F(0,0,1,0)-F(0,0,0,0)]}{2} + \\
&\quad + m^* p^{(0)}_{\rm AB}\frac{[F(0,0,0,1)-F(0,0,0,0)]}{2} + \ldots\Big]
\end{aligned}
\tag{24}
$$

where the terms denoted by '...' are all of second or higher order in $p^{(0)}_{\rm AA}$ and $p^{(0)}_{\rm BB}$. The average over mating units can in the wild type population be obtained by substituting $m^* = m$, $(p^{(0)*}_{\rm AA}, p^{(0)*}_{\rm AB}) = (p^{(0)}_{\rm AA}, p^{(0)}_{\rm AB})$ $N^{(0)*} = N$ in Eqn. (24).

If one of the parents in an even generation mating unit possesses an A allele, then the allele will be prevalent among the offspring and grandoffspring of the mating unit, so we cannot assume that it is rare when applying Eqns. (4–12). We can, however, expand the dependence of these quantities in μ. From Equation (24), we can see that the leading order is obtained by expanding to first order in μ when $u = (0,0,0,0)$ and to zeroth order when $u \in \{(1,0,0,0),(0,1,0,0),(0,0,1,0),(0,0,0,1)\}$. The results of this expansion are given in Table 2.

1.3.2 Monomorphic population

Using the expressions for $(\gamma_{\rm AA}, \gamma_{\rm AB}, \gamma_{\rm BB})$ in Table 2, and the expansion (24) of Eqn. (15), we find that the genotype abundances of a wild type population with polyandry m just before the limitation event are

$$\begin{pmatrix} \tilde{n}_{\rm AA} \\ \tilde{n}_{\rm AB} \\ \tilde{n}_{\rm BB} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ \frac{NR^2}{4} \end{pmatrix} + \begin{pmatrix} 0 \\ 1 \\ -1 \end{pmatrix} NR^2\mu + p^{(0)}_{\rm AA} \begin{pmatrix} \frac{xNR^2(m+1)}{16m} \\ \frac{NR^2(3m-1)}{8m} \\ \frac{NR^2(1-7m)}{16m} \end{pmatrix} + p^{(0)}_{\rm AB} \begin{pmatrix} \frac{xNR^2(m+1)}{64m} \\ \frac{NR^2(7m-1)}{32m} \\ \frac{NR^2(1-15m)}{64m} \end{pmatrix} + \ldots . \tag{25}$$

Summing the rows in Eqn. (25), the total population size just before the limitation event is

$$\tilde{n}_{\rm AA} + \tilde{n}_{\rm AB} + \tilde{n}_{\rm BB} = \frac{NR^2}{4}\left(1 - \frac{(m+1)(1-x)}{16m}(4p^{(0)}_{\rm AA} + p^{(0)}_{\rm AB})\right) + \ldots . \tag{26}$$

Combining Eqns. (14), (25) and (26), the population at generation 2 is

$$\begin{pmatrix} n^{(2)}_{\rm AA} \\ n^{(2)}_{\rm AB} \\ n^{(2)}_{\rm BB} \end{pmatrix} = N \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} + \begin{pmatrix} 0 \\ 4 \\ -4 \end{pmatrix} N\mu + Np^{(0)}_{\rm AA} \begin{pmatrix} \frac{x(m+1)}{4m} \\ \frac{3m-1}{2m} \\ \frac{2-6m-x(m+1)}{4m} \end{pmatrix} + Np^{(0)}_{\rm AB} \begin{pmatrix} \frac{x(m+1)}{16m} \\ \frac{7m-1}{8m} \\ \frac{2-14m-x(m+1)}{16m} \end{pmatrix} . \tag{27}$$

At equilibrium, the genotype frequencies will be the same at all generations, i.e. we would have $n^{(2)}_{\rm AA} = Np^{(0)}_{\rm AA}$, $n^{(2)}_{\rm AB} = Np^{(0)}_{\rm AB}$. Substituting these values into Eqn. (27) yields

$$\begin{aligned} \begin{pmatrix} p^{(0)}_{\rm AA} \\ p^{(0)}_{\rm AB} \end{pmatrix} &= \begin{pmatrix} \frac{x(m+1)}{4m} & \frac{x(m+1)}{16m} \\ \frac{3m-1}{2m} & \frac{7m-1}{8m} \end{pmatrix} \begin{pmatrix} p^{(0)}_{\rm AA} \\ p^{(0)}_{\rm AB} \end{pmatrix} + \begin{pmatrix} 0 \\ 4\mu \end{pmatrix} \\ \Rightarrow \begin{pmatrix} p^{(0)}_{\rm AA} \\ p^{(0)}_{\rm AB} \end{pmatrix} &= \begin{pmatrix} \frac{2x}{1-x} \\ \frac{8[4m-x(m+1)]}{(m+1)(1-x)} \end{pmatrix} \mu . \end{aligned} \tag{28}$$

Eqn. (28) gives the genotype frequency at even generations in equilibrium. The genotype frequencies at *odd* generations will also reach an equilibrium, but will differ from Eqn. (28). However, the total population at odd generations, summed over all broods, is just the result of random mating between all the individuals at the even generation. The total genotype abundances at odd generations are therefore

$$(n^{(1)}_{\rm AA}, n^{(1)}_{\rm AB}, n^{(1)}_{\rm BB}) = \frac{RN}{2}(xq^2, 2q(1-q), (1-q)^2), \tag{29}$$

where $q = (p^{(0)}_{\rm AA} + \frac{p^{(0)}_{\rm AB}}{2})(1-\mu) + (1 - p^{(0)}_{\rm AA} - \frac{p^{(0)}_{\rm AB}}{2})\mu$ is the A allele frequency among the gametes forming this generation. The allele frequency among the odd generation is then $p = \frac{n^{(1)}_{\rm AA} + \frac{n^{(1)}_{\rm AB}}{2}}{n^{(1)}_{\rm AA} + n^{(1)}_{\rm AB} + n^{(1)}_{\rm BB}}$, so by applying Eqns (28) and (29) we get, to leading order,

$$\begin{aligned} p &= \frac{xq^2 + q(1-q)}{1 - q^2(1-x)} \\ &= \frac{17m + 1 - 3x(m+1)}{(m+1)(1-x)}\mu + \ldots . \end{aligned} \tag{30}$$

In the derivation of Eqn. (28) we have assumed that $p^{(0)}_{\rm AA}$ and $p^{(0)}_{\rm AB}$ are numerically small. Equations (4–12) can be solved numerically for any parameter values, and numerical results are compared with the small μ resault (28) in Fig. 1. The values of μ are the same as those used in the simulations in the paper. We see that the approximation is very good for the smaller values of μ and x, but breaks down for larger μ when $(1-x)$ is small. This is because of the factor $\frac{1}{1-x}$ on the right hand side of (28), which causes $n^{(0)}_{\rm AB}$ to be of order 1 when $8\mu \sim (1-x)$.

1.3.3 Invasion of polyandrous mutant

The dynamics of a rare mutant with a different polyandry phenotype m^* in the small-μ limit can be obtained by applying the expansion (24) to Eqn. (17), using the expressions for $\gamma_{\rm AA}, \gamma_{\rm AB}, \gamma_{\rm BB}$ from Table 2 with $m \to m^*$ [taking out a factor of

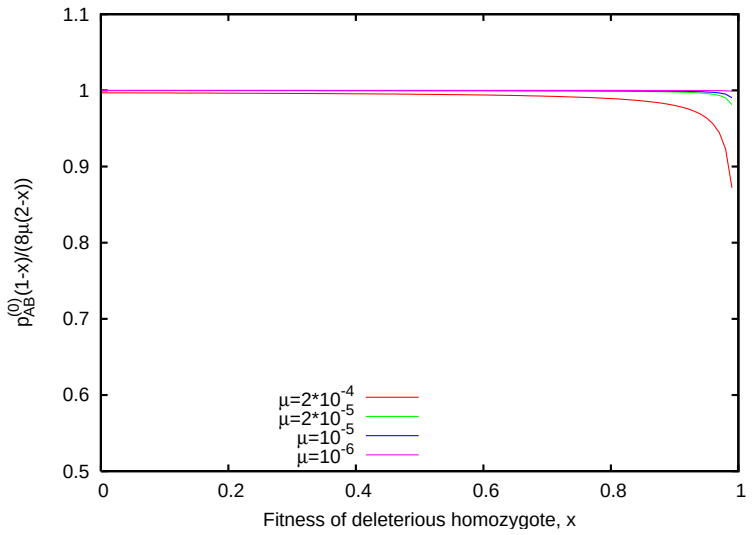

Figure 1: Comparison of the low-mutation rate approximation with with numerical results for finite μ, for the monandrous case $m = 1$. The y-axis shows the measured value of $p^{(0)}_{\mathrm{AB}}$ divided by the theoretical value from Equation (28).

