

Density-dependent ARTs Analysis

Sarah P. Flanagan

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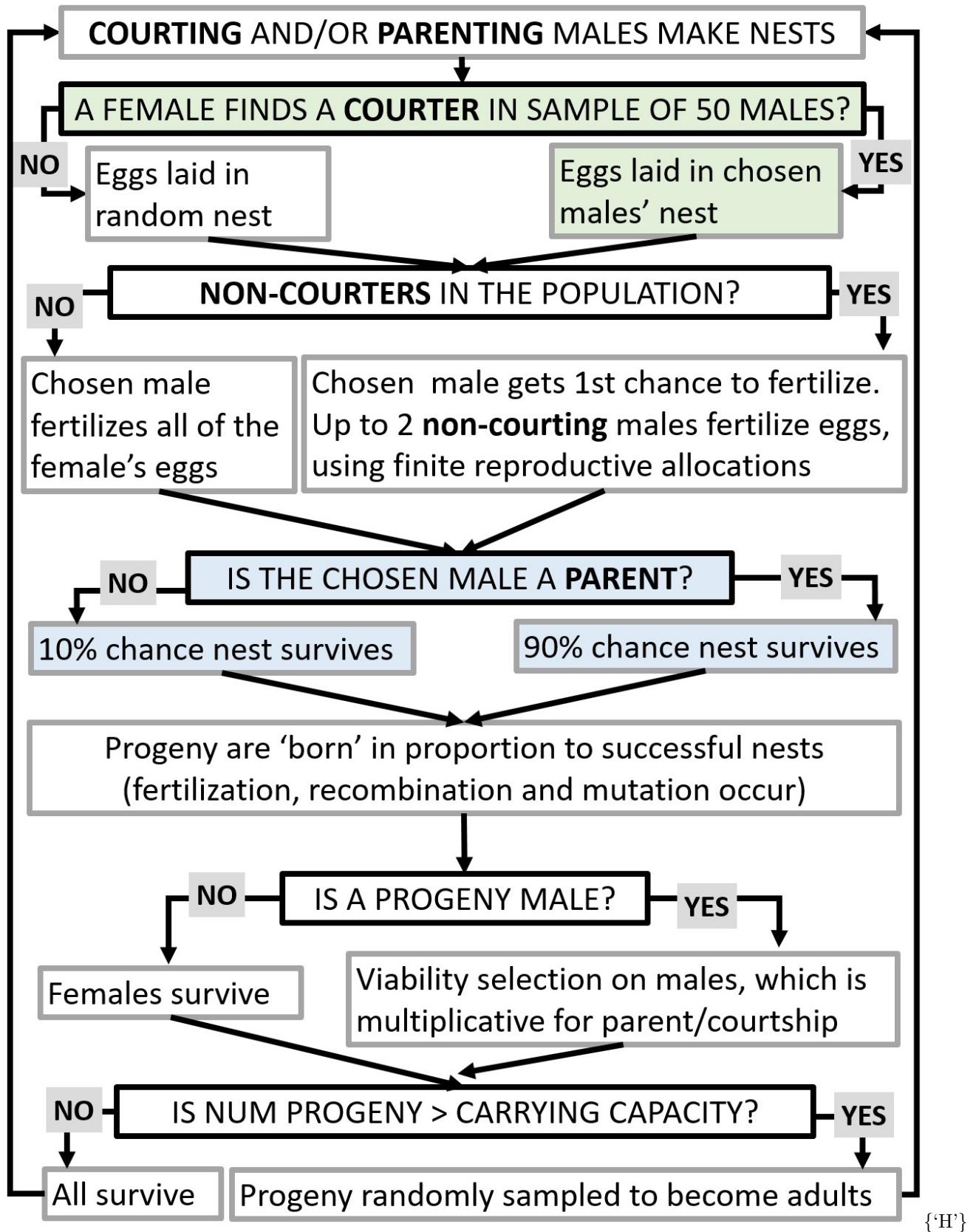
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The purpose of this model is to understand how genetic architectures of alternative reproductive tactics impact their maintenance in populations. I'm using an individual-based simulation model with different selection scenarios, types of alternative 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

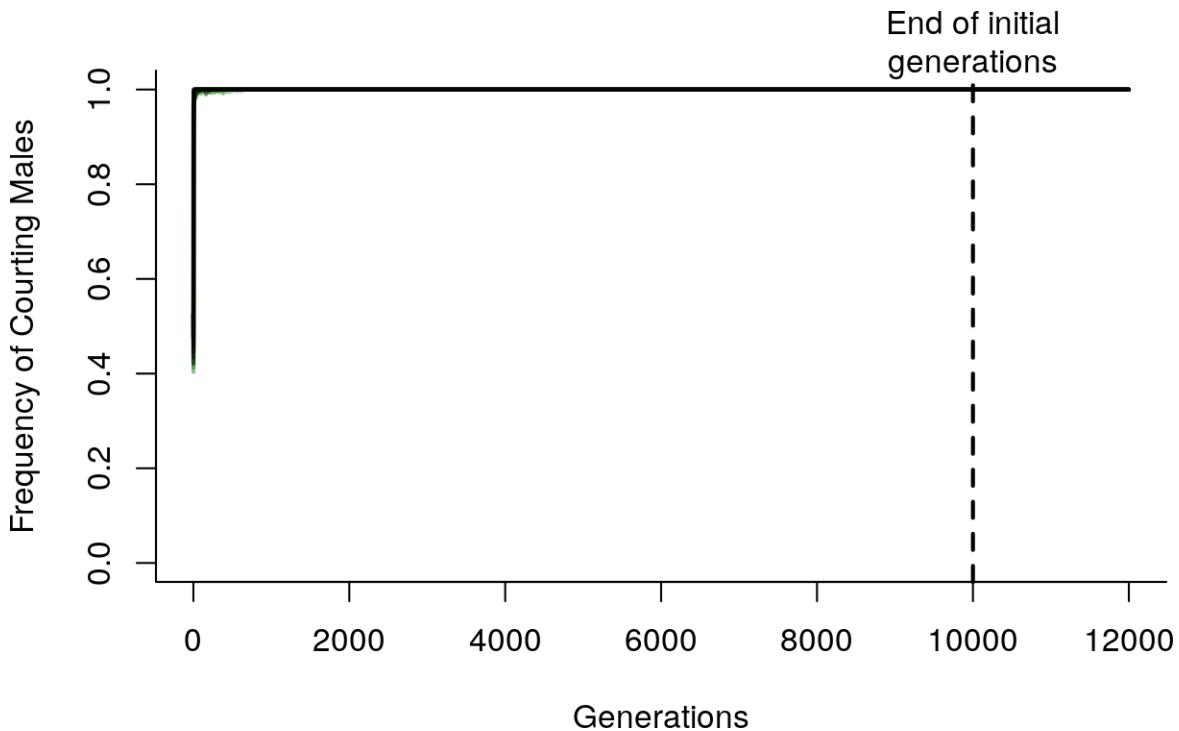


Figure 1: Frequency of the counter morph with unlinked additive genetic variances in all of the replicates

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	1.92829	0
counter_unlinked_1_summary.txt_2	1	1.92650	0
counter_unlinked_1_summary.txt_3	1	1.90038	0
counter_unlinked_1_summary.txt_4	1	2.00000	0
counter_unlinked_2_summary.txt_1	1	2.04517	0
counter_unlinked_2_summary.txt_2	1	1.97030	0
counter_unlinked_2_summary.txt_3	1	2.01623	0
counter_unlinked_2_summary.txt_4	1	1.87925	0
counter_unlinked_3_summary.txt_1	1	2.04098	0
counter_unlinked_3_summary.txt_2	1	1.92085	0
counter_unlinked_3_summary.txt_3	1	2.04938	0
counter_unlinked_3_summary.txt_4	1	1.99399	0
counter_unlinked_4_summary.txt_1	1	2.03666	0
counter_unlinked_4_summary.txt_2	1	2.11416	0
counter_unlinked_4_summary.txt_3	1	2.09205	0
counter_unlinked_4_summary.txt_4	1	2.04499	0
counter_unlinked_5_summary.txt_1	1	2.02429	0
counter_unlinked_5_summary.txt_2	1	1.97628	0
counter_unlinked_5_summary.txt_3	1	2.05339	0
counter_unlinked_5_summary.txt_4	1	2.16450	0

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

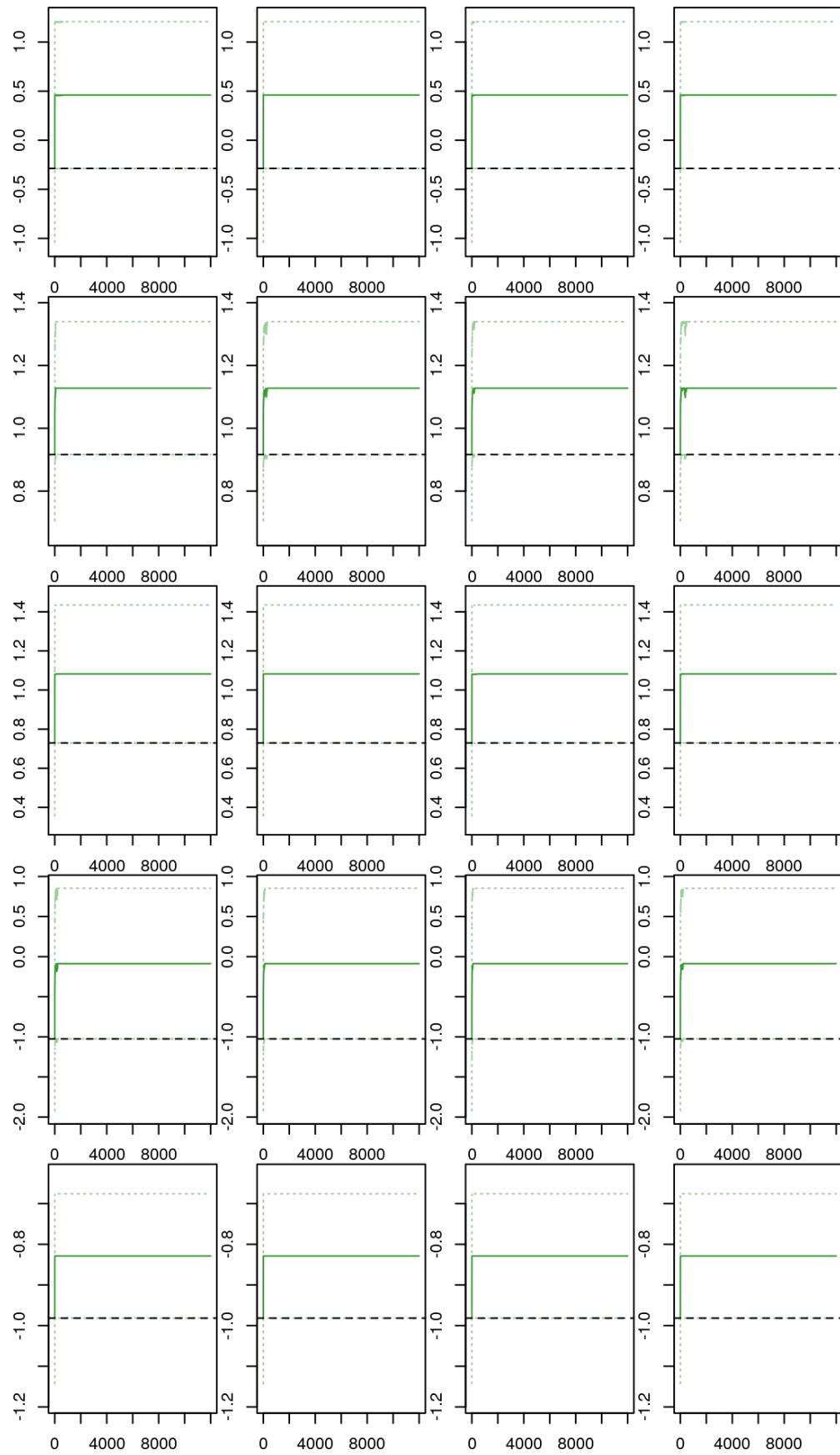


Figure 2: Evolution of courtship trait with unlinked loci. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

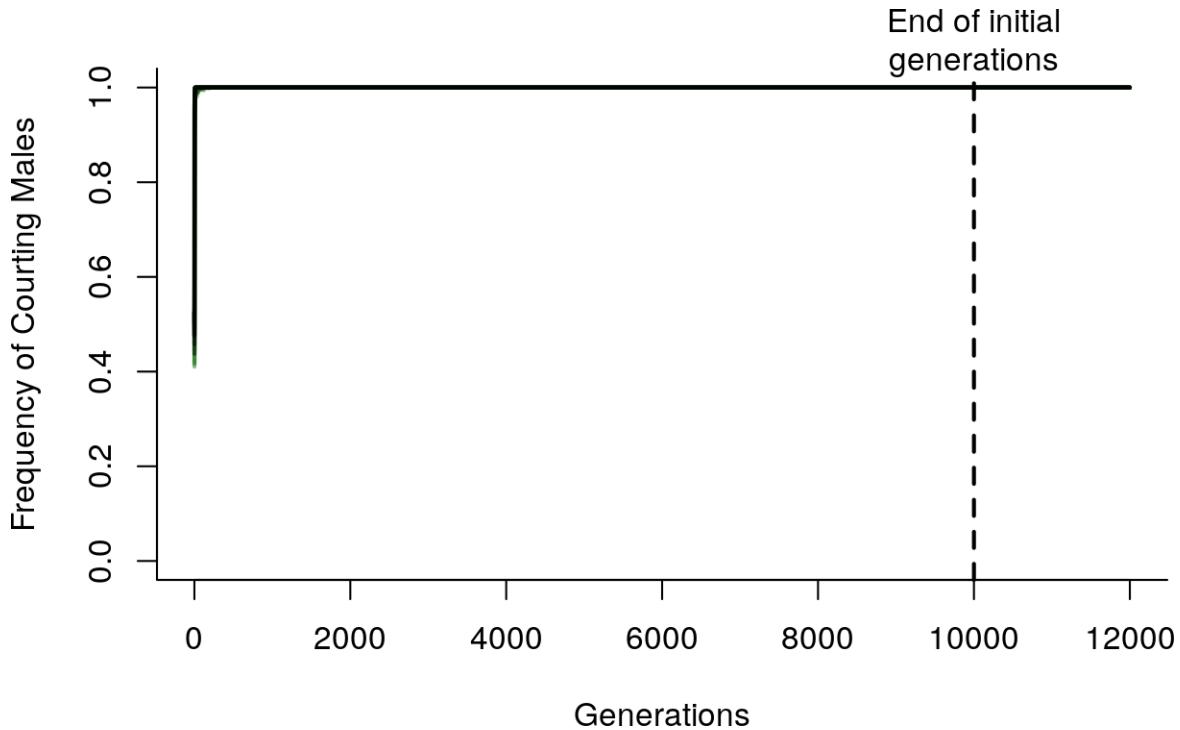


Figure 3: Frequency of the counter morph with unlinked additive genetic variances and without viability selection in all of the replicates

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	2.06186	0
counter_unlinked_novs_1_summary.txt_2	1	2.01207	0
counter_unlinked_novs_1_summary.txt_3	1	2.04499	0
counter_unlinked_novs_1_summary.txt_4	1	2.00401	0
counter_unlinked_novs_2_summary.txt_1	1	1.94932	0
counter_unlinked_novs_2_summary.txt_2	1	2.06612	0
counter_unlinked_novs_2_summary.txt_3	1	2.04082	0
counter_unlinked_novs_2_summary.txt_4	1	2.06612	0
counter_unlinked_novs_3_summary.txt_1	1	2.03252	0
counter_unlinked_novs_3_summary.txt_2	1	1.95312	0
counter_unlinked_novs_3_summary.txt_3	1	2.00401	0
counter_unlinked_novs_3_summary.txt_4	1	2.05761	0
counter_unlinked_novs_4_summary.txt_1	1	2.05761	0
counter_unlinked_novs_4_summary.txt_2	1	1.98807	0
counter_unlinked_novs_4_summary.txt_3	1	1.99601	0
counter_unlinked_novs_4_summary.txt_4	1	1.89394	0
counter_unlinked_novs_5_summary.txt_1	1	2.02020	0

	CourterFreq	CourterW	NonCourterW
courter_unlinked_novs_5_summary.txt_2	1	1.90114	0
courter_unlinked_novs_5_summary.txt_3	1	2.08333	0
courter_unlinked_novs_5_summary.txt_4	1	2.10084	0

