

Density-dependent ARTs Analysis

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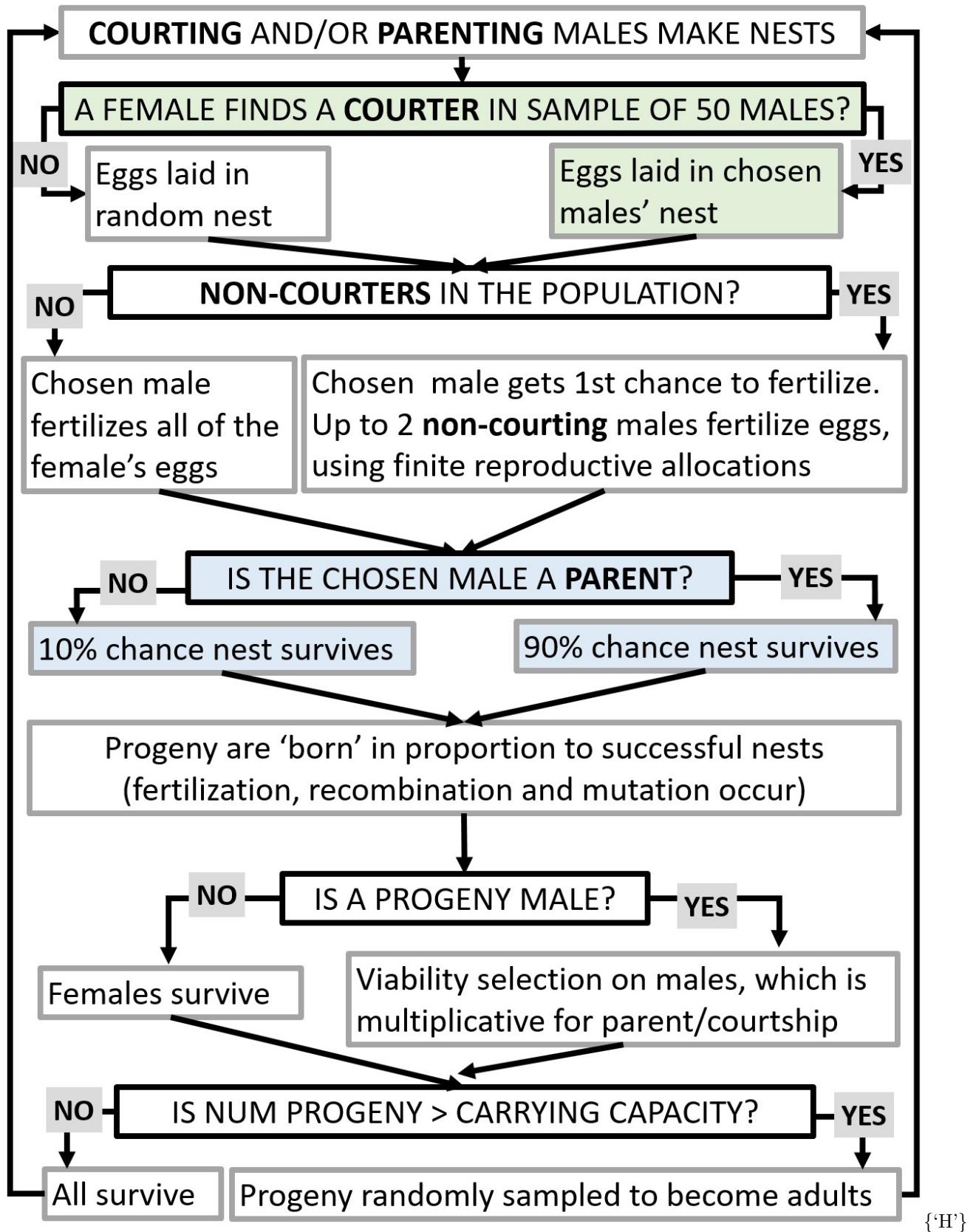
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The purpose of this model is to understand how genetic architectures of alternative reproductive tactics impact their maintenance in populations. I'm using an individual-based simulation model with different selection scenarios, types of alternative tactics, and genetic architectures (genome-wide additive genetic variance, supergenes, expression networks).

Overview of the model

Males can be courters or not-courters and parents or not-parents. When the model is run with both traits, this results in four possible morphs: counter/parent, counter/not-parent, not-counter/parent, and not-counter/not-parent. Generations are non-overlapping and there is one reproductive bout per generation. In each generation, the population follows the following timeline:



each step is explained in further detail below.

1. Choosing a nest

A female samples 50 males and chooses a male to nest with based on his courtship trait. If there are no courtship traits in the model, she chooses based on the male's parental trait. If she does not encounter an acceptable male, she does not nest. If she encounters multiple equally-acceptable males, she randomly selects one of them.

2. Fertilization

Once a female decides to nest, up to three males can fertilize the nest. Courters and parental males can contribute more sperm than non-courter and non-parental males: $r_{courter} = r_{parent} = 8$ and $r_{non-courter} = r_{non-parent} = 4$. A counter/non-parent has $r_{non-parent}$ and a non-counter/parent has r_{parent} . The male with whom the female is nesting gets $r_{parent}/\Sigma n_{sperm}$ and additional non-parental males (up to 2) get $(r_{non-parent} * 0.5/\Sigma n_{sperm})$, where Σn_{sperm} is the total number of sperm contributed by all of the males, weighted by the sperm competition factor (0.5 is the default for all males except the nesting male). So, when a female mates with one counter and two non-parentals, $\Sigma n_{sperm} = r_{courter} + 2*(0.5*r_{sneaker})$, where $r_{courter} = 8$ and $r_{sneaker} = 4$, therefore $\Sigma n_{sperm} = 12$.

That being said, every time a male mates he uses his sperm, so after one mating where a counter fertilizes 50% of the female's 4 eggs, he only has 6 sperm for his next mating.

3. Nest Survival

Before the babies can survive, the nest has to survive. This step is only relevant when parental traits are in the model - if only the courtship trait is specified, then all progeny in the nest survive at this point. When males have the parental trait, if the female has given eggs to a non-parental male (because she chose based on courtship traits), then the nest has a 10% chance of surviving. If the female has given eggs to a parental male, the nest has a 90% chance of surviving.

4. Density-dependent survival

Once the identities of the surviving nests are known—along with the identities of the parents, including sneaker parents—the offspring are created in the simulation. The offspring are created to fill the full carrying capacity of the population, with the numbers per nest being equally divided among all surviving offspring. This allows the population to maintain a constant population size (prior to viability selection) while maintaining the relative successes of the given genotypes/morphs.

5. Viability selection

Before becoming adults, the offspring experience viability selection. Courters and parental males are disfavored in viability selection, with a survival probability of 0.9950125. If an individual is both a counter and a parental male, the survival probability is 0.9900498. Non-courters and non-parental males have survival probabilities of 1.

Evaluating equilibrium

After 10000 generations, I begin tracking the change in frequency of the counter and parent traits, and do so for 2000 additional generations. I calculate the variance in the change in frequency over those 2000 generations. I declare an equilibrium ('stasis') has been reached if the last change in frequency of both traits is less than the variance in changes in frequency.

Unlinked additive genetic variance

In these cases, the traits are encoded by a number (50) of loci, whose alleles contribute additively to determine the trait value. These alleles are all freely recombining and are not adhered to any physical genomic location (aka this is a classical quantitative genetics approach). The overall trait value is compared to a population-level threshold (which is static, in these cases), and if the trait value is above the threshold the male takes the parent or counter morph and if it is below he does not. Below, I'm showing the results from 10 replicates of each scenario.

Courter trait

Females choose nests based on whether the male is a counter or not, and they all prefer counters all of the time (the female preference does not have a genetic basis and does not evolve). The only way that non-counters produce offspring is through sneaking, but all males can be sneakers (both counters and non-counters). Because parental care is not incorporated in this model, all nests survive.

With viability selection

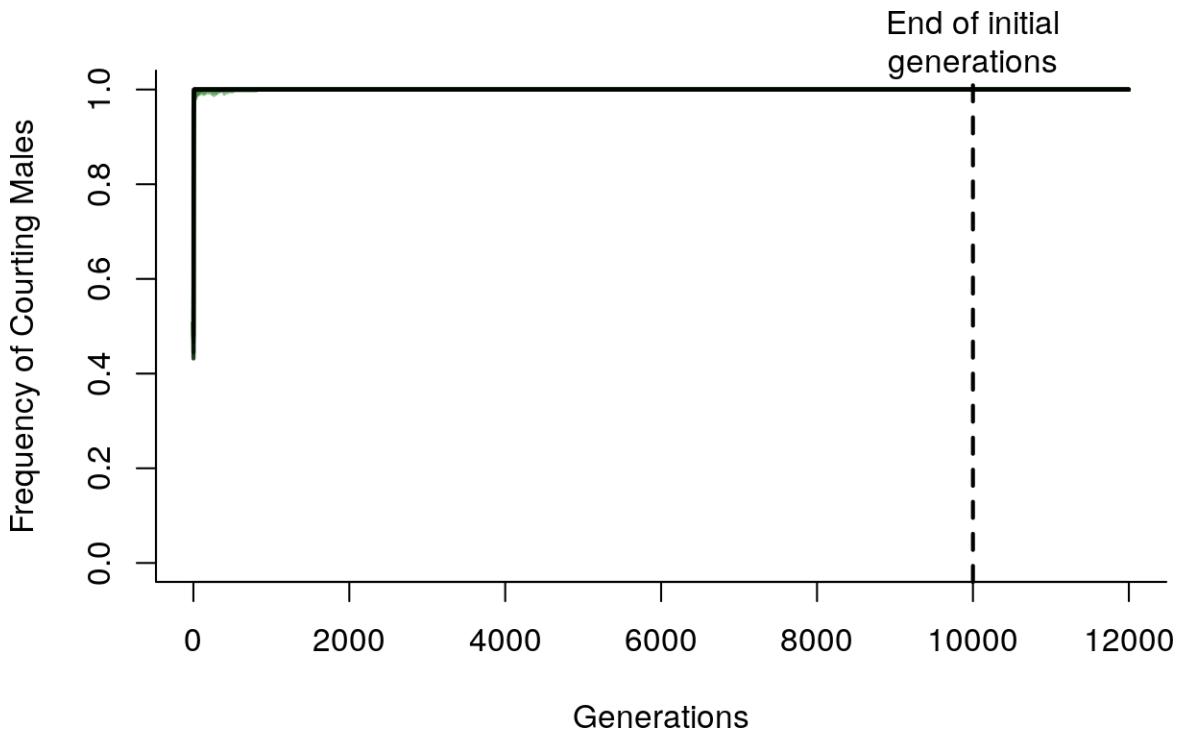


Figure 1: Frequency of the counter morph with unlinked additive genetic variances in all of the replicates

Of the 20 replicates, 20 reached a steady state by 10000 generations. The different runs all overlap, suggesting that they all converge on the same outcome: all males are counters. This result is also obvious by inspecting a table of counter frequencies and fitnesses in the final generation of the runs.

In some cases, major differences emerge between scenarios with viability selection and without, so below I present each case with and without viability selection

Table 1: Frequency of courters in final generation of runs with unlinked additive genetic variances

	CounterFreq	CounterW	NonCounterW
counter_unlinked_1_summary.txt_1	1	2.07708	0
counter_unlinked_1_summary.txt_2	1	2.04330	0
counter_unlinked_1_summary.txt_3	1	1.99799	0
counter_unlinked_1_summary.txt_4	1	2.00605	0
counter_unlinked_2_summary.txt_1	1	2.07708	0
counter_unlinked_2_summary.txt_2	1	2.04330	0
counter_unlinked_2_summary.txt_3	1	1.99799	0
counter_unlinked_2_summary.txt_4	1	2.00605	0
counter_unlinked_3_summary.txt_1	1	1.90267	0
counter_unlinked_3_summary.txt_2	1	2.00604	0
counter_unlinked_3_summary.txt_3	1	1.93933	0
counter_unlinked_3_summary.txt_4	1	1.99198	0
counter_unlinked_4_summary.txt_1	1	2.02020	0
counter_unlinked_4_summary.txt_2	1	1.97628	0
counter_unlinked_4_summary.txt_3	1	1.87970	0
counter_unlinked_4_summary.txt_4	1	1.93798	0
counter_unlinked_5_summary.txt_1	1	2.02020	0
counter_unlinked_5_summary.txt_2	1	1.97628	0
counter_unlinked_5_summary.txt_3	1	1.87970	0
counter_unlinked_5_summary.txt_4	1	1.93798	0

We may also be interested in the evolution of the counter trait values, which reflects the additive effects of all loci.

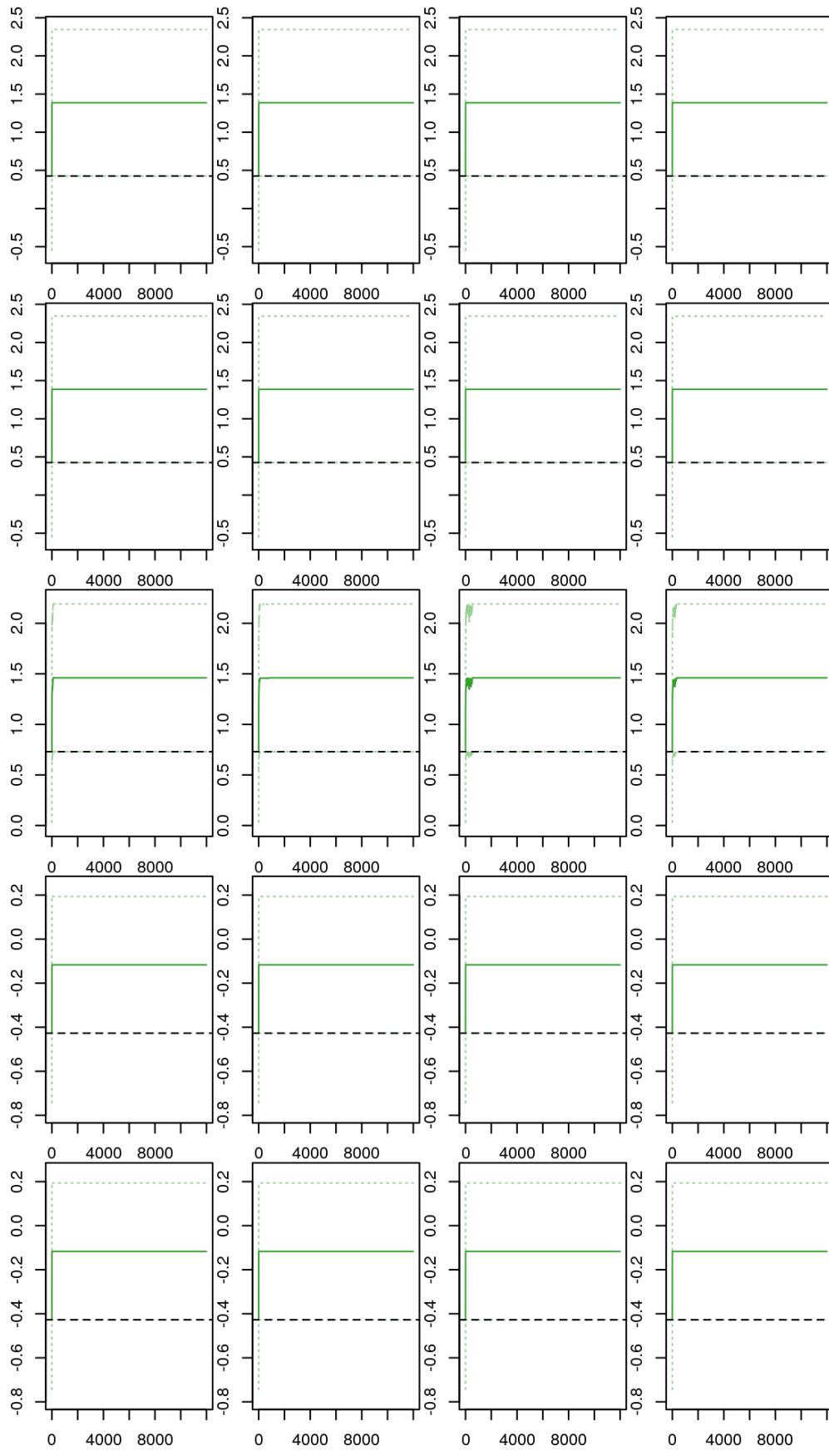


Figure 2: Evolution of courtship trait with unlinked loci. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

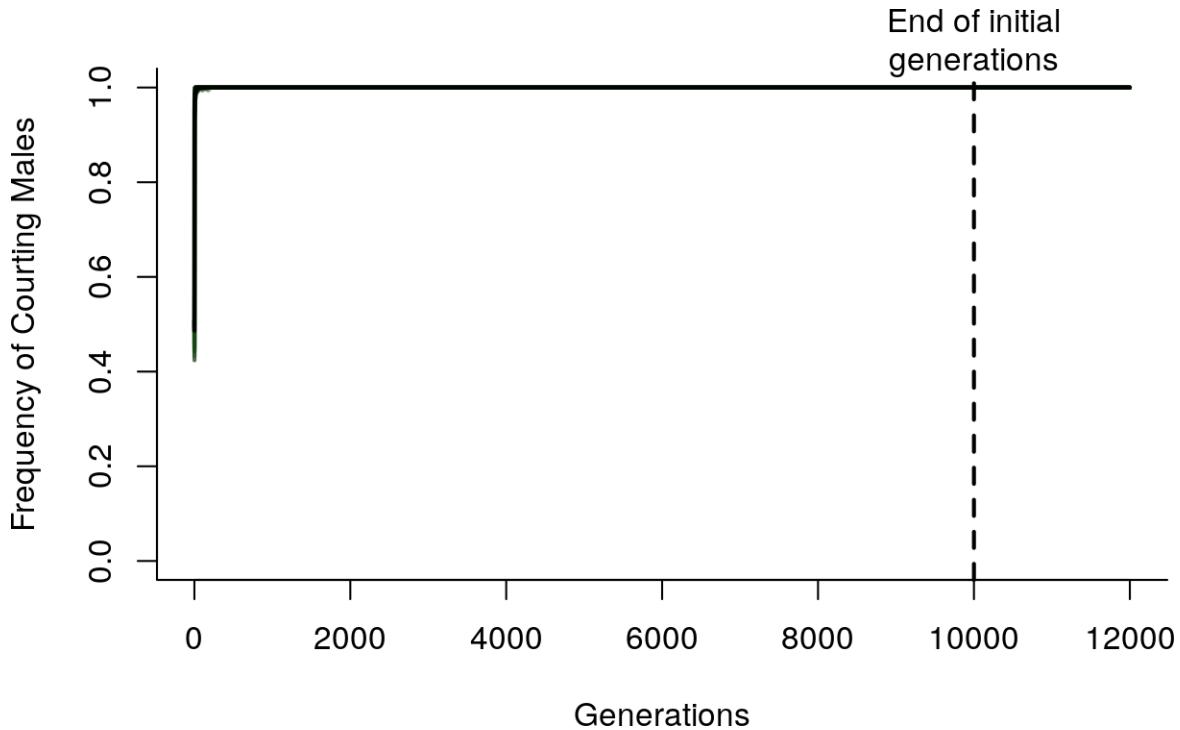


Figure 3: Frequency of the counter morph with unlinked additive genetic variances and without viability selection in all of the replicates

Of the 20 replicates, 20 reached a steady state by 10000 generations. The different runs all overlap, suggesting that they all converge on the same outcome: all males are counters. This result is also obvious by inspecting a table of counter frequencies and fitnesses in the final generation of the runs.

Table 2: Frequency of counters in final generation of runs with unlinked additive genetic variances and no viability selection

	CounterFreq	CounterW	NonCounterW
counter_unlinked_novs_1_summary.txt_1	1	1.90476	0
counter_unlinked_novs_1_summary.txt_2	1	1.94932	0
counter_unlinked_novs_1_summary.txt_3	1	2.13675	0
counter_unlinked_novs_1_summary.txt_4	1	1.97239	0
counter_unlinked_novs_2_summary.txt_1	1	1.90476	0
counter_unlinked_novs_2_summary.txt_2	1	1.94932	0
counter_unlinked_novs_2_summary.txt_3	1	2.13675	0
counter_unlinked_novs_2_summary.txt_4	1	1.97239	0
counter_unlinked_novs_3_summary.txt_1	1	2.01207	0
counter_unlinked_novs_3_summary.txt_2	1	2.02840	0
counter_unlinked_novs_3_summary.txt_3	1	1.99203	0
counter_unlinked_novs_3_summary.txt_4	1	1.97628	0
counter_unlinked_novs_4_summary.txt_1	1	1.91571	0
counter_unlinked_novs_4_summary.txt_2	1	1.91571	0
counter_unlinked_novs_4_summary.txt_3	1	1.94553	0
counter_unlinked_novs_4_summary.txt_4	1	1.95312	0
counter_unlinked_novs_5_summary.txt_1	1	2.02429	0

	CourterFreq	CourterW	NonCourterW
courter_unlinked_novs_5_summary.txt_2	1	2.13220	0
courter_unlinked_novs_5_summary.txt_3	1	1.94553	0
courter_unlinked_novs_5_summary.txt_4	1	2.00000	0

We may also be interested in the evolution of the counter trait values, which reflects the additive effects of all loci.