$\frac{N^{(0)*}R^2}{4}$ for clarity]

$$\frac{4}{N^{(0)*}R^2}\begin{pmatrix}\tilde{n}^*_{\mathrm{AA}}\\ \tilde{n}^*_{\mathrm{AB}}\\ \tilde{n}^*_{\mathrm{BB}}\end{pmatrix} = \begin{pmatrix}0\\0\\1\end{pmatrix} + \begin{pmatrix}0\\4\\-4\end{pmatrix}\mu + p^{(0)*}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4}\\ \frac{1}{2}\\ -\frac{3}{4}\end{pmatrix} + p^{(0)*}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16}\\ \frac{3}{8}\\ -\frac{7}{16}\end{pmatrix} + \\ + p^{(0)}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4m^*}\\ \frac{2m^*-1}{2m^*}\\ \frac{1-4m^*}{4m^*}\end{pmatrix} + p^{(0)}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16m^*}\\ \frac{4m^*-1}{8m^*}\\ \frac{1-8m^*}{16m^*}\end{pmatrix} + \ldots \tag{31}$$

Combining Eqns. (26) and (28), we see that, for the wild type population constant population N, the mortality rate at the population limitation event is $\frac{N}{\tilde{n}_{\mathrm{AA}}+\tilde{n}_{\mathrm{AB}}+\tilde{n}_{\mathrm{AB}}} = \frac{4}{R^2(1-2\mu)}$. Substituting (31) into Eqn. (18), the mutant genotype abundances after the population limitation event are

$$\frac{1}{N^{(0)*}}\begin{pmatrix}n^{(2)*}_{\mathrm{AA}}\\ n^{(2)*}_{\mathrm{AB}}\\ n^{(2)*}_{\mathrm{BB}}\end{pmatrix} = \begin{pmatrix}0\\0\\1\end{pmatrix} + \begin{pmatrix}0\\4\\-2\end{pmatrix}\mu + p^{(0)*}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4}\\ \frac{1}{2}\\ -\frac{3}{4}\end{pmatrix} + p^{(0)*}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16}\\ \frac{3}{8}\\ -\frac{7}{16}\end{pmatrix} + \\ + p^{(0)}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4m^*}\\ \frac{2m^*-1}{2m^*}\\ \frac{1-4m^*}{4m^*}\end{pmatrix} + p^{(0)}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16m^*}\\ \frac{4m^*-1}{8m^*}\\ \frac{1-8m^*}{16m^*}\end{pmatrix} + \ldots \tag{32}$$

To find the invasion rate of the mutant, we consider the quasistationary state where the mutant population increases by a constant amount per double generation. If we define r as the invasion rate per *single* generation, then in this quasistationary state we would have $\frac{1}{N^{(0)*}}(n^{(2)*}_{\mathrm{AA}}, n^{(2)*}_{\mathrm{AB}}, n^{(2)*}_{\mathrm{BB}}) = \frac{(1+r)^2}{N^{(0)*}}(n^{(0)*}_{\mathrm{AA}}, n^{(0)*}_{\mathrm{AB}}, n^{(0)*}_{\mathrm{BB}}) \approx (1+2r)(p^{(0)*}_{\mathrm{AA}}, p^{(0)*}_{\mathrm{AB}}, p^{(0)*}_{\mathrm{BB}})$, where we have assumed that r is small (which will be the case if the deleterious allele is rate). Substituting this into eqn (32) gives

$$(1+2r)\begin{pmatrix}p^{(0)*}_{\mathrm{AA}}\\ p^{(0)*}_{\mathrm{AB}}\\ 1-p^{(0)*}_{\mathrm{AA}}-p^{(0)*}_{\mathrm{AB}}\end{pmatrix} = \begin{pmatrix}0\\0\\1\end{pmatrix} + \begin{pmatrix}0\\4\\-2\end{pmatrix}\mu + p^{(0)*}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4}\\ \frac{1}{2}\\ -\frac{3}{4}\end{pmatrix} + p^{(0)*}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16}\\ \frac{3}{8}\\ -\frac{7}{16}\end{pmatrix} + \\ + p^{(0)}_{\mathrm{AA}}\begin{pmatrix}\frac{x}{4m^*}\\ \frac{2m^*-1}{2m^*}\\ \frac{1-4m^*}{4m^*}\end{pmatrix} + p^{(0)}_{\mathrm{AB}}\begin{pmatrix}\frac{x}{16m^*}\\ \frac{4m^*-1}{8m^*}\\ \frac{1-8m^*}{16m^*}\end{pmatrix} + \ldots \tag{33}$$

The first two rows of equation (33) give, to lowest order,

$$\begin{aligned}
\begin{pmatrix} p_{\rm AA}^{(0)*} \\ p_{\rm AB}^{(0)*} \end{pmatrix} &= \begin{pmatrix} \frac{x}{4} & \frac{x}{16} \\ \frac{1}{2} & \frac{3}{8} \end{pmatrix} \begin{pmatrix} p_{\rm AA}^{(0)*} \\ p_{\rm AB}^{(0)*} \end{pmatrix} + \begin{pmatrix} \frac{x}{4m^*} p_{\rm AA}^{(0)} + \frac{x}{16m^*} p_{\rm AB}^{(0)} \\ \frac{2m^*-1}{2m^*} p_{\rm AA}^{(0)} + \frac{4m^*-1}{8m^*} p_{\rm AB}^{(0)} + 4\mu \end{pmatrix} \\
\Rightarrow \begin{pmatrix} p_{\rm AA}^{(0)*} \\ p_{\rm AB}^{(0)*} \end{pmatrix} &= \frac{16}{10-3x} \begin{pmatrix} \frac{5}{8} & \frac{x}{16} \\ \frac{1}{2} & 1-\frac{x}{4} \end{pmatrix} \begin{pmatrix} \frac{x}{4m^*} p_{\rm AA}^{(0)} + \frac{x}{16m^*} p_{\rm AB}^{(0)} \\ \frac{2m^*-1}{2m^*} p_{\rm AA}^{(0)} + \frac{4m^*-1}{8m^*} p_{\rm AB}^{(0)} + 4\mu \end{pmatrix} \\
\Rightarrow \frac{1}{4} p_{\rm AA}^{(0)*} + \frac{9}{16} p_{\rm AB}^{(0)*} &= \frac{16}{10-3x} \begin{pmatrix} \frac{1}{4} & \frac{9}{16} \end{pmatrix} \begin{pmatrix} \frac{5}{8} & \frac{x}{16} \\ \frac{1}{2} & 1-\frac{x}{4} \end{pmatrix} \begin{pmatrix} \frac{x}{4m^*} p_{\rm AA}^{(0)} + \frac{x}{16m^*} p_{\rm AB}^{(0)} \\ \frac{2m^*-1}{2m^*} p_{\rm AA}^{(0)} + \frac{4m^*-1}{8m^*} p_{\rm AB}^{(0)} + 4\mu \end{pmatrix} \\
&= \frac{16}{10-3x} \left(\frac{7x + (18-4x)(2m^*-1)}{64m^*} p_{\rm AA}^{(0)} + \frac{7x + (18-4x)(4m^*-1)}{256m^*} p_{\rm AB}^{(0)} + \frac{9-2x}{4}\mu \right) \qquad (34)
\end{aligned}$$

Using the linear combination of $p_{\rm AA}^{(0)*}$and $p_{\rm AB}^{(0)*}$ in Eqn. (34), the third row of Eqn. (33) gives, to lowest order,

$$\begin{aligned}
2r &= -2\mu + \frac{1}{4} p_{\rm AA}^{(0)*} + \frac{9}{16} p_{\rm AB}^{(0)*} + \frac{1-4m^*}{4m^*} p_{\rm AA}^{(0)} + \frac{1-8m^*}{16m^*} p_{\rm AB}^{(0)} \\
&= \frac{16-2x}{10-3x}\mu + \frac{(m^*+2)(x-1)}{(10-3x)m^*} p_{\rm AA}^{(0)} + \frac{(m^*+1)(x-1)}{2m^*(10-3x)} p_{\rm AB}^{(0)} \\
&= \frac{16(m^*-m)}{(10-3x)m^*(m+1)} \\
\Rightarrow r &= \frac{8(m^*-m)}{(10-3x)m^*(m+1)}, \qquad (35)
\end{aligned}$$

where we have used Eqn. (28) to substitute for $p_{\rm AA}^{(0)}, p_{\rm AB}^{(0)}$.