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

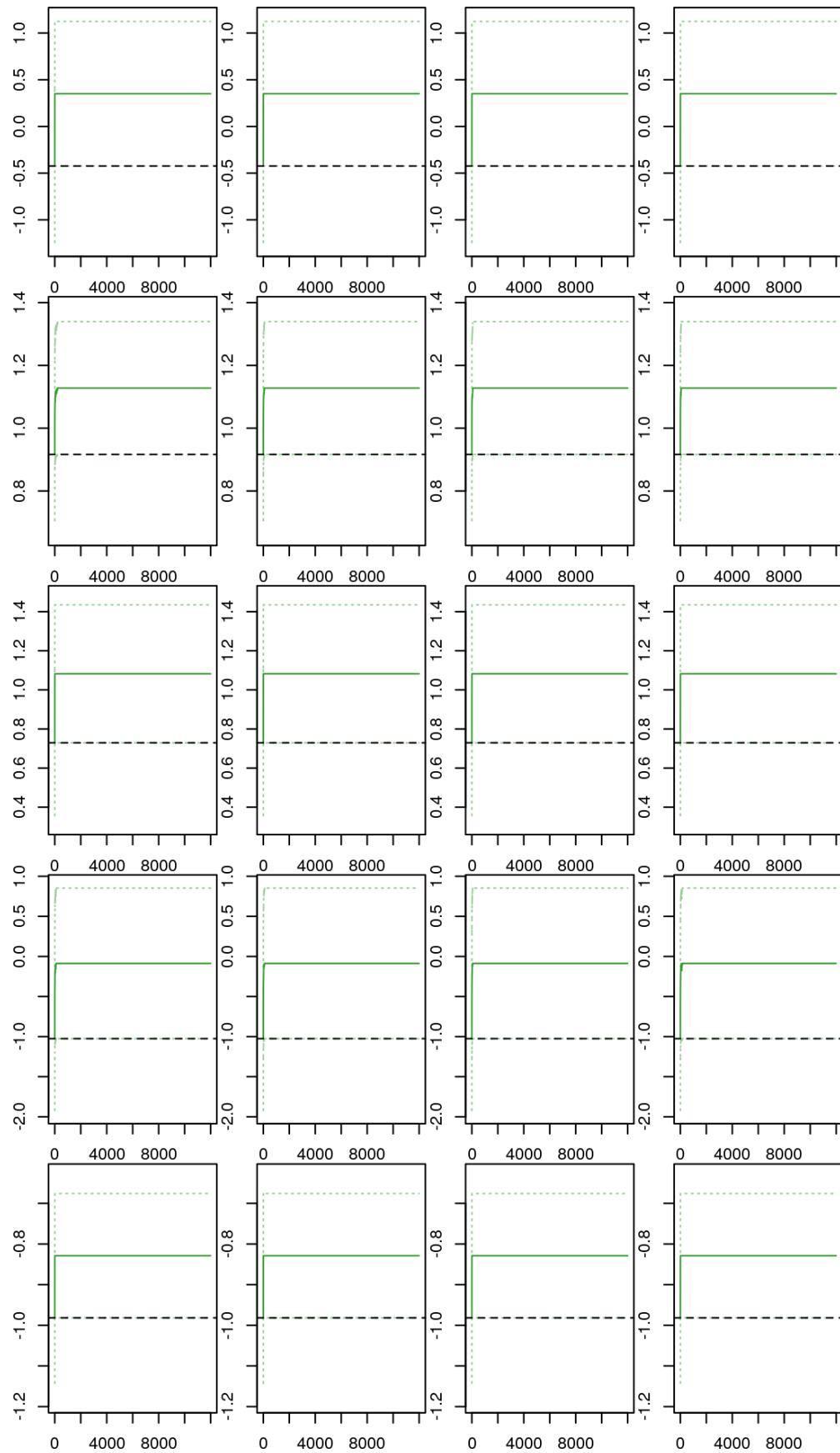


Figure 4: Evolution of courtship trait with unlinked loci and no viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

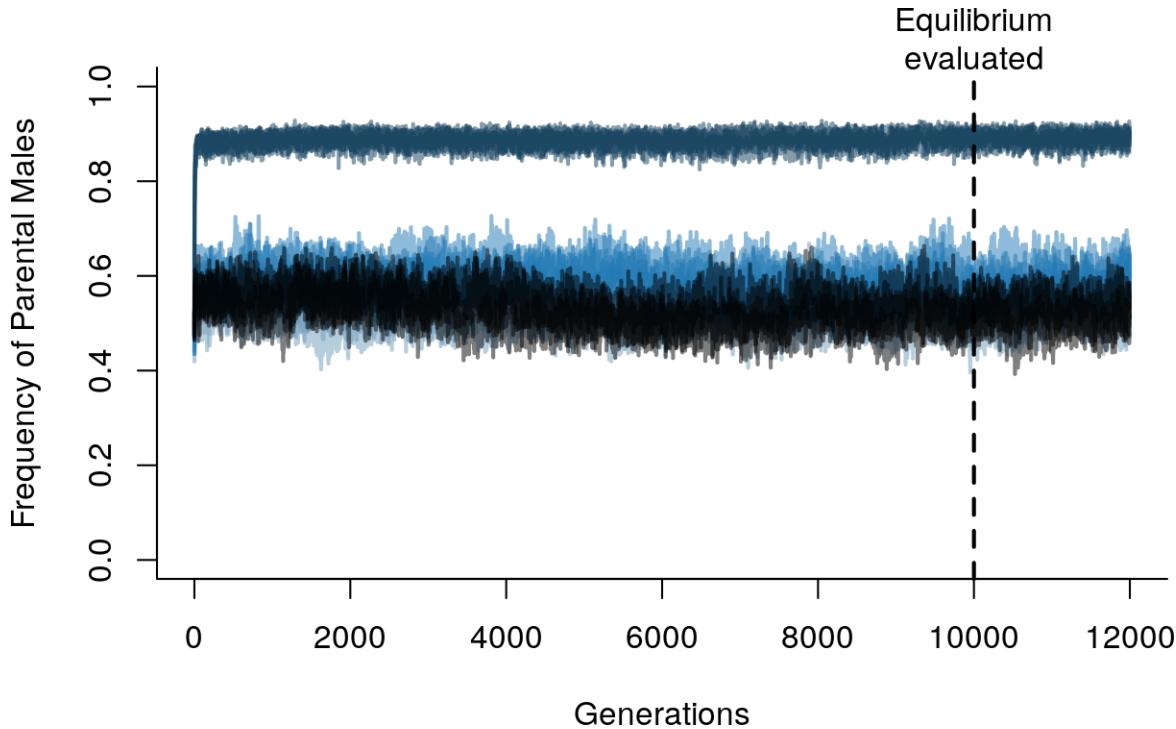


Figure 5: Frequency of parent morph with unlinked loci (each color represents a different replicate)

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	0.621901	1.61462	0.311475
parent_unlinked_1_summary.txt_2	0.472505	1.53879	0.281853
parent_unlinked_1_summary.txt_3	0.556000	1.54676	0.283784
parent_unlinked_1_summary.txt_4	0.553061	1.63838	0.296804
parent_unlinked_2_summary.txt_1	0.600840	1.60839	0.326316
parent_unlinked_2_summary.txt_2	0.636364	1.62222	0.316667
parent_unlinked_2_summary.txt_3	0.602851	1.50000	0.446154
parent_unlinked_2_summary.txt_4	0.599589	1.60959	0.317949
parent_unlinked_3_summary.txt_1	0.881553	1.62775	1.131150
parent_unlinked_3_summary.txt_2	0.875494	1.72686	0.841270
parent_unlinked_3_summary.txt_3	0.884921	1.67937	0.672414
parent_unlinked_3_summary.txt_4	0.908915	1.62687	0.808511
parent_unlinked_4_summary.txt_1	0.510776	1.50633	0.207048
parent_unlinked_4_summary.txt_2	0.525667	1.60156	0.324675

	ParentFreq	ParentW	NonParentW
parent_unlinked_4_summary.txt_3	0.531828	1.52510	0.377193
parent_unlinked_4_summary.txt_4	0.474308	1.59167	0.289474
parent_unlinked_5_summary.txt_1	0.857977	1.56689	0.794521
parent_unlinked_5_summary.txt_2	0.854331	1.63825	0.621622
parent_unlinked_5_summary.txt_3	0.833659	1.52582	0.694118
parent_unlinked_5_summary.txt_4	0.840637	1.67773	0.575000

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

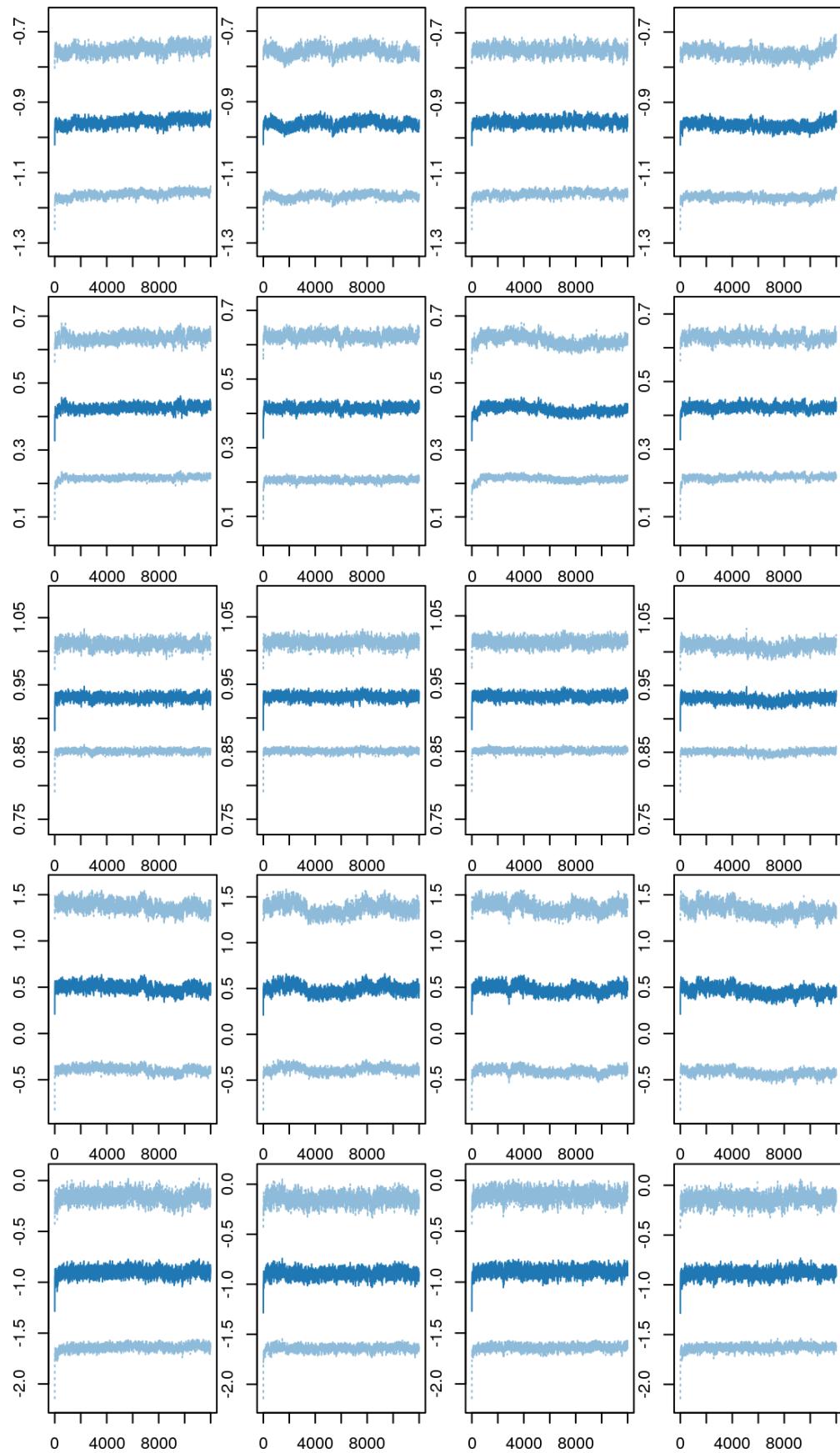


Figure 6: Evolution of parenting trait values with additive genetic variation. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

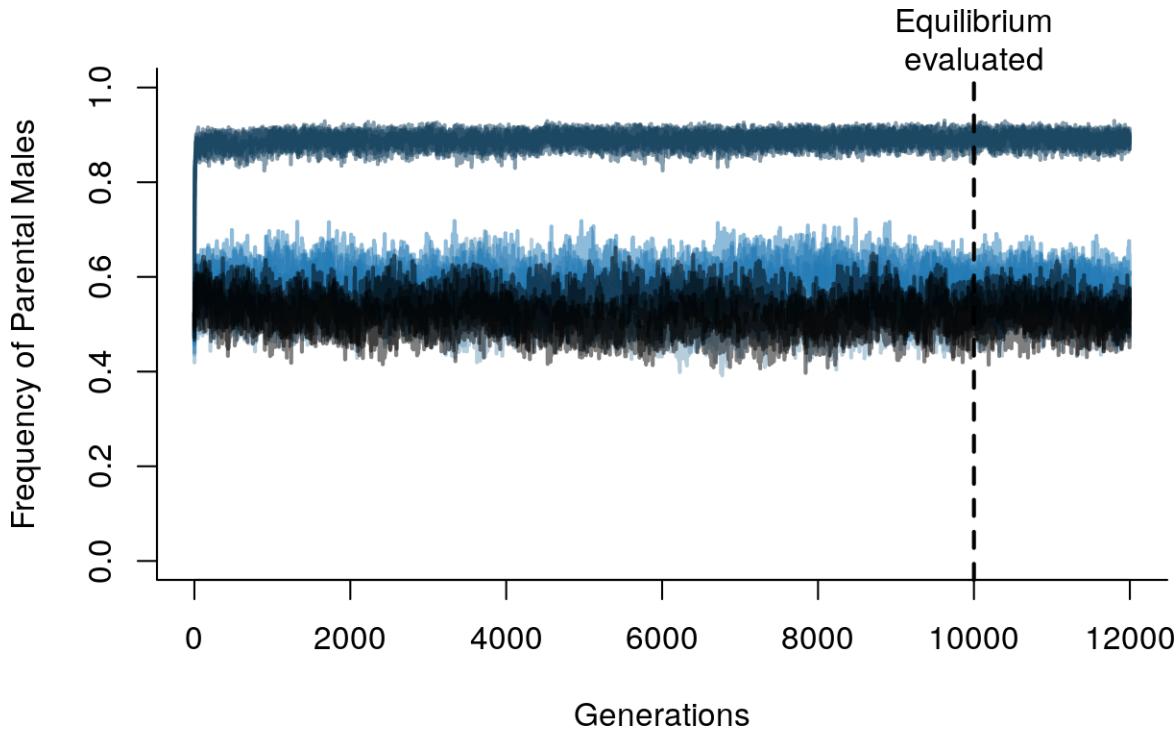


Figure 7: Frequency of parent morph with unlinked loci without viability selection for all replicates

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	0.609037	1.38387	0.211055
parent_unlinked_novs_1_summary.txt_2	0.478846	1.36145	0.298893
parent_unlinked_novs_1_summary.txt_3	0.509128	1.64542	0.276860
parent_unlinked_novs_1_summary.txt_4	0.565392	1.40569	0.421296
parent_unlinked_novs_2_summary.txt_1	0.606426	1.39404	0.331633
parent_unlinked_novs_2_summary.txt_2	0.511538	1.30451	0.255906
parent_unlinked_novs_2_summary.txt_3	0.548708	1.37681	0.277533
parent_unlinked_novs_2_summary.txt_4	0.555332	1.52536	0.339367
parent_unlinked_novs_3_summary.txt_1	0.892276	1.63554	0.660377
parent_unlinked_novs_3_summary.txt_2	0.912281	1.63248	0.666667
parent_unlinked_novs_3_summary.txt_3	0.889336	1.68326	0.909091
parent_unlinked_novs_3_summary.txt_4	0.897590	1.62416	1.039220
parent_unlinked_novs_4_summary.txt_1	0.542094	1.57955	0.322870
parent_unlinked_novs_4_summary.txt_2	0.493230	1.29804	0.347328
parent_unlinked_novs_4_summary.txt_3	0.519924	1.29927	0.320158
parent_unlinked_novs_4_summary.txt_4	0.515267	1.46667	0.232283
parent_unlinked_novs_5_summary.txt_1	0.861660	1.56193	0.728571
parent_unlinked_novs_5_summary.txt_2	0.860784	1.63554	0.605634
parent_unlinked_novs_5_summary.txt_3	0.868421	1.59307	0.714286
parent_unlinked_novs_5_summary.txt_4	0.845842	1.67146	0.763158