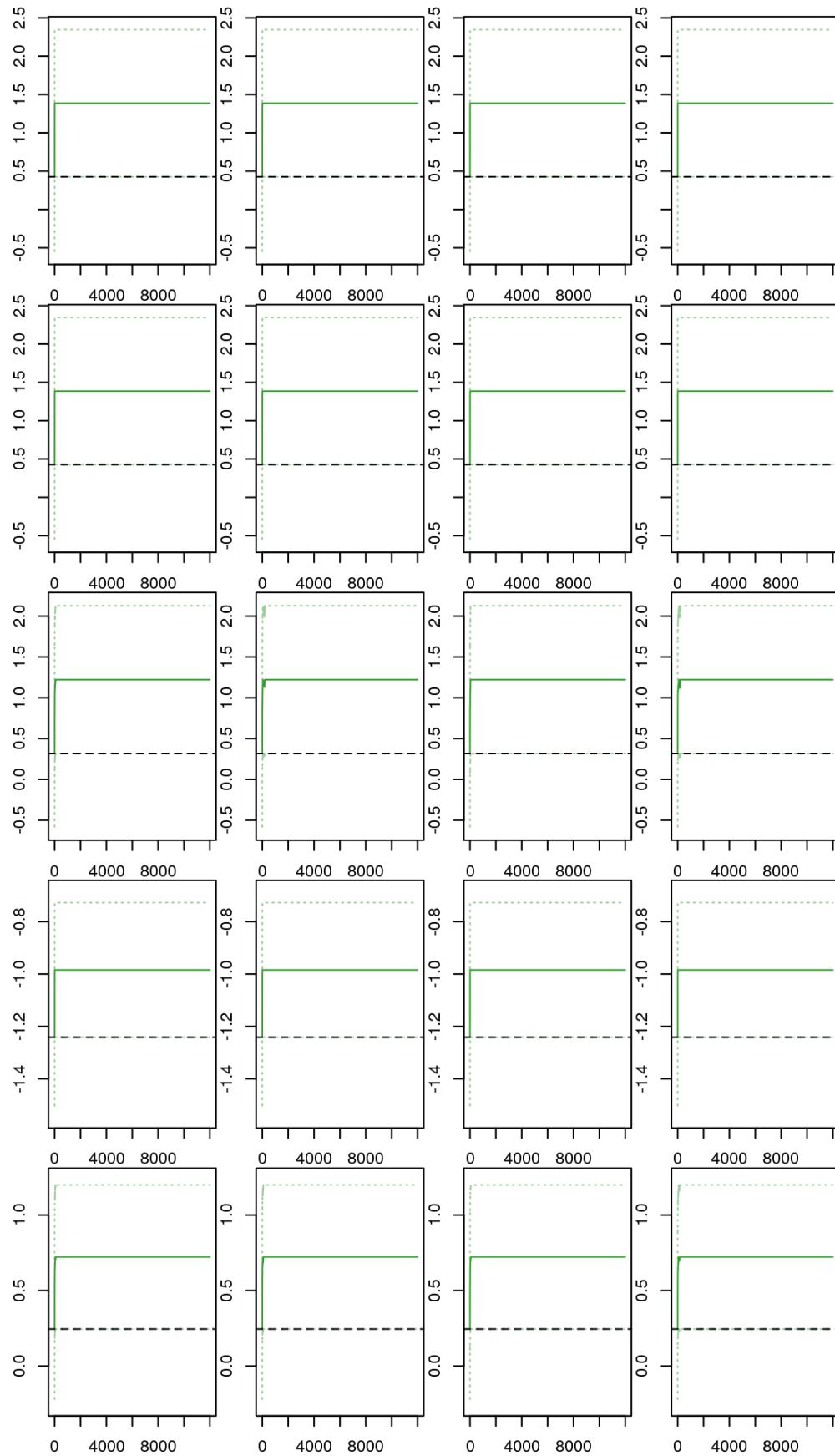


Figure 4: Evolution of courtship trait with unlinked loci and no viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Parental trait

In this case, there are no courtship traits so females lay eggs in nests randomly. Non-parental males will sneak fertilizations in parental males' nests. Parental males provide care that allows nests to have a 90% chance of survival. The female preference does not have a genetic basis and does not evolve.

With viability selection

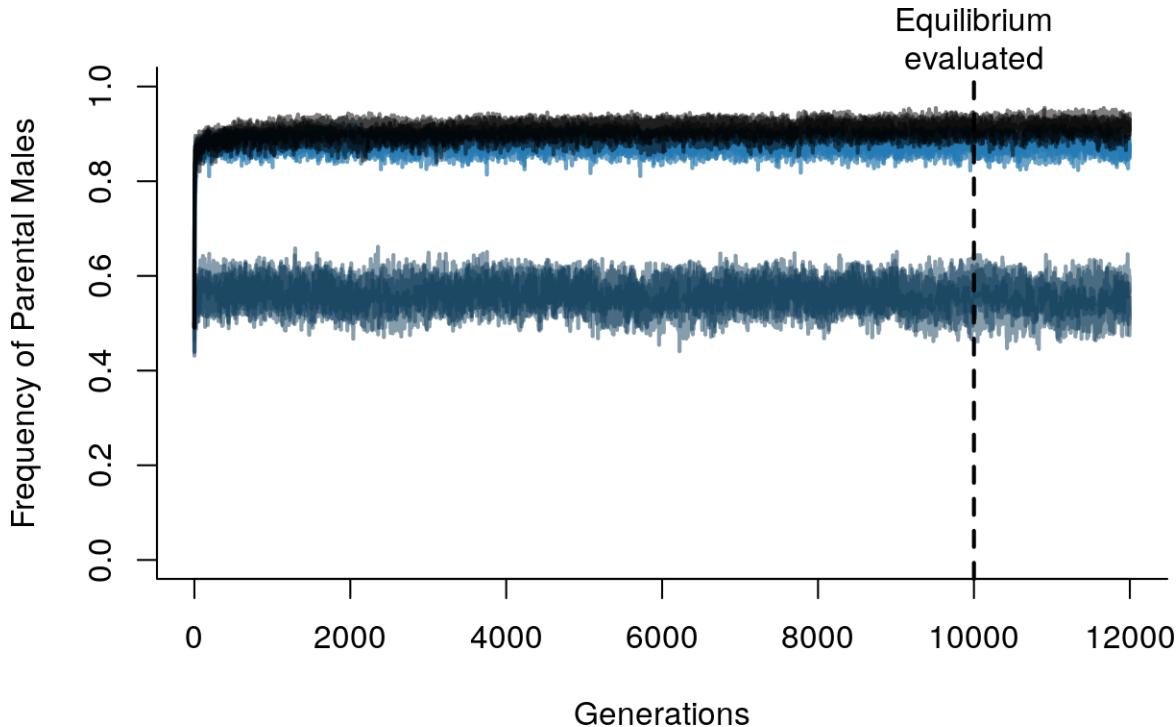


Figure 5: Frequency of parent morph with unlinked loci (each color represents a different replicate)

Again, inference is facilitated by looking at the final frequencies and fitnesses in each replicate:

Table 3: Frequency of parents in final generation

	ParentFreq	ParentW	NonParentW
parent_unlinked_1_summary.txt_1	0.875717	1.54803	0.569231
parent_unlinked_1_summary.txt_2	0.863281	1.64027	0.771429
parent_unlinked_1_summary.txt_3	0.873494	1.66207	0.746032
parent_unlinked_1_summary.txt_4	0.866534	1.71264	0.746269
parent_unlinked_2_summary.txt_1	0.875717	1.54803	0.569231
parent_unlinked_2_summary.txt_2	0.863281	1.64027	0.771429
parent_unlinked_2_summary.txt_3	0.873494	1.66207	0.746032
parent_unlinked_2_summary.txt_4	0.866534	1.71264	0.746269
parent_unlinked_3_summary.txt_1	0.545977	1.49474	0.291139
parent_unlinked_3_summary.txt_2	0.517625	1.31900	0.250000
parent_unlinked_3_summary.txt_3	0.568898	1.55017	0.315068
parent_unlinked_3_summary.txt_4	0.528736	1.50000	0.300813
parent_unlinked_4_summary.txt_1	0.907445	1.75388	1.021740
parent_unlinked_4_summary.txt_2	0.930769	1.60124	1.222220

	ParentFreq	ParentW	NonParentW
parent_unlinked_4_summary.txt_3	0.908184	1.64396	0.869565
parent_unlinked_4_summary.txt_4	0.927856	1.72570	0.666667
parent_unlinked_5_summary.txt_1	0.501976	1.31496	0.269841
parent_unlinked_5_summary.txt_2	0.521042	1.33846	0.334728
parent_unlinked_5_summary.txt_3	0.570499	1.76046	0.333333
parent_unlinked_5_summary.txt_4	0.584071	1.54545	0.361702

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Let's take a look at how the parent trait values evolve

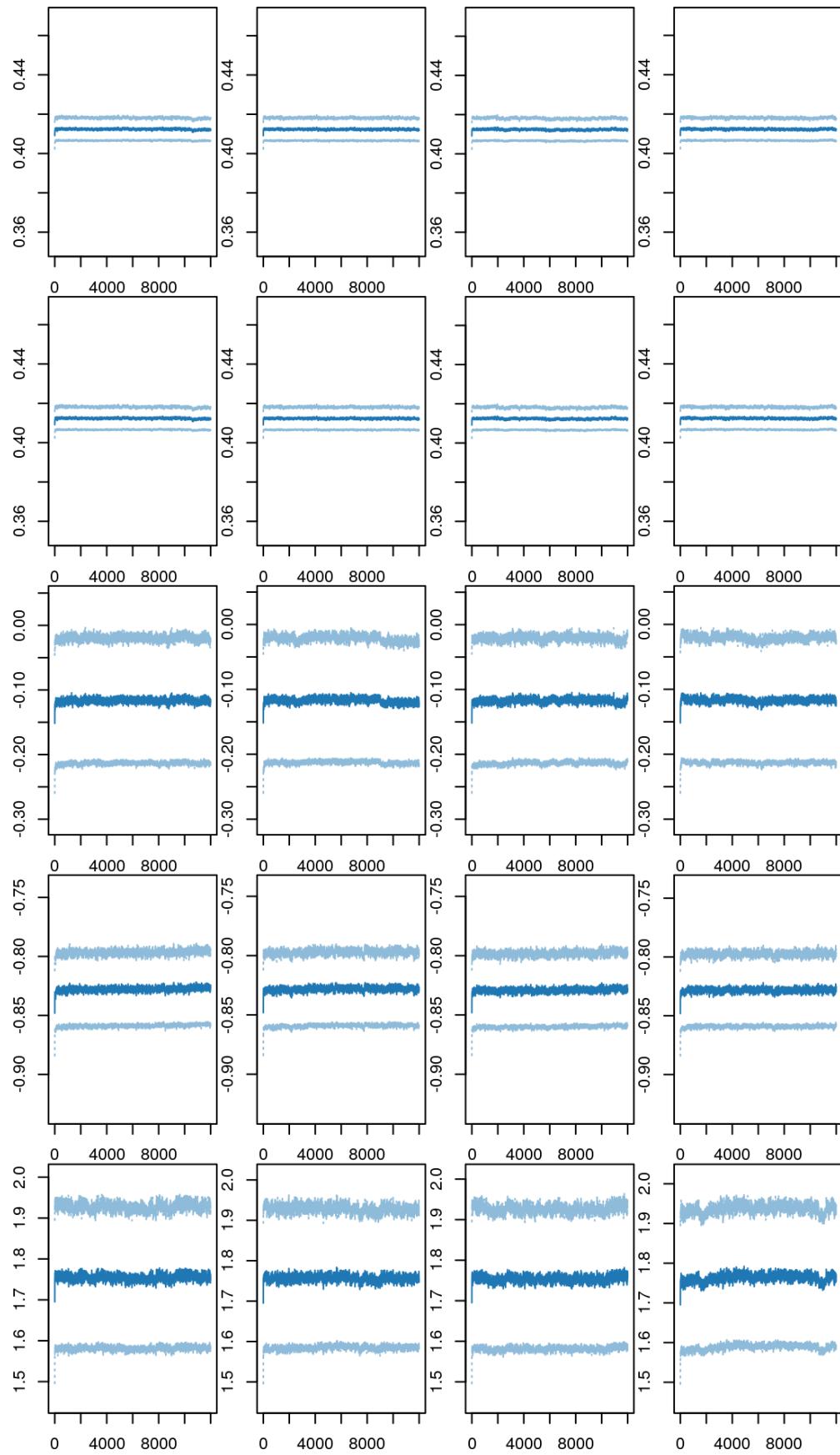


Figure 6: Evolution of parenting trait values with additive genetic variation. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

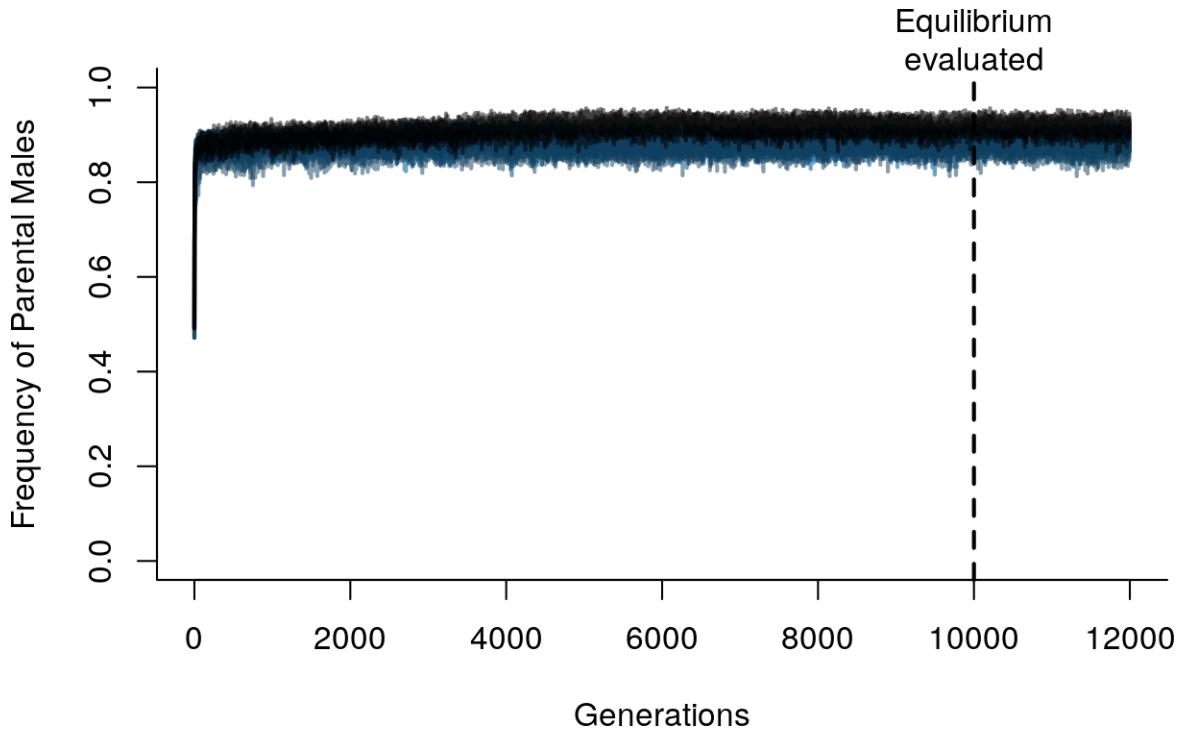


Figure 7: Frequency of parent morph with unlinked loci without viability selection for all replicates

Again, let's look at the final frequencies and fitnesses in each replicate:

Table 4: Frequency of parents in final generation

	ParentFreq	ParentW	NonParentW
parent_unlinked_novs_1_summary.txt_1	0.889546	1.70067	0.928571
parent_unlinked_novs_1_summary.txt_2	0.895464	1.59031	1.169810
parent_unlinked_novs_1_summary.txt_3	0.885932	1.56009	0.816667
parent_unlinked_novs_1_summary.txt_4	0.907692	1.65678	0.916667
parent_unlinked_novs_2_summary.txt_1	0.889546	1.70067	0.928571
parent_unlinked_novs_2_summary.txt_2	0.895464	1.59031	1.169810
parent_unlinked_novs_2_summary.txt_3	0.885932	1.56009	0.816667
parent_unlinked_novs_2_summary.txt_4	0.907692	1.65678	0.916667
parent_unlinked_novs_3_summary.txt_1	0.875728	1.53659	0.812500
parent_unlinked_novs_3_summary.txt_2	0.886869	1.67426	0.982143
parent_unlinked_novs_3_summary.txt_3	0.853707	1.72770	0.684932
parent_unlinked_novs_3_summary.txt_4	0.873706	1.68246	0.934426
parent_unlinked_novs_4_summary.txt_1	0.933884	1.74779	1.250000
parent_unlinked_novs_4_summary.txt_2	0.910646	1.59708	0.744681
parent_unlinked_novs_4_summary.txt_3	0.922921	1.64615	1.184210
parent_unlinked_novs_4_summary.txt_4	0.911067	1.59436	0.800000
parent_unlinked_novs_5_summary.txt_1	0.578313	1.50000	0.219048
parent_unlinked_novs_5_summary.txt_2	0.553606	1.39437	0.497817
parent_unlinked_novs_5_summary.txt_3	0.575049	1.57288	0.311927
parent_unlinked_novs_5_summary.txt_4	0.538603	1.29352	0.250996

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Let's take a look at how the parent trait values evolve

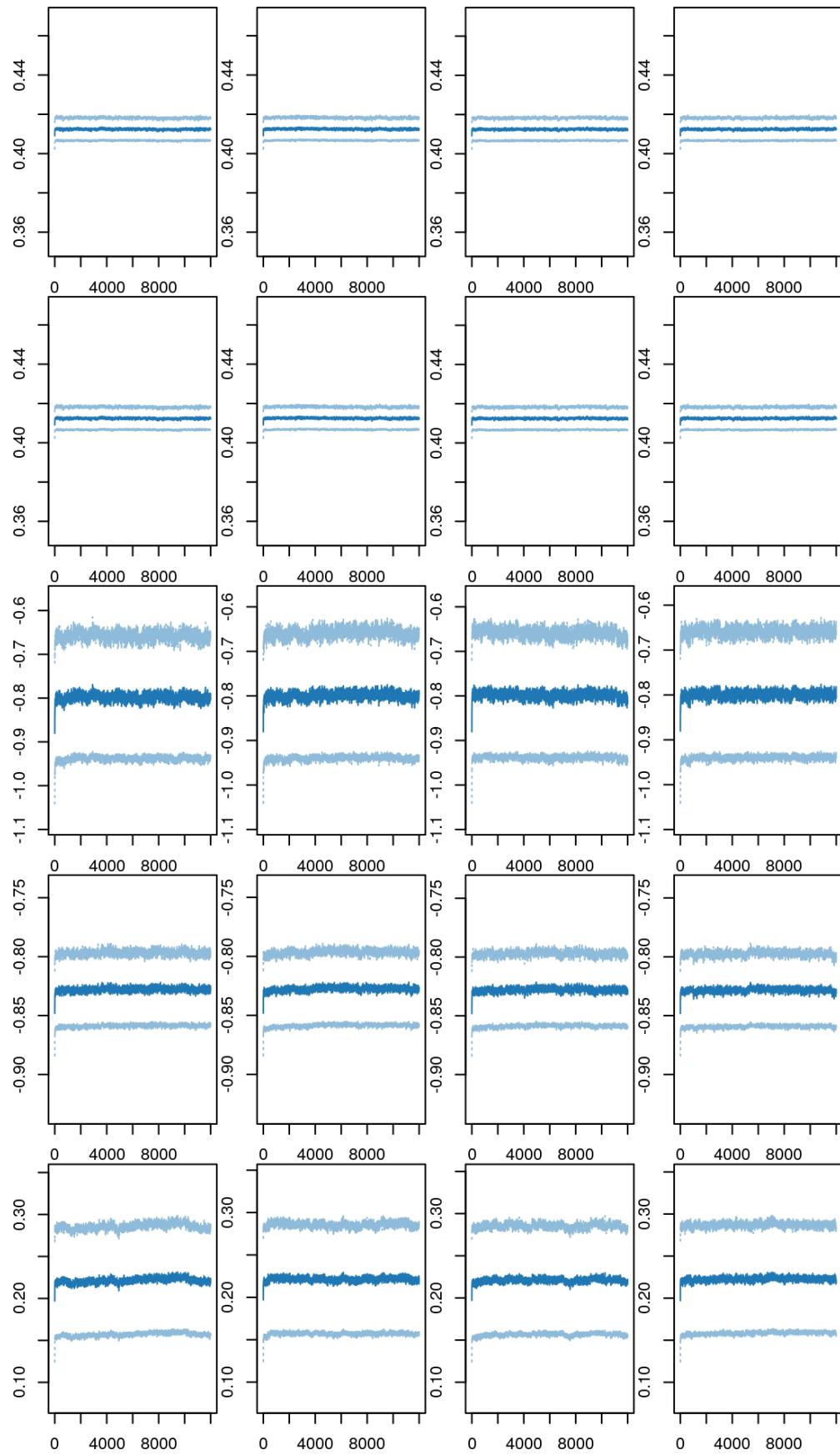
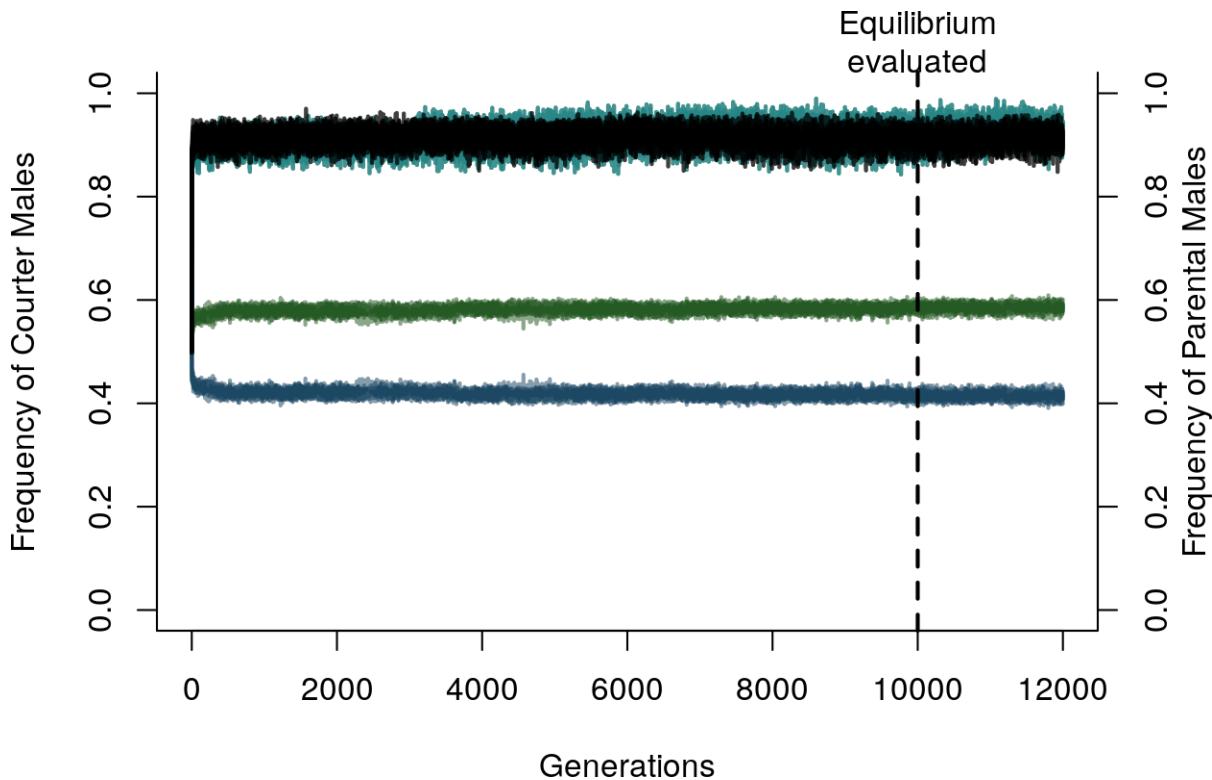


Figure 8: Evolution of parenting trait values with additive genetic variation and no viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Courtship and Parental Traits

Females choose nests based on males' courtship trait (they all only nest with courting males, and the female preference does not have a genetic basis and does not evolve), and then the survival of the nest depends on whether the courting male is also a parental male. If the chosen male is a parental male, the nest has a 90% chance of survival. Otherwise, it only has a 10% chance. Non-courtiers and non-parents can reproduce through sneaking.

With viability selection



The different runs have different outcomes.

Let's look at the morph frequencies for each run.