Since r has the same sign as (m^*-m), higher degrees of polyandry are always favoured in the absence of costs to mating. If there is a cost κ to each mating event, then the mutant population will grow at a rate $(1+r)(1-\kappa)^{m^*-m} \approx r-(m^*-m)\kappa$ relative to the wild type.

1.3.4 Inbreeding depression

Using Equations (19–23) and (29) for the monandrous case $m=1$, the average fitness on selfing is

$$\begin{aligned}
E(W_{\rm S}) &= \frac{x+3}{4} 2q + 1 - 2q + O(\mu^2) \\
&= 1 - \frac{3(3-x)\mu}{2} + O(\mu^2) \qquad (36)
\end{aligned}$$

and the fitness on outbreeding is

$$E(W_{\rm O}) = 1 + O(\mu^2). \qquad (37)$$

Therefore, the inbreeding depression is

$$\delta = 1 - \frac{3(3-x)\mu}{2} + O(\mu^2) \qquad (38)$$

1.3.5 Generalisation to $L \neq 1$

The case of general L and m is difficult to analyse, as the loci are not necessarily statistically independent. However, we show in Section 2.2.1 that the loci are indeed independent in the monandrous case $m=1$, and that they are approximately independent in the case when the deleterious alleles are rare.

Independence of loci implies that, if the fraction of individuals of different genotypes for the one-locus case are $p_{\rm AA}, p_{\rm AB}, p_{\rm BB}$, then for the L-locus case the probability that an individual has $l_{\rm AA}, l_{\rm AB}, l_{\rm BB}$ loci of genotype AA, AB, and BB is multinomial:

$$\Pr(l_{\rm AA}, l_{\rm AB}, l_{\rm BB}) = \frac{L!}{l_{\rm AA}! l_{\rm AB}! l_{\rm BB}!} (p_{\rm AA})^{l_{\rm AA}} (p_{\rm AB})^{l_{\rm AB}} (p_{\rm BB})^{l_{\rm BB}}.$$

Consider a quantity F whose value for the L-locus case is the product of single-locus values for the genotype at each locus. If $F(AA)$, $F(AB)$,$F(BB)$ are the single-locus values for genotypes AA, AB, BB, then the average value for the L-locus case is

$$\begin{aligned}
&\textstyle\sum_{l_{\rm AA}+l_{\rm AB}+l_{\rm BB}=L} \Pr(l_{\rm AA}, l_{\rm AB}, l_{\rm BB}) (F(AA))^{l_{\rm AA}} (F(AB))^{l_{\rm AB}} (F(BB))^{l_{\rm BB}} \\
&= [F(AA)p_{\rm AA} + F(AB)p_{\rm AB} + F(BB)p_{\rm BB}]^L, \qquad (39)
\end{aligned}$$

i.e. the average for the single-locus case raised to the L'th power.

Monandrous wild type equilibrium. The independence of the loci imply that the allele frequency at odd generations is still p from equation (29), and Eqn. (3) from the paper obtains for the case $m = 1$.

Invasion by a biandrous mutant. Since fitness is a product of factors over loci, the growth rate for the population is the L'th power of the growth rate in the single-locus case. If $1 + r_1$ is the relative rate of growth of the mutant growth rate for the single-locus case, the relative growth rate will be $(1 + r_1)^L \approx 1 + r_1 L$. The invasion rate $r = r_1 L$ in Eqnation (4) of the paper obtains by multiplying Eqn. (35) in this appendix by L for the case $m^* = 2$, $m = 1$.

Inbreeding depression. The fitness on selfing and outcrossing are the L-th powers of the single-locus values, so using Eqns. (36) and (37) the inbreeding depression is

$$\begin{aligned} \delta &= 1 - [1 - \frac{3(3-x)\mu}{2} + O(\mu^2)]^L \\ &= \frac{3(3-x)\mu L}{2} + O(\mu^2 L) \end{aligned} \tag{40}$$

which is Eqn. (4) of the paper.

1.4 Overdominant trait

We now consider the case of symmetric overdominance, $x = y$, $0 < x < 1$. By symmetry, both alleles have average frequency $\frac{1}{2}$ over the whole population, so we cannot exploit the rarity of some genotypes to develop a perturbation analysis. Since polymorphism is maintained even in the absence of mutation, and the genotype frequencies are insensitive to the mutation rate, we shall in this section assume that $\mu = 0$. Though we present in this section results for symmetric overdominance, polymorphism is also maintained in this model in the asymmetric case $x \neq y$ (see section 3.2).

An analytical solution of Equations (4–18) is possible, but since it requires the solution of a cubic equation we shall simply present the results of numerical iterations of these equations.

1.4.1 Equilibrium monomprphic population

The genotype abundances at equilibrium can be readily obtained by iterating Equations (4–15). The heterozygosity at even generations, $\frac{n_{\mathrm{AB}}^{(0)}}{N}$, is shown in Figure 2. For purposes of comparison, we have also included the result for the case where there is random mating at all generations, which can straightforwardly be obtained[3]. We see that the heterozygosity increases as the number of mates is increased, i.e. as the degree of inbreeding is reduced.

1.4.2 Invasion by a mutant

The rate of invasion by which a mutant with a different degree of polyandry m^* from the wild type can be obtained by the methods in section 1.2.2. These invasion rates are illustrated in Figure 3. We find that the growth rate is positive for $m^* > m$, and negative for $m^* < m$. Therefore, in the absence of costs to mating, polyandry will invade, the optimal level of polyandry being $m = \infty$.

If, however, there is a cost κ per mate, then the growth rate of the mutant relative to the wild type will be

$$\begin{aligned} [1 + r(m^*, m)][1 - \kappa]^{m^* - m} &\approx 1 + r(m^*, m) - (m^* - m)\kappa \\ &= 1 + (m^* - m)[\frac{r(m^*, m)}{(m^* - m)} - \kappa] \end{aligned} \tag{41}$$

The mutant will therefore invade if $(m^* - m)[\frac{r(m^*,m)}{(m^*-m)} - \kappa] > 0$, i.e. if

$$\begin{array}{c} \text{either } \frac{r(m^*,m)}{(m^*-m)} > \kappa \text{ and } m^* > m \\ \text{or } \frac{r(m^*,m)}{(m^*-m)} < \kappa \text{ and } m^* < m. \end{array}$$

If there are values m_1 and m_2 for which $m_1 < m_2$ and $\frac{r(m_1,m_2)}{m_1-m_2} < \frac{r(m_2,m_1)}{m_2-m_1}$, i.e. $[-r(m_1, m_2)] < r(m_2, m_1)$, then both conditions can be satisfied simultaneously, and a mixed strategy will evolve when $\frac{r(m_1,m_2)}{m_1-m_2} < \kappa < \frac{r(m_2,m_1)}{m_2-m_1}$. Figure 4 shows the ratio $\frac{r(m+1,m)}{[-r(m,m+1)]}$ as a function of x for different values of m, and we do indeed find that this ratio is greater than 1. The phase diagram is illustrated in figure 5, showing that there are regions where two strategies can coexist.