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

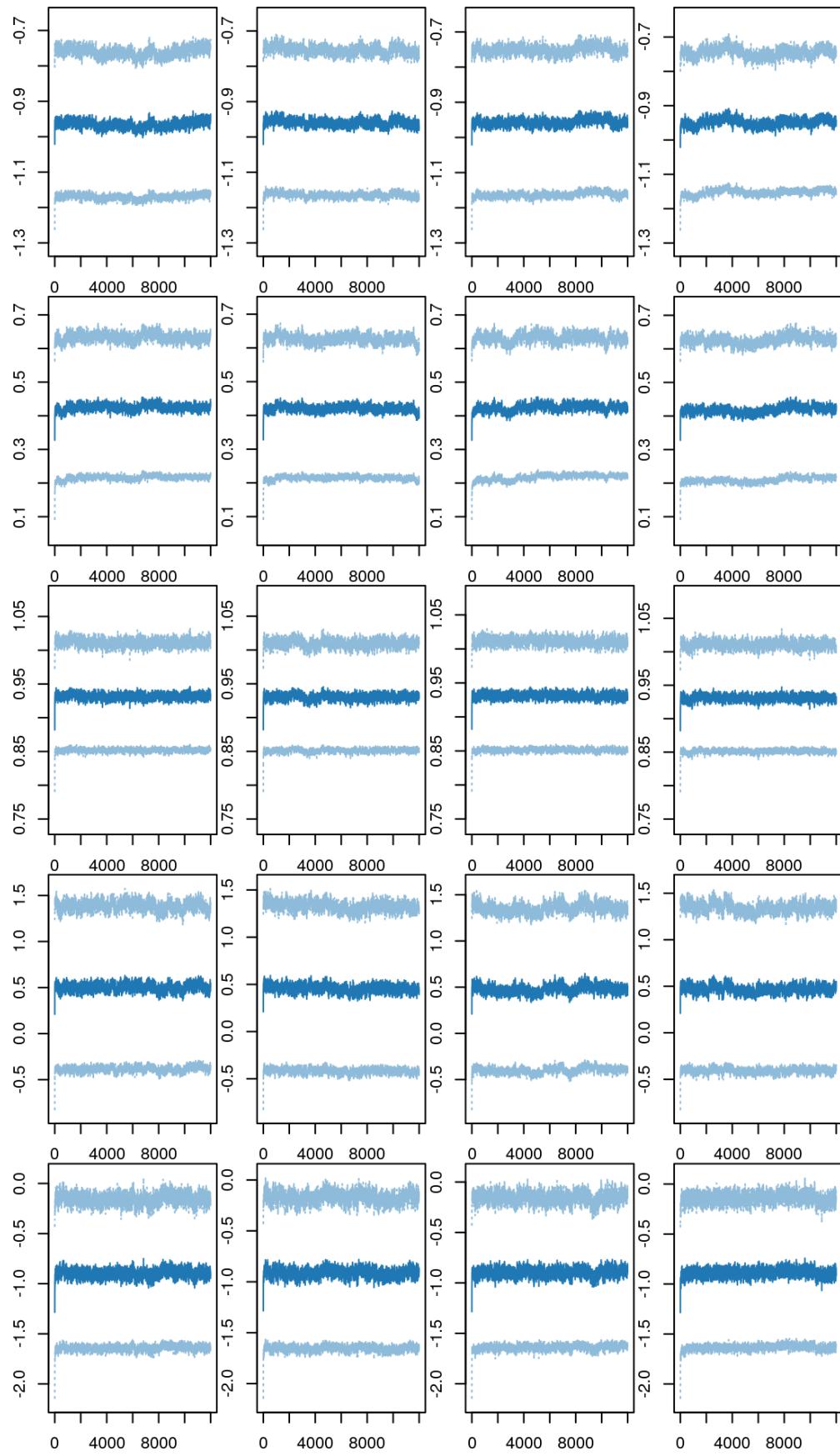
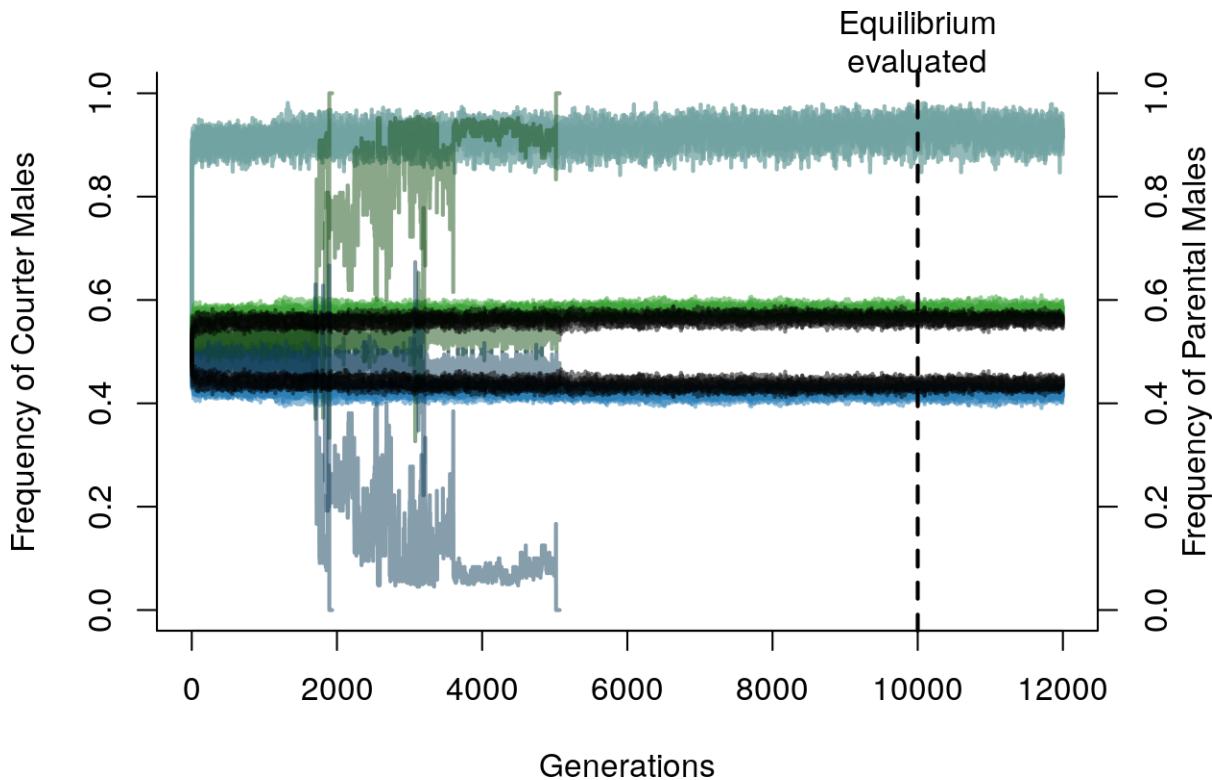


Figure 8: Evolution of parenting trait values with additive genetic variation and no viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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.

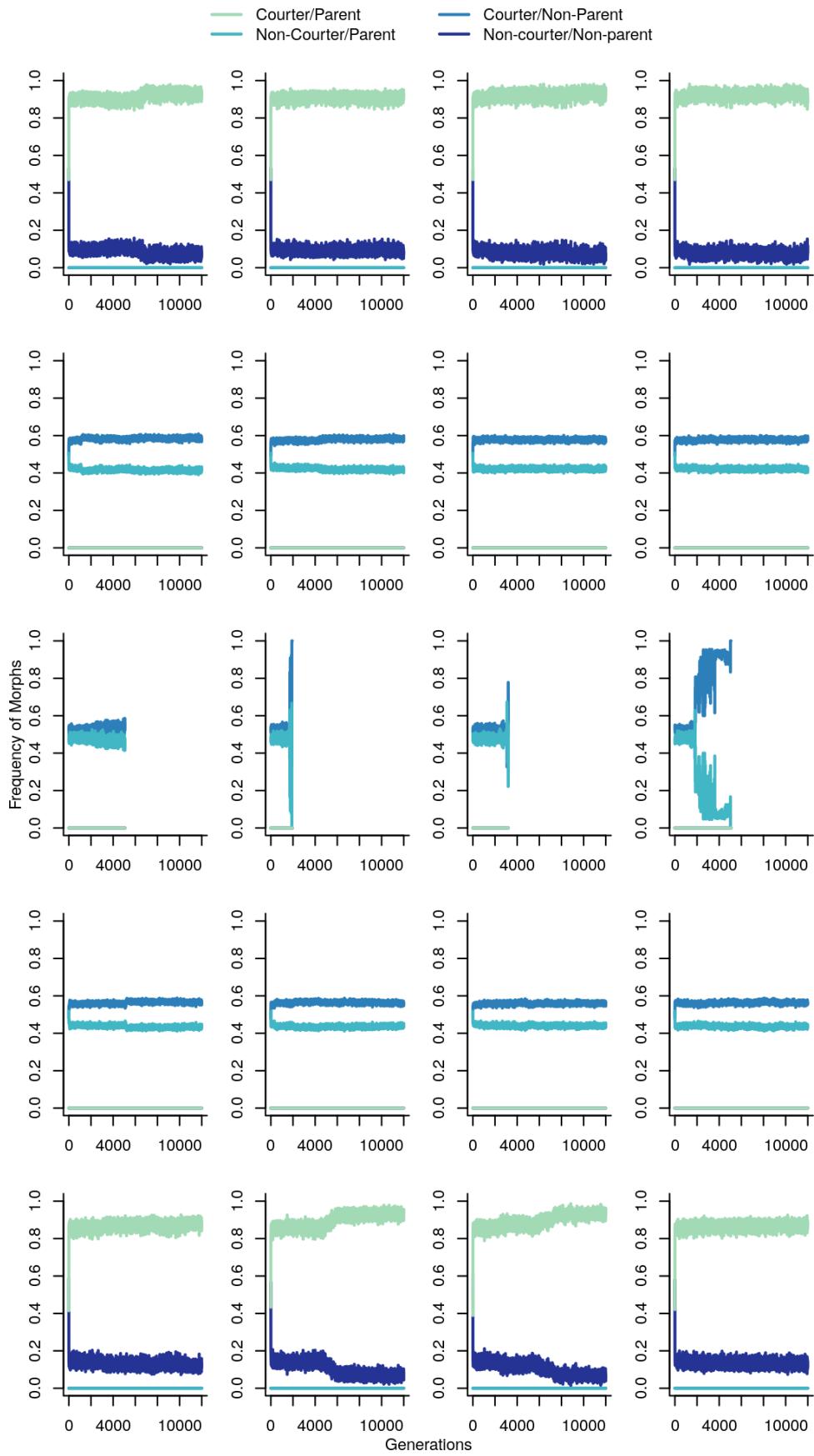


Figure 9: Frequency of the 4 morphs in each rep with unlinked genetic variation

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	Parent
parent-courter_unlinked_1_summary.txt_1	11999	Pop0	940	455	485	1000	-0
parent-courter_unlinked_1_summary.txt_2	11999	Pop1	1000	502	498	1000	-0
parent-courter_unlinked_1_summary.txt_3	11999	Pop2	944	464	480	1000	-0
parent-courter_unlinked_1_summary.txt_4	11999	Pop3	947	477	470	1000	-0
parent-courter_unlinked_2_summary.txt_1	11999	Pop0	941	457	484	1000	0
parent-courter_unlinked_2_summary.txt_2	11999	Pop1	932	456	476	1000	0
parent-courter_unlinked_2_summary.txt_3	11999	Pop2	917	438	479	993	0
parent-courter_unlinked_2_summary.txt_4	11999	Pop3	944	462	482	1000	0
parent-courter_unlinked_3_summary.txt_1	5068	Pop0	725	381	344	837	0
parent-courter_unlinked_3_summary.txt_2	1933	Pop1	4	4	0	0	0
parent-courter_unlinked_3_summary.txt_3	3202	Pop2	4	4	0	0	0
parent-courter_unlinked_3_summary.txt_4	5067	Pop3	12	2	10	8	0
parent-courter_unlinked_4_summary.txt_1	11999	Pop0	967	480	487	1000	-0
parent-courter_unlinked_4_summary.txt_2	11999	Pop1	966	481	485	1000	-0
parent-courter_unlinked_4_summary.txt_3	11999	Pop2	966	491	475	1000	-0
parent-courter_unlinked_4_summary.txt_4	11999	Pop3	965	477	488	1000	-0
parent-courter_unlinked_5_summary.txt_1	11999	Pop0	976	511	465	1000	0
parent-courter_unlinked_5_summary.txt_2	11999	Pop1	942	472	470	1000	0
parent-courter_unlinked_5_summary.txt_3	11999	Pop2	943	468	475	1000	0
parent-courter_unlinked_5_summary.txt_4	11999	Pop3	989	489	500	1000	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.

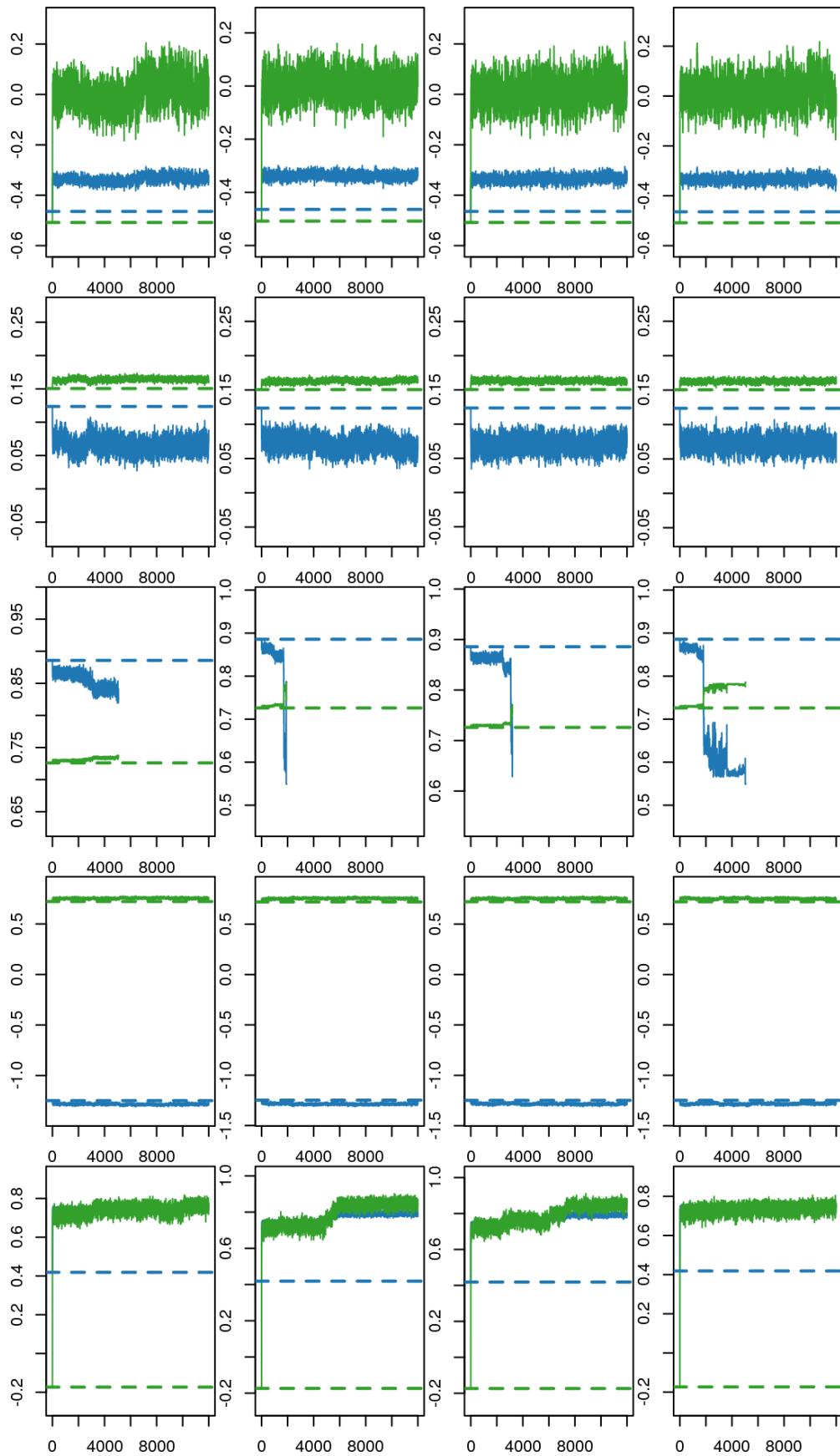
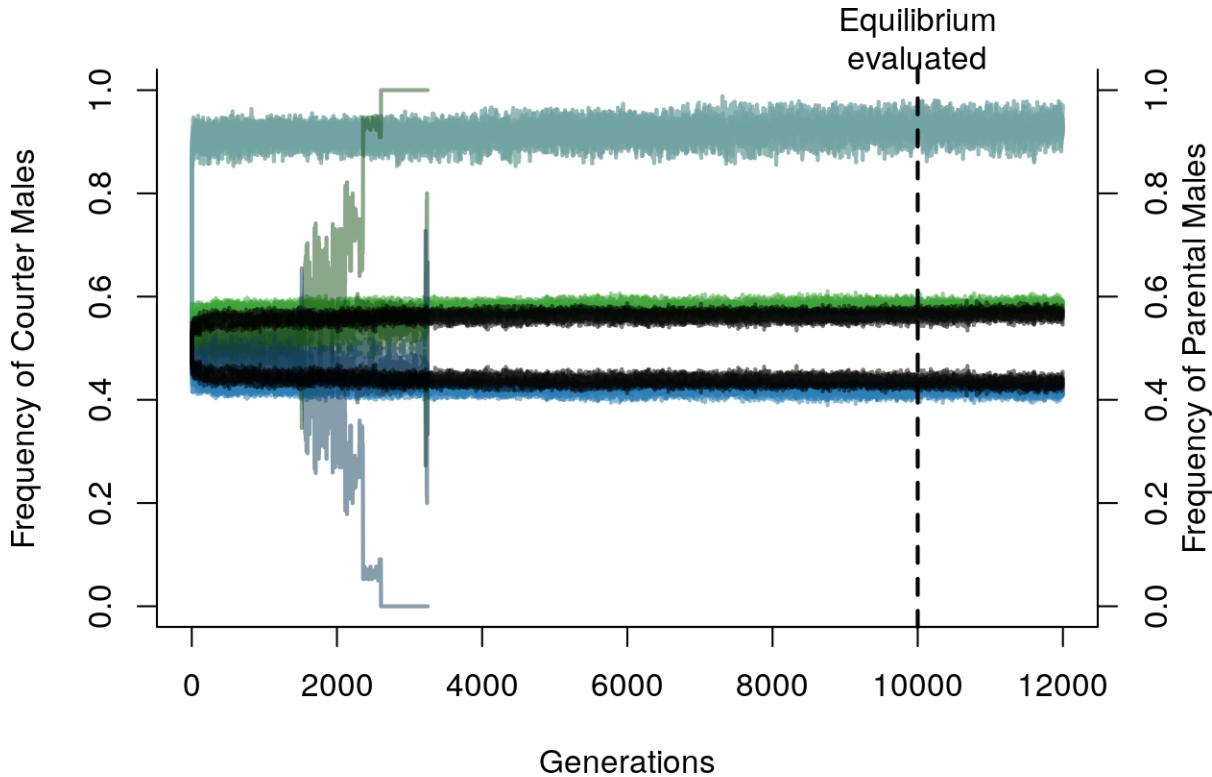


Figure 10: Evolution of the counter and parenting trait values in each rep with unlinked genetic variation. Dotted line shows the thresholds determining if males become courters (green) or parents (blue)

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.