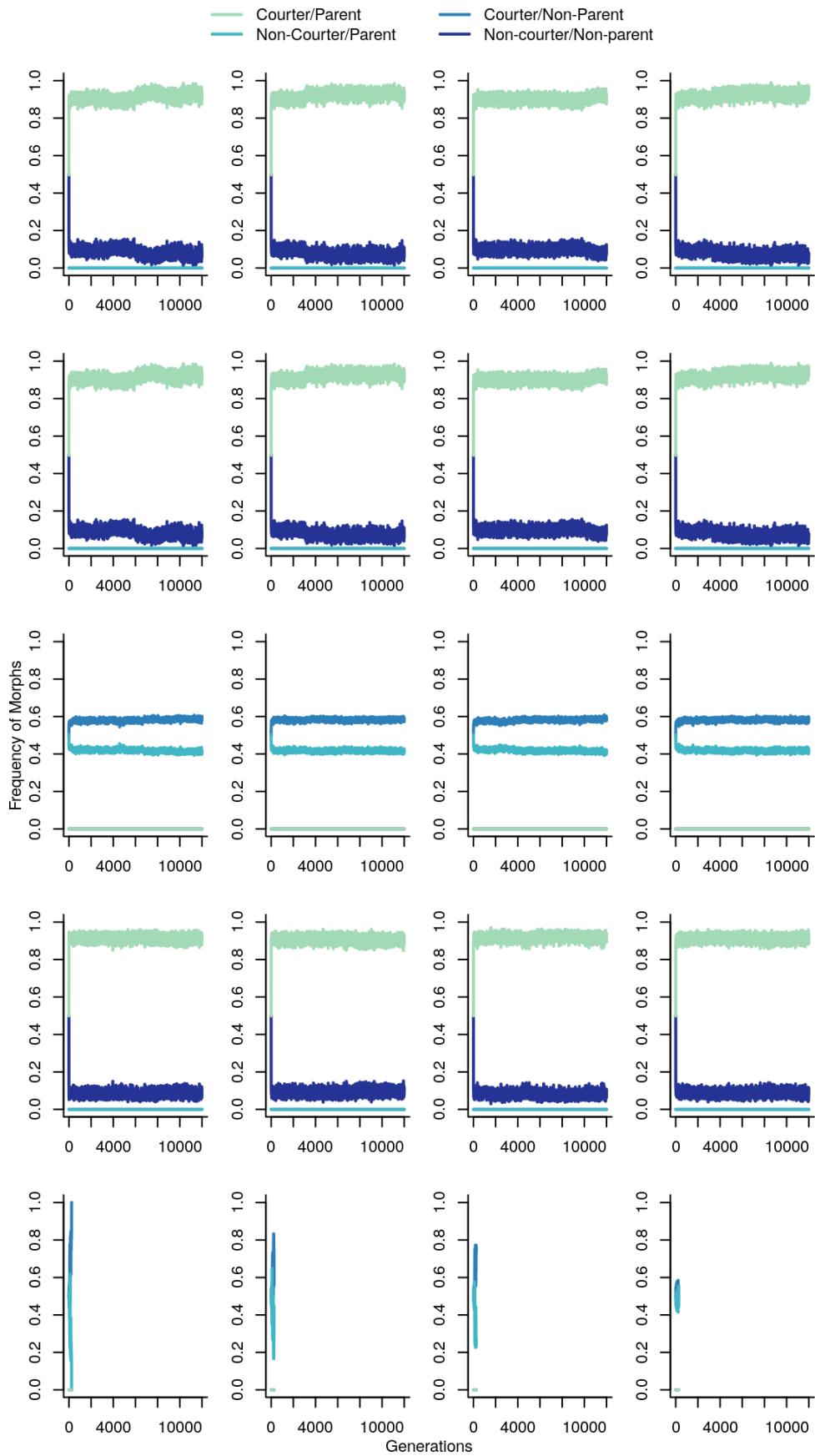


Figure 9: Frequency of the 4 morphs in each rep with unlinked genetic variation

In some of the runs the population crashed after few generations. This is obvious when looking at the final frequencies in a table as well:

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	Parer
parent-courter_unlinked_1_summary.txt_1	11999	Pop0	919	462	457	1000	0
parent-courter_unlinked_1_summary.txt_2	11999	Pop1	933	458	475	1000	0
parent-courter_unlinked_1_summary.txt_3	11999	Pop2	969	453	516	1000	0
parent-courter_unlinked_1_summary.txt_4	11999	Pop3	944	493	451	1000	0
parent-courter_unlinked_2_summary.txt_1	11999	Pop0	919	462	457	1000	0
parent-courter_unlinked_2_summary.txt_2	11999	Pop1	933	458	475	1000	0
parent-courter_unlinked_2_summary.txt_3	11999	Pop2	969	453	516	1000	0
parent-courter_unlinked_2_summary.txt_4	11999	Pop3	944	493	451	1000	0
parent-courter_unlinked_3_summary.txt_1	11999	Pop0	987	501	486	1000	0
parent-courter_unlinked_3_summary.txt_2	11999	Pop1	984	488	496	1000	0
parent-courter_unlinked_3_summary.txt_3	11999	Pop2	981	479	502	1000	0
parent-courter_unlinked_3_summary.txt_4	11999	Pop3	983	485	498	1000	0
parent-courter_unlinked_4_summary.txt_1	11999	Pop0	987	509	478	1000	0
parent-courter_unlinked_4_summary.txt_2	11999	Pop1	989	514	475	1000	0
parent-courter_unlinked_4_summary.txt_3	11999	Pop2	1000	505	495	1000	0
parent-courter_unlinked_4_summary.txt_4	11999	Pop3	1000	526	474	1000	0
parent-courter_unlinked_5_summary.txt_1	256	Pop0	4	3	1	4	-0
parent-courter_unlinked_5_summary.txt_2	256	Pop1	27	18	9	29	-0
parent-courter_unlinked_5_summary.txt_3	256	Pop2	36	20	16	52	-0
parent-courter_unlinked_5_summary.txt_4	256	Pop3	304	163	141	295	-0

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a courter.

If we look at how the two traits evolved, we see that in the runs when the population crashed the trait values did not immediately evolve above the thresholds (unlike in the other runs) – and that the parent threshold started out much lower than the courter threshold. It may be that the threshold value plays a key role in determining the fate of the populations.

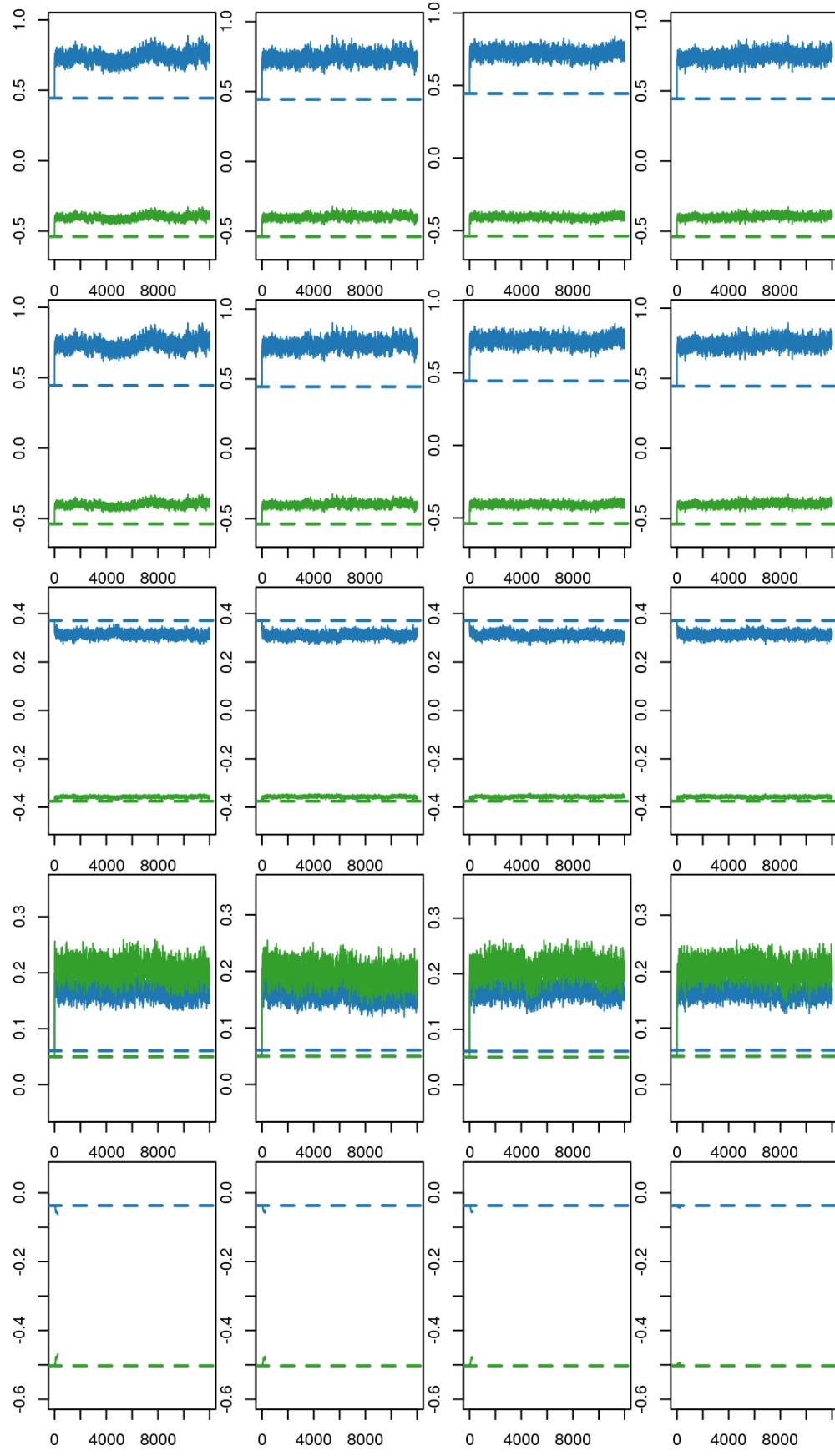
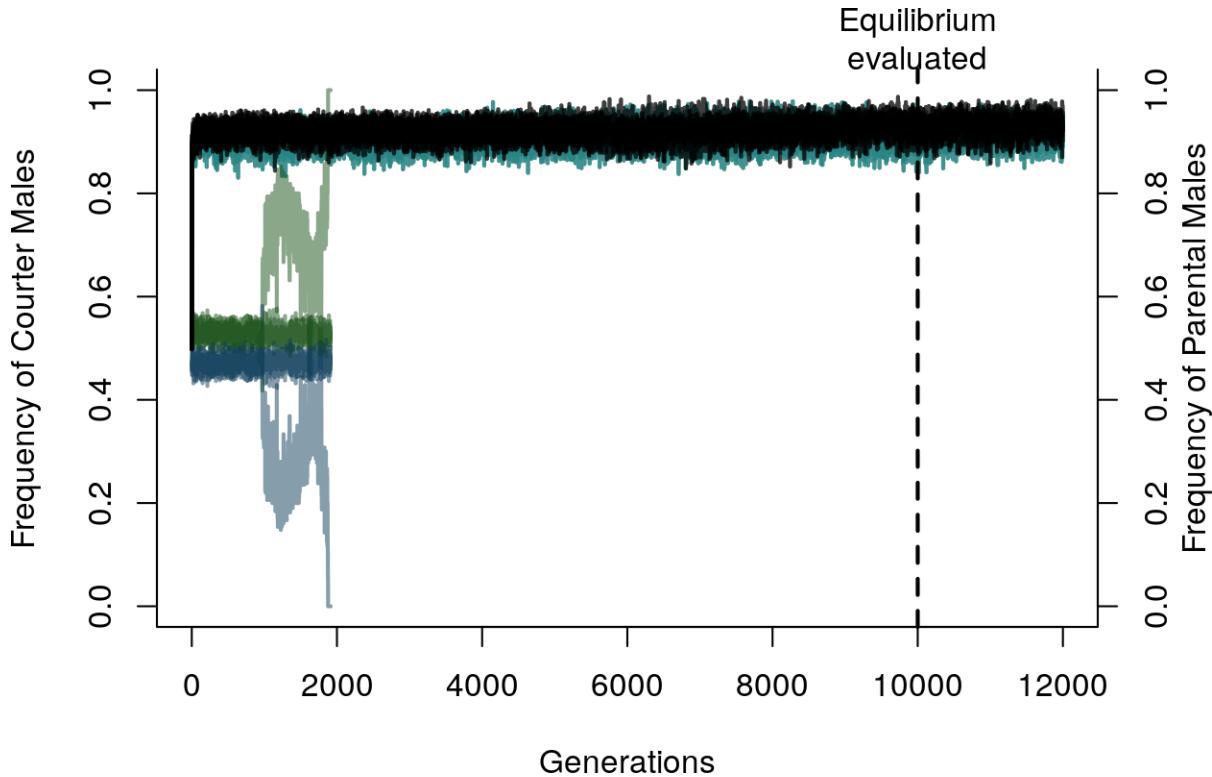


Figure 10: Evolution of the counter and parenting trait values in each rep with unlinked genetic variation.
Dotted line shows the thresholds determining if males become courters (green) or parents (blue)

Without viability selection

This scenario – unlinked loci contributing to the additive genetic variances of courtship and parental traits – is one where having viability selection or not having viability selection is important.



The different runs have different outcomes, but none of the runs crashed. Clearly, the crashing of the populations seen above is due to viability selection.

Let's look at the morph frequencies for each run.

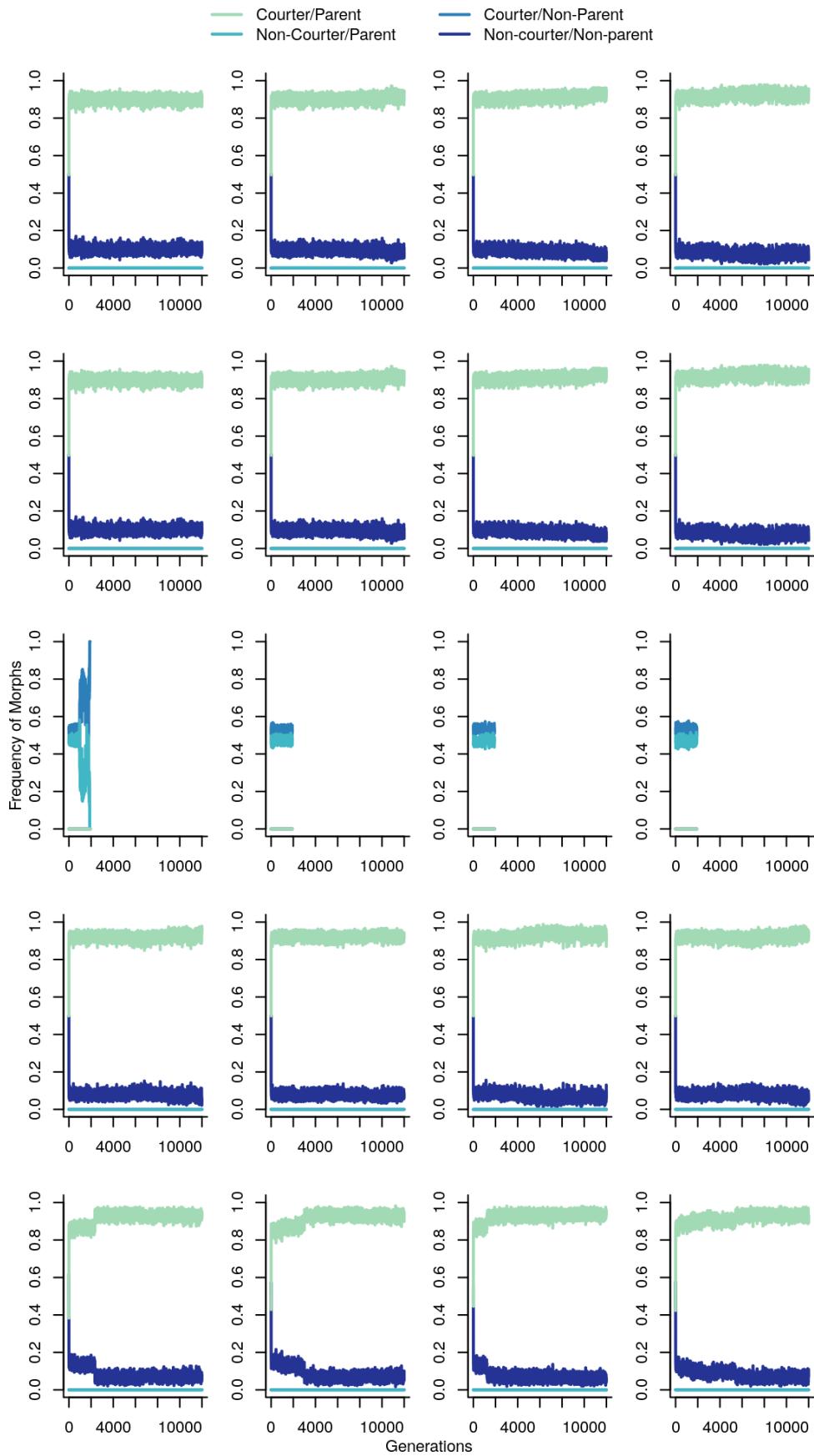


Figure 11: Frequency of the 4 morphs in each rep with unlinked genetic variation and no viability selection

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_unlinked_novs_1_summary.txt_1	11999	Pop0	1000	496	504	1000
parent-courter_unlinked_novs_1_summary.txt_2	11999	Pop1	956	478	478	1000
parent-courter_unlinked_novs_1_summary.txt_3	11999	Pop2	971	481	490	1000
parent-courter_unlinked_novs_1_summary.txt_4	11999	Pop3	952	463	489	1000
parent-courter_unlinked_novs_2_summary.txt_1	11999	Pop0	1000	496	504	1000
parent-courter_unlinked_novs_2_summary.txt_2	11999	Pop1	956	478	478	1000
parent-courter_unlinked_novs_2_summary.txt_3	11999	Pop2	971	481	490	1000
parent-courter_unlinked_novs_2_summary.txt_4	11999	Pop3	952	463	489	1000
parent-courter_unlinked_novs_3_summary.txt_1	1913	Pop0	6	1	5	4
parent-courter_unlinked_novs_3_summary.txt_2	1913	Pop1	977	496	481	1000
parent-courter_unlinked_novs_3_summary.txt_3	1913	Pop2	908	462	446	956
parent-courter_unlinked_novs_3_summary.txt_4	1913	Pop3	900	464	436	1000
parent-courter_unlinked_novs_4_summary.txt_1	11999	Pop0	944	456	488	1000
parent-courter_unlinked_novs_4_summary.txt_2	11999	Pop1	1000	534	466	1000
parent-courter_unlinked_novs_4_summary.txt_3	11999	Pop2	946	469	477	1000
parent-courter_unlinked_novs_4_summary.txt_4	11999	Pop3	944	470	474	1000
parent-courter_unlinked_novs_5_summary.txt_1	11999	Pop0	952	458	494	1000
parent-courter_unlinked_novs_5_summary.txt_2	11999	Pop1	947	469	478	1000
parent-courter_unlinked_novs_5_summary.txt_3	11999	Pop2	953	487	466	1000
parent-courter_unlinked_novs_5_summary.txt_4	11999	Pop3	948	448	500	1000

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a courter.

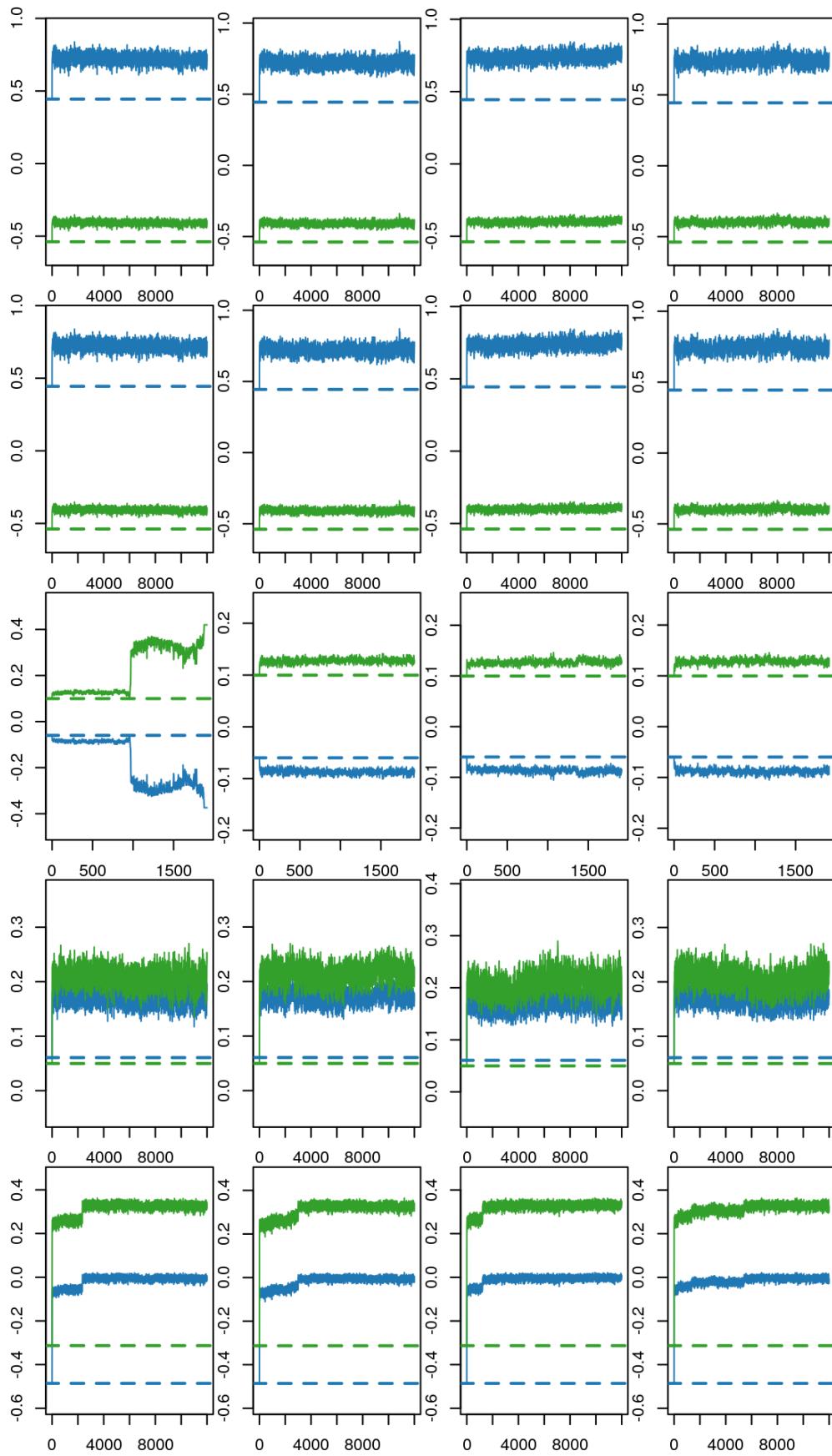


Figure 12: Evolution of the courtship and parenting trait values in each rep with unlinked genetic variation and without viability selection. Green represents courtship²³ trait values and blue represents parental trait values, and the dotted lines are the thresholds

When the counter/parent and non-counter/non-parent morphs are maintained in populations, the counter threshold is higher than the parental threshold. When the non-counter/parent and counter/non-parent morphs are maintained, the parental threshold is higher than the counter threshold.

