SUPPLEMENTARY MATERIAL

Quasi-Hardy-Weinberg equilibrium

In the derivation of the model we assume that selection is weak enough such that genotypes remain in approximately Hardy-Weinberg proportions after selection. This 'quasi-Hardy-Weinberg equilibrium' (QHW) assumption is invoked because selection generally causes very little departure from the frequencies expected at Hardy-Weinberg Equilibrium (HWE) (see Nagylaki 1976), and therefore the assumption allows for very simple (but approximate) solutions that are within order s^2 (or $\delta[s^2]$) of the exact expectation (where s represents a generic measure of the strength of selection). The 'error' in the approximations can be expressed as the difference between the frequencies of the genotype classes after selection and the frequency expected under HWE given the allele frequencies after selection. The deviations from HWE are symmetrical, with the two homozygote classes having equal deviations and the sum of the deviation of the homozygote classes always being equal and opposite to the deviation of the heterozygote. The magnitude of the deviation (ε) (which represents the deviation of the homozygote classes or half the deviation of the heterozygote class) has the value (with the heterozygotes having a deviation of $+2\varepsilon$ and the homozygotes having a deviation of $-\varepsilon$):

$$\varepsilon = \frac{p_2^2 p_1^2 d_o[2 + d_o + d_m + a_m(p_1 - p_2)] + (\tfrac{1}{2} p_1 p_2)^2 [2a_o + a_m + d_m(p_2 - p_1)]^2}{\overline{w}^2} \qquad \text{(S1)}$$

If we consider the magnitude of any of the genetic effects on total fitness as being generically captured by the selection parameter s (so all genetic effects are weighted by s), then we can see that the deviation caused by additive direct and maternal effects and dominance maternal effects are on the order of s^2, while the deviation caused by a direct dominance effect is on the order of s (Nagylaki 1976). Furthermore, because of the scaling of these effects by the square of the product of the allele frequencies, all deviations tend to be very small unless selection is very strong. Most importantly with respect to the model presented in the main text, maternal effects only contribute a very small deviation from HWE, and therefore the approximations under the assumption of QHW will capture the evolutionary and statistical properties with only minor error that is $\sim O(s^2)$.

In Figure S1 we illustrate the deviations from Hardy-Weinberg frequencies caused by selection under several scenarios. Because the deviations are very small (eq. S1) the illustrations all assume relatively strong selection (genetic effects are scaled to be ~5 to 20% of mean fitness measured when both alleles are at equal frequency) and only cases for direct effects are illustrated since maternal effects contribute a similar pattern, but with smaller deviations. All cases with weaker selection results in deviations that are smaller than the thickness of the lines in the plot and therefore appear the same as the case of additive direct effects illustrated in Figure S1 panel A (see also Wade 1979).

In Figure S2 we illustrate the error in the predicted evolutionary trajectory introduced by the QHW approximation compared to the exact dynamics. The QHW does not alter the evolutionary trajectories when there are only direct effects since the deviation from the H-W expectation in the genotype frequencies of adults is irrelevant under random mating (since each generation starts in H-W proportions). Consequently, we only illustrate scenarios where there are maternal effects with or without direct effects. Because deviations from H-W proportions are generally small and have a correspondingly small influence on evolutionary

dynamics, the scenarios illustrated in Figure 2 assume very strong selection (with genetic effects having a magnitude of ca. 20% of mean fitness when both alleles are at equal frequency).

Multi-locus model

To understand how the single locus models translates into a model with two or more loci we briefly present a two-locus case, which provides results that logically extend to the *N* locus case (cf. Nagylaki 1993). We focus on the evolutionary properties of the multi-locus system and do not present an analysis of the variance components for which the multi-locus case is a simple extension of the single-locus case. In the two-locus model, we add a second locus (the B locus) that has two alleles, B_1, and B_2, which have frequencies x_1 and x_2 respectively. Unless otherwise stated, we follow all of the assumptions for the A locus model examined in the main text. To keep track of the direct and maternal effects of the two loci we add a subscript that indicates the locus having the effect; i.e., the A locus has direct effects $a_{o(A)}$ and $d_{o(A)}$, while the B locus has effects $a_{o(B)}$ and $d_{o(B)}$; likewise, the A locus has maternal effects $a_{m(A)}$ and $d_{m(A)}$, while the B locus has effects $a_{m(B)}$ and $d_{m(B)}$. As in the single locus case, we assume that these genetic effects are effects on fitness when considering evolutionary properties of the model.