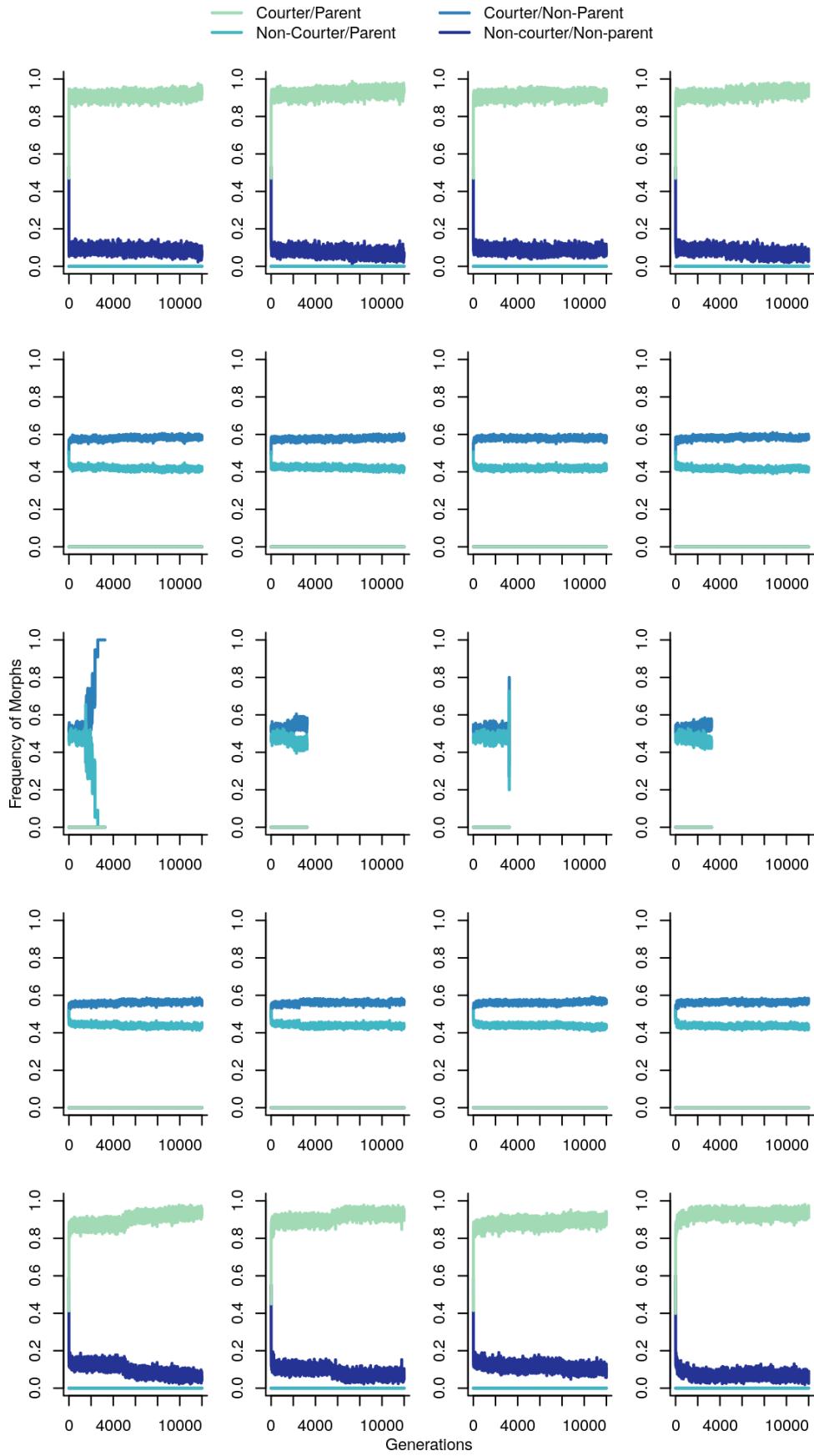


Figure 11: Frequency of the 4 morphs in each rep with unlinked genetic variation and no viability selection

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_unlinked_novs_1_summary.txt_1	11999	Pop0	936	459	477	1000
parent-courter_unlinked_novs_1_summary.txt_2	11999	Pop1	944	454	490	1000
parent-courter_unlinked_novs_1_summary.txt_3	11999	Pop2	1000	488	512	1000
parent-courter_unlinked_novs_1_summary.txt_4	11999	Pop3	948	489	459	1000
parent-courter_unlinked_novs_2_summary.txt_1	11999	Pop0	941	461	480	1000
parent-courter_unlinked_novs_2_summary.txt_2	11999	Pop1	944	459	485	1000
parent-courter_unlinked_novs_2_summary.txt_3	11999	Pop2	942	469	473	1000
parent-courter_unlinked_novs_2_summary.txt_4	11999	Pop3	943	453	490	1000
parent-courter_unlinked_novs_3_summary.txt_1	3251	Pop0	23	12	11	37
parent-courter_unlinked_novs_3_summary.txt_2	3251	Pop1	742	376	366	849
parent-courter_unlinked_novs_3_summary.txt_3	3250	Pop2	8	3	5	4
parent-courter_unlinked_novs_3_summary.txt_4	3250	Pop3	744	377	367	818
parent-courter_unlinked_novs_4_summary.txt_1	11999	Pop0	967	492	475	1000
parent-courter_unlinked_novs_4_summary.txt_2	11999	Pop1	968	490	478	1000
parent-courter_unlinked_novs_4_summary.txt_3	11999	Pop2	965	471	494	1000
parent-courter_unlinked_novs_4_summary.txt_4	11999	Pop3	967	483	484	1000
parent-courter_unlinked_novs_5_summary.txt_1	11999	Pop0	950	504	446	1000
parent-courter_unlinked_novs_5_summary.txt_2	11999	Pop1	944	457	487	1000
parent-courter_unlinked_novs_5_summary.txt_3	11999	Pop2	972	487	485	1000
parent-courter_unlinked_novs_5_summary.txt_4	11999	Pop3	947	465	482	1000

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

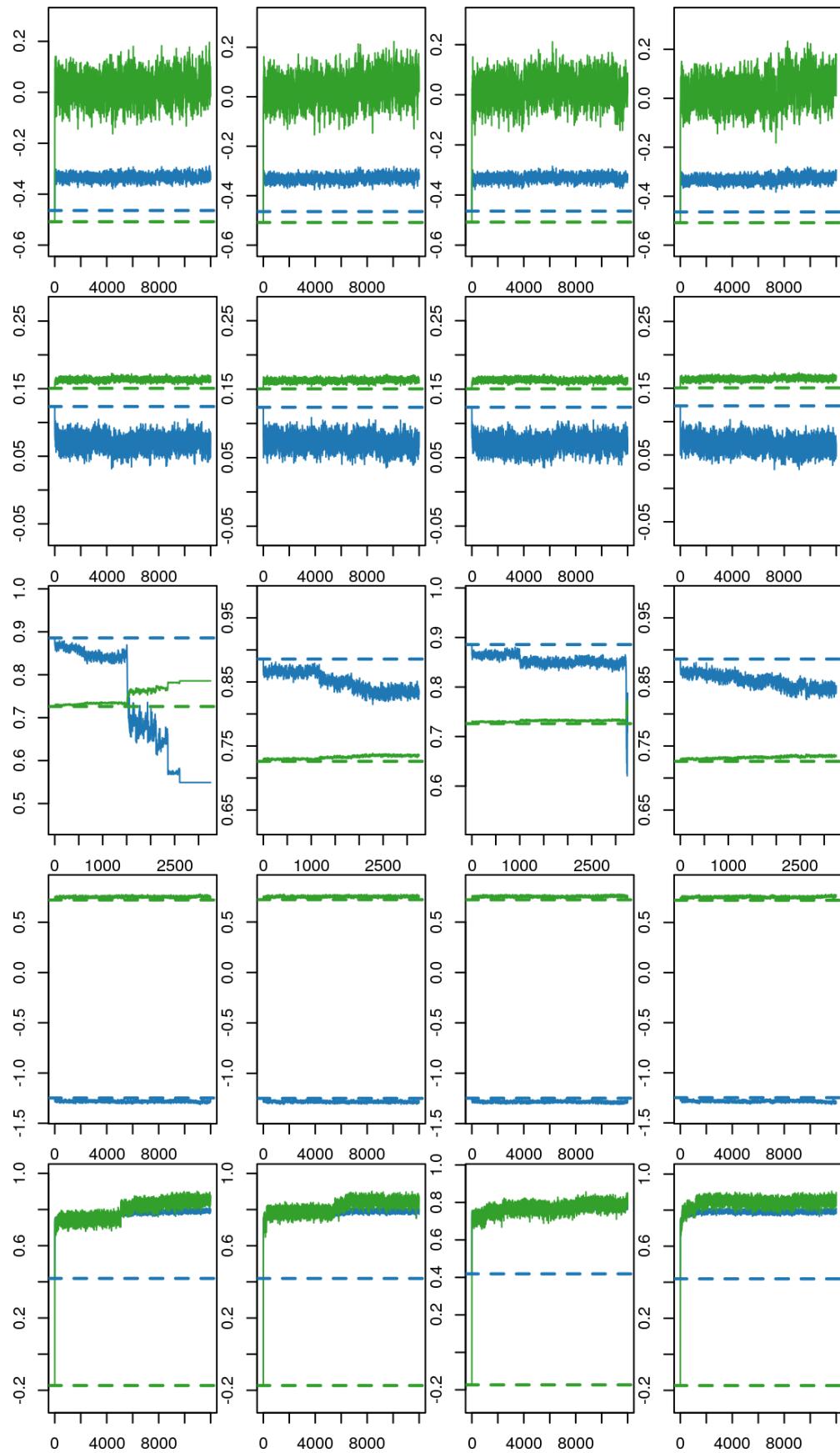


Figure 12: Evolution of the courtier and parenting trait values in each rep with unlinked genetic variation and without viability selection. Green represents courtship trait values and blue represents parental trait values, and the dotted lines are the thresholds

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

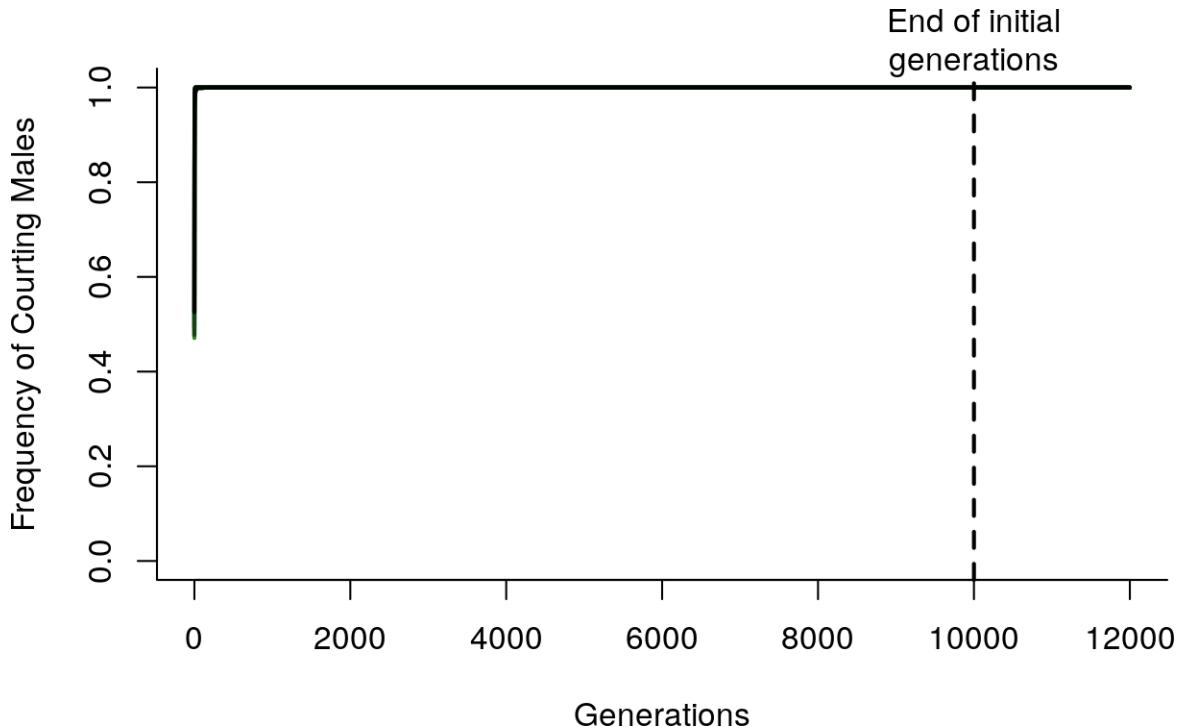


Figure 13: Frequency of the counter morph with linked QTLs (each color represents a different replicate)

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	1.92308	0

	CounterFreq	CounterW	NonCounterW
courter_linked_1_summary.txt_2	1	1.92678	0
courter_linked_1_summary.txt_3	1	2.02020	0
courter_linked_1_summary.txt_4	1	2.09644	0
courter_linked_2_summary.txt_1	1	2.01616	0
courter_linked_2_summary.txt_2	1	1.98397	0
courter_linked_2_summary.txt_3	1	1.91205	0
courter_linked_2_summary.txt_4	1	1.96078	0
courter_linked_3_summary.txt_1	1	2.01212	0
courter_linked_3_summary.txt_2	1	2.02653	0
courter_linked_3_summary.txt_3	1	1.95098	0
courter_linked_3_summary.txt_4	1	1.98008	0
courter_linked_4_summary.txt_1	1	1.94510	0
courter_linked_4_summary.txt_2	1	1.86304	0
courter_linked_4_summary.txt_3	1	2.01829	0
courter_linked_4_summary.txt_4	1	2.01414	0
courter_linked_5_summary.txt_1	1	2.02020	0
courter_linked_5_summary.txt_2	1	2.08333	0
courter_linked_5_summary.txt_3	1	2.02020	0
courter_linked_5_summary.txt_4	1	1.90114	0

Every replicate has the courtship trait go to fixation.

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

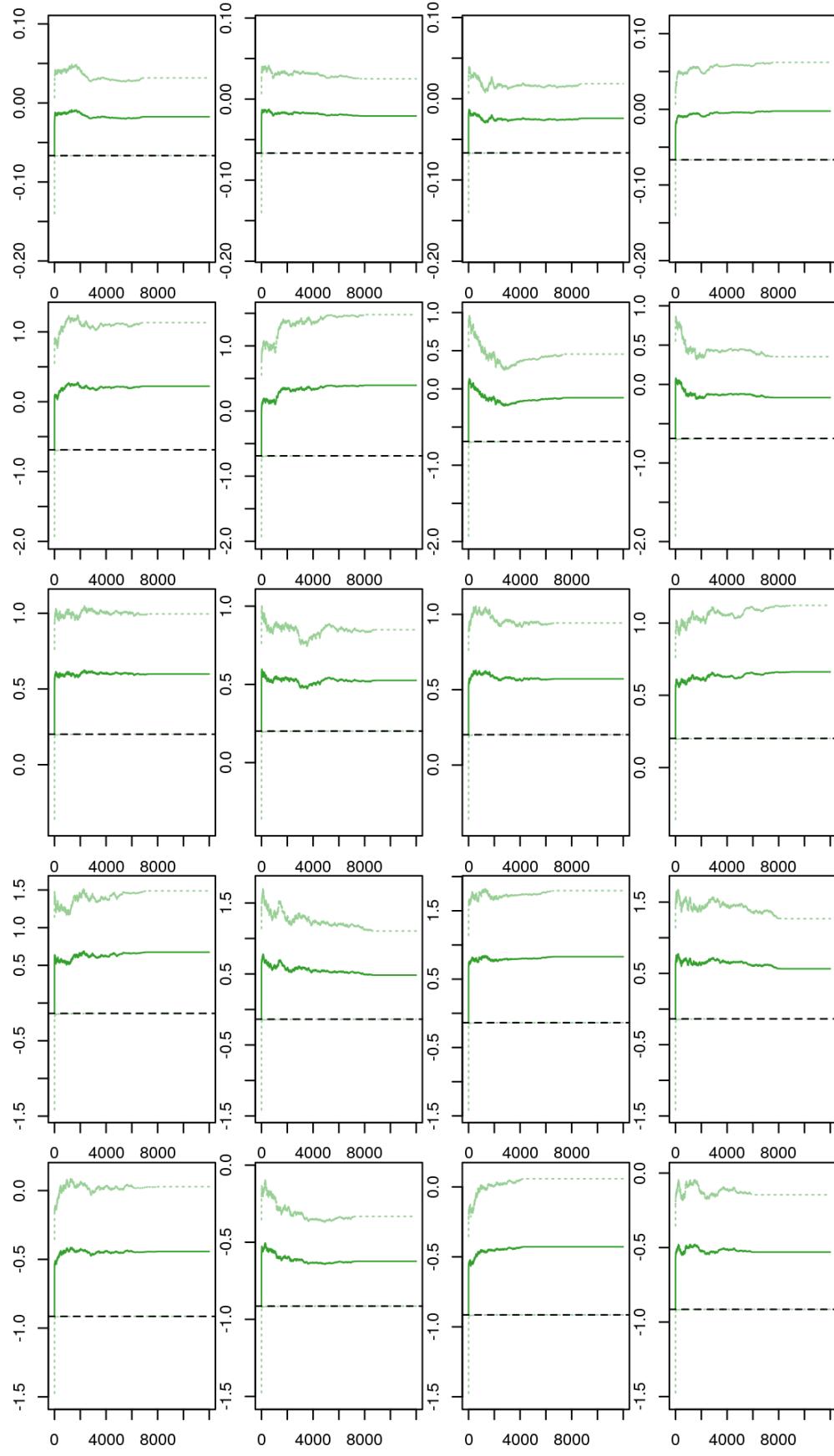


Figure 14: Evolution of courtship trait with linked loci. Green dotted lines are the standard deviations of the traits and the black dotted line is the threshold