Linked additive genetic variance

In these cases, the traits are encoded by a number (50) of loci, whose alleles contribute additively to determine the trait value. These alleles anchored on chromosomes, equally distributed among the chromosomes (4). The overall trait value is compared to a population-level threshold (which is static, in these cases), and if the trait value is above the threshold the male takes the parent or counter morph and if it is below he does not. Below, I'm showing the results from 10 replicates of each scenario.

Courter trait

With viability selection

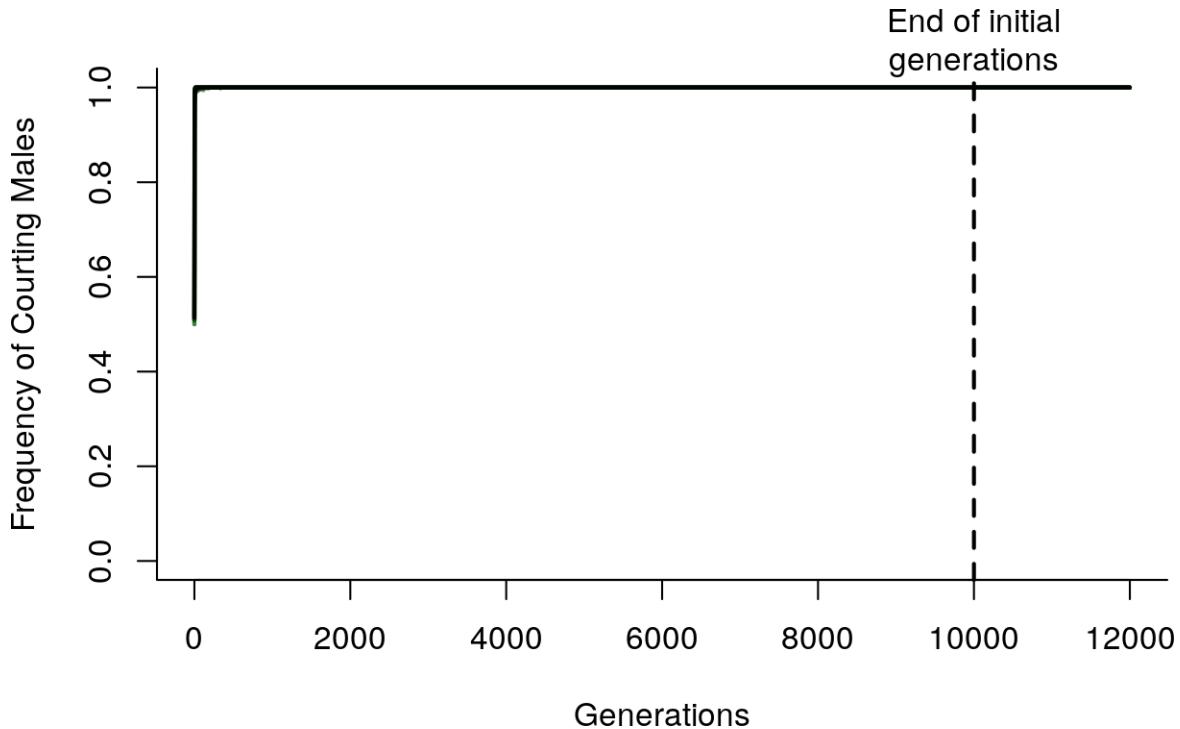


Figure 13: Frequency of the counter morph with linked QTLs (each color represents a different replicate)

When only the courtship trait is included in the simulation, 20 of the 20 replicates reached an equilibrium by 10000 generations.

This is further evidenced by looking at a table of trait values and fitnesses in the final generation of each replicate

Table 7: Frequency of counters with linked QTLs in final generation

	CounterFreq	CounterW	NonCounterW
counter_linked_1_summary.txt_1	1	2.02449	0

	CounterFreq	CounterW	NonCounterW
counter_linked_1_summary.txt_2	1	1.97217	0
counter_linked_1_summary.txt_3	1	2.12580	0
counter_linked_1_summary.txt_4	1	2.03689	0
counter_linked_2_summary.txt_1	1	2.02449	0
counter_linked_2_summary.txt_2	1	1.97217	0
counter_linked_2_summary.txt_3	1	2.12580	0
counter_linked_2_summary.txt_4	1	2.03689	0
counter_linked_3_summary.txt_1	1	2.15054	0
counter_linked_3_summary.txt_2	1	2.05339	0
counter_linked_3_summary.txt_3	1	2.04499	0
counter_linked_3_summary.txt_4	1	2.04918	0
counter_linked_4_summary.txt_1	1	2.07516	0
counter_linked_4_summary.txt_2	1	2.12876	0
counter_linked_4_summary.txt_3	1	1.97421	0
counter_linked_4_summary.txt_4	1	2.02642	0
counter_linked_5_summary.txt_1	1	2.00401	0
counter_linked_5_summary.txt_2	1	1.94553	0
counter_linked_5_summary.txt_3	1	2.06186	0
counter_linked_5_summary.txt_4	1	2.00803	0

Every replicate has the courtship trait go to fixation.

Let's also evaluate the evolution of the courtship trait values:

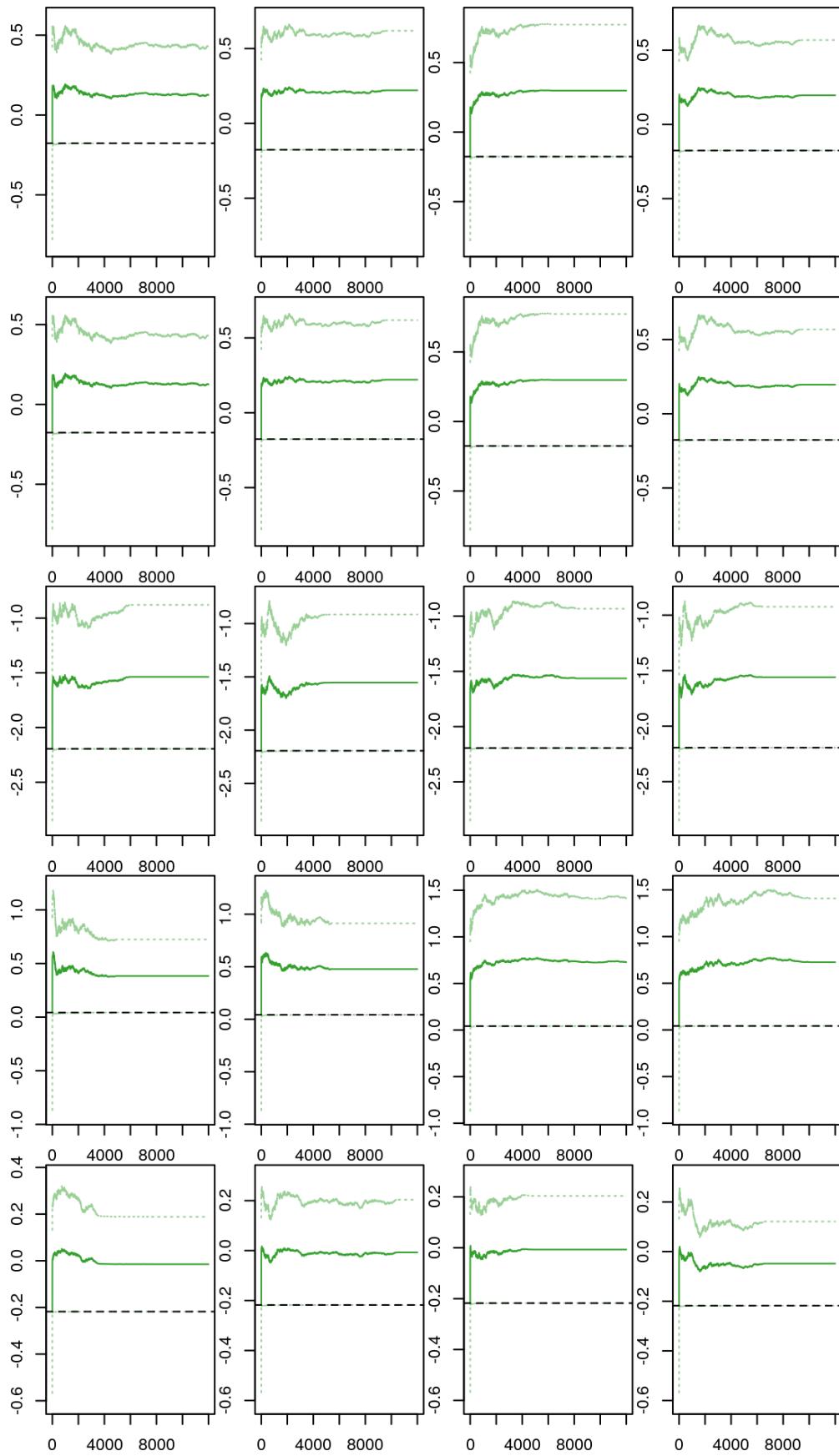


Figure 14: Evolution of courtship trait with linked loci. Green dotted lines are the standard deviations of the traits and the black dotted line is the threshold

In every case, the trait values evolve above the threshold.

Without viability selection

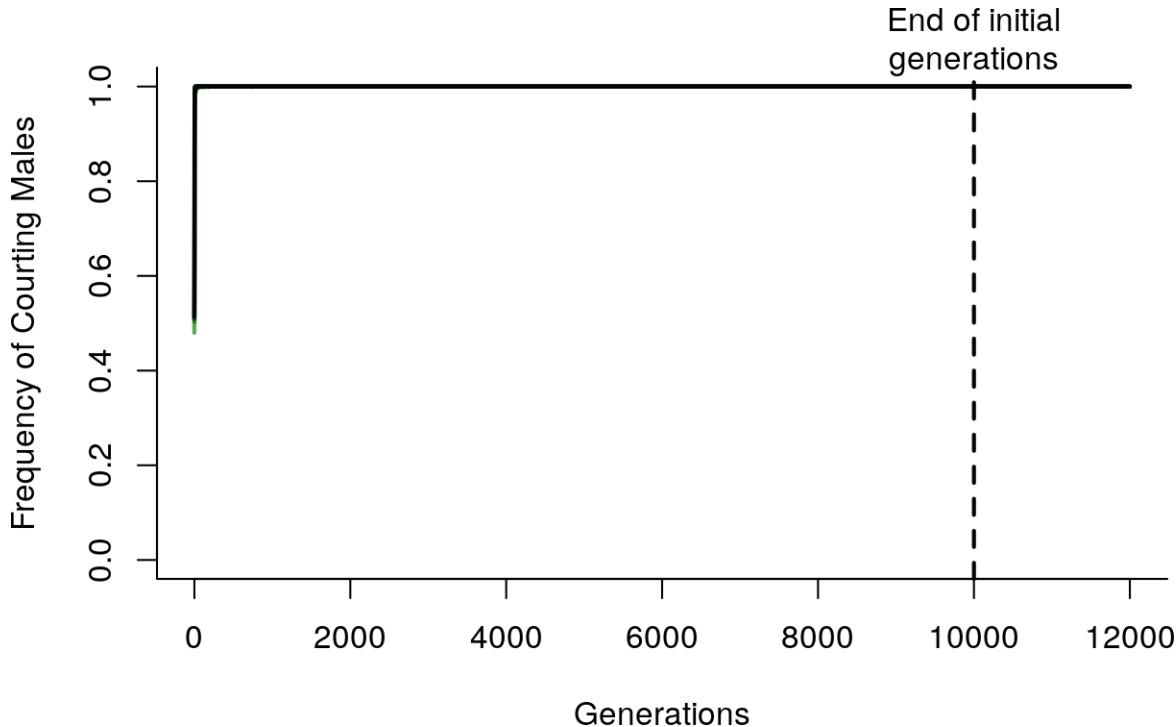


Figure 15: Frequency of the courtship trait with linked QTLs and no viability selection (each color represents a different replicate)

When only the courtship trait is included in the simulation, 0 of the 20 replicates reached an equilibrium by 10000 generations.

This is further evidenced by looking at a table of trait values and fitnesses in the final generation of each replicate

Table 8: Frequency of courters with linked QTLs in final generation

	CounterFreq	CounterW	NonCounterW
counter_linked_novs_1_summary.txt_1	1	2.05339	0
counter_linked_novs_1_summary.txt_2	1	2.11864	0
counter_linked_novs_1_summary.txt_3	1	1.92308	0
counter_linked_novs_1_summary.txt_4	1	2.02020	0
counter_linked_novs_2_summary.txt_1	1	1.90840	0
counter_linked_novs_2_summary.txt_2	1	1.87617	0
counter_linked_novs_2_summary.txt_3	1	1.98807	0
counter_linked_novs_2_summary.txt_4	1	2.03666	0
counter_linked_novs_3_summary.txt_1	1	2.07469	0
counter_linked_novs_3_summary.txt_2	1	1.99203	0
counter_linked_novs_3_summary.txt_3	1	1.99601	0
counter_linked_novs_3_summary.txt_4	1	1.91571	0
counter_linked_novs_4_summary.txt_1	1	2.04082	0

	CourterFreq	CourterW	NonCourterW
courter_linked_novs_4_summary.txt_2	1	2.04918	0
courter_linked_novs_4_summary.txt_3	1	2.12314	0
courter_linked_novs_4_summary.txt_4	1	2.01207	0
courter_linked_novs_5_summary.txt_1	1	2.06186	0
courter_linked_novs_5_summary.txt_2	1	1.94553	0
courter_linked_novs_5_summary.txt_3	1	2.08333	0
courter_linked_novs_5_summary.txt_4	1	1.87970	0

Every rep has the courtship trait go to fixation.

Let's also evaluate the evolution of the courtship trait values:

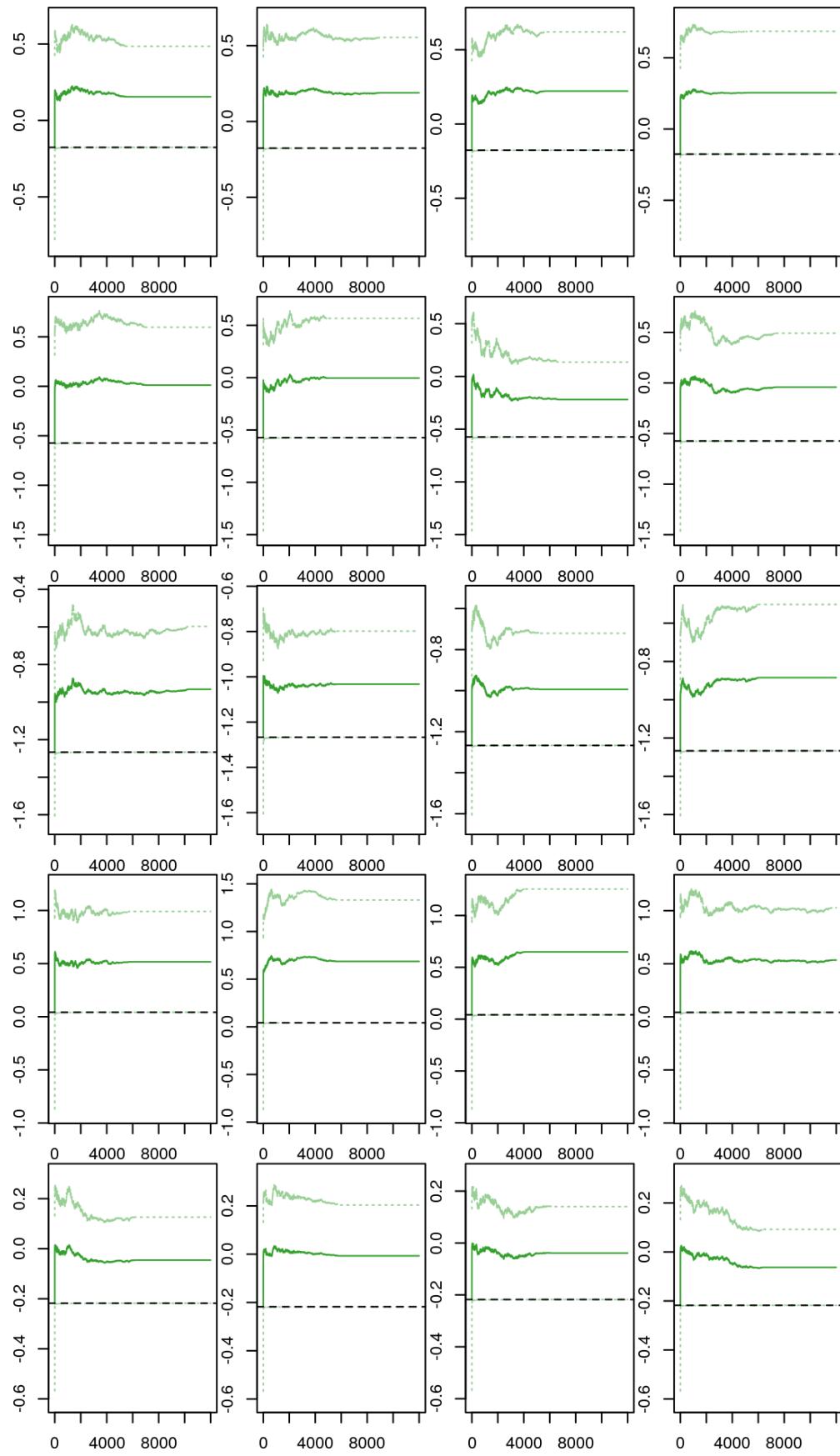


Figure 16: Evolution of courtship trait with linked loci and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

The case with only the courtship trait does not differ qualitatively with or without viability selection.

Parental trait

With viability selection

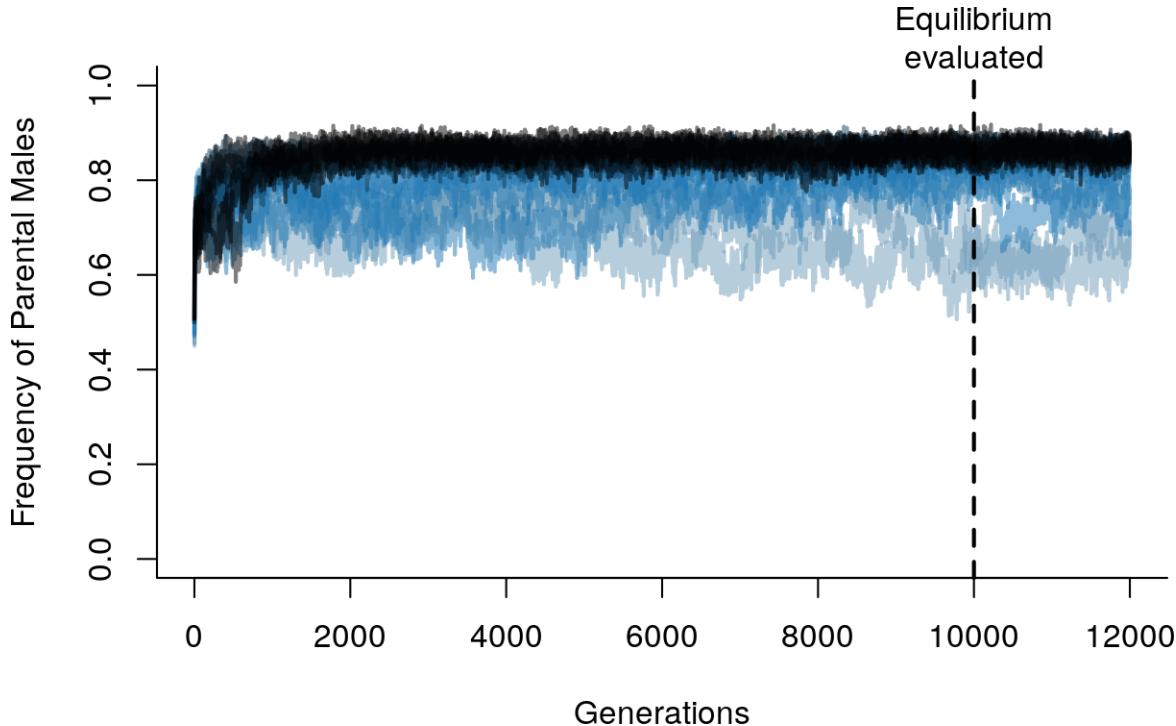


Figure 17: Frequency of parent morph with linked QTLs (each color represents a different replicate)

When only the parental trait is included in the model with linked QTLs, variable outcomes can be reached – although all include each rep reaching some stable state with minor fluctuations.