[3]The allele frequencies $a_{\mathrm{mat}} = a_{\mathrm{pat}} = \frac{1}{2}$ at all generations, so using Eqns. (1–3) and then setting total population size=N we get $\frac{n_{\mathrm{AB}}}{N} = \frac{1}{1+x}$

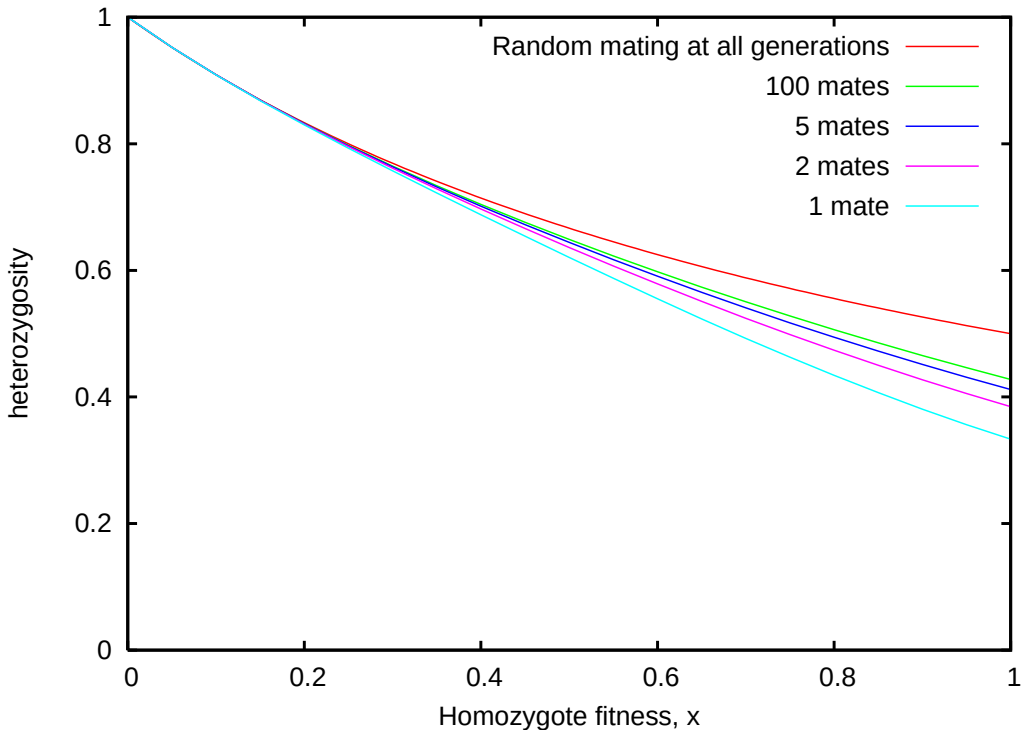

Figure 2: Heterozygosity in equilibrium for a population where all females are equally polyandrous, with a single overdominant locus.

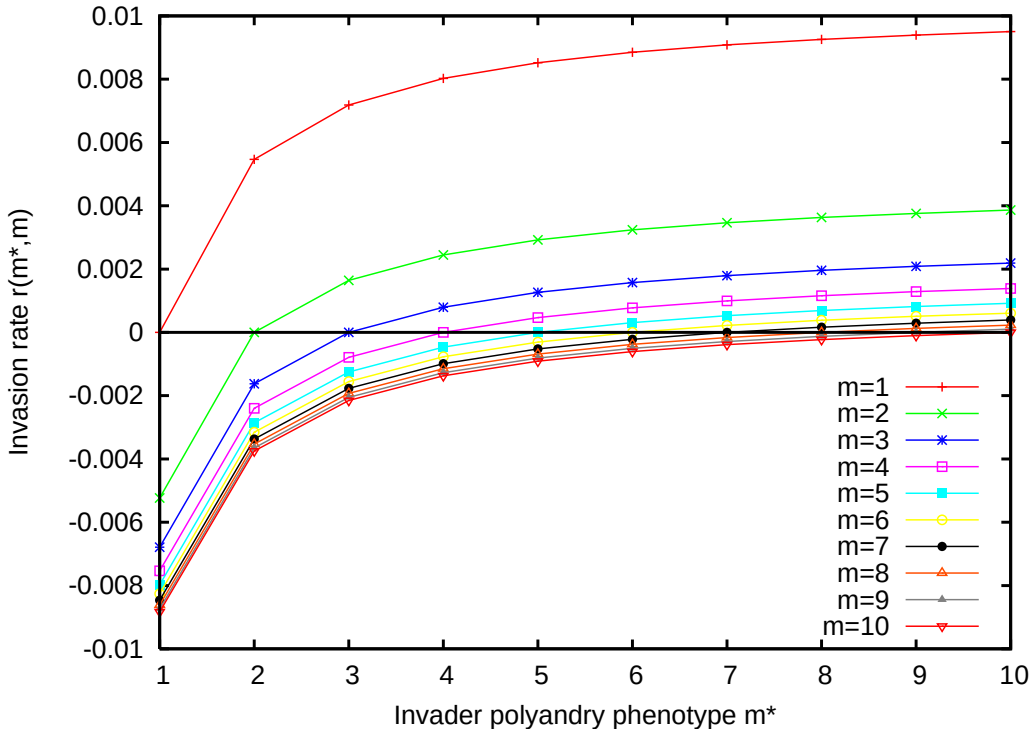

Figure 3: Invasion rate by a mutant with polyandry phenotype m^* in a wild type population with phenotype m. Single overdominant locus, homozygote fitness $x = 0.5$.

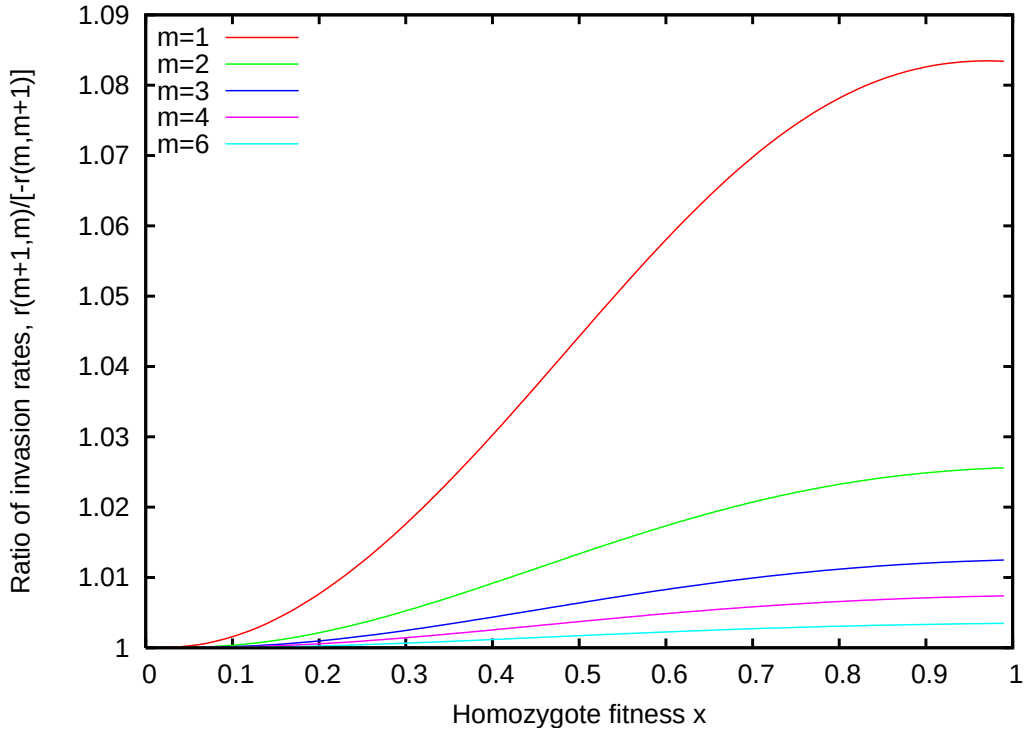

Figure 4: Ratio of the rate of invasion for phenotype $m+1$ in wild type m to the negative rate of invasion by m in wild type $m+1$. Since this ratio is > 1, a mixed strategy where m and $m+1$ are mutually invasible is possible when the cost per mating is set appropriately.