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

Without viability selection

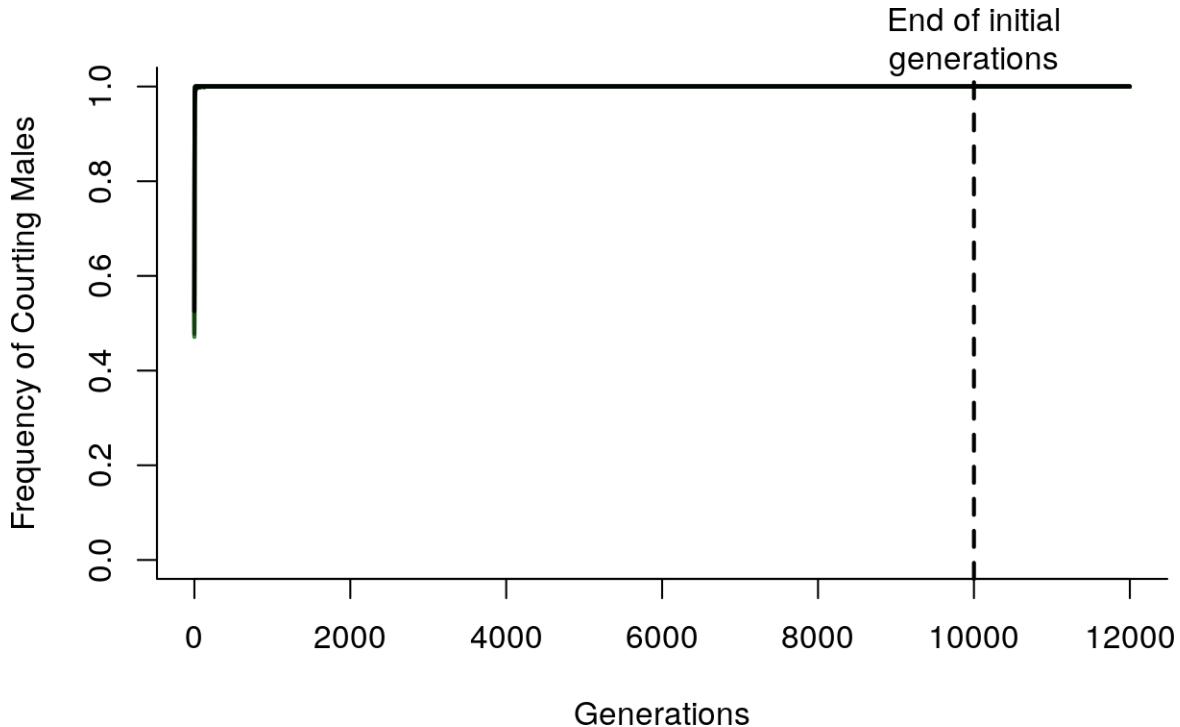


Figure 15: Frequency of the courtship trait with linked QTLs and no viability selection (each color represents a different replicate)

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 courtiers with linked QTLs in final generation

	CounterFreq	CounterW	NonCounterW
counter_linked_novs_1_summary.txt_1	1	2.03252	0
counter_linked_novs_1_summary.txt_2	1	2.01207	0
counter_linked_novs_1_summary.txt_3	1	1.96078	0
counter_linked_novs_1_summary.txt_4	1	1.97628	0
counter_linked_novs_2_summary.txt_1	1	1.98413	0
counter_linked_novs_2_summary.txt_2	1	2.18818	0
counter_linked_novs_2_summary.txt_3	1	2.00000	0
counter_linked_novs_2_summary.txt_4	1	1.98807	0
counter_linked_novs_3_summary.txt_1	1	2.06186	0
counter_linked_novs_3_summary.txt_2	1	2.05761	0
counter_linked_novs_3_summary.txt_3	1	2.02840	0
counter_linked_novs_3_summary.txt_4	1	2.01207	0
counter_linked_novs_4_summary.txt_1	1	2.04082	0

	CourterFreq	CourterW	NonCourterW
courter_linked_novs_4_summary.txt_2	1	1.98807	0
courter_linked_novs_4_summary.txt_3	1	2.11416	0
courter_linked_novs_4_summary.txt_4	1	2.06186	0
courter_linked_novs_5_summary.txt_1	1	1.95695	0
courter_linked_novs_5_summary.txt_2	1	1.90476	0
courter_linked_novs_5_summary.txt_3	1	1.93050	0
courter_linked_novs_5_summary.txt_4	1	1.97239	0

Every rep has the courtship trait go to fixation.

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

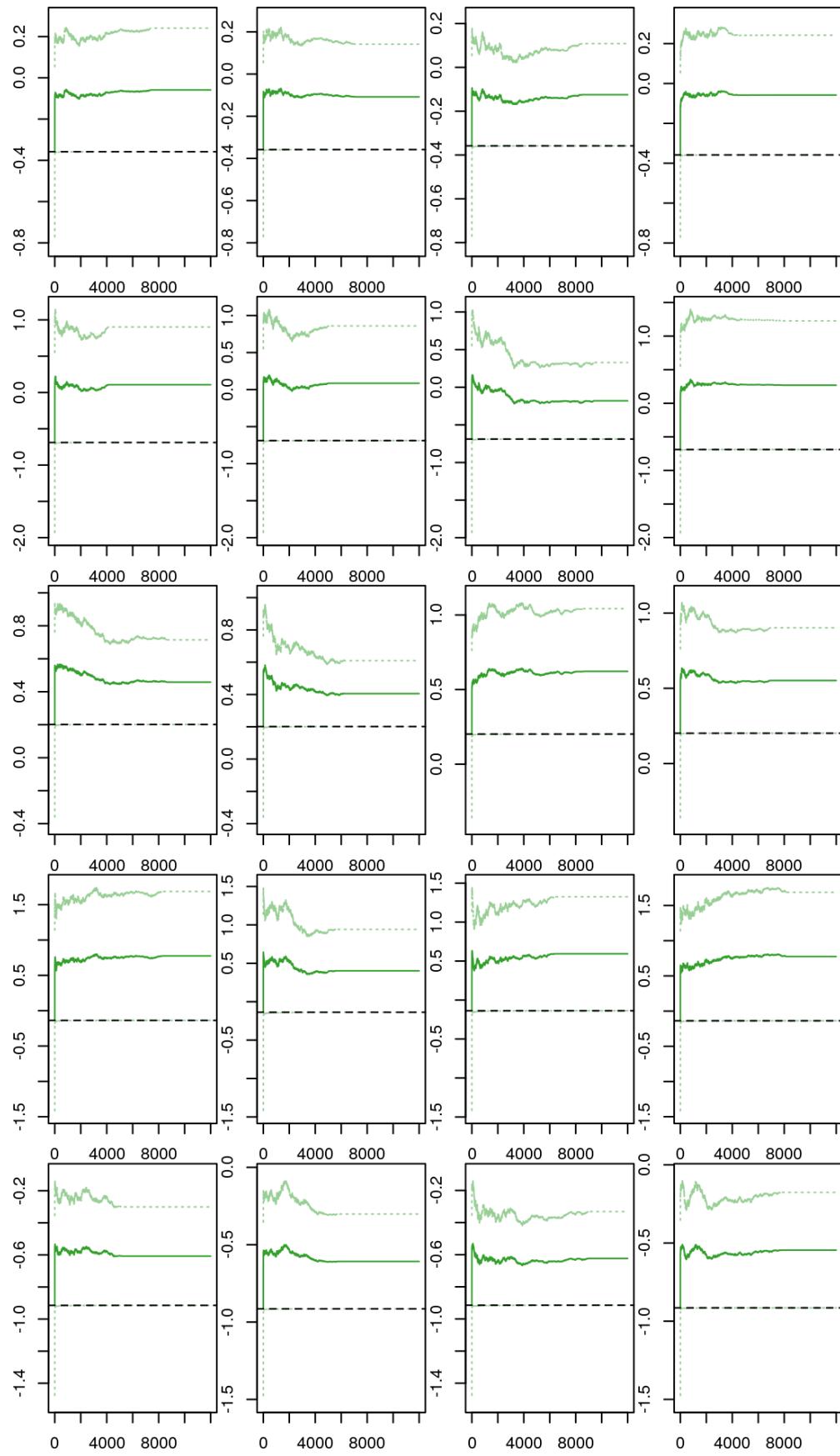


Figure 16: Evolution of courtship trait with linked loci and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

Parental trait

With viability selection

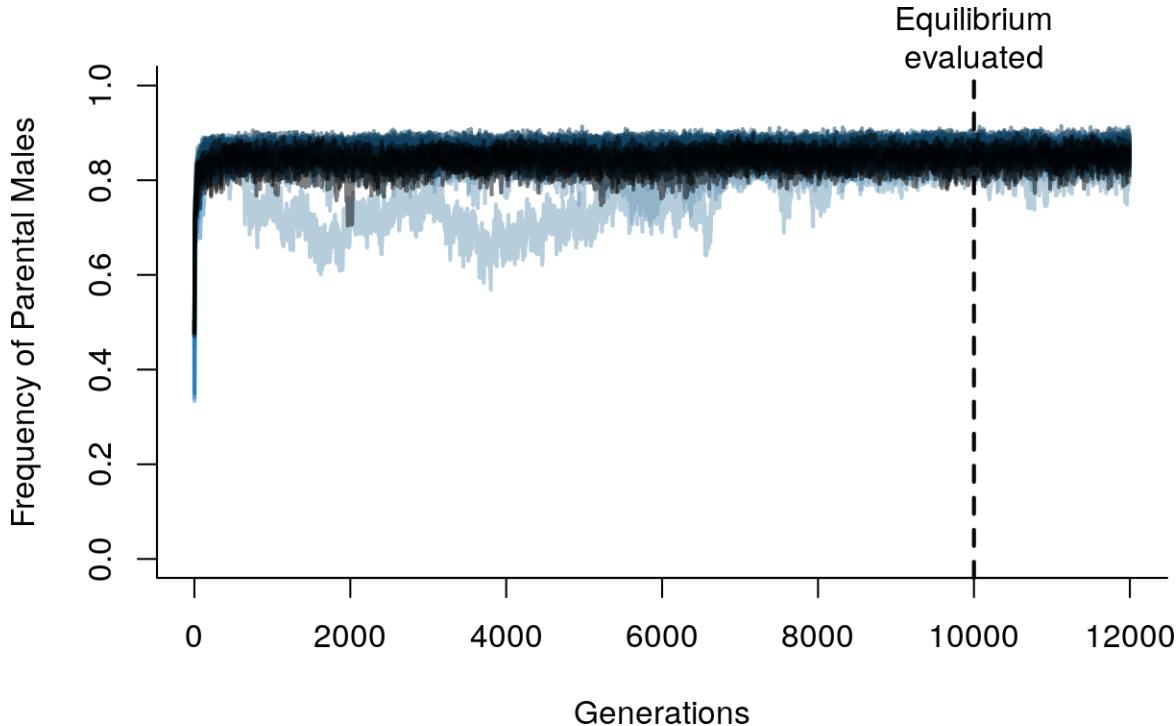


Figure 17: Frequency of parent morph with linked QTLs (each color represents a different replicate)

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	0.807843	1.50000	0.642857
parent_linked_1_summary.txt_2	0.853608	1.71739	0.718310
parent_linked_1_summary.txt_3	0.845238	1.58216	0.653846
parent_linked_1_summary.txt_4	0.811623	1.58025	0.702128
parent_linked_2_summary.txt_1	0.866530	1.74882	0.723077
parent_linked_2_summary.txt_2	0.846449	1.59864	0.587500
parent_linked_2_summary.txt_3	0.886100	1.55773	0.627119
parent_linked_2_summary.txt_4	0.868627	1.53950	0.731343
parent_linked_3_summary.txt_1	0.881526	1.67198	0.644068
parent_linked_3_summary.txt_2	0.863724	1.60222	0.563380
parent_linked_3_summary.txt_3	0.873267	1.65079	0.671875
parent_linked_3_summary.txt_4	0.878543	1.73272	1.033330
parent_linked_4_summary.txt_1	0.870968	1.59259	0.852941
parent_linked_4_summary.txt_2	0.853801	1.61416	0.680000
parent_linked_4_summary.txt_3	0.831663	1.63373	0.523810

	ParentFreq	ParentW	NonParentW
parent_linked_4_summary.txt_4	0.853360	1.69928	0.722222
parent_linked_5_summary.txt_1	0.839583	1.69479	0.649351
parent_linked_5_summary.txt_2	0.832661	1.67797	0.481928
parent_linked_5_summary.txt_3	0.777328	1.63542	0.481818
parent_linked_5_summary.txt_4	0.802348	1.59756	0.653465

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:

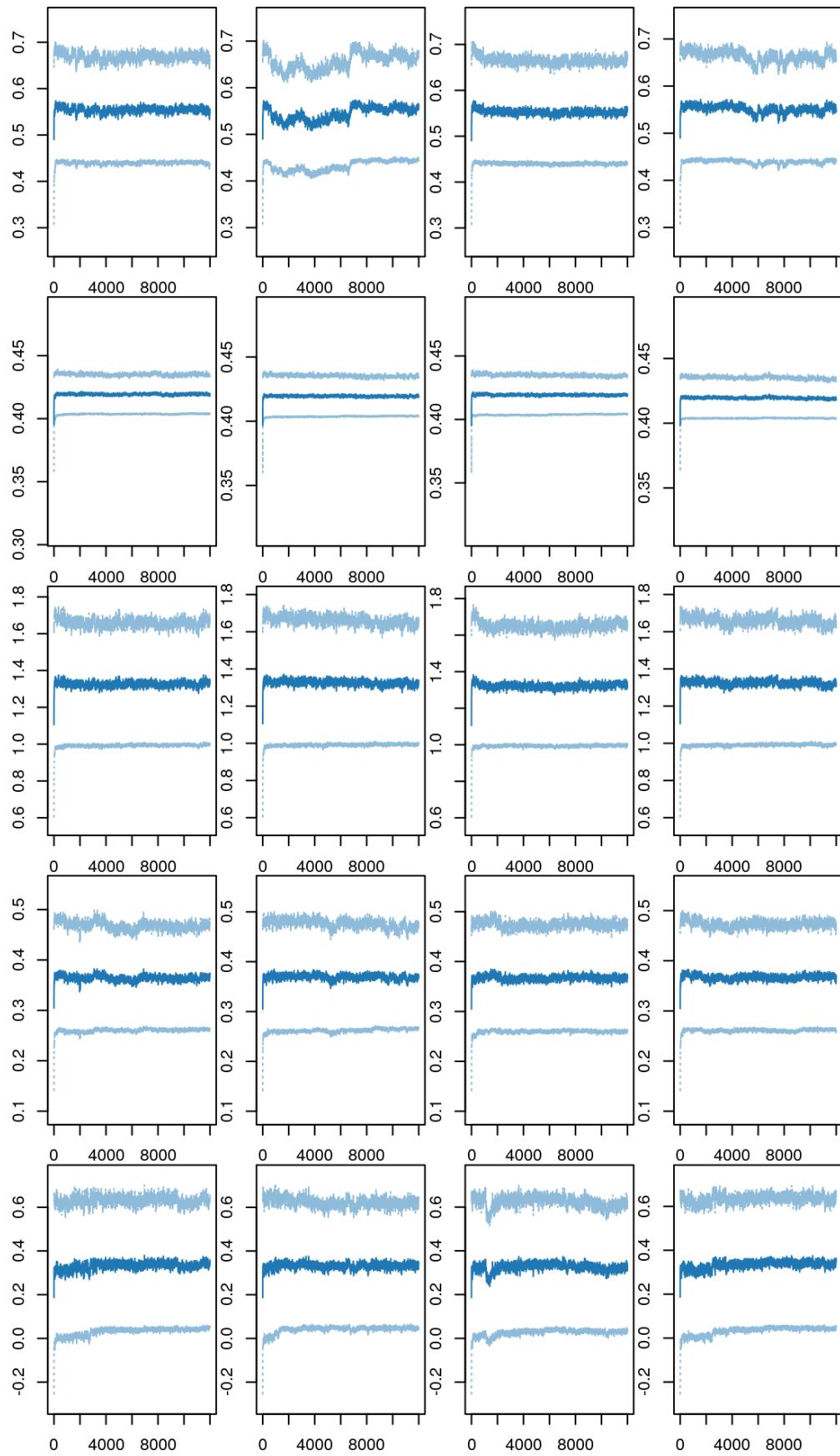


Figure 18: Evolution of parenting trait values with linked QTLs. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

Without viability selection

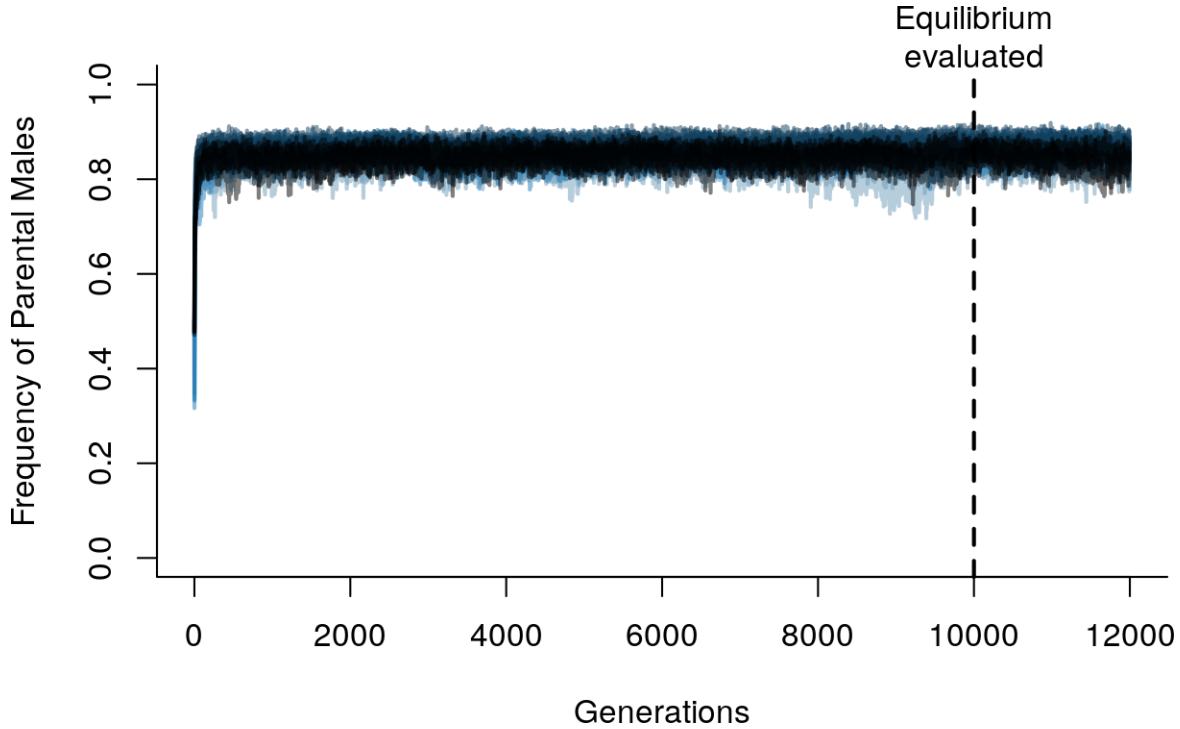


Figure 19: Frequency of parent morph with linked QTLs without viability selection (each color represents a different replicate)