Table 9: Frequency of parents with linked QTLs in final generation

	ParentFreq	ParentW	NonParentW
parent_linked_1_summary.txt_1	0.636538	1.36556	0.285714
parent_linked_1_summary.txt_2	0.766798	1.59278	0.406780
parent_linked_1_summary.txt_3	0.694332	1.62099	0.397351
parent_linked_1_summary.txt_4	0.831439	1.59453	0.629213
parent_linked_2_summary.txt_1	0.848303	1.64471	0.539474
parent_linked_2_summary.txt_2	0.761996	1.55919	0.379032
parent_linked_2_summary.txt_3	0.728324	1.51058	0.609929
parent_linked_2_summary.txt_4	0.865759	1.62472	0.695652
parent_linked_3_summary.txt_1	0.873684	1.82169	0.766667
parent_linked_3_summary.txt_2	0.867617	1.69953	0.646154
parent_linked_3_summary.txt_3	0.858586	1.64471	0.714286
parent_linked_3_summary.txt_4	0.861386	1.77471	0.671429
parent_linked_4_summary.txt_1	0.851240	1.70631	0.944444
parent_linked_4_summary.txt_2	0.859155	1.73068	0.657143
parent_linked_4_summary.txt_3	0.872428	1.68868	1.016130

	ParentFreq	ParentW	NonParentW
parent_linked_4_summary.txt_4	0.875000	1.64977	0.709677
parent_linked_5_summary.txt_1	0.849237	1.59101	0.607595
parent_linked_5_summary.txt_2	0.690608	1.37600	0.488095
parent_linked_5_summary.txt_3	0.837255	1.52693	0.506024
parent_linked_5_summary.txt_4	0.853465	1.63341	0.608108

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

The evolution of the trait values may shed light on the variable outcomes:

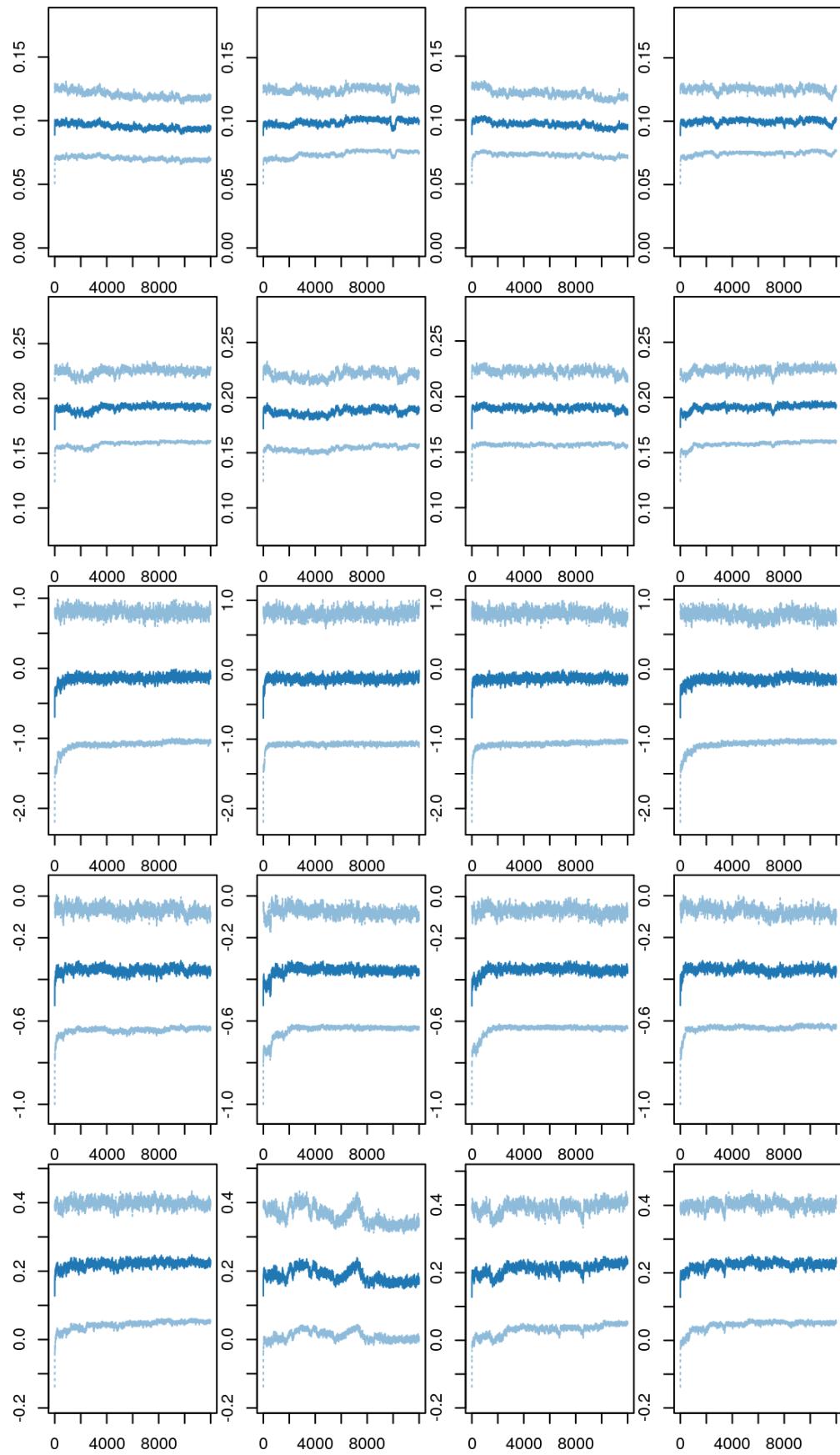


Figure 18: Evolution of parenting trait values with linked QTLs. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Fluctuations around a relatively stable trait mean match the fluctuations around a fairly stable frequency of parental males.

Without viability selection

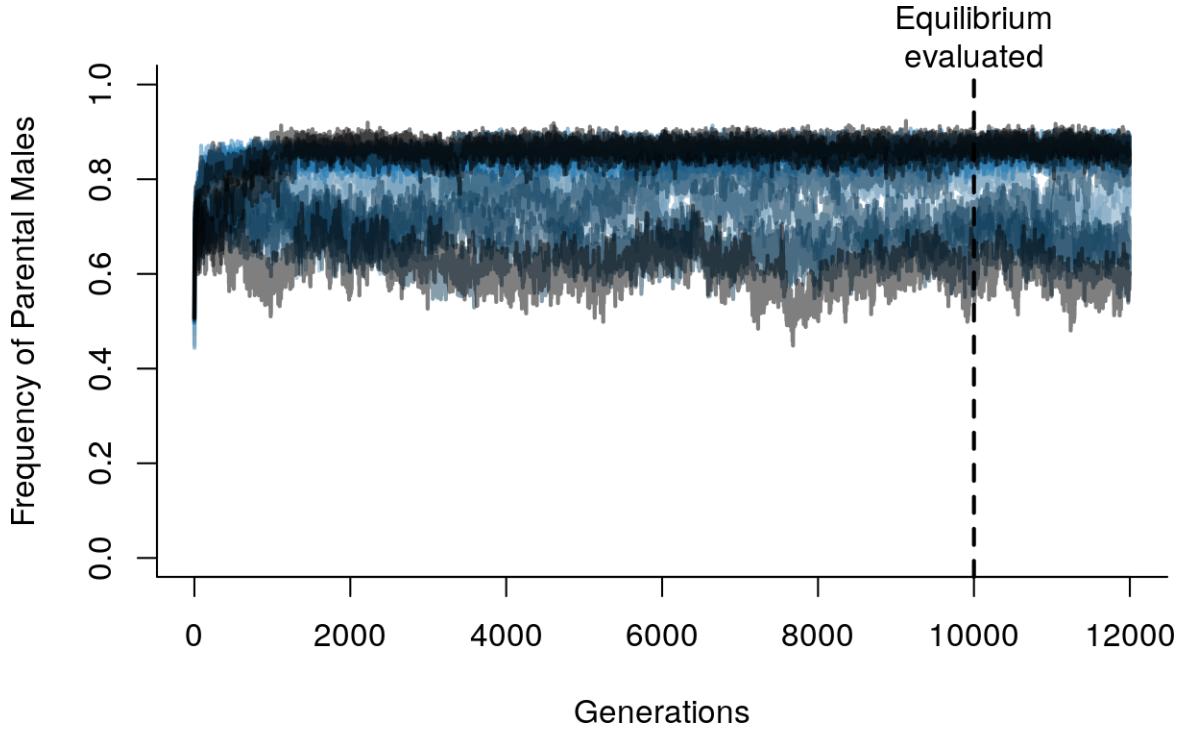


Figure 19: Frequency of parent morph with linked QTLs without viability selection (each color represents a different replicate)

When only the parental trait is included in the model with linked QTLs, variable outcomes can be reached – although all include each rep reaching some stable state with minor fluctuations.

Table 10: Frequency of parents with linked QTLs in final generation, with no viability selection

	ParentFreq	ParentW	NonParentW
parent_linked_novs_1_summary.txt_1	0.830116	1.51628	0.420455
parent_linked_novs_1_summary.txt_2	0.794175	1.53545	0.452830
parent_linked_novs_1_summary.txt_3	0.811861	1.72292	0.586957
parent_linked_novs_1_summary.txt_4	0.750973	1.45855	0.468750
parent_linked_novs_2_summary.txt_1	0.838710	1.71635	0.650000
parent_linked_novs_2_summary.txt_2	0.851626	1.69928	0.726027
parent_linked_novs_2_summary.txt_3	0.861660	1.61468	0.571429
parent_linked_novs_2_summary.txt_4	0.892925	1.57602	0.982143
parent_linked_novs_3_summary.txt_1	0.808468	1.70324	0.536842
parent_linked_novs_3_summary.txt_2	0.608696	1.44410	0.410628
parent_linked_novs_3_summary.txt_3	0.669903	1.63188	0.288235
parent_linked_novs_3_summary.txt_4	0.704501	1.53056	0.397351
parent_linked_novs_4_summary.txt_1	0.876310	1.80861	0.932203
parent_linked_novs_4_summary.txt_2	0.599593	1.55932	0.324873

	ParentFreq	ParentW	NonParentW
parent_linked_novs_4_summary.txt_3	0.843444	1.51972	0.587500
parent_linked_novs_4_summary.txt_4	0.855397	1.75238	0.619718
parent_linked_novs_5_summary.txt_1	0.730382	1.47934	0.485075
parent_linked_novs_5_summary.txt_2	0.845703	1.62356	0.481013
parent_linked_novs_5_summary.txt_3	0.820866	1.68825	0.472527
parent_linked_novs_5_summary.txt_4	0.834661	1.60143	0.397590

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Looking at the evolution of trait values reflects the same patterns:

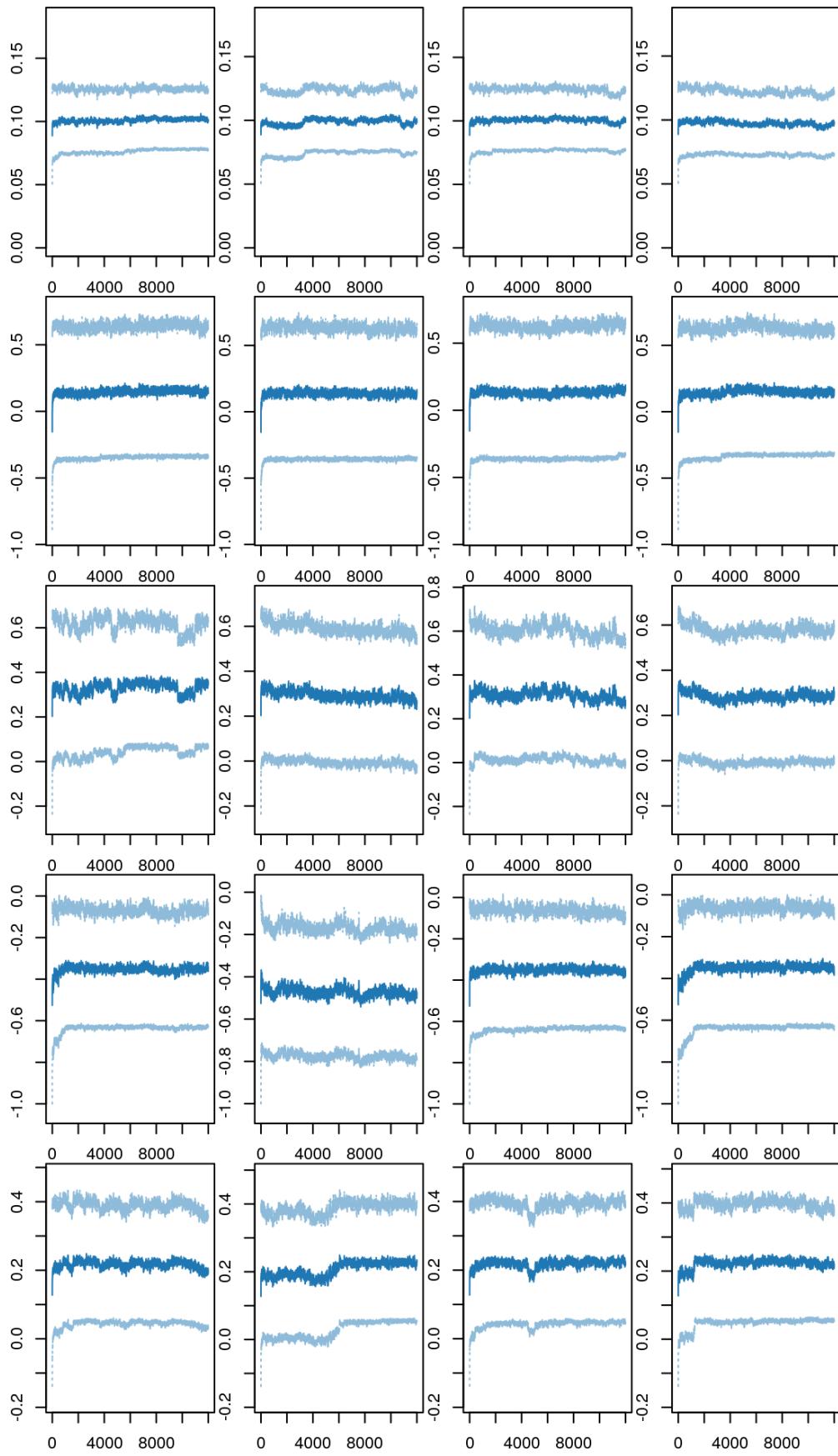


Figure 20: Evolution of parenting trait values with linked QTLs and without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Courtship and Parental Traits

Including both courtship and parental traits, along with linked loci, causes the outcomes to be less predictable – same as in the case of unanchored/unlinked genetic loci.

With viability selection

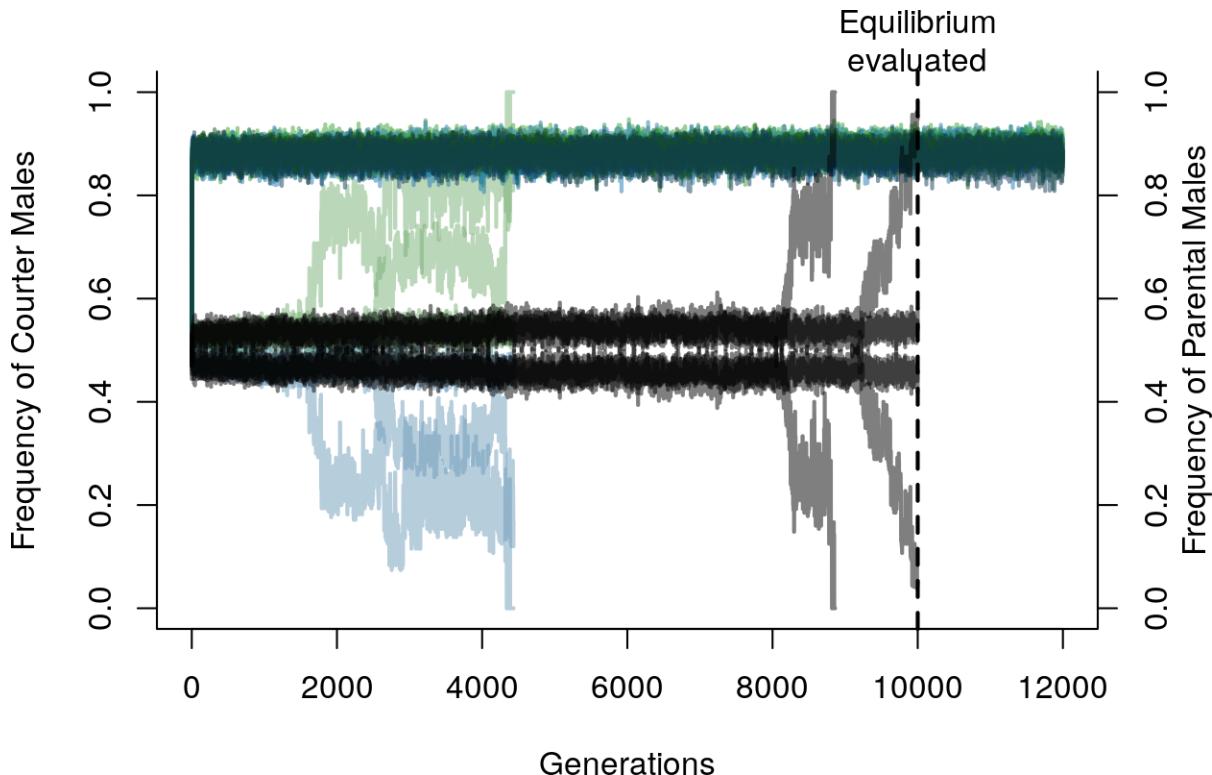


Figure 21: Frequency of the two morphs with linked QTLs (counter = green, parent = blue)

Because of the variable outcomes, it is useful to visualize the frequencies of the four morphs with each rep in its own graph.

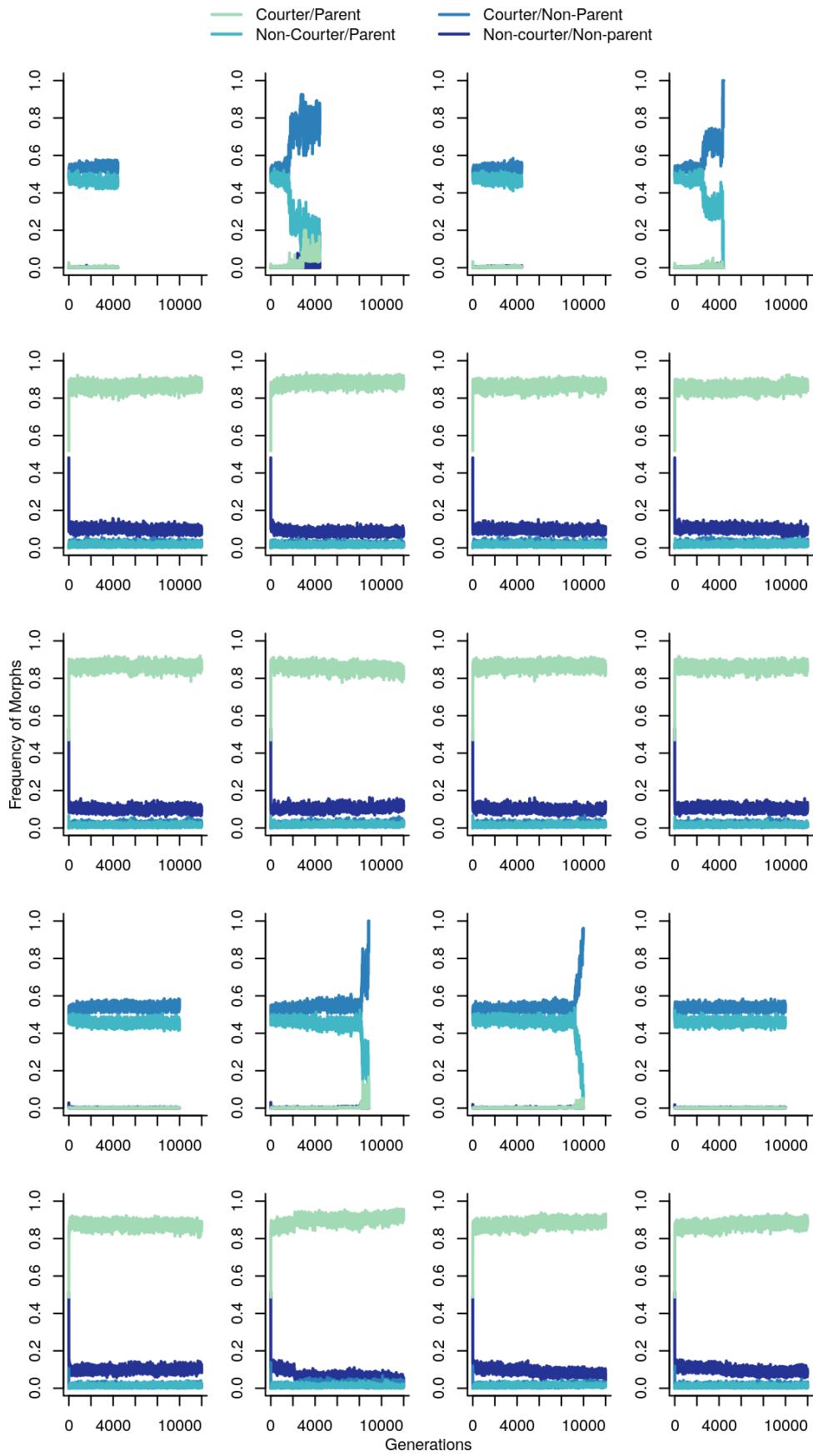


Figure 22: Frequency of the 4 morphs in each rep with linked QTLs

In some of the runs the population crashed after few generations. This is obvious both from the figures and when looking at the final frequencies in a table as well (pay attention to the generation number column):

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	ParentT
parent-courter_linked_1_summary.txt_1	4433	Pop0	695	362	333	770	-0.17
parent-courter_linked_1_summary.txt_2	4433	Pop1	48	18	30	63	-0.17
parent-courter_linked_1_summary.txt_3	4433	Pop2	702	357	345	762	-0.17
parent-courter_linked_1_summary.txt_4	4432	Pop3	6	1	5	4	-0.17
parent-courter_linked_2_summary.txt_1	11999	Pop0	1000	534	466	1000	-0.81
parent-courter_linked_2_summary.txt_2	11999	Pop1	999	509	490	1000	-0.81
parent-courter_linked_2_summary.txt_3	11999	Pop2	1000	522	478	1000	-0.81
parent-courter_linked_2_summary.txt_4	11999	Pop3	1000	517	483	1000	-0.81
parent-courter_linked_3_summary.txt_1	11999	Pop0	1000	504	496	1000	0.02
parent-courter_linked_3_summary.txt_2	11999	Pop1	999	502	497	1000	0.02
parent-courter_linked_3_summary.txt_3	11999	Pop2	1000	489	511	1000	0.02
parent-courter_linked_3_summary.txt_4	11999	Pop3	1000	507	493	1000	0.02
parent-courter_linked_4_summary.txt_1	10001	Pop0	825	414	411	920	0.38
parent-courter_linked_4_summary.txt_2	8861	Pop1	4	4	0	0	0.38
parent-courter_linked_4_summary.txt_3	10000	Pop2	52	19	33	72	0.38
parent-courter_linked_4_summary.txt_4	10000	Pop3	866	436	430	952	0.38
parent-courter_linked_5_summary.txt_1	11999	Pop0	1000	510	490	1000	0.46
parent-courter_linked_5_summary.txt_2	11999	Pop1	958	474	484	1000	0.46
parent-courter_linked_5_summary.txt_3	11999	Pop2	964	493	471	1000	0.46
parent-courter_linked_5_summary.txt_4	11999	Pop3	989	503	486	1000	0.46

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a counter. However, 5 of those reps with variation actually crashed.

The problems arise with the counter/non-parent and non-counter/parent morphs start to coexist.