The properties of a multi-locus system differ from those of a single locus system as a consequence of associations between loci. Consequently, the critical aspect to consider when examining the difference between the single-locus model presented in the text and the possibility of a multi-locus genetic architecture is the contribution of linkage disequilibrium (LD) between loci. To account for associations between loci we build genotypes from the four possible two-locus haploptypes: A_1B_1, A_1B_2, A_2B_1, A_2B_2. To develop a two-generation

model in which we can model the influence of the maternal and offspring genomes, we can define the frequencies of the four possible haplotypes in the parental generation, $t-1$, denoted h_{ij}, where i indicates the subscript of the A locus allele and j indicates the subscript of the B locus allele. The degree of LD between the two loci at generation $(t-1)$ is denoted D, where $D = (h_{11}h_{22} - h_{12}h_{21})$. If we measure allele frequencies and the value of LD (D) after selection in the parental generation but before selection in the offspring (so that allele frequencies do not change between generations, but LD does due to recombination), we can express the frequencies of haplotypes in the offspring generation as a function of their frequency in the parent generation and D:

$$\begin{aligned} h_{11} &= p_1 x_1 + \tfrac{1}{2} D = h_{11} - \tfrac{1}{2} D \\ h_{12} &= p_1 x_2 - \tfrac{1}{2} D = h_{12} + \tfrac{1}{2} D \\ h_{21} &= p_2 x_1 - \tfrac{1}{2} D = h_{21} + \tfrac{1}{2} D \\ h_{22} &= p_2 x_2 + \tfrac{1}{2} D = h_{22} - \tfrac{1}{2} D \end{aligned} \qquad \text{(S2)}$$

The ½ in equations (S2) represents the reduction in LD due to free recombination. These haplotype frequencies are used to generate the frequencies of all maternal-offspring two-locus genotype combinations under the assumption that there is random union of gametes.

In the case of two loci, mean fitness is essentially the same as in the single locus case (eq. 4), with the influence of the two loci being entirely additive (NB, mean fitness is not affected by LD):

$$\begin{aligned} \overline{w} = \mu &+ (p_1 - p_2)(a_{o(A)} + a_{m(A)}) + 2p_1p_2(d_{o(A)} + d_{m(A)}) \\ &+ (x_1 - x_2)(a_{o(B)} + a_{m(B)}) + 2x_1x_2(d_{o(B)} + d_{m(B)}) \end{aligned}, \qquad \text{(S3)}$$

To understand how selection affects patterns of association we can examine the evolutionary change in LD. This is most clearly (and simply) illustrated by assuming that the system starts in linkage equilibrium (LE) and then examining the amount of LD that is built by selection in a generation. We denote this evolutionary change in LD as ΔD_0, which has the value:

$$\Delta D_0 = -\frac{\left[\begin{array}{l} p_1 p_2 x_1 x_2 \\ \left(a_{o(A)} + \frac{1}{2} a_{m(A)} - (d_{o(A)} + \frac{1}{2} d_{m(A)})(p_1 - p_2)\right) \\ \left(a_{o(B)} + \frac{1}{2} a_{m(B)} - (d_{o(B)} + \frac{1}{2} d_{m(B)})(x_1 - x_2)\right) \end{array}\right]}{2\overline{w}^2} \qquad \text{(S4)}$$

Which clearly demonstrates that the degree of LD built by selection will generally be very small (Nagylaki 1993) because the magnitude of LD depends on the product of the strength of selection on the two loci (i.e., the product of their effects on fitness), meaning that LD will generally be ~$O(s^2)$ (Nagylaki 1993), and therefore will be negligible unless selection is strong. Because these deviations from LE are generally very small, the multi-locus system can be considered to remain in 'quasi-linkage equilibrium' (QLE) (Kimura 1965; Nagylaki 1976, 1993).