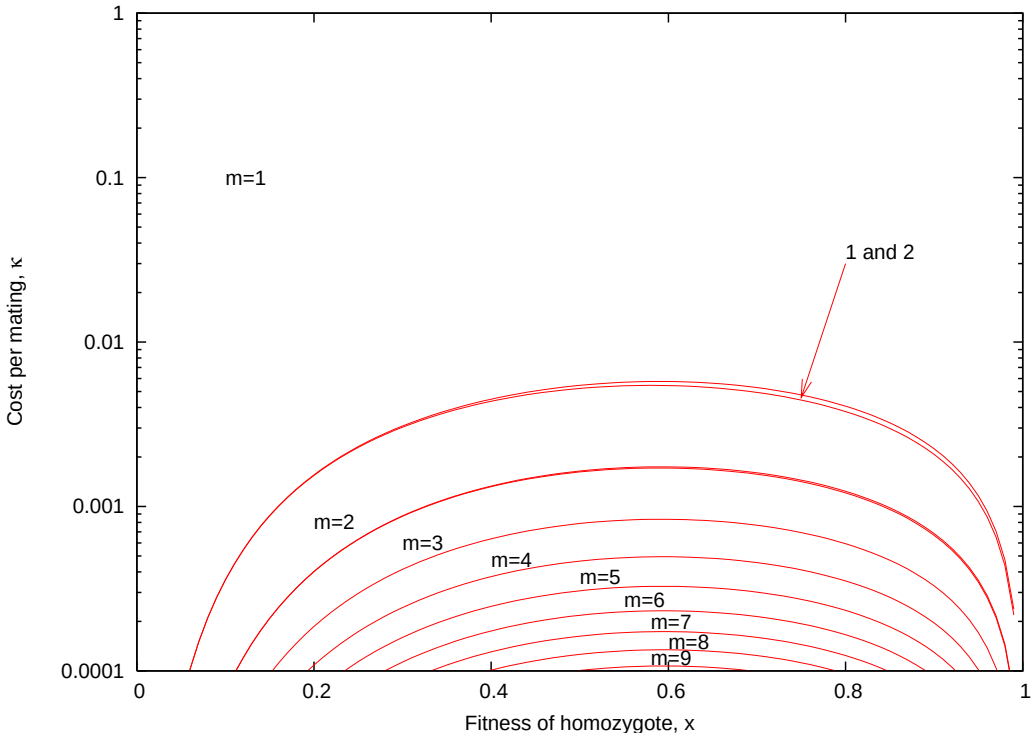

Figure 5: Phase diagram showing the ESS level of polyandry $m$for a single overdominant locus, as a function of homozygote fitness x and cost per mating κ. At each boundary, there is a thin region where mixed strategies are possible.

1.4.3 Inbreeding depression

While it is laborious to derive analytically the genotype frequencies at even generations, the total abundance of genotypes at odd generations may be obtained straightforwardly. By symmetry, the allele frequency is always $\frac{1}{2}$, so from Eqns. (1–3) the genotype frequencies at the odd generations are $(p^{(1)}_{\rm AA}, p^{(1)}_{\rm AB}, p^{(1)}_{\rm BB}) = \frac{1}{2(1+x)}(x, 2, x)$. Using Eqns. (22) and (23), the fitness of in- and outbreeding individuals at odd generations are

$$E(W_{\rm S}) = \frac{R}{2(1+x)}(2x^2+x+1) \tag{42}$$

$$E(W_{\rm O}) = \frac{R(x+1)}{2}. \tag{43}$$

Since the loci are independent when the females are monogamous, we can calculate the ratio of inbreeding to outbreeding fitness for general L using Eqn. (39), and hence the inbreeding depression for general L is

$$\delta = 1 - \left(\frac{2x^2+x+1}{(x+1)^2}\right)^L, \tag{44}$$

which is Equation (6) in the manuscript.

2 Are the loci independent?

Inbreeding can cause nonrandom associations between genotypes at different loci, even in the absence of linkage or selection (Bennet J.H. & Binet F.E., Heredity **10** 51–56 (1956)). This makes it difficult to generalise results for a single-locus model to the multilocus case. In this section we shall discuss the conditions under which the loci will have independent dynamics in our model.

We shall adopt a slightly different notation from the previous section, in order to make this discussion as general as possible. Let us assume that there are L unlinked loci, with the genotype being expressed as an L-tuple $G = \{g_i\}$ of the genotypes g_i at each locus i. Let us assume that each locus has a multiplicative effect, i.e. the number of offspring of genotype $G_c = \{g_{ci}\}$ arising from a mother of genotype $G_m = \{g_{mi}\}$ mated with a father of genotype $G_p = \{g_{pi}\}$ can be expressed in the form $\Omega(G_m, G_p, G_c) = \prod_i \omega_i(g_{mi}, g_{pi}, g_{ci})$, where ω_i represents the relative contribution from each locus. We make no assumptions here about the number of alleles at the locus, the expression type of trait (recessive, overdominant,...) or the presence of mutation. The fitness of the mating unit is

$$\begin{aligned}
\Phi(G_m, G_p) &= \sum_{G_c} \Omega(G_m, G_p, G_c) \\
&= \sum_{G_c} \prod_i \omega_i(g_{mi}, g_{pi}, g_{ci}) \\
&= \left[\sum_{g_{c1}} \omega_1(g_{m1}, g_{p1}, g_{c1})\right]\left[\sum_{g_{c2}} \omega_2(g_{m2}, g_{p2}, g_{c2})\right]\cdots\left[\sum_{g_{cL}} \omega_L(g_{mL}, g_{pL}, g_{cL})\right] \\
&= \prod_i \phi_i(g_{mi}, g_{pi}),
\end{aligned}$$

where $\phi_i(g_{mi}, g_{pi}) = \sum_{g_{ci}} \omega_i(g_{mi}, g_{pi}, g_{ci})$ is the contribution to the fitness from locus i. The final equality holds because the sum over all genotypes can be factorised into independent sums over each locus.

2.1 Monandrous female

Consider a female of genotype G_m that outbreeds with a single male of genotype G_p, where all of her offspring breed with members of the same brood. The number of matings in the brood between offspring of genotype $G_{c_1} = \{g_{c_1 i}\}$,$G_{c_2} = \{g_{c_2 i}\}$ will be $\frac{1}{2}\Omega(G_m, G_p, G_{c_1})\frac{\Omega(G_m, G_p, G_{c_2})}{\Phi(G_m, G_p)}$, so the number of grandoffspring of genotype $G_g = \{g_{gi}\}$ is

$$\Gamma(G_m, G_p, G_g) = \sum_{G_{c_1}, G_{c_2}} \frac{1}{2}\Omega(G_{c_1}, G_{c_2}, G_g)\Omega(G_m, G_p, G_{c_1})\frac{\Omega(G_m, G_p, G_{c_2})}{\Phi(G_m, G_p)}$$

$$
\begin{aligned}
&= \frac{1}{2}\sum_{G_{c_1},G_{c_2}}\prod_i \omega_i(g_{c_1 i},g_{c_2 i},g_{gi})\omega_i(g_{mi},g_{pi},g_{c_1 i})\frac{\omega_i(g_{mi},g_{pi},g_{c_2 i})}{\phi_i(g_{mi},g_{pi})}\\
&= \frac{1}{2}\prod_i \gamma_i(g_{mi},g_{pi},g_{gi}),
\end{aligned}
$$

where

$$
\gamma_i(g_{mi},g_{pi},g_{gi}) = \sum_{g_{c_1 i},g_{c_2 i}} \omega_i(g_{c_1 i},g_{c_2 i},g_{gi})\omega_i(g_{mi},g_{pi},g_{c_1 i})\frac{\omega_i(g_{mi},g_{pi},g_{c_2 i})}{\phi_i(g_{mi},g_{pi})}.
$$

If there are $N_o(G_o)$ individuals of genotype $G_o = \{g_{oi}\}$ at the initial outbreeding generation, then the number of matings between genotype G_m and G_p is

$$
M(G_m,G_p) = \frac{1}{2}\frac{N_o(G_m)N_o(G_p)}{N_{oT}},
$$

where N_{oT} is the total number of individuals in the population at this generation. The total number of individuals of genotype G_g at the grandchild generation will then be

$$
N_g(G_g) \;=\; \sum_{G_m,G_p}\Gamma(G_m,G_p,G_g)M(G_m,G_p).
$$

If we assume that $N_o(G_o) = N_{oT}\prod_i p_{oi}(g_{oi})$, which states that the loci are independent (i.e. in identity equilibrum) at the outbreeding generation, then

$$
\begin{aligned}
N_g(G_g) &= \frac{1}{4}N_{oT}\sum_{G_m,G_p}\prod_i \gamma_i(g_{mi},g_{pi},g_{gi})p_{oi}(g_{mi})p_{oi}(g_{pi})\\
&= \frac{1}{4}N_{oT}\prod_i p_{gi}(g_{gi}),
\end{aligned}
$$

where $p_{gi}(g_{gi}) = \sum_{g_{mi},g_{pi}}\gamma_i(g_{mi},g_{pi},g_{gi})p_{oi}(g_{mi})p_{oi}(g_{pi})$. That is, if the loci are independent at the initial generation, they will remain independent at all subsequent generations.