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	0.854582	1.64103	0.808219
parent_linked_novs_1_summary.txt_2	0.867188	1.61261	1.000000
parent_linked_novs_1_summary.txt_3	0.799603	1.56328	0.504950
parent_linked_novs_1_summary.txt_4	0.833333	1.65647	0.682353
parent_linked_novs_2_summary.txt_1	0.855711	1.74941	0.750000
parent_linked_novs_2_summary.txt_2	0.864583	1.75904	0.938462
parent_linked_novs_2_summary.txt_3	0.855072	1.65617	0.971429
parent_linked_novs_2_summary.txt_4	0.850103	1.70048	0.890411
parent_linked_novs_3_summary.txt_1	0.879377	1.57301	0.532258
parent_linked_novs_3_summary.txt_2	0.868217	1.54018	0.602941
parent_linked_novs_3_summary.txt_3	0.872917	1.72076	0.688525
parent_linked_novs_3_summary.txt_4	0.867647	1.71671	0.952381
parent_linked_novs_4_summary.txt_1	0.815416	1.74129	0.648352
parent_linked_novs_4_summary.txt_2	0.848723	1.55556	0.558442

	ParentFreq	ParentW	NonParentW
parent_linked_novs_4_summary.txt_3	0.840816	1.72573	0.576923
parent_linked_novs_4_summary.txt_4	0.838912	1.71571	0.376623
parent_linked_novs_5_summary.txt_1	0.822180	1.51163	0.677419
parent_linked_novs_5_summary.txt_2	0.770526	1.60656	0.422018
parent_linked_novs_5_summary.txt_3	0.814346	1.73575	0.579545
parent_linked_novs_5_summary.txt_4	0.775758	1.71615	0.648649

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:

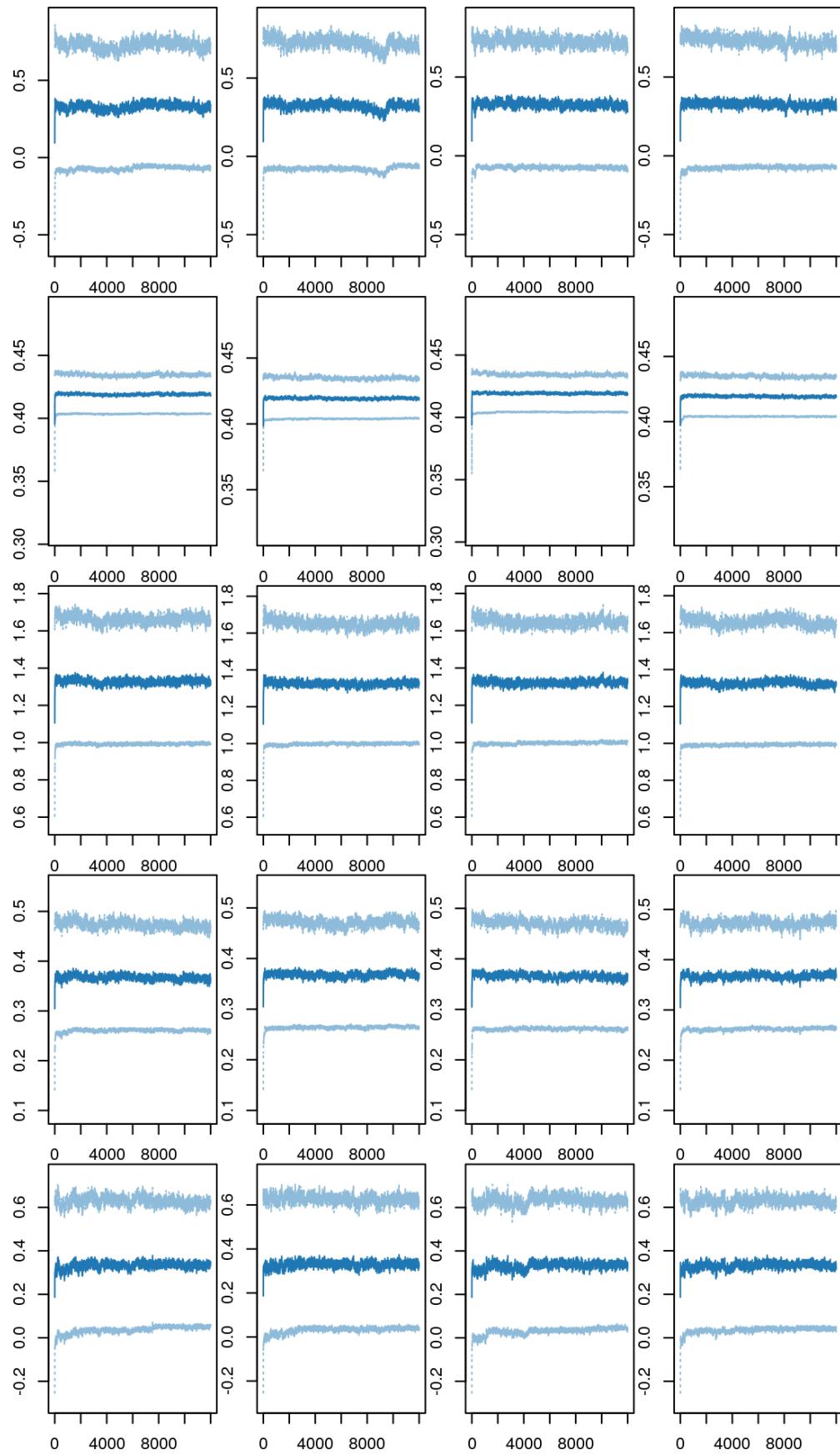


Figure 20: Evolution of parenting trait values with linked QTLs and without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

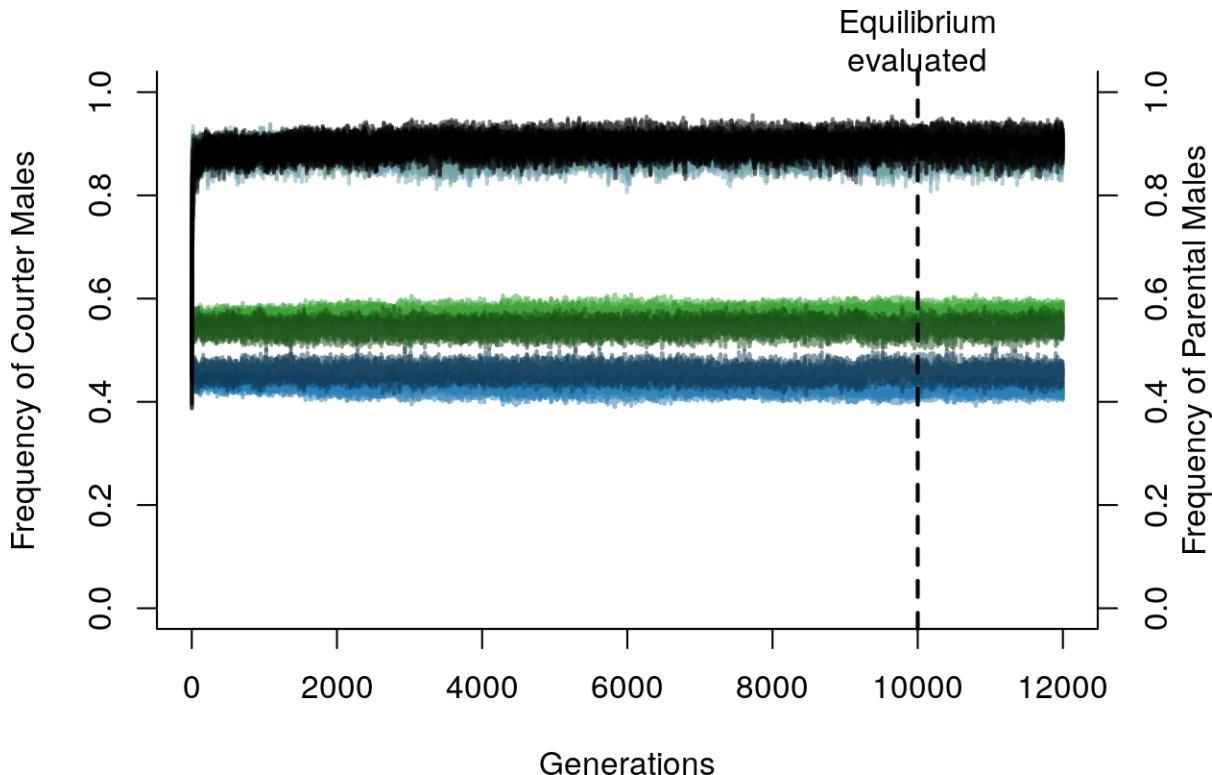


Figure 21: Frequency of the two morphs with linked QTLs (counter = green, parent = blue)

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

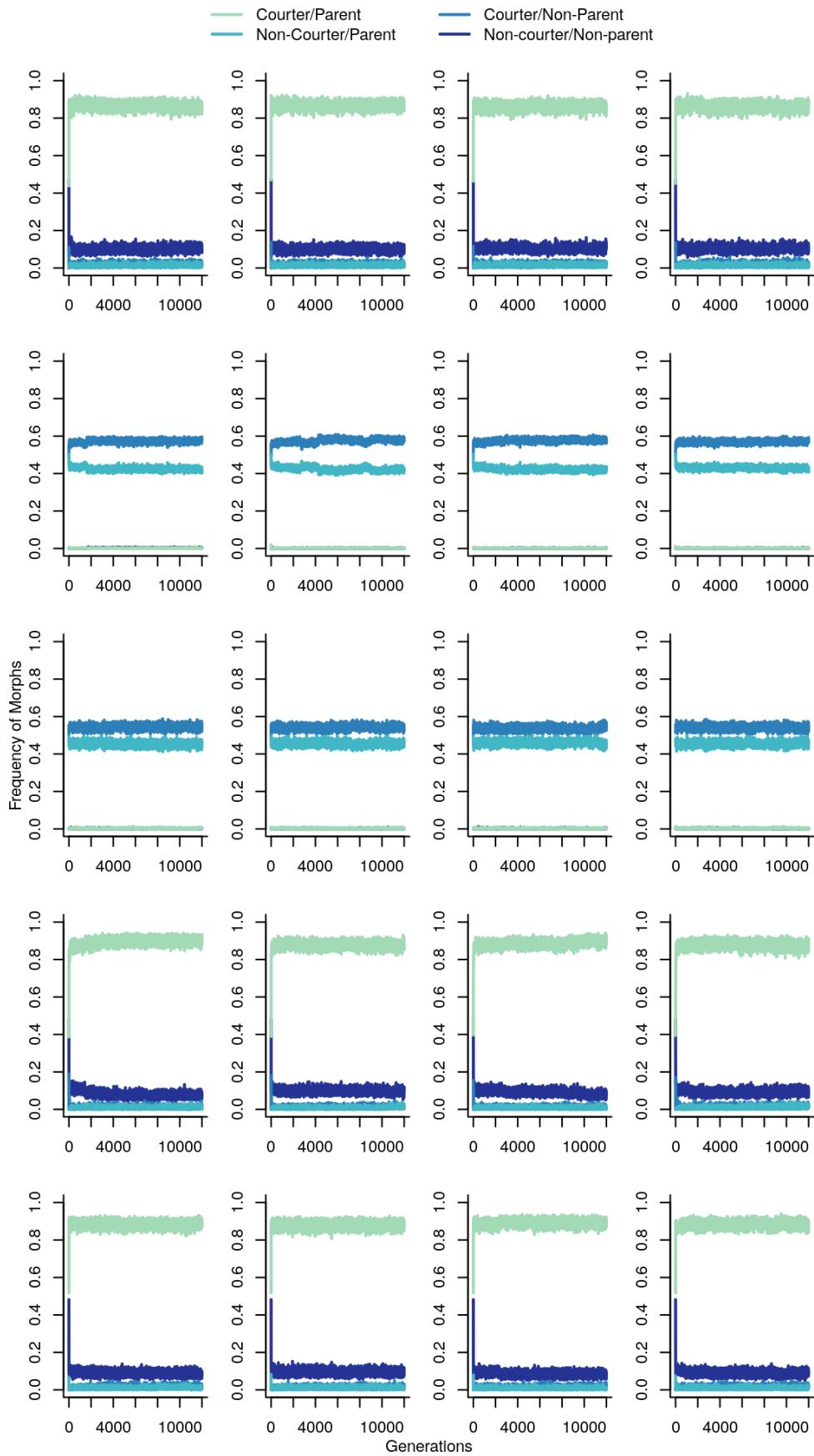


Figure 22: Frequency of the 4 morphs in each rep with linked QTLs

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	11999	Pop0	1000	480	520	1000	0.9
parent-courter_linked_1_summary.txt_2	11999	Pop1	1000	491	509	1000	0.9
parent-courter_linked_1_summary.txt_3	11999	Pop2	1000	484	516	1000	0.9
parent-courter_linked_1_summary.txt_4	11999	Pop3	999	486	513	1000	0.9
parent-courter_linked_2_summary.txt_1	11999	Pop0	950	475	475	1000	-0.2
parent-courter_linked_2_summary.txt_2	11999	Pop1	935	455	480	1000	-0.2
parent-courter_linked_2_summary.txt_3	11999	Pop2	926	446	480	1000	-0.2
parent-courter_linked_2_summary.txt_4	11999	Pop3	951	466	485	1000	-0.2
parent-courter_linked_3_summary.txt_1	11999	Pop0	1000	497	503	1000	-0.5
parent-courter_linked_3_summary.txt_2	11999	Pop1	1000	515	485	1000	-0.5
parent-courter_linked_3_summary.txt_3	11999	Pop2	1000	513	487	1000	-0.5
parent-courter_linked_3_summary.txt_4	11999	Pop3	1000	513	487	1000	-0.5
parent-courter_linked_4_summary.txt_1	11999	Pop0	975	475	500	1000	0.8
parent-courter_linked_4_summary.txt_2	11999	Pop1	972	483	489	1000	0.8
parent-courter_linked_4_summary.txt_3	11999	Pop2	987	498	489	1000	0.8
parent-courter_linked_4_summary.txt_4	11999	Pop3	976	477	499	1000	0.8
parent-courter_linked_5_summary.txt_1	11999	Pop0	1000	495	505	1000	-0.1
parent-courter_linked_5_summary.txt_2	11999	Pop1	1000	491	509	1000	-0.1
parent-courter_linked_5_summary.txt_3	11999	Pop2	1000	529	471	1000	-0.1
parent-courter_linked_5_summary.txt_4	11999	Pop3	1000	502	498	1000	-0.1

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a counter. However, 0 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:

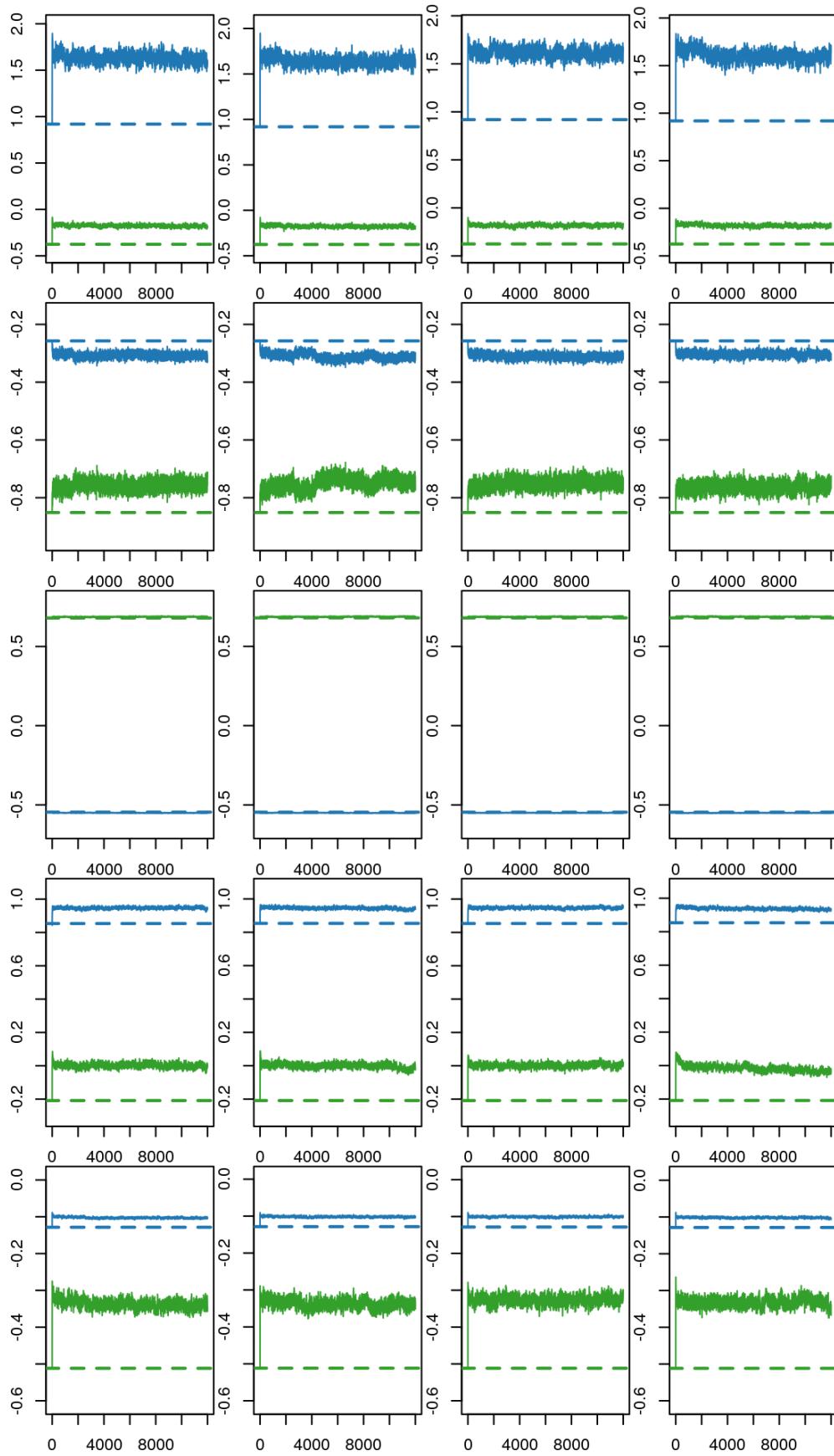


Figure 23: Evolution of the counter and parenting trait values in each rep with linked genetic variation