The LD generated by selection essentially contributes an 'error' deviation from the equations derived under the assumption of QLE for evolutionary change in allele frequencies at each of the two loci. The expressions for evolutionary change in allele frequencies at the A and B loci have the same form (i.e., Δx_1 is the same as the equation for Δp_1, except the subscripting for the genetic effects is reversed), so for simplicity we consider evolutionary changes in the frequency of the A_1 (cf. eq. 6 in the main text):

$$\Delta p_1 = \frac{p_1 p_2 \left[\left(a_{o(A)} + \frac{1}{2} a_{m(A)} \right) + (p_2 - p_1)\left(d_{o(A)} + \frac{1}{2} d_{m(A)} \right) \right]}{\overline{w}} - D \frac{\left(a_{o(B)} + a_{m(B)} \right) + (x_2 - x_1)\left(d_{o(B)} + d_{m(B)} \right)}{2\overline{w}} \quad \text{(S5).}$$

The term on the first line in eq. (S5) is identical to the evolutionary change derived in the single locus case (eq. 6), while the second line gives the deviation from the single locus expectation caused by selection on the B locus. This deviation is a function of both the magnitude of LD (D), which is expected to be on the order of s^2, and the strength of selection on the B locus, which is on the order of s, and consequently the total deviation in the evolutionary change at the A locus from the expectation under the single locus model (eq. 6) caused by selection in a multi-locus system is $\sim O(s^3)$ (but is $\sim O[s^2]$ for direct dominance effects) As a result, the evolution of each individual locus in a multi-locus system with an arbitrary number of loci will approximately follow the trajectory and dynamics expected under the single locus model, with the error in that approximation being $\sim O(s^3)$. More importantly, contribution of LD to evolutionary change (eq. S5) generally affects the rate but not the overall trajectory of evolution. As a result, the fundamental evolutionary dynamics expected at each locus in a multi-locus system will follow the pattern expected under the QLE approximation, even if the exact rate differs slightly from that expected.

The evolutionary trajectories for several arbitrary patterns of genetic effects for the single locus expectation under the QLE assumption and the exact expectation calculated using equations (S4) for the evolution of LD and (S5) for the evolution of allele frequencies are illustrated in Figure S3. Note that, to achieve a perceivable difference between the single locus expectation under the QLE assumption and the exact expectation selection needs to be relatively strong (i.e., genetic effects are ca. >10% of mean fitness), which is consistent with the expectation of the error.

References

Kimura, M. 1965. Attainment of quasilinkage equilibrium when gene frequencies are changiung by natural selection. Genetics 52:875-890.

Nagylaki, T. 1976. The evolution of one- and two-locus systems. Genetics 83:583-600.

Nagylaki, T. 1993. The evolution of multilocus systems under weak selection. Genetics 134:627-647.

Wade, M. J. 1979. The evolution of social interactions by family selection. American Naturalist 113:399-417.

Figure S1. Comparison of genotype frequencies after selection to the Hardy-Weinberg expectation. In each case the blue line gives the actual frequency after selection while the red line gives the Hardy-Weinberg frequency based on the allele frequency after selection. The genotype that each of the lines corresponds to are only labelled in the first figure since the order remains the same in all figures (likewise for the axes). The lines for the heterozygote frequencies are for the unordered heterozygote (i.e., the sum of the frequencies of the reciprocal heterozygotes). Unless selection is very strong and the two alleles are at intermediate frequencies the two lines are too close to visualize the difference and appear as a purple blend of the two lines. A-C show the case of an additive direct effect (a_o) with values of 0.05, 0.10 and 0.20 respectively while D-F show cases of a dominance direct effect (d_o) with these same respective values.

Figure S2. Evolutionary trajectories at the A locus (illustrated as the frequency of the A_1 allele, p_1, through generations) comparing the QHW approximation with the exact dynamics. For the QHW scenario the change each generation was calculated using equation (6), while for the exact dynamics we allowed selection to cause parental genotype frequencies (as we as the associated allele frequencies) to deviate from the H-W proportions and calculated the frequencies of the maternal-offspring genotype combinations each generation assuming random mating (which were then used to calculate offspring fitness and further changes in allele frequencies the following generation, and so on). Because selection needs to be relatively strong to generate discernable differences between the QHW approximation with the exact dynamics we assume that genetic effects on fitness are scaled to ca. 20% of mean fitness in magnitude when both alleles are at equal frequency (i.e., genetic effects have a fixed absolute size, and therefore the effect on relative fitness depends on allele frequencies as mean fitness increases through evolutionary time). The six scenarios illustrated are: **A)** the

locus has an additive maternal effect ($a_m = 0.2$), **B)** the locus has an dominance maternal effect ($d_m = 0.2$), : **C)** the locus has both an additive direct and maternal effect ($a_o = a_m = 0.2$), **D)** the locus has both a dominance direct effect and an additive maternal effect ($d_o = a_m = 0.2$), **E)** the locus has both an additive direct effect and a dominance maternal effect ($a_o = d_m = 0.2$), and **F)** the locus has both a dominance direct and maternal effect ($d_o = d_m = 0.2$). For each case the blue symbol gives the approximation under the QHW assumption, while the red symbol gives the exact value calculated by iteration. Axes are only labelled for the first panel (A) since they are the same for all (A-F).