2.2 Biandrous female

Consider now an outbreeding female of genotype G_m that mates with two males, respectively of genotype $G_{p_1} = \{g_{p_1 i}\}$, $G_{p_2} = \{g_{p_2 i}\}$. We use $\Omega_B(G_m,G_{p_1},G_{p_2},G_c)$ to denote the number of offspring of genotype G_c in her brood. Assuming the female divides her eggs equally among the offspring of either male, Ω_B will contain contributions from both males in the form

$$
\Omega_B(G_m,G_{p_1},G_{p_2},G_c) = \frac{1}{2}\Omega(G_m,G_{p_1},G_c) + \frac{1}{2}\Omega(G_m,G_{p_2},G_c),
$$

and her fitness will be

$$
\Phi_B(G_m,G_{p_1},G_{p_2}) = \frac{1}{2}\Phi(G_m,G_{p_1}) + \frac{1}{2}\Phi(G_m,G_{p_2}).
$$

In contrast to the monandrous case, neither Ω_B nor Φ_B factorises into a product of single-locus factors. As we shall see, this leads to the loci no longer being independent.

When the offspring interbreed with other members of the brood, each female will again take two mates. The number of matings between a mother of genotype G_{c_1} and father G_{c_2} will be

$$
\Omega_B(G_m,G_{p_1},G_{p_2},G_{c_1})\frac{\Omega_B(G_m,G_{p_1},G_{p_2},G_{c_2})}{\Phi_B(G_m,G_{p_1},G_{p_2})}
$$

Each mating combination is represented twice as many times as if the females were monandrous at this generation, but the females devote only half of their eggs to each mate. The number of grandoffspring of genotype G_g will be

$$
\begin{aligned}
\Gamma_B(G_m,G_{p_1},G_{p_2},G_g) &= \sum_{G_{c_1},G_{c_2}}\frac{1}{2}\Omega(G_{c_1},G_{c_2},G_g)\Omega_B(G_m,G_{p_1},G_{p_2},G_{c_1})\frac{\Omega_B(G_m,G_{p_1},G_{p_2},G_{c_2})}{\Phi_B(G_m,G_{p_1},G_{p_2})}\\
&= \sum_{G_{c_1},G_{c_2}}\frac{1}{8}\frac{\Omega(G_{c_1},G_{c_2},G_g)}{\Phi_B(G_m,G_{p_1},G_{p_2})}\times
\end{aligned}
$$

$$
\begin{aligned}
& [\Omega(G_m, G_{p_1}, G_{c_1}) + \Omega(G_m, G_{p_2}, G_{c_1})][\Omega(G_m, G_{p_1}, G_{c_2}) + \Omega(G_m, G_{p_2}, G_{c_2})] \\
= & \frac{1}{8\Phi_B(G_m, G_{p_1}, G_{p_2})} \times \\
& [\prod_i \psi_i(g_{mi}, g_{p_1 i}, g_{p_1 i}) + \prod_i \psi_i(g_{mi}, g_{p_1 i}, g_{p_2 i}) + \prod_i \psi_i(g_{mi}, g_{p_2 i}, g_{p_1 i}) + \prod_i \psi_i(g_{mi}, g_{p_2 i}, g_{p_2 i})]
\end{aligned}
$$

where

$$
\psi_i(g_{mi}, g_{p_a i}, g_{p_b i}) = \sum_{g_{c_1}, g_{c_2}} \omega_i(g_{mi}, g_{p_b i}, g_{c_1 i}) \omega_i(g_{mi}, g_{p_b i}, g_{c_2 i})
$$

If we assume that the loci are independent at the initial outbreeding generation, so that the number of mating units with genotype G_m, G_{p_1}, G_{p_2} is $\frac{1}{2} N_o(G_m) \frac{N_o(G_{p_1}) N_o(G_{p_2})}{N_{oT}^2} = \frac{1}{2} N_{oT} \prod_i p_{oi}(g_{mi}) p_{oi}(g_{p_1 i}) p_{oi}(g_{p_2 i})$, then the total number of grandoffspring of genotype G_g will be

$$
\begin{aligned}
N_g(G_g) &= \sum_{G_m, G_{p_1}, G_{p_2}} \Gamma_B(G_m, G_{p_1}, G_{p_2}, G_g) \times \frac{1}{2} N_{oT} \prod_i p_{oi}(g_{mi}) p_{oi}(g_{p_1 i}) p_{oi}(g_{p_2 i}) \\
&= \sum_{G_m, G_{p_1}, G_{p_2}} \frac{N_{oT}}{16\Phi_B(G_m, G_{p_1}, G_{p_2})} \times \\
&\quad [\prod_i \psi_i(g_{mi}, g_{p_1 i}, g_{p_1 i}) + \prod_i \psi_i(g_{mi}, g_{p_1 i}, g_{p_2 i}) + \prod_i \psi_i(g_{mi}, g_{p_2 i}, g_{p_1 i}) + \prod_i \psi_i(g_{mi}, g_{p_2 i}, g_{p_2 i})] \\
&\quad \times \prod_i p_{oi}(g_{mi}) p_{oi}(g_{p_1 i}) p_{oi}(g_{p_2 i}) \\
&= \sum_{G_m, G_{p_1}, G_{p_2}} \frac{N_{oT} \prod_i p_{oi}(g_{mi}) p_{oi}(g_{p_1 i}) p_{oi}(g_{p_2 i})}{4} \frac{[\prod_i \psi_i(g_{mi}, g_{p_1}, g_{p_1}) + \prod_i \psi_i(g_{mi}, g_{p_1}, g_{p_2})]}{[\prod_i \phi_i(g_{mi}, g_{p_1 i}) + \prod_i \phi_i(g_{mi}, g_{p_2 i})]},
\end{aligned} \tag{45}
$$

where in the last line we have used symmetry to note that $\psi_i(g_{mi}, g_{p_a i}, g_{p_b i}) = \psi_i(g_{mi}, g_{p_b i}, g_{p_a i})$ and $\Phi_B(G_m, G_{p_1}, G_{p_2}) = \Phi_B(G_m, G_{p_2}, G_{p_1})$.

The result on the right hand side of (45) cannot be written as the product of single-locus terms. One reason for this is the denominator, which is the sum of two products which represent the total number offspring a female has by either father. However, even if these numbers are the same the numerator contains a sum of two terms, respectively representing the offspring full-sib and half-sib matings. The population is temporarily separated into two sub-populations, which have different levels of inbreeding and therefore have different levels of heterozygosity. Even if each the loci in each sub-population were statistically independent, the sum of these two populations will not be. The loci are therefore not, in general, independent when the females are biandrous.

2.2.1 Deleterious recessive trait

The terms in the denominator of Eqn. (45) represent the total number of offspring of the female by different fathers. There are certainly genotype combinations for which these numbers are not equal. However, if the abundance of the deleterious allele is q, then these differ by an amount that is typically of order Lq^2x. Therefore, if $q = O(\mu)$, to order μ we will have $\prod_i \phi_i(g_{mi}, g_{p_1 i}) = \prod_i \phi_i(g_{mi}, g_{p_2 i})]$ for the mating units that contribute to the dynamics to leading order. Meanwhile, since we are only interested in the terms in (45) to linear order in μ, the terms which interest us will simply be additive. Therefore, we can assume the loci are independent to first order in μ.