Looking at the trait value evolution may help us understand why some of the runs resulted in extinction:

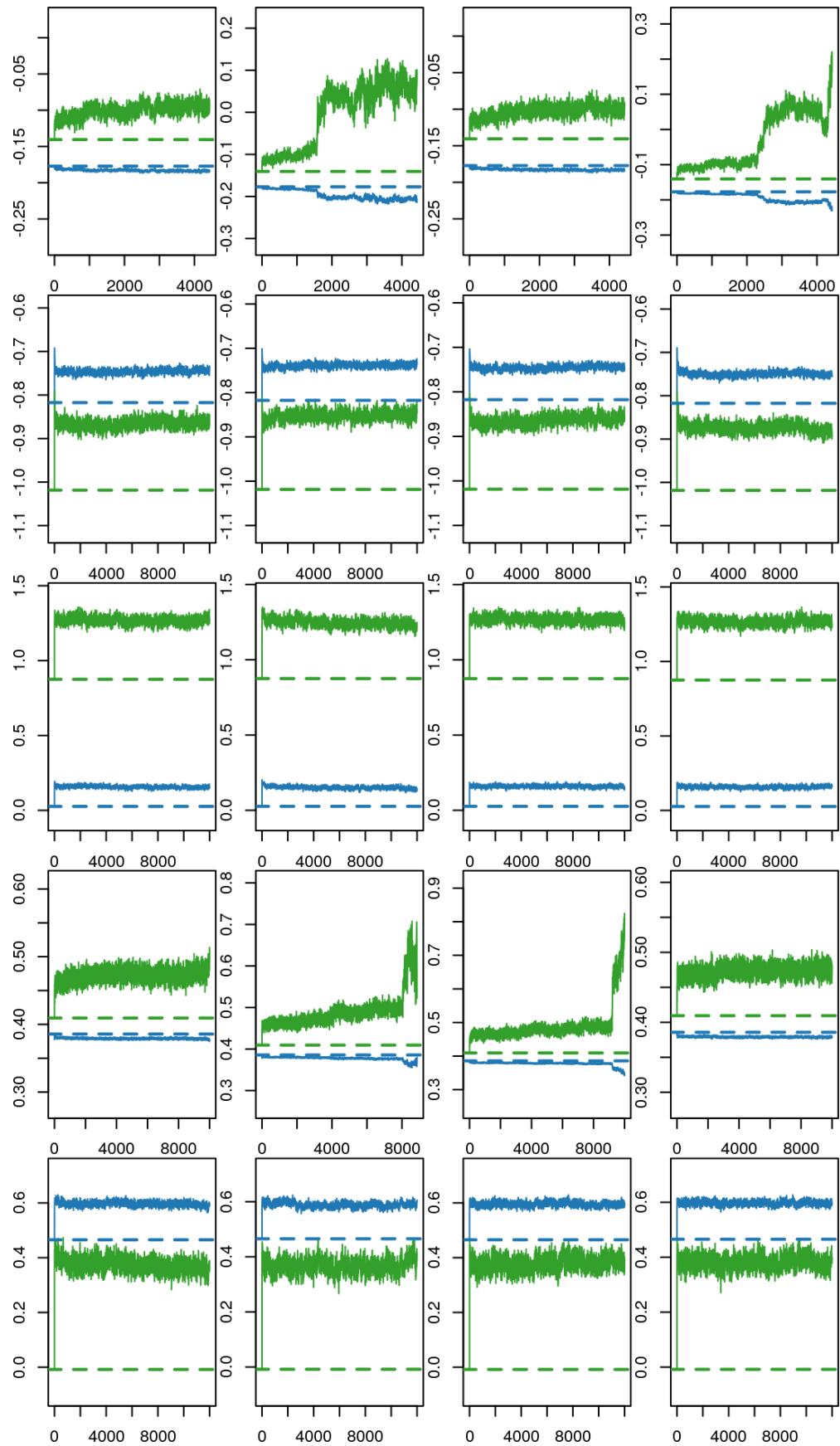


Figure 23: Evolution of the counter and parenting trait values in each rep with linked genetic variation

Without viability selection

Same as in the case of unlinked genetic variances, removing viability selection prevents the populations from crashing.

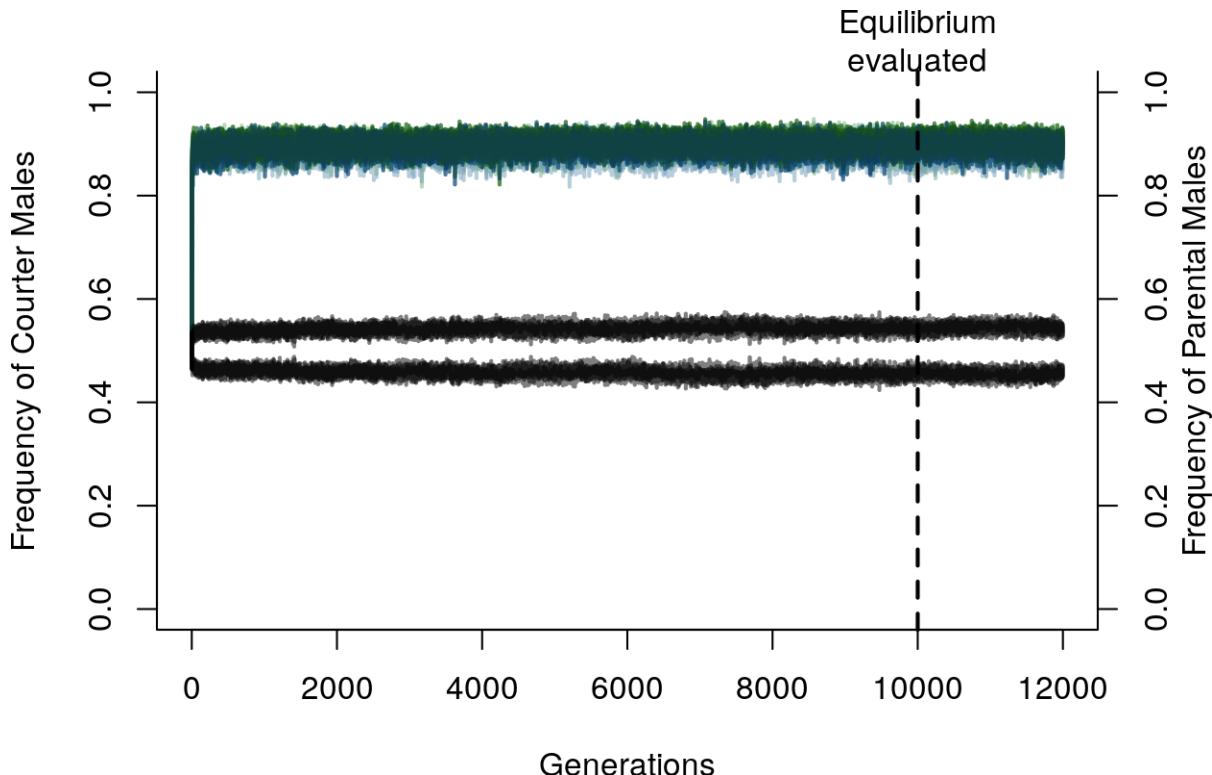


Figure 24: Frequency of the two morphs with linked QTLs and without viability selection (courter = green, parent = blue)

Because of the variable outcomes, it is useful to visualize the frequencies of the four morphs with each rep in its own graph.

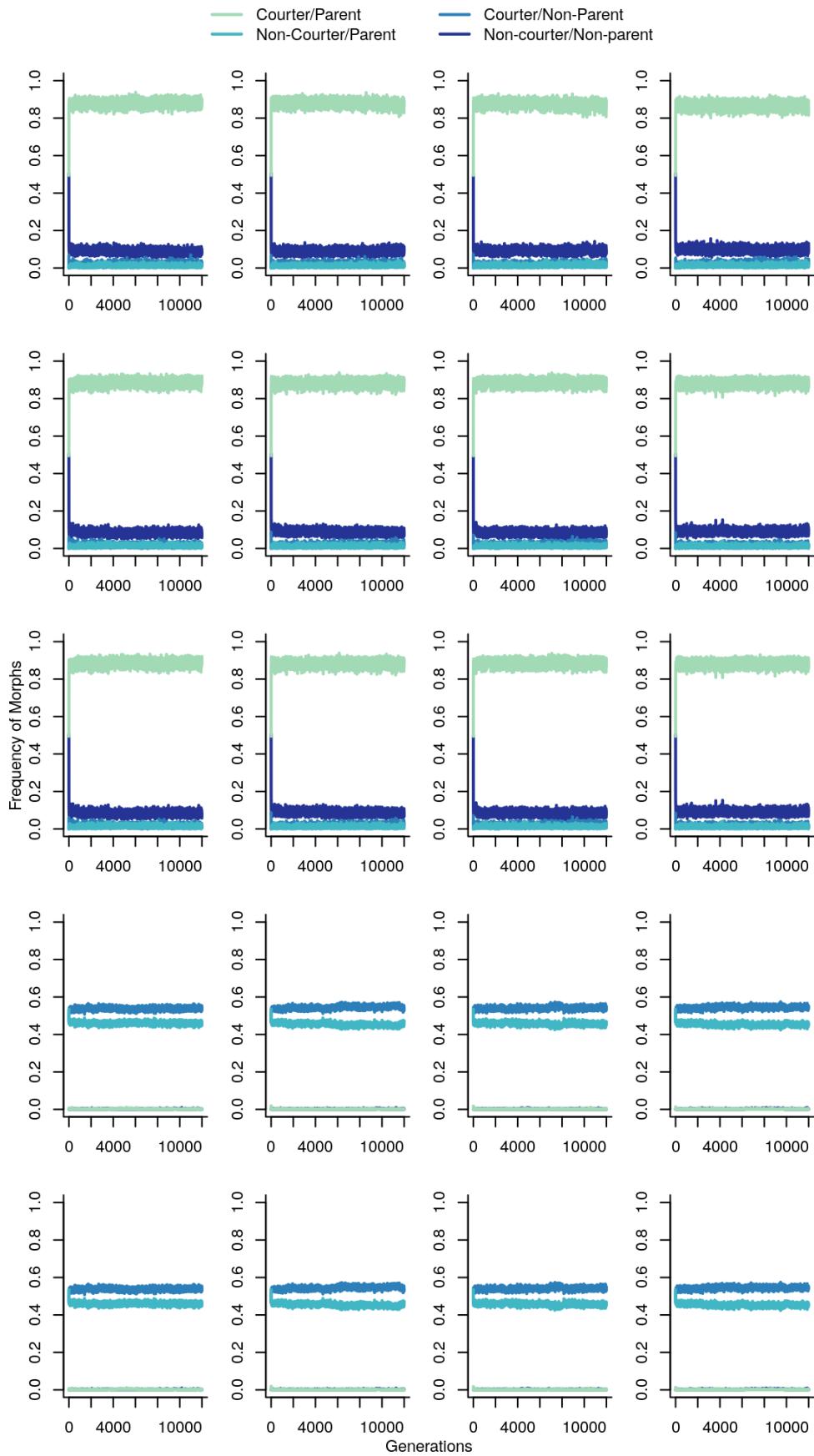


Figure 25: Frequency of the 4 morphs in each rep with linked QTLs without viability selection

In some of the runs the population crashed after few generations. This is obvious both from the figures and when looking at the final frequencies in a table as well (pay attention to the generation number column):

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	P
parent-courter_linked_novs_1_summary.txt_1	11999	Pop0	1000	480	520	1000	
parent-courter_linked_novs_1_summary.txt_2	11999	Pop1	993	499	494	1000	
parent-courter_linked_novs_1_summary.txt_3	11999	Pop2	989	461	528	1000	
parent-courter_linked_novs_1_summary.txt_4	11999	Pop3	993	513	480	1000	
parent-courter_linked_novs_2_summary.txt_1	11999	Pop0	1000	493	507	1000	
parent-courter_linked_novs_2_summary.txt_2	11999	Pop1	1000	526	474	1000	
parent-courter_linked_novs_2_summary.txt_3	11999	Pop2	1000	506	494	1000	
parent-courter_linked_novs_2_summary.txt_4	11999	Pop3	1000	467	533	1000	
parent-courter_linked_novs_3_summary.txt_1	11999	Pop0	1000	493	507	1000	
parent-courter_linked_novs_3_summary.txt_2	11999	Pop1	1000	526	474	1000	
parent-courter_linked_novs_3_summary.txt_3	11999	Pop2	1000	506	494	1000	
parent-courter_linked_novs_3_summary.txt_4	11999	Pop3	1000	467	533	1000	
parent-courter_linked_novs_4_summary.txt_1	11999	Pop0	980	512	468	1000	
parent-courter_linked_novs_4_summary.txt_2	11999	Pop1	980	499	481	1000	
parent-courter_linked_novs_4_summary.txt_3	11999	Pop2	979	504	475	1000	
parent-courter_linked_novs_4_summary.txt_4	11999	Pop3	983	515	468	1000	
parent-courter_linked_novs_5_summary.txt_1	11999	Pop0	980	512	468	1000	
parent-courter_linked_novs_5_summary.txt_2	11999	Pop1	980	499	481	1000	
parent-courter_linked_novs_5_summary.txt_3	11999	Pop2	979	504	475	1000	
parent-courter_linked_novs_5_summary.txt_4	11999	Pop3	983	515	468	1000	

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs have two morphs coexisting. Looking at the trait value evolution may help us understand why some of the runs resulted in extinction:

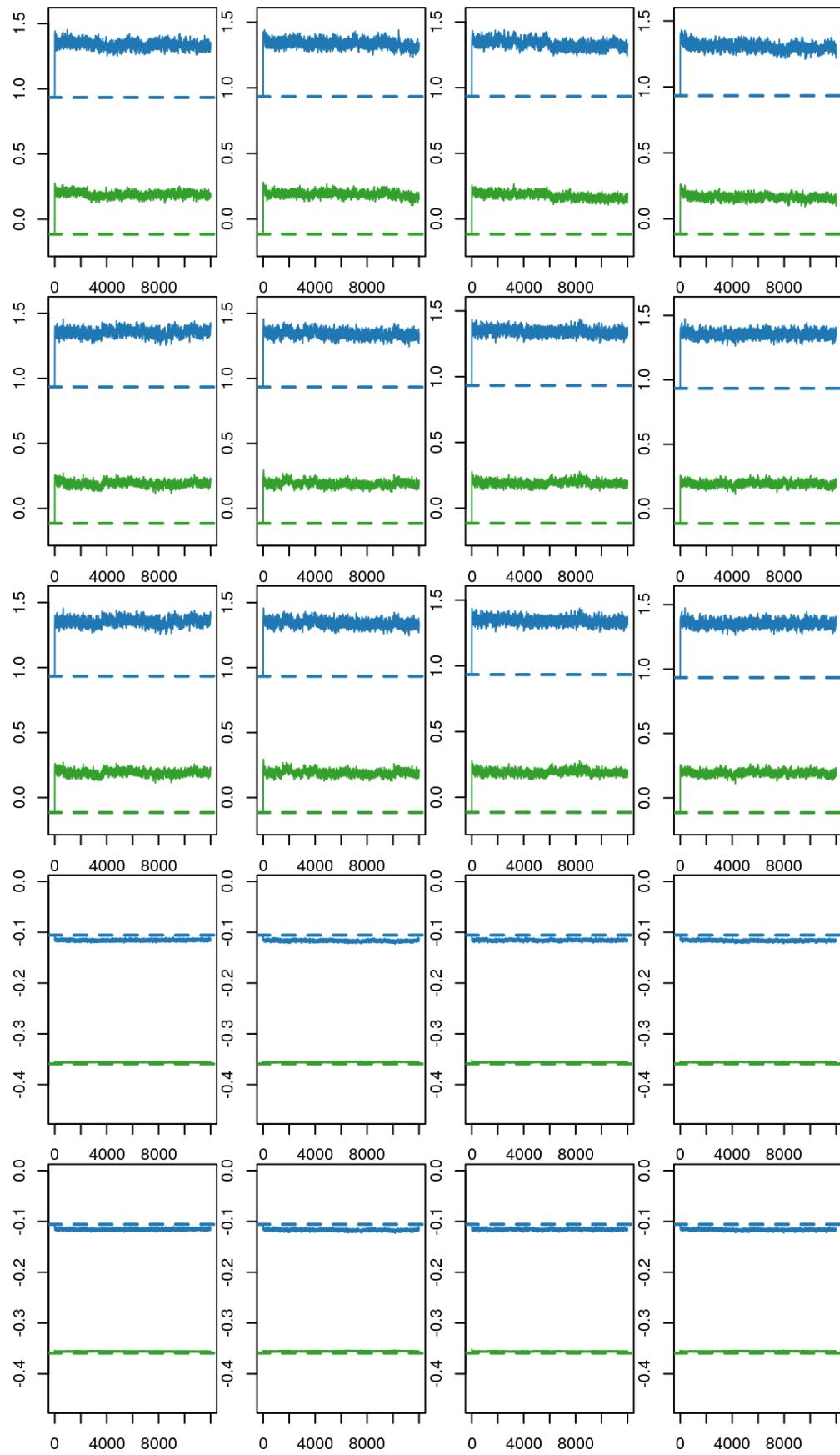


Figure 26: Evolution of the counter and parenting trait values in each rep with linked genetic variation and no viability selection

Same as with unlinked variation, when the parental threshold is higher than the courtship threshold, the non-courter/parent and parent/non-courter coexist.

Supergenes

In these cases, the loci (50) are all located in one region of a chromosome, and that region has reduced recombination. As above, the overall trait value is compared to a population-level threshold (which is static, in these cases), and if the trait value is above the threshold the male takes the parent or courter morph and if it is below he does not. Below, I'm showing the results from 10 replicates of each scenario.

Courter trait

With viability selection

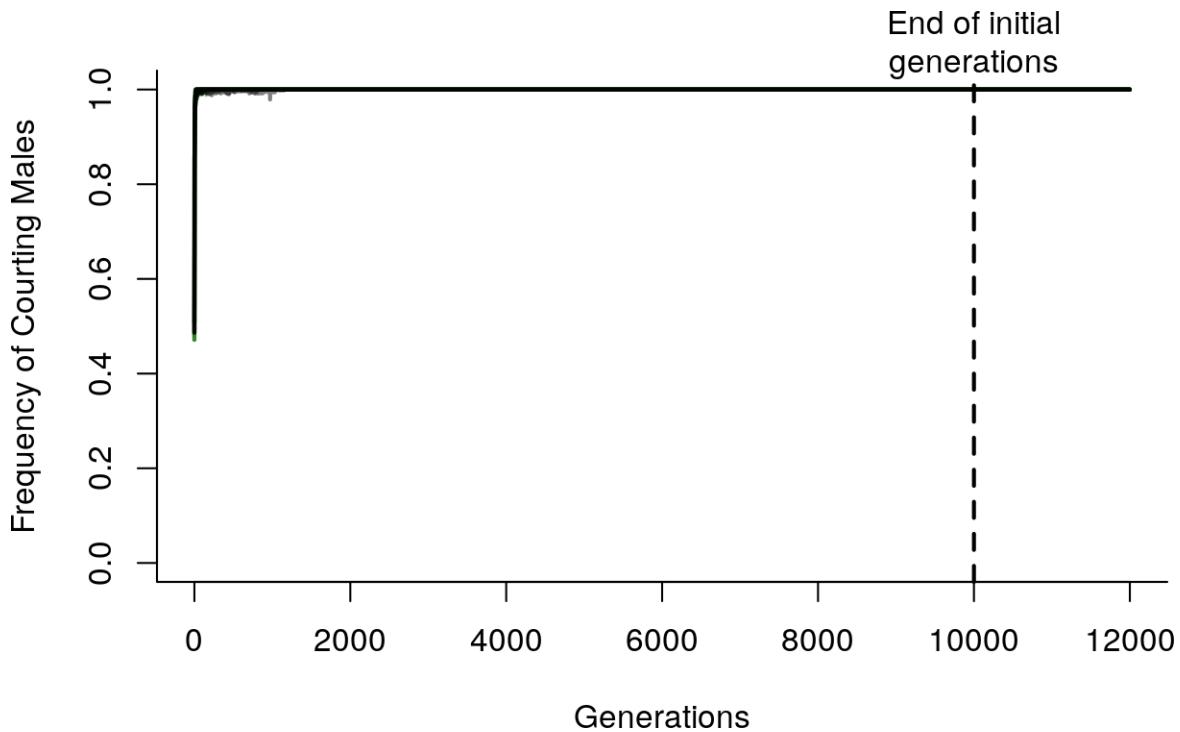


Figure 27: Frequency of the courter morph with supergenes (each color represents a different replicate)

Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Table 13: Frequency of courters with supergenes in final generation

	CourterFreq	CourterW	NonCourterW
courter_supergene_1_summary.txt_1	1	1.94129	0
courter_supergene_1_summary.txt_2	1	2.04107	0
courter_supergene_1_summary.txt_3	1	1.95098	0
courter_supergene_1_summary.txt_4	1	2.04733	0
courter_supergene_2_summary.txt_1	1	1.98603	0
courter_supergene_2_summary.txt_2	1	2.05144	0
courter_supergene_2_summary.txt_3	1	1.97624	0

	CounterFreq	CounterW	NonCounterW
counter_supergene_2_summary.txt_4	1	1.98403	0
counter_supergene_3_summary.txt_1	1	2.02429	0
counter_supergene_3_summary.txt_2	1	2.04959	0
counter_supergene_3_summary.txt_3	1	1.94727	0
counter_supergene_3_summary.txt_4	1	1.93217	0
counter_supergene_4_summary.txt_1	1	1.96850	0
counter_supergene_4_summary.txt_2	1	1.96078	0
counter_supergene_4_summary.txt_3	1	1.96850	0
counter_supergene_4_summary.txt_4	1	1.76056	0
counter_supergene_5_summary.txt_1	1	1.80435	0
counter_supergene_5_summary.txt_2	1	1.97809	0
counter_supergene_5_summary.txt_3	1	1.99399	0
counter_supergene_5_summary.txt_4	1	1.94706	0

Looking at the evolution of the trait values:

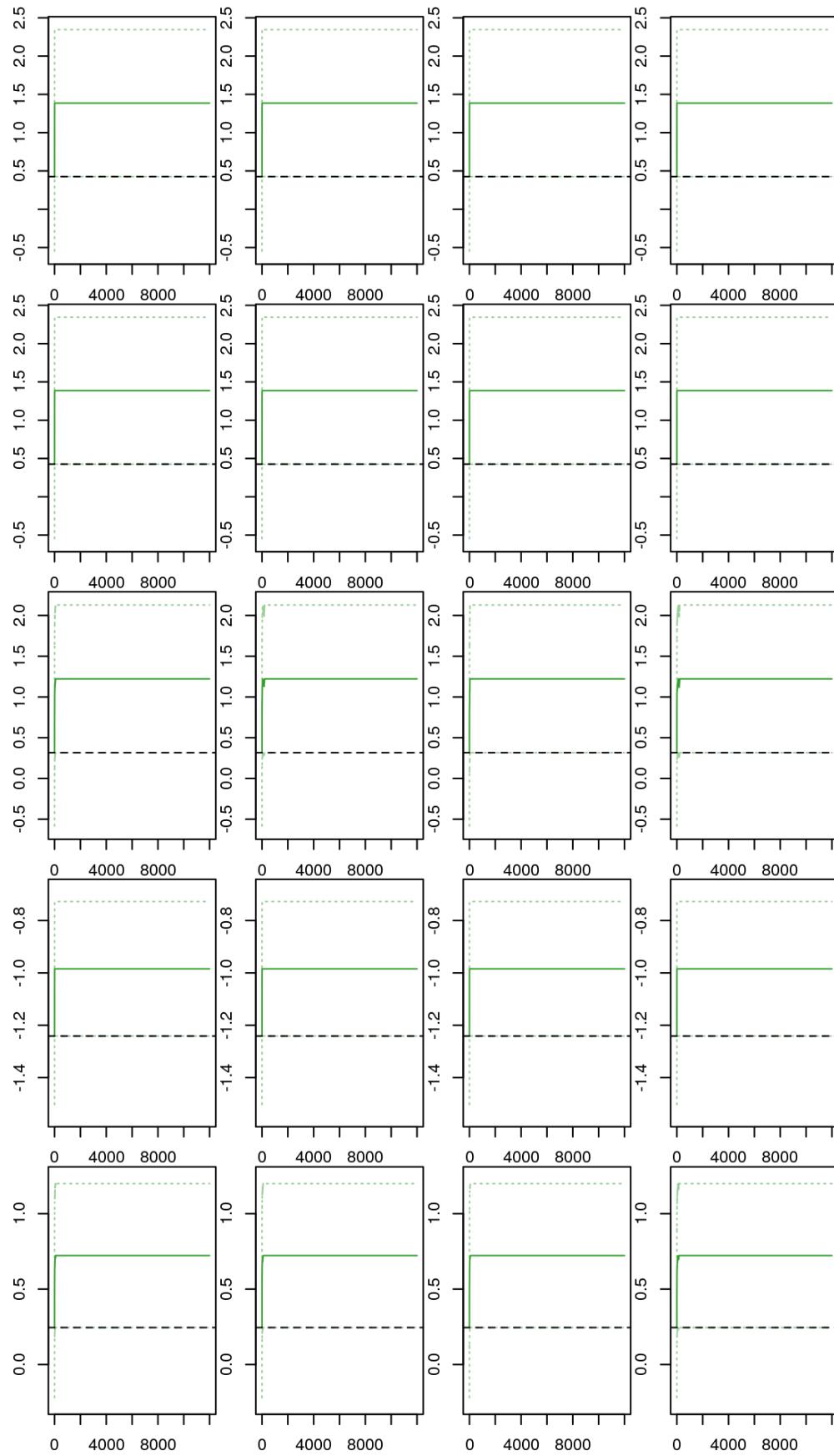


Figure 28: Evolution of courtship trait with a supergene. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