Figure S3. Evolutionary trajectories at the A locus (illustrated as the frequency of the A_1 allele, p_1, through generations) for the single locus case and the two locus case for a series of arbitrary scenarios. For the single locus case, evolutionary changes were iterated through generations using equation (6), while for the two locus case, evolutionary changes each generation were calculated iteratively using equation (S3) for evolutionary change in LD and (S4) for evolutionary change in allele frequencies (with evolutionary change at the B locus being calculated using the analogous expression as S4, but for change in the frequency of the B_1 allele, which is not shown). The four scenarios illustrated are: **A)** both loci have additive direct and maternal effects (where $a_{o(A)} = a_{o(B)} = a_{m(A)} = a_{m(B)} = 0.2$), **B)** the A locus has an additive direct effect (where $a_{o(A)} = 0.2$), while the B locus has an additive maternal effect (where $a_{m(B)} = 0.4$). **C)** the A locus has an additive maternal effect (where $a_{m(A)} = 0.4$), while the B locus has a dominance maternal effect (where $d_{m(B)} = 0.8$), **D)** both loci have dominance direct and maternal effects (where $d_{o(A)} = d_{o(B)} = d_{m(A)} = d_{m(B)} = 0.4$). For each case the blue symbol gives the approximation under the QLE assumption, while the red symbol gives the exact value from the multi-locus iteration.

Figure S1

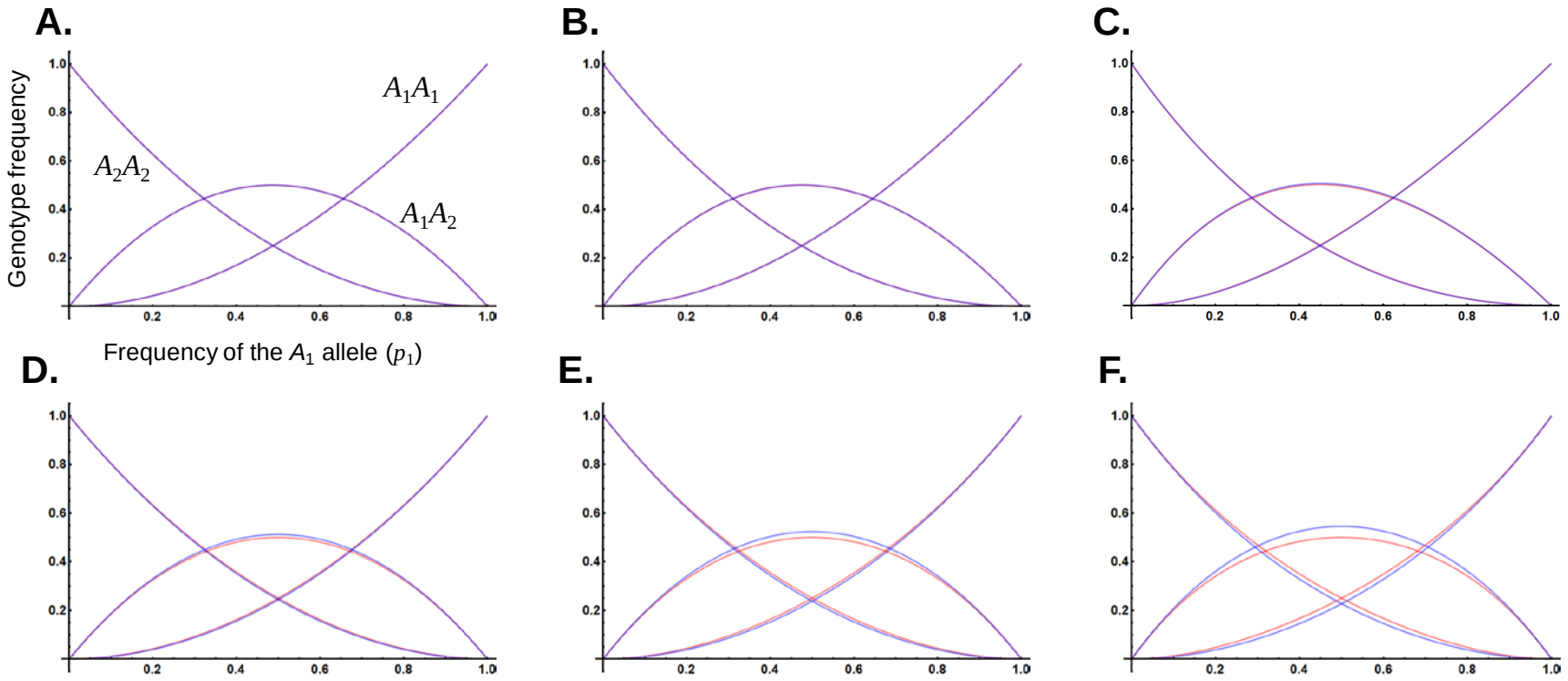
A.
B.
C.
D.
E.
F.
Genotype frequency
A_1A_1
A_2A_2
A_1A_2
Frequency of the A_1 allele (p_1)
1.0
0.8
0.6
0.4
0.2
0.2
0.4
0.6
0.8
1.0