2.2.2 Overdominant trait

For the overdominant case, we can no longer assume that all relevant broods have the same size. Figure 6 shows the departures from independence in a biandrous population with two unlinked, symmetrically overdominant loci. We find that there is an overrepresentation of doubly-homozygous individuals, and also of doubly-heterozygous individuals. Note that the effect persists in the neutral limit $x \to 1$, which shows that the effect is due to the combination of two sub populations with different levels of inbreeding, rather than the differing brood sizes of different mating units. However, the effect is very weak, being no more that about 1%, so we expect that extensions of one-locus results to the multi-locus case by assuming independent loci will be a good approximation. This is indeed borne out by the simultaion results in the paper.

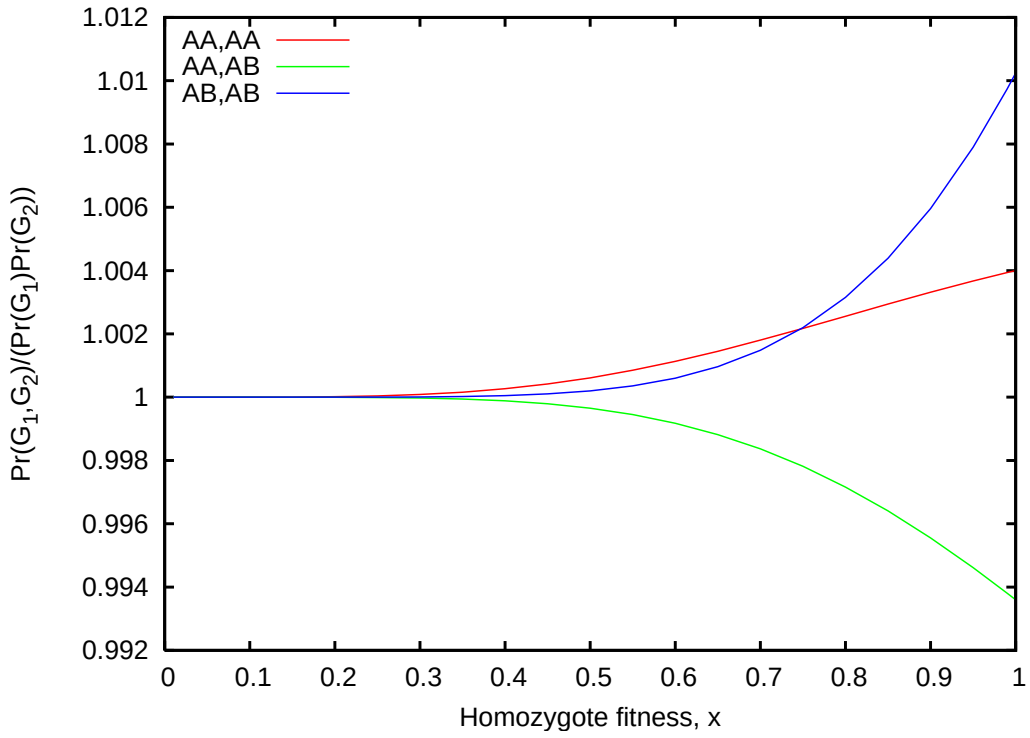

Figure 6: Identity disequilibrium for two symmetrically overdominant loci. The y-axis shows the ratio $\frac{Pr(G_1,G_2)}{Pr(G_1)Pr(G_2)}$, the numerator being the joint probability $Pr(G_1, G_2)$ of having genotype G_1at locus 1 and genotype G_2 at locus 2. the demoninator being the product of the marginal probabilities $Pr(G_1)$ and $Pr(G_2)$ of having each genotype at these loci. If the loci were statistically independent, then this ration would always equal unity.

3 Fixation of alleles in finite populations

Genetic drift in finite populations can cause alleles to go to fixation, i.e. all individuals have the same homozygous genotype, even when this genotype has lower fitness than others. This is one of the ways in which finite populations behave differently from infinite populations, and the effect is stronger when alleles are only mildly deleterious, and when populations are smaller. In this section, we shall quantify the effect of fixation on the equilibrium behaviour of our model. We shall consider the case of a single locus and monandrous females. In finite populations the loci are no longer guaranteed to be statistical independent, so the behaviour of the many-locus case cannot necessarily be straightforwardly extrapolated.

3.1 Deleterious recessive trait

Here, we consider the case where the fitness of AA, AB, and BB genotypes is x, 1, and 1 respectively. If mutations are rare, when a deleterious allele is generated it will typically either go to extinction (most likely) or to fixation in a short space of time. The population will therefore spend most of its time either as all AA or all BB homozygotes, with short transition periods between these states. We can therefore treat it as a two-state Markov process.

Let $f_B(x)$ be the probability that, starting with a single B allele in an otherwise AA population, the population drifts to become saturated BB homozygotes, and $f_A(x)$ be the the probability that, starting with a single A allele in an otherwise BB population, the population drifts to become saturated AA homozygotes. If μN is the probability at which mutations arise, the transition rates between the states are

$$\begin{array}{ll} \text{AA} \to \text{AA at rate} & \mu N(1-f_B) \\ \text{AA} \to \text{BB at rate} & \mu N f_B \\ \text{BB} \to \text{AA at rate} & \mu N f_A \\ \text{BB} \to \text{BB at rate} & \mu N(1-f_A). \end{array}$$

The fixation probability is the fraction of time that the locus is heterozygous AA, i.e.

$$P_{\text{fix}} = \frac{f_A(x)}{f_A(x)+f_B(x)}. \tag{46}$$

Note that P_{fix} is independent of μ, provided μ is small.

The probability f_A can be measured from simulations by starting with a single A allele in a wiltype BB population, and recording the fraction of realisations where all individuals become AA before they all become BB. f_B can be measured in a similar fashion. Figure 7 shows the resulting fixation probability P_{fix} inferred via equation (46). The fixation probability is found to decay exponentially with large N; the curves are fits of the form $a\exp(-bN)$to the large-N tail. The figure shows that we expect no significant degree of fixation for $x \leq 0.9$ unless the population size is very small, but when $N = 50$ and $x = 0.99$ we expect the deleterious allele to be fixed at as many as $\approx 20\%$ of the loci.

3.2 Asymmetric, overdominant trait

A finite population will always go to fixation in the absence of mutation, but this can take a very long time if both homozygotes have the same fitness x. Figure 8 shows the time to fixation T_{fixation}(in double generations) for a population with a single, symmetrically overdominant locus. The lines are fits of the form $\log T = aN+b$, with $a = 0.0414\pm0.0008$, 0.0154 ± 0.0002, 0.0078 ± 0.0001 for $x = 0.95$, 0.98, 0.99 respectively, suggesting $a = c(1-x)$, with $c = 0.80 \pm 0.04$ (standard errors). The fits predict that the time to fixation for $N = 1000$ should be $> 2.6 \times 10^8$ for $x = 0.98$ and $> 10^{19}$ for $x = 0.95$.

The rate at which new mutations appear in the population is μN, but in most cases the mutant allele will go extinct before it becomes prevalent. For the neutral case $x = 1$, the probability that a mutant allele will reach the equilibrium frequency $\frac{1}{2}$ before going extinct is approximately $\frac{1}{N}$; this probability will be greater when $x \neq 1$, because selection favours polymorphism. Therefore, once an allele is fixed, the typical time before it becomes prevalent is approximately μ^{-1} or less. A given locus will therefore remain polymorphic, and the infinite-N results for the population genetics applicable, provided $T_{\text{fixation}} > \mu^{-1}$. For $\mu = 10^{-5}$–10^{-6}, we need $T_{\text{fixation}} \approx 10^5$ or 10^6.