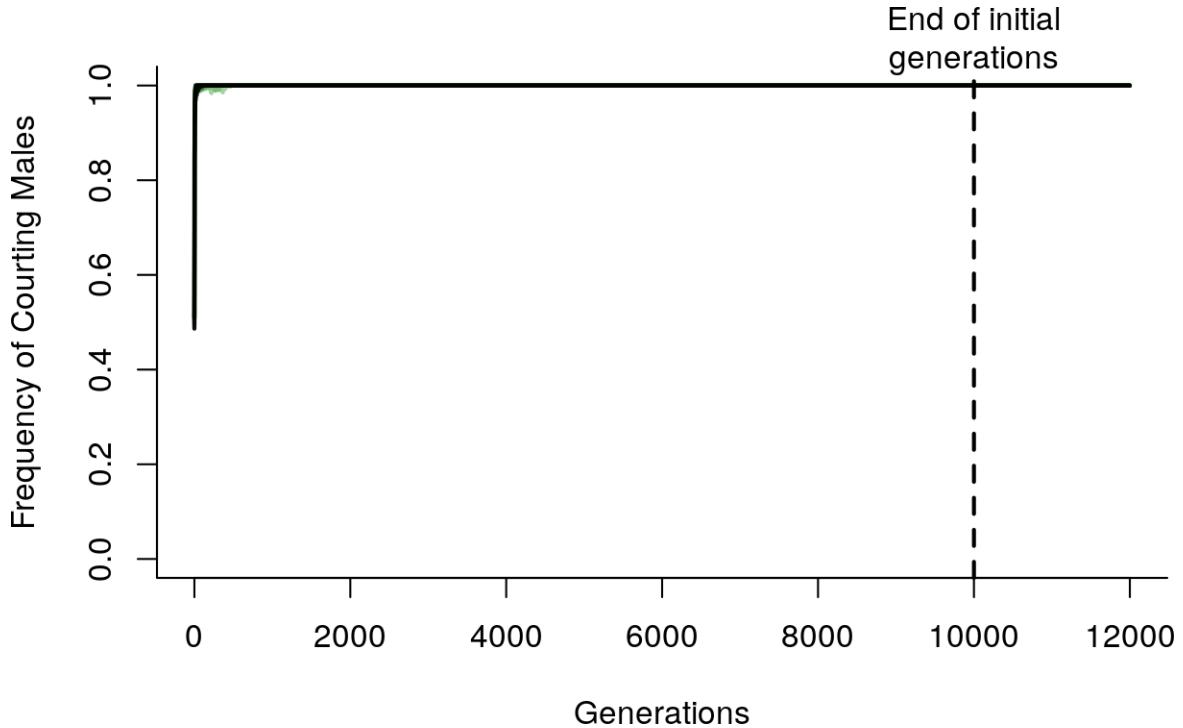


Figure 29: Frequency of the counter morph with supergenes without viability selection (each color represents a different replicate)

Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Table 14: Frequency of counters with supergenes in final generation with no viability selection

	CounterFreq	CounterW	NonCounterW
counter_supergene_novs_1_summary.txt_1	1	2.06186	0
counter_supergene_novs_1_summary.txt_2	1	1.98020	0
counter_supergene_novs_1_summary.txt_3	1	1.94553	0
counter_supergene_novs_1_summary.txt_4	1	1.96464	0
counter_supergene_novs_2_summary.txt_1	1	1.91571	0
counter_supergene_novs_2_summary.txt_2	1	2.01613	0
counter_supergene_novs_2_summary.txt_3	1	2.03252	0
counter_supergene_novs_2_summary.txt_4	1	1.99203	0
counter_supergene_novs_3_summary.txt_1	1	1.93424	0
counter_supergene_novs_3_summary.txt_2	1	2.00803	0
counter_supergene_novs_3_summary.txt_3	1	1.96464	0
counter_supergene_novs_3_summary.txt_4	1	1.98807	0
counter_supergene_novs_4_summary.txt_1	1	1.93424	0
counter_supergene_novs_4_summary.txt_2	1	2.00803	0
counter_supergene_novs_4_summary.txt_3	1	1.96464	0
counter_supergene_novs_4_summary.txt_4	1	1.98807	0
counter_supergene_novs_5_summary.txt_1	1	1.89753	0
counter_supergene_novs_5_summary.txt_2	1	1.93424	0
counter_supergene_novs_5_summary.txt_3	1	1.98807	0

	CourterFreq	CourterW	NonCourterW
courter_supergene_novs_5_summary.txt_4	1	2.08768	0

Looking at the evolution of the trait values:

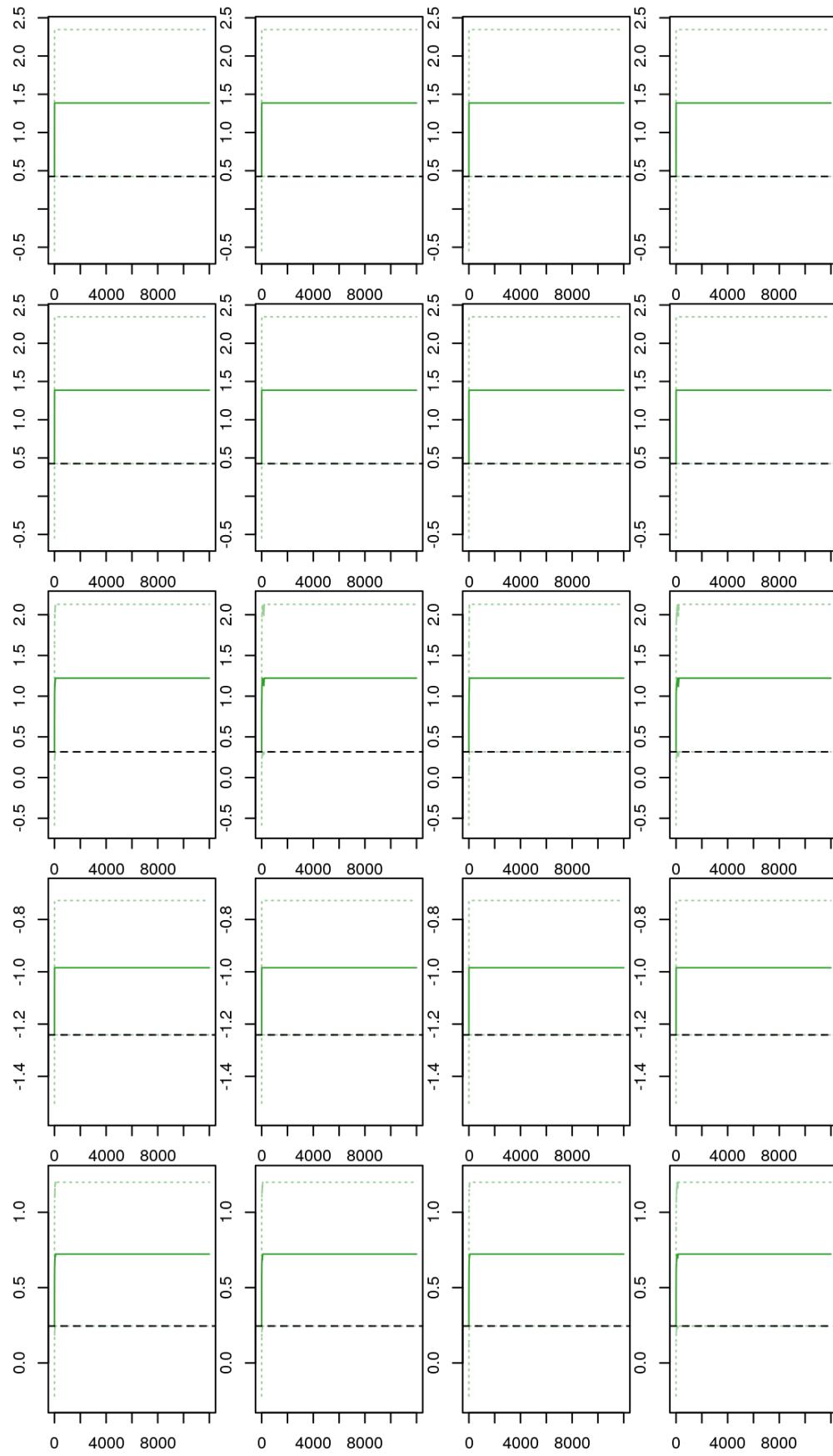


Figure 30: Evolution of courtship trait with a supergene and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Parental trait

With viability selection

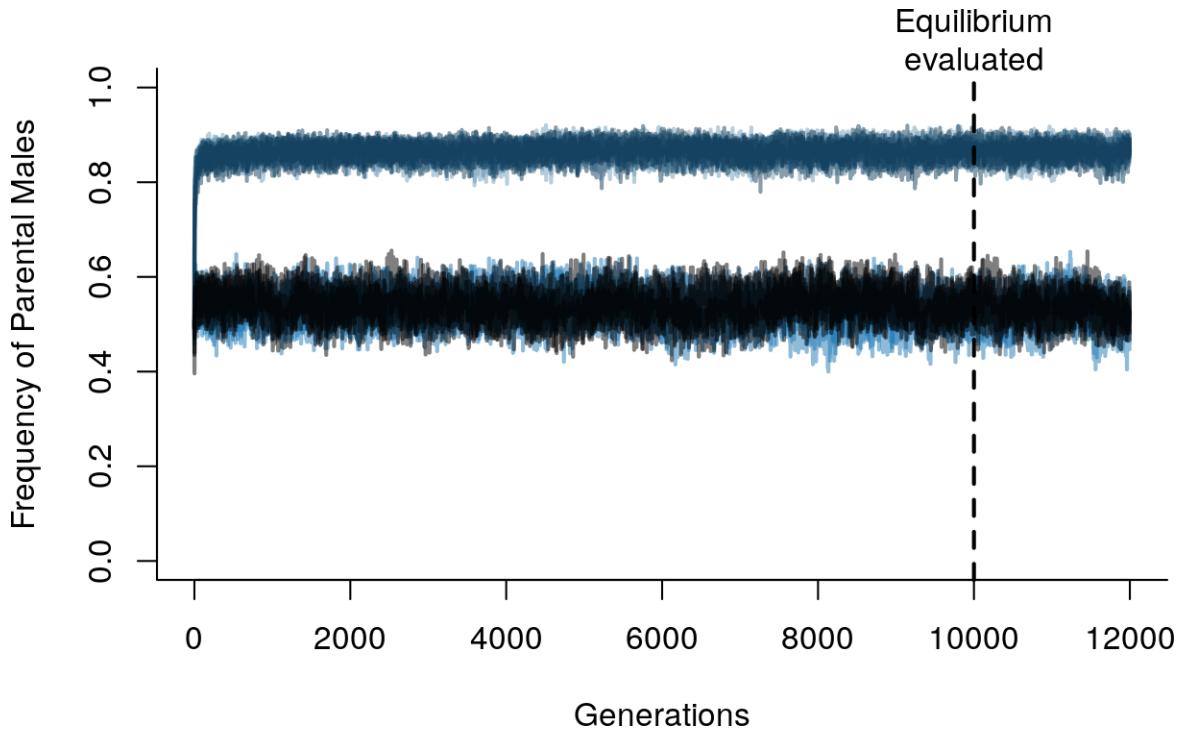


Figure 31: Frequency of parent morph with supergenes (each color represents a different replicate)

Table 15: Frequency of parents with supergenes in final generation

	ParentFreq	ParentW	NonParentW
parent_supergene_1_summary.txt_1	0.859244	1.77262	0.791045
parent_supergene_1_summary.txt_2	0.873727	1.66667	0.596774
parent_supergene_1_summary.txt_3	0.851852	1.63285	0.805556
parent_supergene_1_summary.txt_4	0.873823	1.52802	0.776119
parent_supergene_2_summary.txt_1	0.517034	1.45349	0.261411
parent_supergene_2_summary.txt_2	0.557769	1.54643	0.252252
parent_supergene_2_summary.txt_3	0.463265	1.36564	0.418251
parent_supergene_2_summary.txt_4	0.514344	1.47809	0.219409
parent_supergene_3_summary.txt_1	0.866534	1.60230	0.761194
parent_supergene_3_summary.txt_2	0.880157	1.65179	0.786885
parent_supergene_3_summary.txt_3	0.875248	1.67873	0.730159
parent_supergene_3_summary.txt_4	0.869121	1.74118	0.828125
parent_supergene_4_summary.txt_1	0.520085	1.47561	0.378855
parent_supergene_4_summary.txt_2	0.487179	1.37247	0.269231
parent_supergene_4_summary.txt_3	0.502174	1.70130	0.423581
parent_supergene_4_summary.txt_4	0.525105	1.65600	0.219298
parent_supergene_5_summary.txt_1	0.539370	1.39781	0.358974
parent_supergene_5_summary.txt_2	0.520000	1.34066	0.214286
parent_supergene_5_summary.txt_3	0.518519	1.43214	0.284615
parent_supergene_5_summary.txt_4	0.542074	1.56679	0.320513

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Let's look at the trajectories of the parent traits.

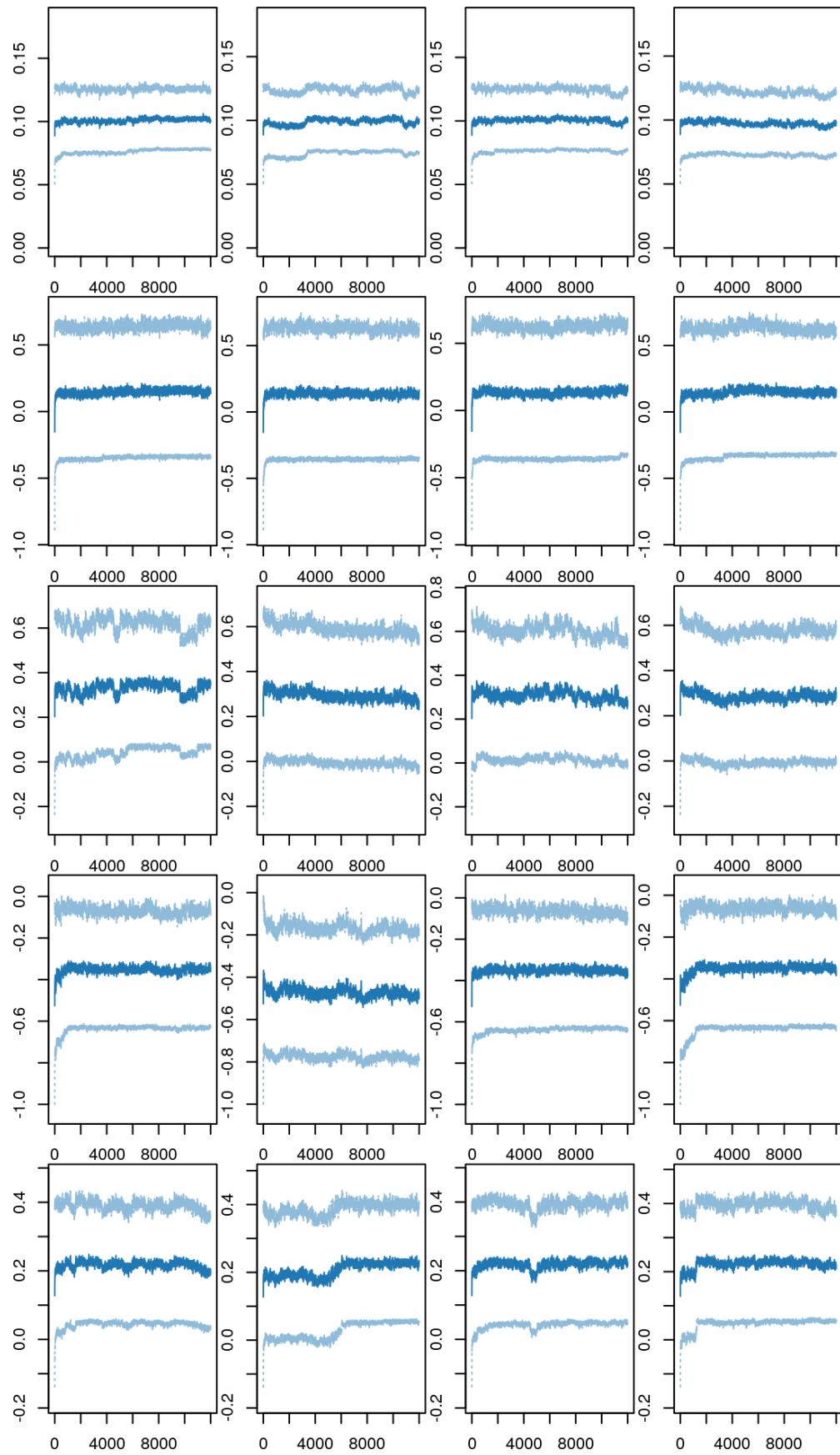


Figure 32: Evolution of parenting trait values with a supergene. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

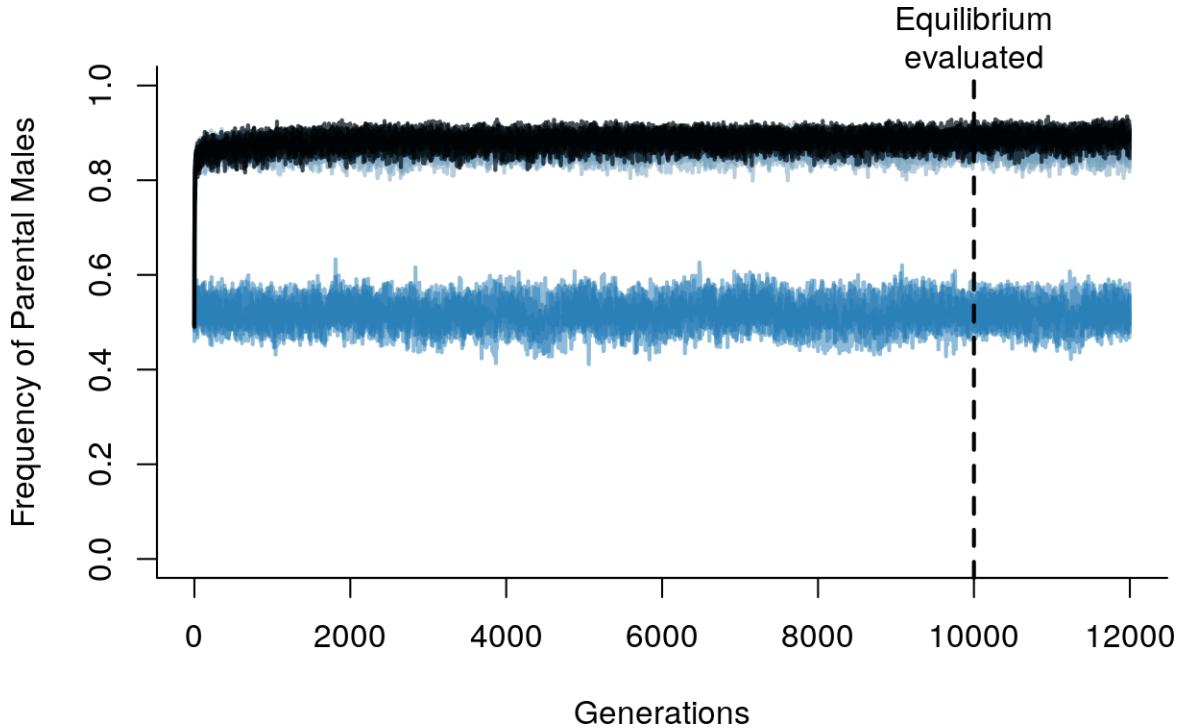


Figure 33: Frequency of parent morph with supergenes without viability selection (each color represents a different replicate)

Table 16: Frequency of parents with supergenes in final generation without viability selection

	ParentFreq	ParentW	NonParentW
parent_supergene_novs_1_summary.txt_1	0.833656	1.62413	0.488372
parent_supergene_novs_1_summary.txt_2	0.868110	1.63492	0.656716
parent_supergene_novs_1_summary.txt_3	0.878193	1.68456	1.048390
parent_supergene_novs_1_summary.txt_4	0.844758	1.61814	0.727273
parent_supergene_novs_2_summary.txt_1	0.557613	1.40959	0.376744
parent_supergene_novs_2_summary.txt_2	0.488978	1.47951	0.247059
parent_supergene_novs_2_summary.txt_3	0.479424	1.36910	0.296443
parent_supergene_novs_2_summary.txt_4	0.508299	1.44082	0.312236
parent_supergene_novs_3_summary.txt_1	0.907514	1.58174	0.895833
parent_supergene_novs_3_summary.txt_2	0.885593	1.77990	0.870370
parent_supergene_novs_3_summary.txt_3	0.907869	1.61099	1.083330
parent_supergene_novs_3_summary.txt_4	0.876797	1.69321	0.750000
parent_supergene_novs_4_summary.txt_1	0.907514	1.58174	0.895833
parent_supergene_novs_4_summary.txt_2	0.885593	1.77990	0.870370
parent_supergene_novs_4_summary.txt_3	0.907869	1.61099	1.083330
parent_supergene_novs_4_summary.txt_4	0.876797	1.69321	0.750000
parent_supergene_novs_5_summary.txt_1	0.580517	1.43836	0.289100
parent_supergene_novs_5_summary.txt_2	0.534483	1.49462	0.246914
parent_supergene_novs_5_summary.txt_3	0.541825	1.50175	0.215768
parent_supergene_novs_5_summary.txt_4	0.533865	1.45522	0.252137

Variation was maintained in 20 of the 20. 0 of the 20 populations crashed. Of the 20 replicates, 20 reached an equilibrium by 10000 generations.

Let's look at the trajectories of the parent traits.