Figure S2

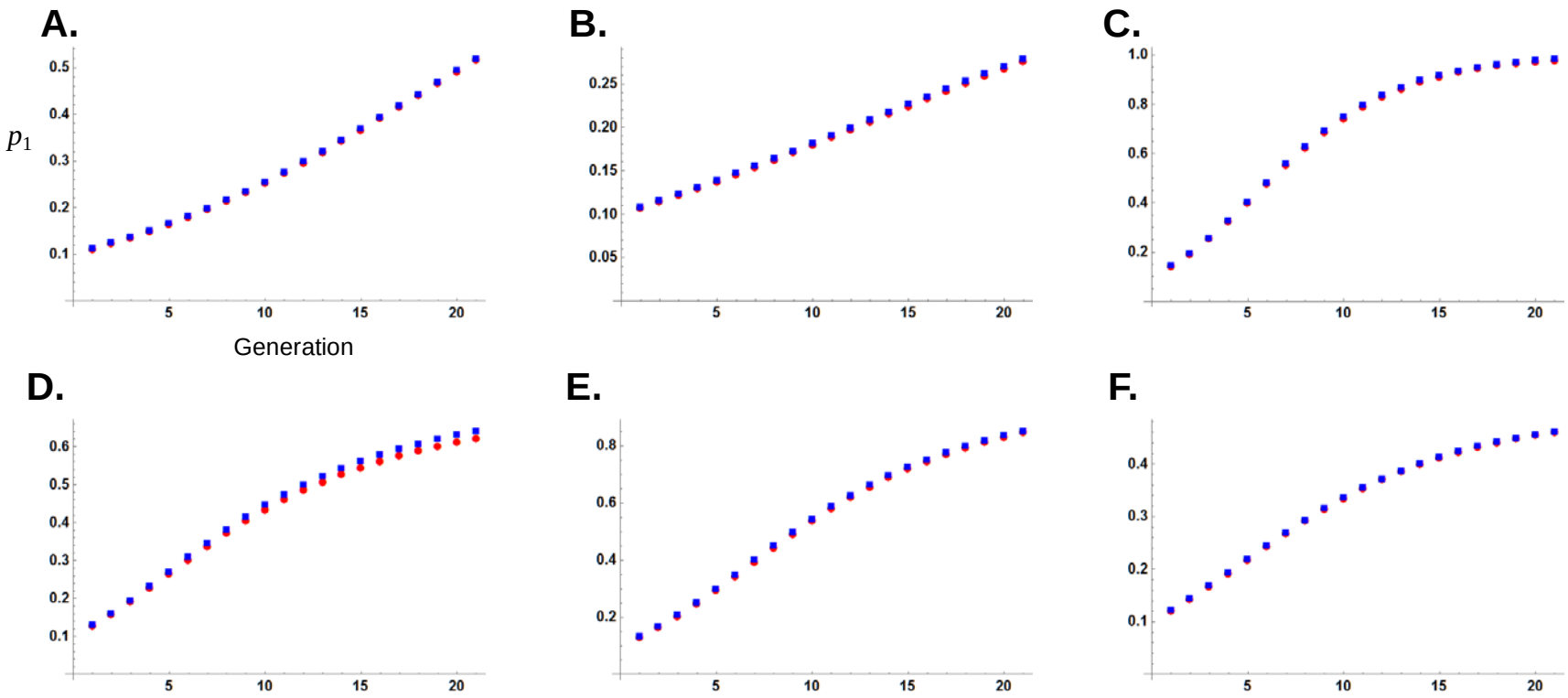

Figure S2

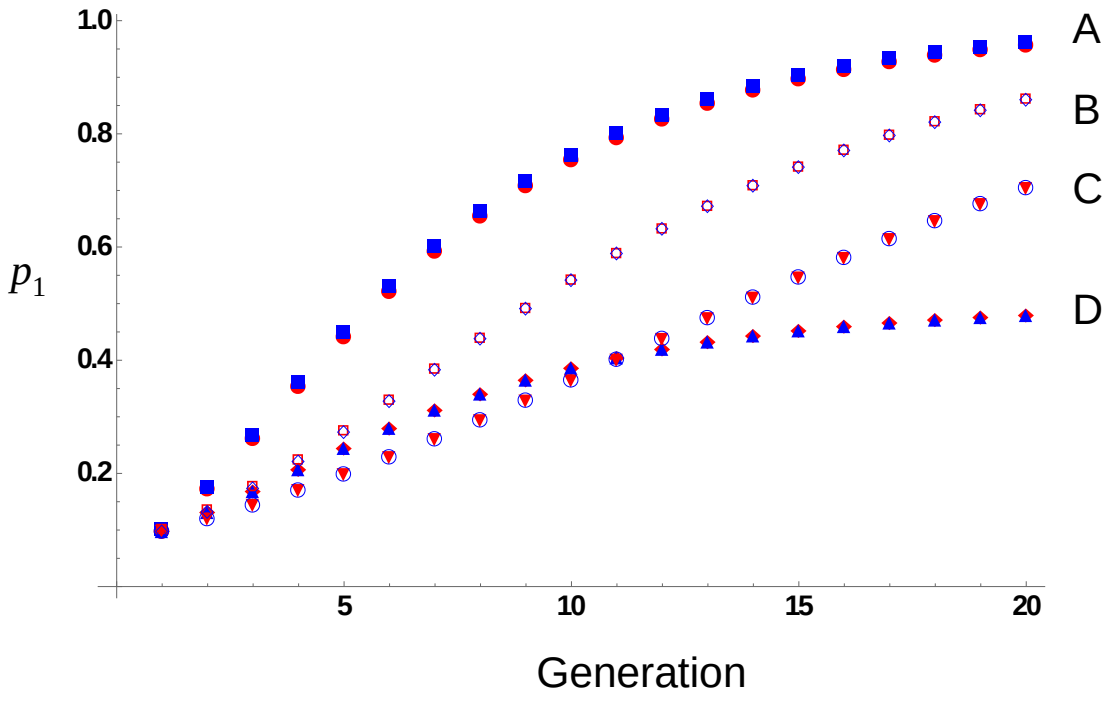

Table S1. The expected phenotypes of offspring as a function of the offspring genotype or maternal genotype. These values are equivalent to the marginal means shown in Table 1, but for the case with inbreeding. See Table 2 for the frequencies under inbreeding.

Genotype			
A_1A_1	A_1A_2	A_2A_1	A_2A_2
Expected phenotype as a function of offspring genotype			
$1+ a_o + a_m + (a_m - d_m)(F-1)p_2$	$1 + d_o + a_m + (a_m - d_m)(F-1)p_2$	$1 + d_o - a_m - (a_m - d_m)(F-1)p_2$	$1 - a_o - a_m - (a_m - d_m)(F-1)p_2$
Expected phenotype as a function of the maternal genotype			
$1 + a_o[F+p_1(1-F)] + d_o(1-F)p_2 + a_m$	$1 + a_o[(1-F)(p_1-p_2)] + d_o(1-F) + d_m$	$1 + a_o[(1-F)(p_1-p_2)] + d_o(1-F) + d_m$	$1 - a_o[F+p_2(1-F)] + d_o(1-F)p_1 - a_m$