Without viability selection

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

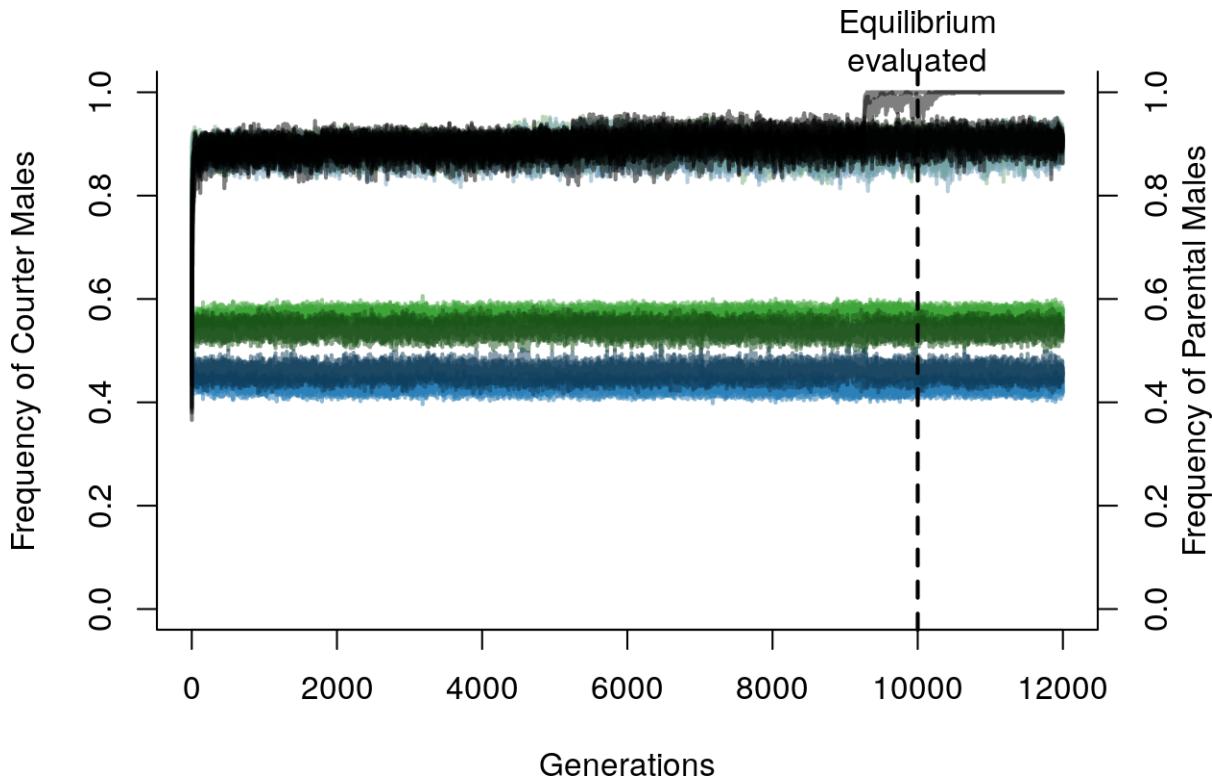


Figure 24: Frequency of the two morphs with linked QTLs and without viability selection (courter = green, parent = blue)

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

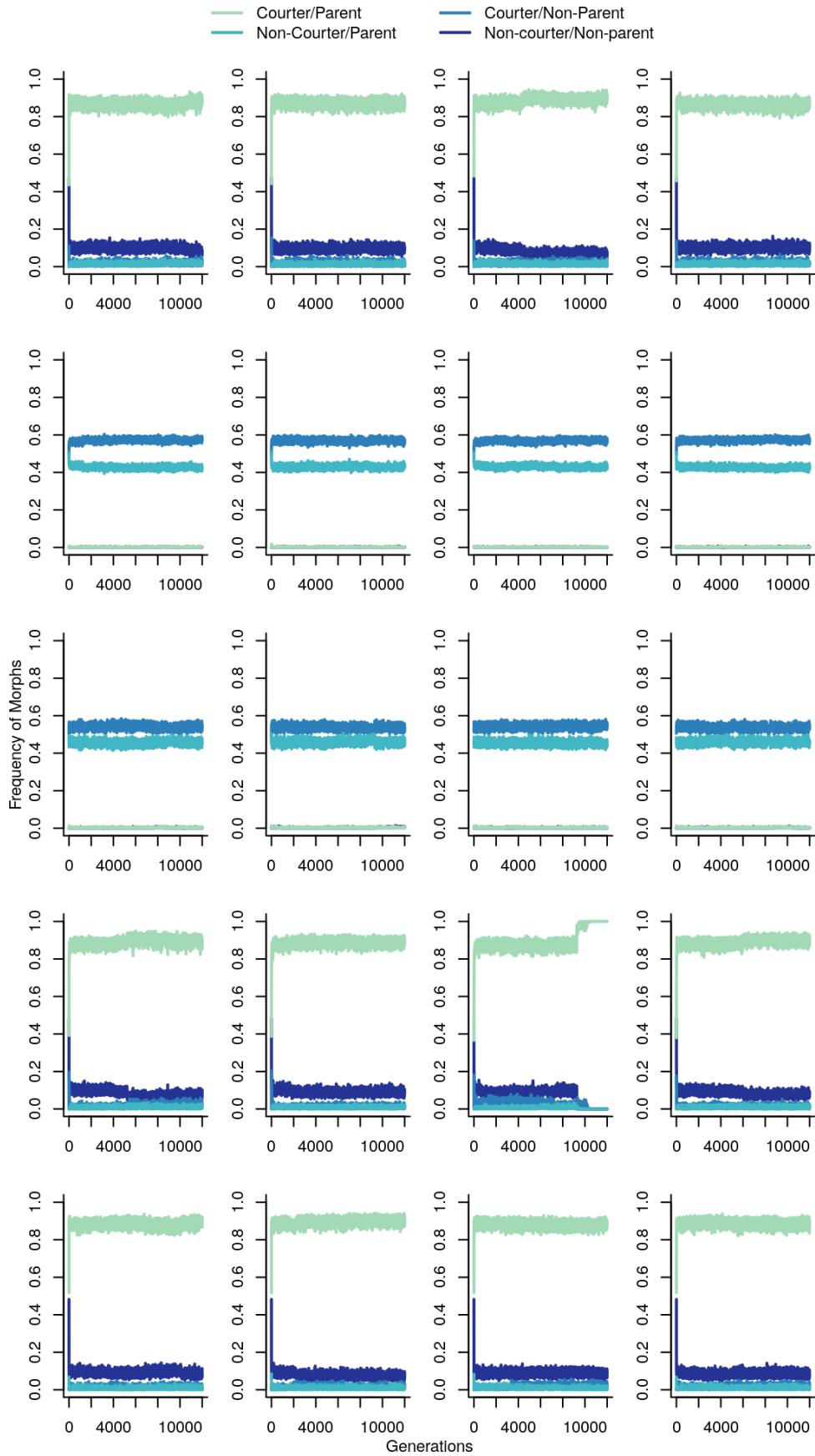


Figure 25: Frequency of the 4 morphs in each rep with linked QTLs without viability selection

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	981	490	491	1000	
parent-courter_linked_novs_1_summary.txt_2	11999	Pop1	1000	504	496	1000	
parent-courter_linked_novs_1_summary.txt_3	11999	Pop2	987	530	457	1000	
parent-courter_linked_novs_1_summary.txt_4	11999	Pop3	1000	505	495	1000	
parent-courter_linked_novs_2_summary.txt_1	11999	Pop0	946	458	488	1000	
parent-courter_linked_novs_2_summary.txt_2	11999	Pop1	881	422	459	955	
parent-courter_linked_novs_2_summary.txt_3	11999	Pop2	938	457	481	1000	
parent-courter_linked_novs_2_summary.txt_4	11999	Pop3	951	460	491	1000	
parent-courter_linked_novs_3_summary.txt_1	11999	Pop0	1000	513	487	1000	
parent-courter_linked_novs_3_summary.txt_2	11999	Pop1	1000	519	481	1000	
parent-courter_linked_novs_3_summary.txt_3	11999	Pop2	1000	513	487	1000	
parent-courter_linked_novs_3_summary.txt_4	11999	Pop3	994	512	482	1000	
parent-courter_linked_novs_4_summary.txt_1	11999	Pop0	958	480	478	1000	
parent-courter_linked_novs_4_summary.txt_2	11999	Pop1	1000	513	487	1000	
parent-courter_linked_novs_4_summary.txt_3	11999	Pop2	956	473	483	1000	
parent-courter_linked_novs_4_summary.txt_4	11999	Pop3	988	503	485	1000	
parent-courter_linked_novs_5_summary.txt_1	11999	Pop0	1000	481	519	1000	
parent-courter_linked_novs_5_summary.txt_2	11999	Pop1	979	492	487	1000	
parent-courter_linked_novs_5_summary.txt_3	11999	Pop2	1000	521	479	1000	
parent-courter_linked_novs_5_summary.txt_4	11999	Pop3	992	488	504	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:

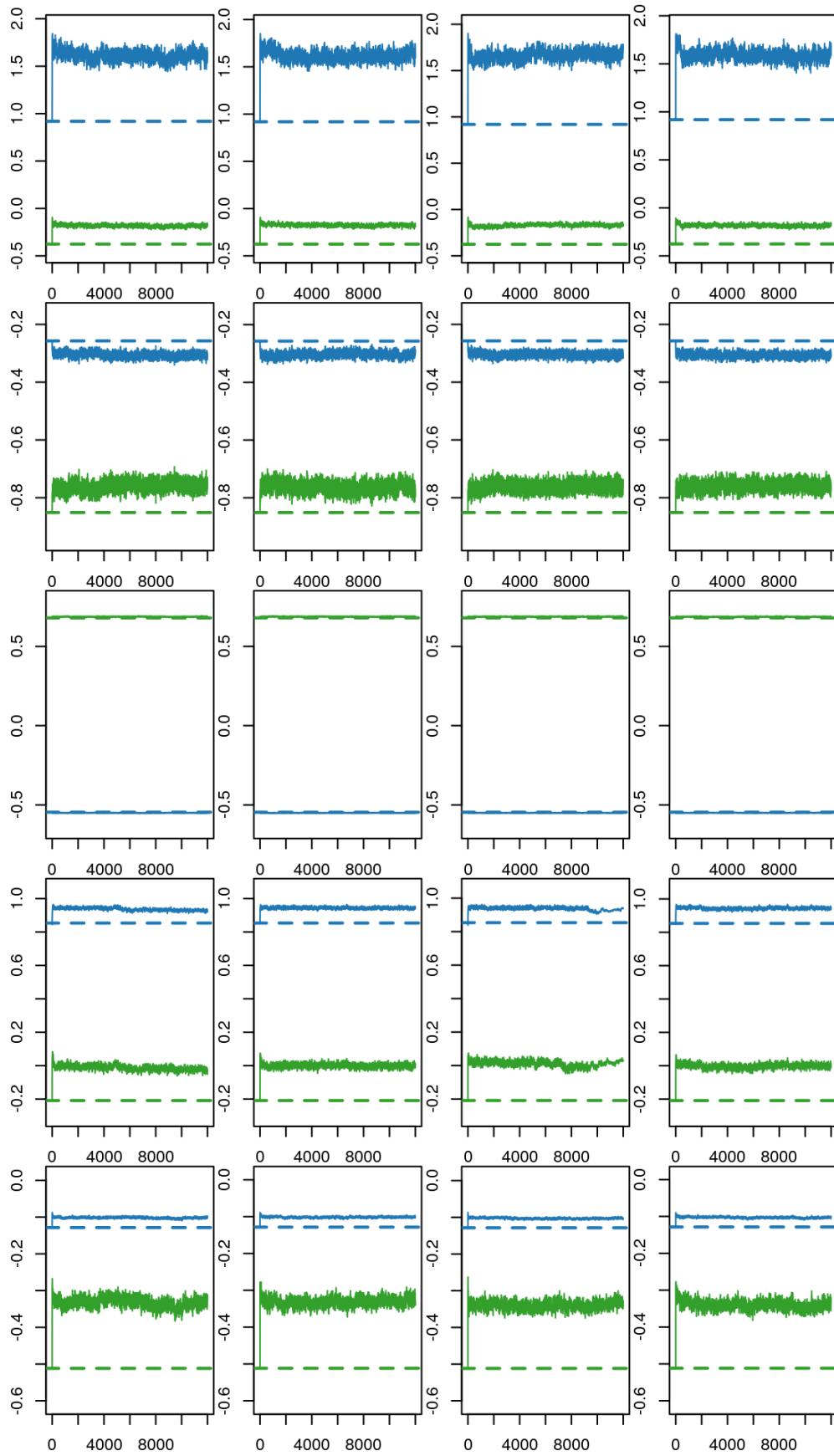


Figure 26: Evolution of the counter and parenting trait values in each rep with linked genetic variation and no viability selection

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

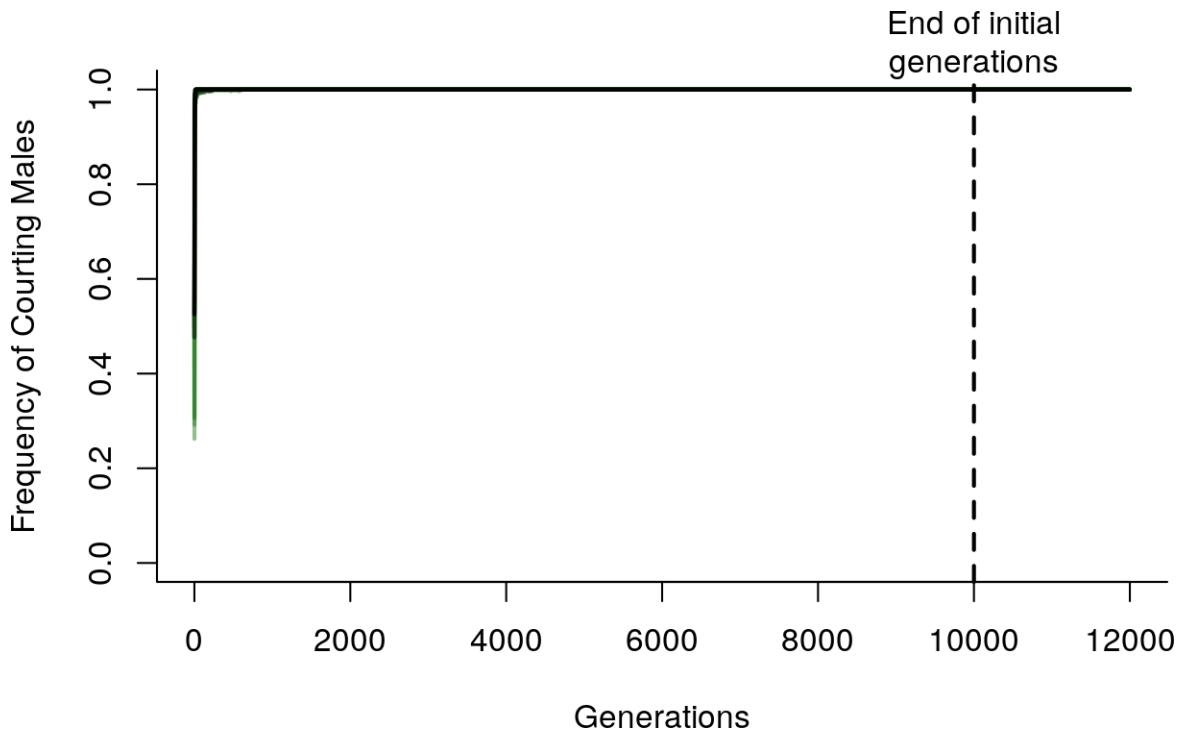


Figure 27: Frequency of the courter morph with supergenes (each color represents a different replicate)

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

Table 13: Frequency of courters with supergenes in final generation

	CounterFreq	CounterW	NonCounterW
courter_supergene_1_summary.txt_1	1	1.90249	0
courter_supergene_1_summary.txt_2	1	2.01826	0
courter_supergene_1_summary.txt_3	1	1.96245	0
courter_supergene_1_summary.txt_4	1	1.96063	0
courter_supergene_2_summary.txt_1	1	2.00201	0
courter_supergene_2_summary.txt_2	1	2.07708	0
courter_supergene_2_summary.txt_3	1	1.87902	0