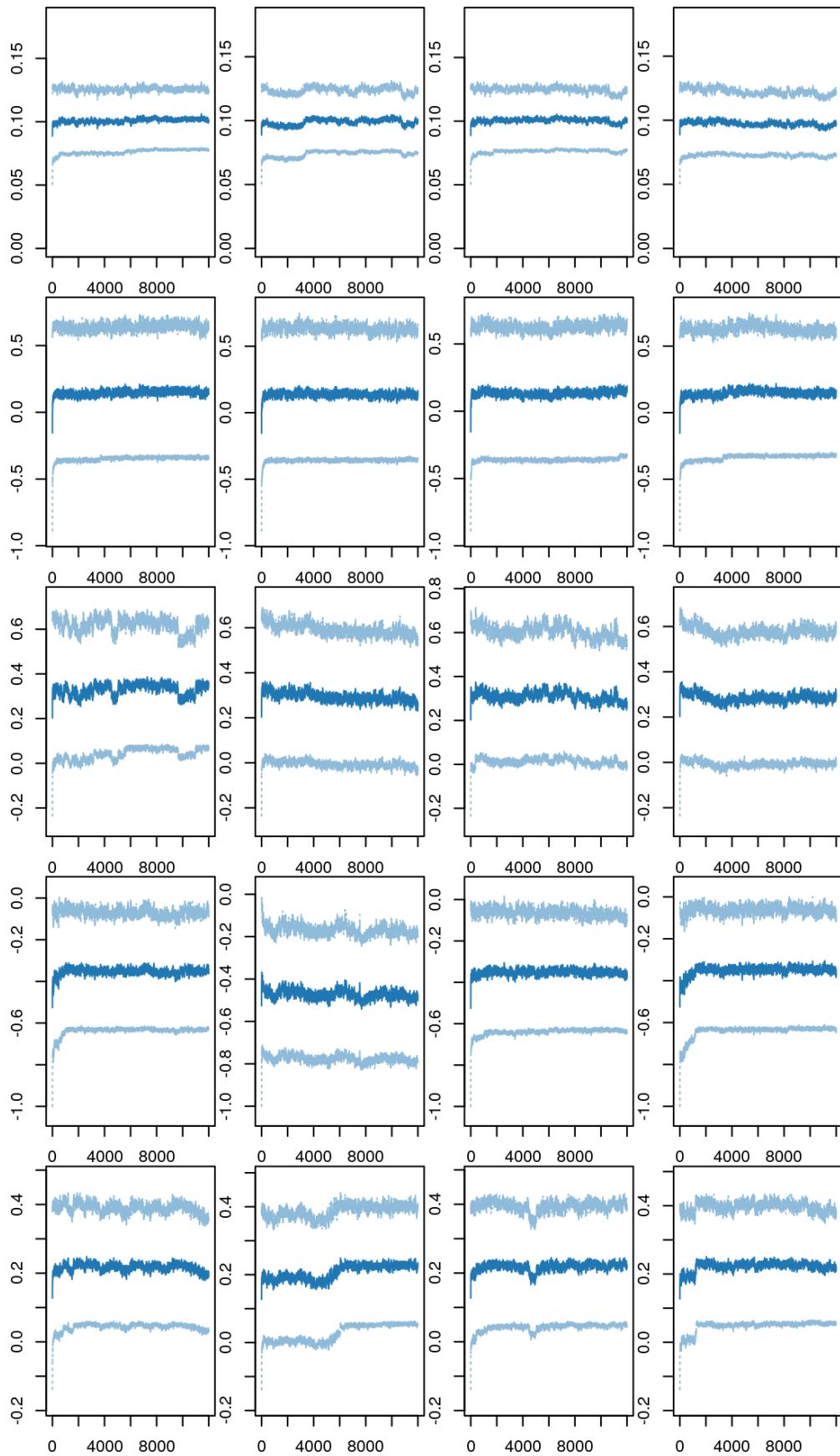


Figure 34: Evolution of parenting trait values with a supergene without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Courtship and Parental Traits

With viability selection

The different runs have different outcomes. To better see this, let's look at the morph frequencies in each rep separately.

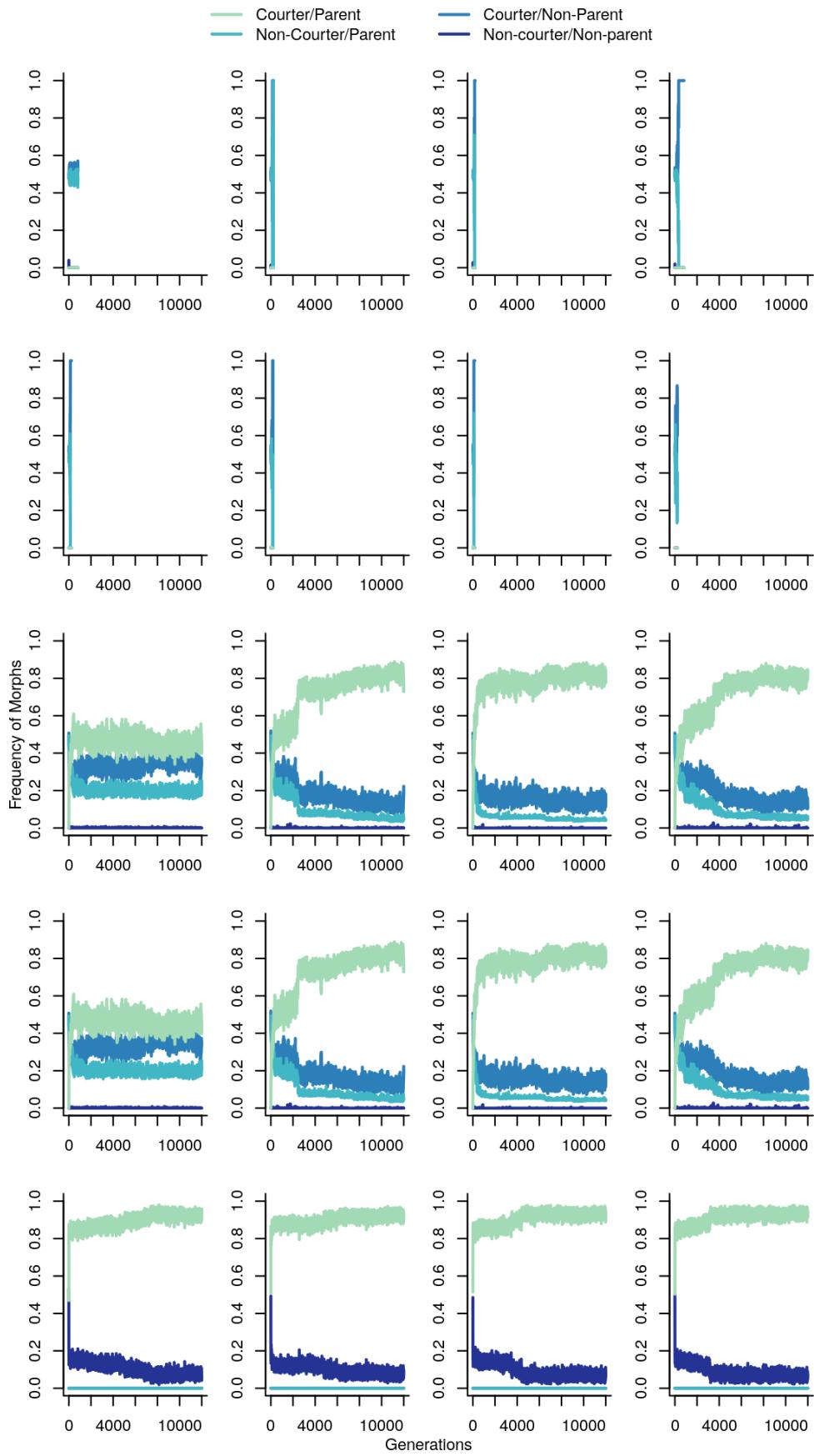


Figure 35: Frequency of the 4 morphs in each rep with supergenes

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	Par
parent-courter_supergene_1_summary.txt_1	825	Pop0	271	137	134	289	-
parent-courter_supergene_1_summary.txt_2	240	Pop1	4	4	0	0	-
parent-courter_supergene_1_summary.txt_3	205	Pop2	4	4	0	0	-
parent-courter_supergene_1_summary.txt_4	824	Pop3	6	6	0	0	-
parent-courter_supergene_2_summary.txt_1	235	Pop0	7	1	6	4	-
parent-courter_supergene_2_summary.txt_2	192	Pop1	4	4	0	0	-
parent-courter_supergene_2_summary.txt_3	168	Pop2	4	4	0	0	-
parent-courter_supergene_2_summary.txt_4	235	Pop3	31	13	18	40	-
parent-courter_supergene_3_summary.txt_1	11999	Pop0	948	489	459	1000	-
parent-courter_supergene_3_summary.txt_2	11999	Pop1	945	470	475	1000	-
parent-courter_supergene_3_summary.txt_3	11999	Pop2	939	490	449	1000	-
parent-courter_supergene_3_summary.txt_4	11999	Pop3	944	450	494	1000	-
parent-courter_supergene_4_summary.txt_1	11999	Pop0	948	489	459	1000	-
parent-courter_supergene_4_summary.txt_2	11999	Pop1	945	470	475	1000	-
parent-courter_supergene_4_summary.txt_3	11999	Pop2	939	490	449	1000	-
parent-courter_supergene_4_summary.txt_4	11999	Pop3	944	450	494	1000	-
parent-courter_supergene_5_summary.txt_1	11999	Pop0	943	450	493	1000	-
parent-courter_supergene_5_summary.txt_2	11999	Pop1	935	460	475	1000	-
parent-courter_supergene_5_summary.txt_3	11999	Pop2	944	469	475	1000	-
parent-courter_supergene_5_summary.txt_4	11999	Pop3	944	470	474	1000	-

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a courter. 8 of those reps with variation went extinct before 10000 generations.

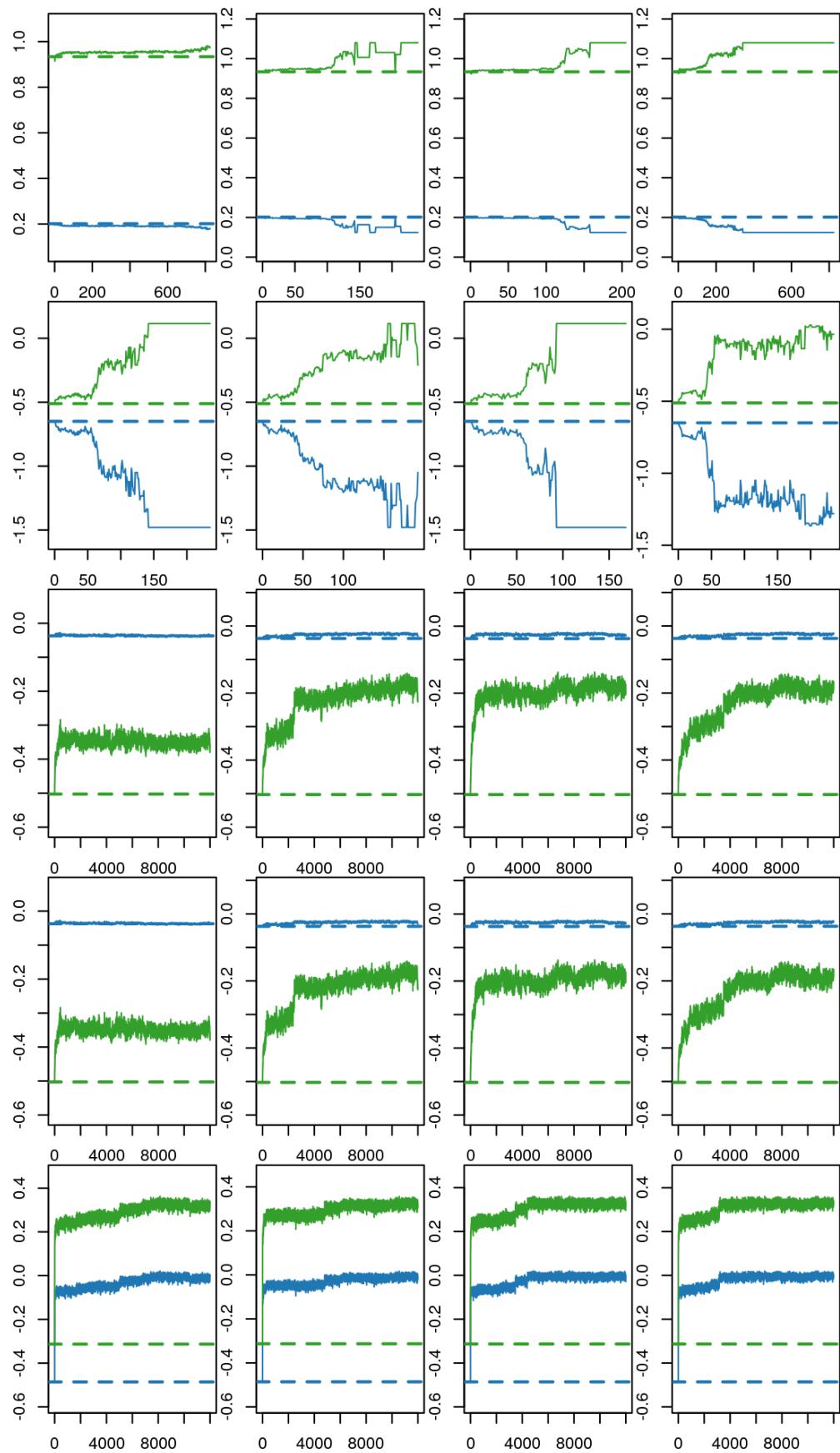


Figure 36: Evolution of the counter and parenting trait values in each rep with a supergene

Without viability selection

The different runs have different outcomes. To better see this, let's look at the morph frequencies in each rep separately.

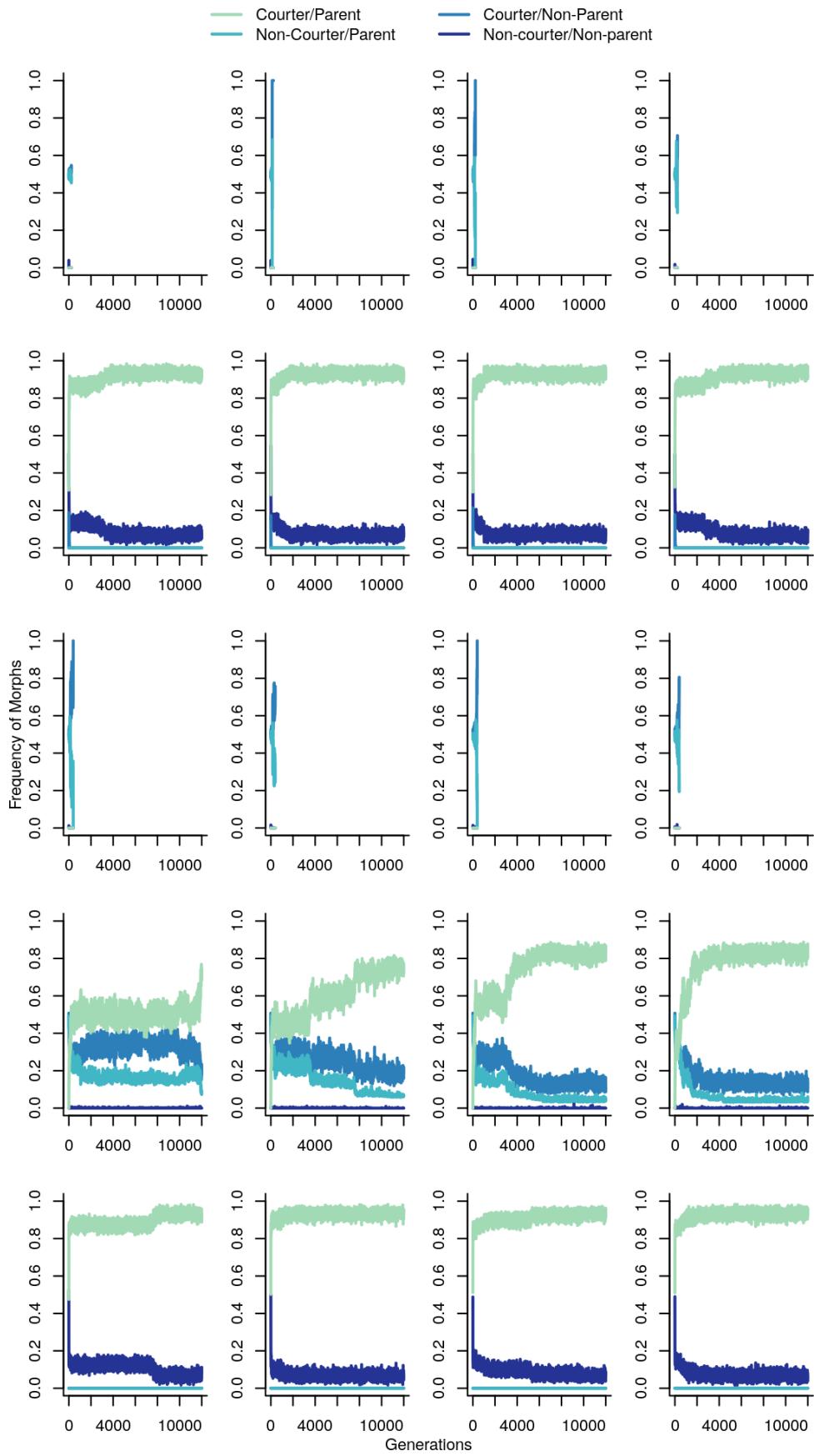


Figure 37: Frequency of the 4 morphs in each rep with supergenes without viability selection

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_supergene_novs_1_summary.txt_1	236	Pop0	663	340	323	724
parent-courter_supergene_novs_1_summary.txt_2	235	Pop1	8	1	7	4
parent-courter_supergene_novs_1_summary.txt_3	235	Pop2	12	7	5	16
parent-courter_supergene_novs_1_summary.txt_4	235	Pop3	35	17	18	47
parent-courter_supergene_novs_2_summary.txt_1	11999	Pop0	957	465	492	1000
parent-courter_supergene_novs_2_summary.txt_2	11999	Pop1	950	491	459	1000
parent-courter_supergene_novs_2_summary.txt_3	11999	Pop2	956	487	469	1000
parent-courter_supergene_novs_2_summary.txt_4	11999	Pop3	956	489	467	1000
parent-courter_supergene_novs_3_summary.txt_1	396	Pop0	12	1	11	4
parent-courter_supergene_novs_3_summary.txt_2	396	Pop1	67	30	37	84
parent-courter_supergene_novs_3_summary.txt_3	396	Pop2	16	5	11	20
parent-courter_supergene_novs_3_summary.txt_4	396	Pop3	80	34	46	103
parent-courter_supergene_novs_4_summary.txt_1	11999	Pop0	948	470	478	1000
parent-courter_supergene_novs_4_summary.txt_2	11999	Pop1	948	458	490	1000
parent-courter_supergene_novs_4_summary.txt_3	11999	Pop2	946	481	465	1000
parent-courter_supergene_novs_4_summary.txt_4	11999	Pop3	943	477	466	1000
parent-courter_supergene_novs_5_summary.txt_1	11999	Pop0	943	493	450	1000
parent-courter_supergene_novs_5_summary.txt_2	11999	Pop1	949	478	471	1000
parent-courter_supergene_novs_5_summary.txt_3	11999	Pop2	956	480	476	1000
parent-courter_supergene_novs_5_summary.txt_4	11999	Pop3	944	470	474	1000

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a counter. 8 of those reps with variation went extinct before 10000 generations.

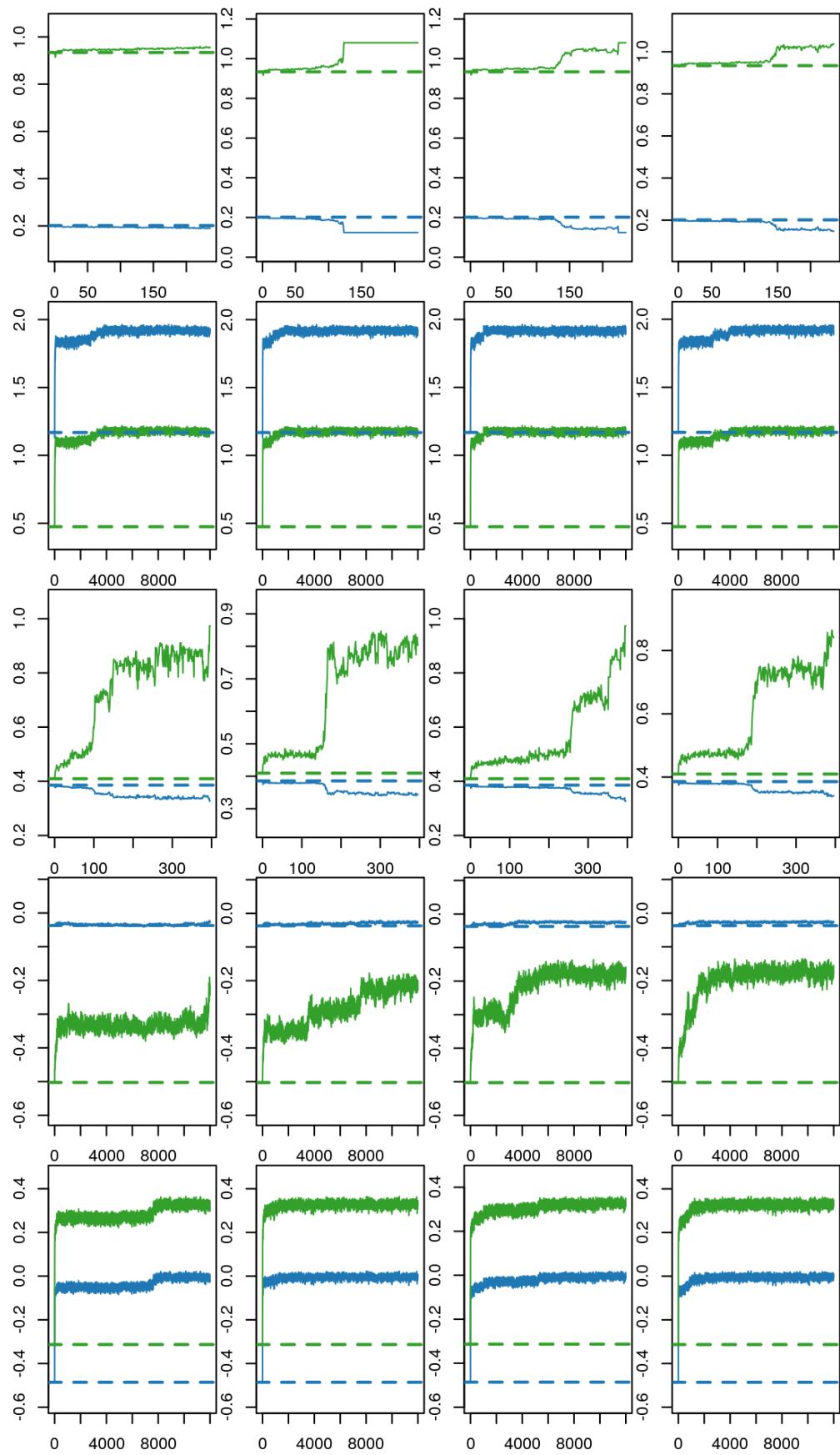


Figure 38: Evolution of the counter and parenting trait values in each rep with a supergene without viability selection

In the case of supergenes, the qualitative outcomes differ substantially between the viability and no-viability runs, but not in terms of populations crashing or surviving – different types of variation can be maintained!

Preliminary conclusions

- Viability selection may be an important factor ofr the model when both parental and coursthip traits are present.
- When single traits are present, the mechanism of inheritance doesn't seem to play a major role.
- Supergenes may facilitate different amounts of variation to be maintained – but it depends on the selective environment.