However, the time to fixation is dramatically reduced when the AA and BB genotypes have different fitness. Indeed, in the extremely asymmetric case it is possible for selection to remove the less fit allele even in an finite population. The red curve in Figure 9 shows the locus of (x, y) points where the less fit allele is just driven to extinction, based on numerical iteration of Eqns. (4–18); the region labelled 'purging' is where there is no polymorphic stable equilibrium. In finite populations, stochastic fluctuations enlarge the region where one allele can become fixed. The black curves in Figure 9 shows the region of parameter space where polymorphism is expected to be maintained for a population of 1000 individuals. The region labelled 'polymorphic' is where the time to extinction was more than 10^6 timesteps in more than 50% of realisations. We finds that there is a region of values around $x = y = 0.95$ where polymorphism is expected to be maintained, but if the trait is extremely asymmetric then one allele will probably go to fixation.

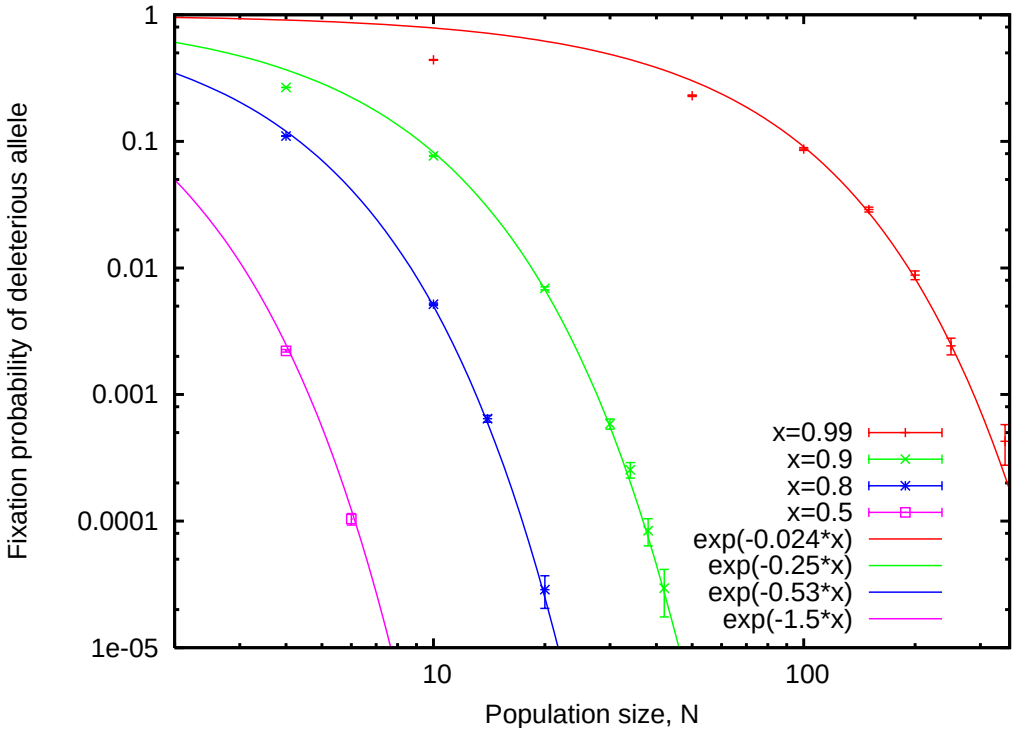

Figure 7: Fixation probability of the deleterious allele, for a single-locus recessive trait.

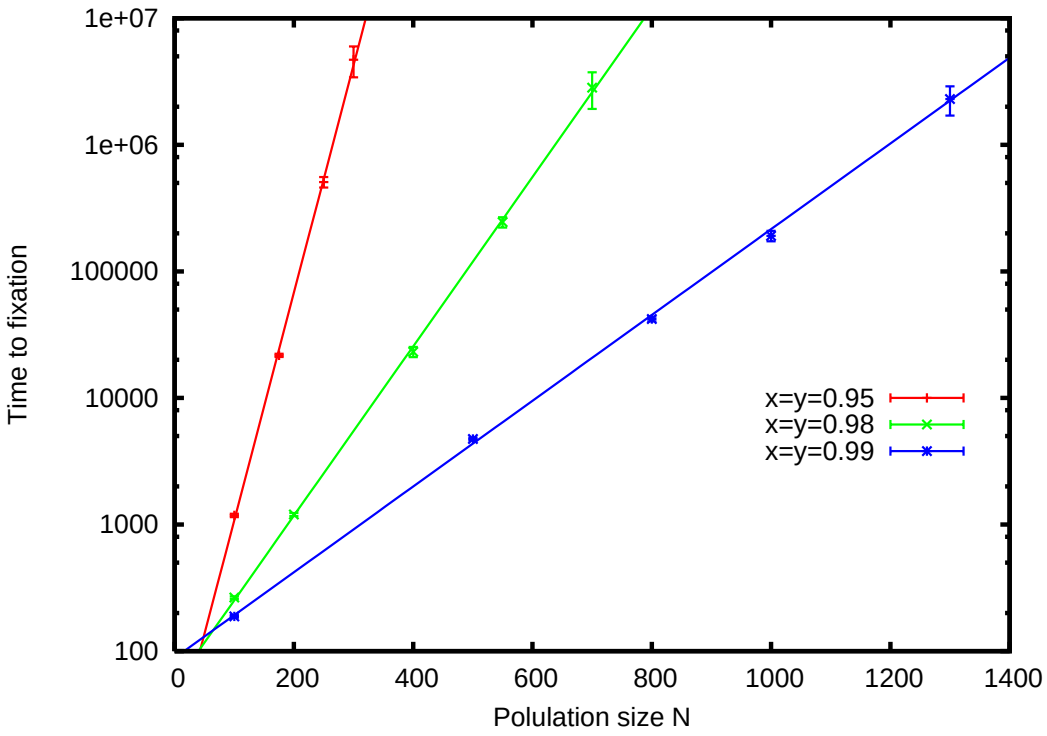

Figure 8: Time to fixation for the symmetric overdominant case.

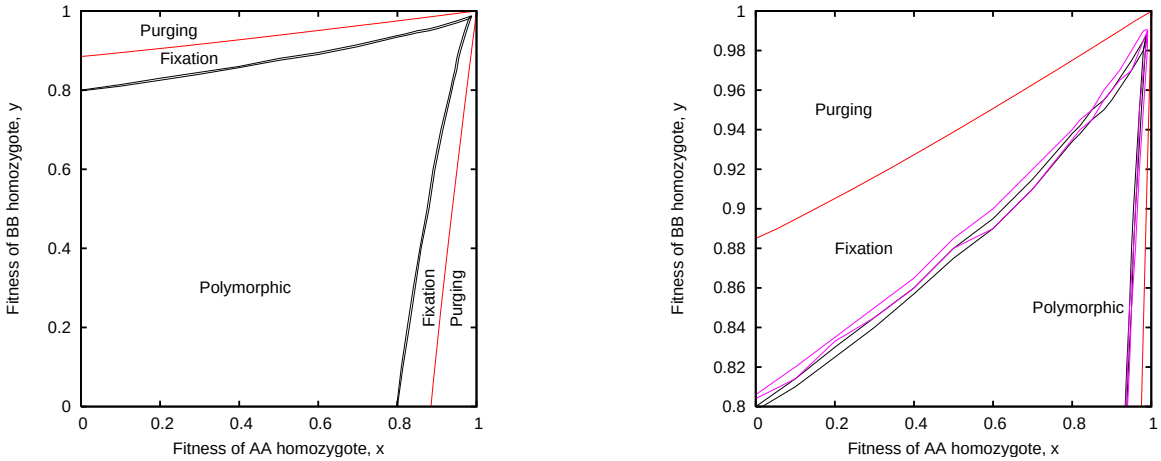

Figure 9: Whether polymorphism persists, or whether one allele goes to fixation, for a population with a single overdominant locus. Left: the region labeled 'Purging' is where selection removes one of the alleles even in an infinite population. The region labelled 'Polymorphic' is where the time to fixation T_{fixation} is more often greater than 10^6 than less, the region labelled 'Fixation' is where T_{fixation} is more often less than 10^6, for a population of size $N = 1000$. The black solid curves delineate the confidence intervals of the curve where $Pr(T_{\text{fixation}} > 10^6) = 0.5$. Right: Same as on the left, but concentrating on $y > 0.8$. Black and red curves as before, magenta curves represent confidence intervals of the curve $Pr(T_{\text{fixation}} > 10^5) = 0.5$.