	CounterFreq	CounterW	NonCounterW
counter_supergene_2_summary.txt_4	1	1.97426	0
counter_supergene_3_summary.txt_1	1	2.14871	0
counter_supergene_3_summary.txt_2	1	2.08787	0
counter_supergene_3_summary.txt_3	1	2.03061	0
counter_supergene_3_summary.txt_4	1	1.92802	0
counter_supergene_4_summary.txt_1	1	2.00000	0
counter_supergene_4_summary.txt_2	1	1.86567	0
counter_supergene_4_summary.txt_3	1	1.93050	0
counter_supergene_4_summary.txt_4	1	1.93050	0
counter_supergene_5_summary.txt_1	1	1.88679	0
counter_supergene_5_summary.txt_2	1	2.04918	0
counter_supergene_5_summary.txt_3	1	2.02429	0
counter_supergene_5_summary.txt_4	1	2.02020	0

Looking at the evolution of the trait values:

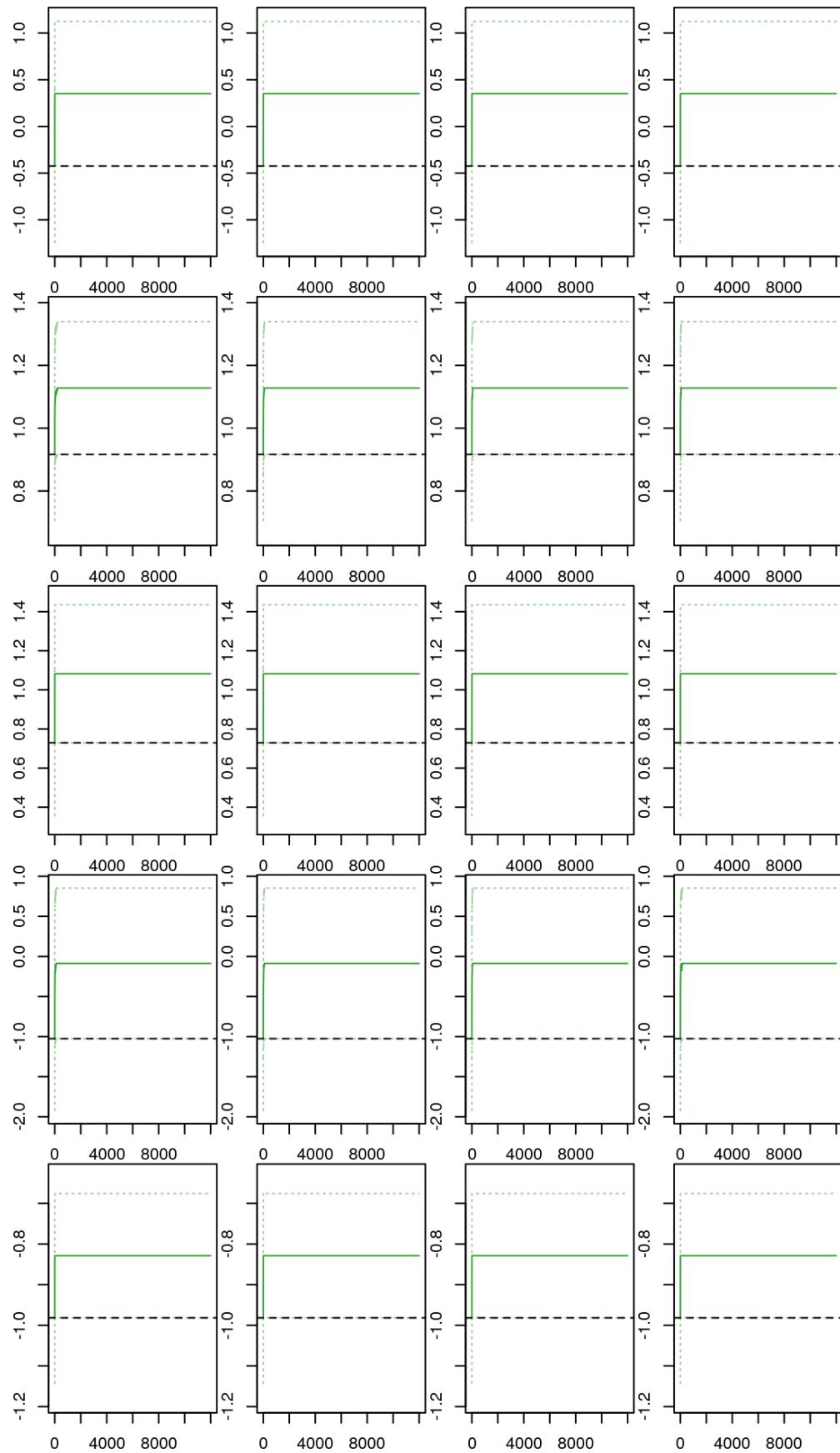


Figure 28: Evolution of courtship trait with a supergene. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

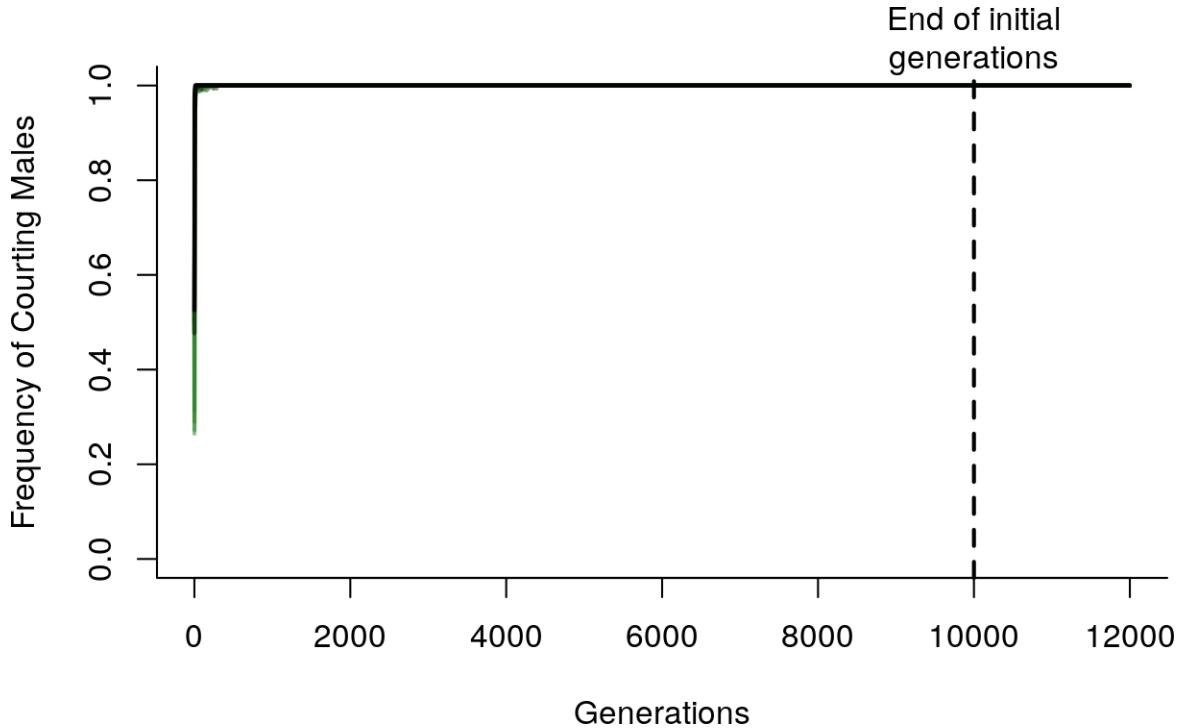


Figure 29: Frequency of the counter morph with supergenes without viability selection (each color represents a different replicate)

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

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

	CounterFreq	CounterW	NonCounterW
counter_supergene_novs_1_summary.txt_1	1	1.98413	0
counter_supergene_novs_1_summary.txt_2	1	2.02840	0
counter_supergene_novs_1_summary.txt_3	1	1.98413	0
counter_supergene_novs_1_summary.txt_4	1	2.00401	0
counter_supergene_novs_2_summary.txt_1	1	1.98020	0
counter_supergene_novs_2_summary.txt_2	1	1.95312	0
counter_supergene_novs_2_summary.txt_3	1	1.99601	0
counter_supergene_novs_2_summary.txt_4	1	2.05761	0
counter_supergene_novs_3_summary.txt_1	1	1.96464	0
counter_supergene_novs_3_summary.txt_2	1	2.02840	0
counter_supergene_novs_3_summary.txt_3	1	2.00401	0
counter_supergene_novs_3_summary.txt_4	1	1.96078	0
counter_supergene_novs_4_summary.txt_1	1	2.03666	0
counter_supergene_novs_4_summary.txt_2	1	2.09205	0
counter_supergene_novs_4_summary.txt_3	1	2.03252	0
counter_supergene_novs_4_summary.txt_4	1	1.96078	0
counter_supergene_novs_5_summary.txt_1	1	1.91205	0
counter_supergene_novs_5_summary.txt_2	1	1.98020	0
counter_supergene_novs_5_summary.txt_3	1	2.00000	0

	CourterFreq	CourterW	NonCourterW
courter_supergene_novs_5_summary.txt_4	1	1.98413	0

Looking at the evolution of the trait values:

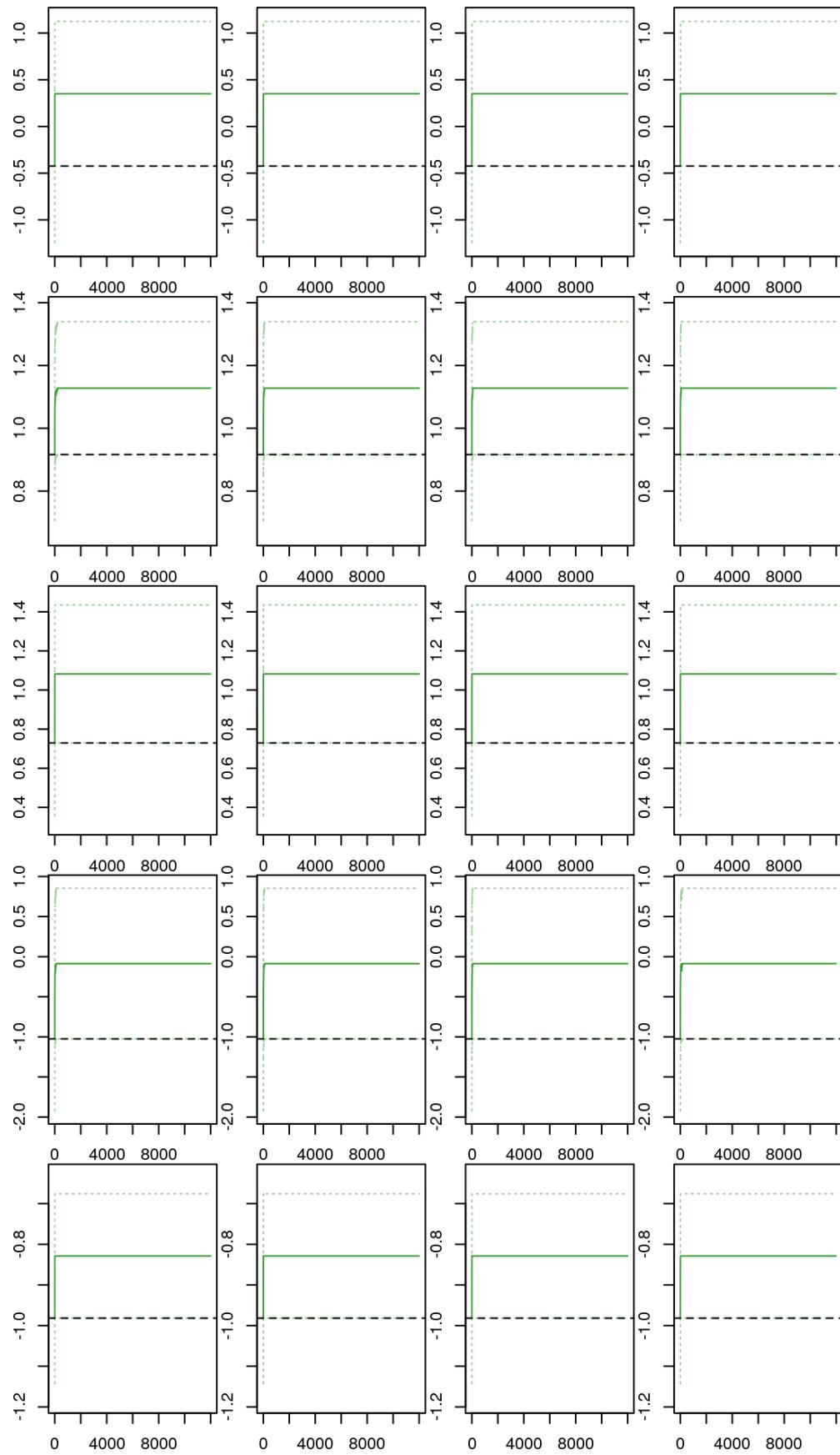


Figure 30: Evolution of courtship trait with a supergene and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Parental trait

With viability selection

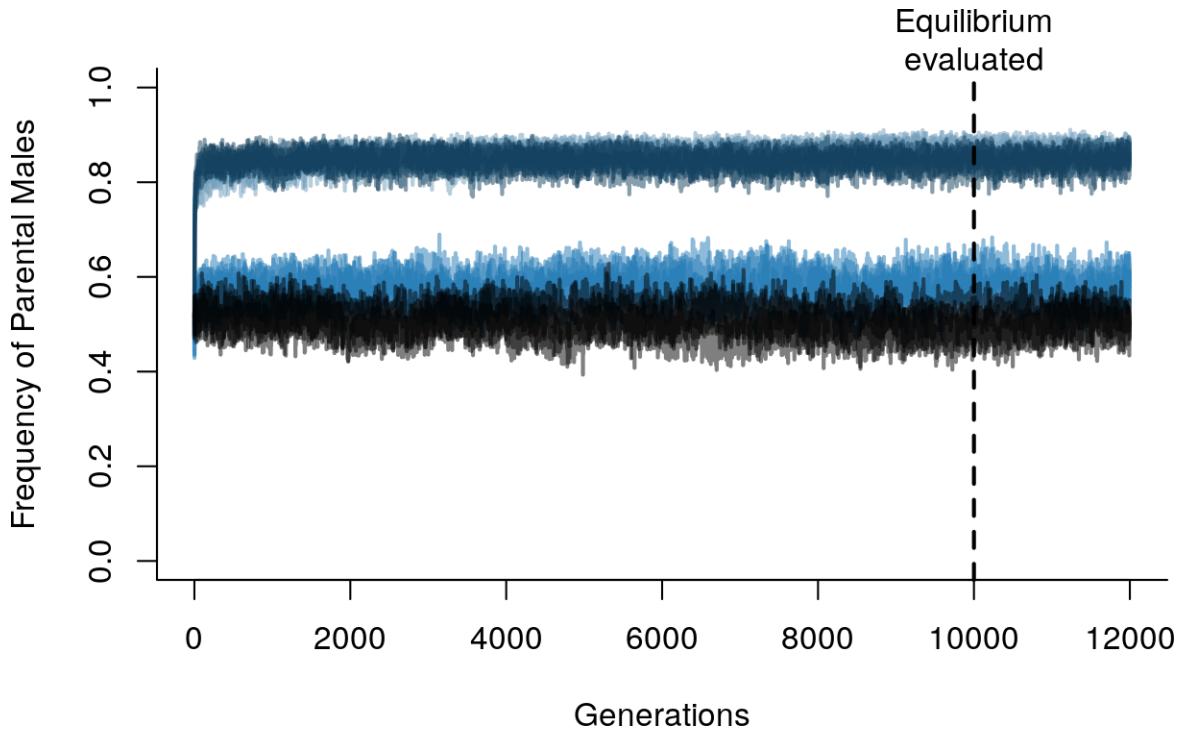


Figure 31: Frequency of parent morph with supergenes (each color represents a different replicate)

Table 15: Frequency of parents with supergenes in final generation

	ParentFreq	ParentW	NonParentW
parent_supergene_1_summary.txt_1	0.882105	1.70406	0.910714
parent_supergene_1_summary.txt_2	0.868787	1.70252	0.651515
parent_supergene_1_summary.txt_3	0.875510	1.67599	0.885246
parent_supergene_1_summary.txt_4	0.885106	1.77404	1.055560
parent_supergene_2_summary.txt_1	0.590814	1.55830	0.331633
parent_supergene_2_summary.txt_2	0.552000	1.51449	0.352679
parent_supergene_2_summary.txt_3	0.586345	1.53425	0.359223
parent_supergene_2_summary.txt_4	0.580247	1.68440	0.338235
parent_supergene_3_summary.txt_1	0.860000	1.56279	0.600000
parent_supergene_3_summary.txt_2	0.844181	1.57009	0.734177
parent_supergene_3_summary.txt_3	0.848861	1.81707	0.452055
parent_supergene_3_summary.txt_4	0.861057	1.58409	0.718310
parent_supergene_4_summary.txt_1	0.505071	1.47177	0.383673
parent_supergene_4_summary.txt_2	0.513185	1.51383	0.225000
parent_supergene_4_summary.txt_3	0.474849	1.30085	0.218391
parent_supergene_4_summary.txt_4	0.504132	1.50410	0.279167
parent_supergene_5_summary.txt_1	0.823183	1.54177	0.555556
parent_supergene_5_summary.txt_2	0.857977	1.61224	0.465753
parent_supergene_5_summary.txt_3	0.838384	1.64096	0.575000
parent_supergene_5_summary.txt_4	0.832998	1.53623	0.759036

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.

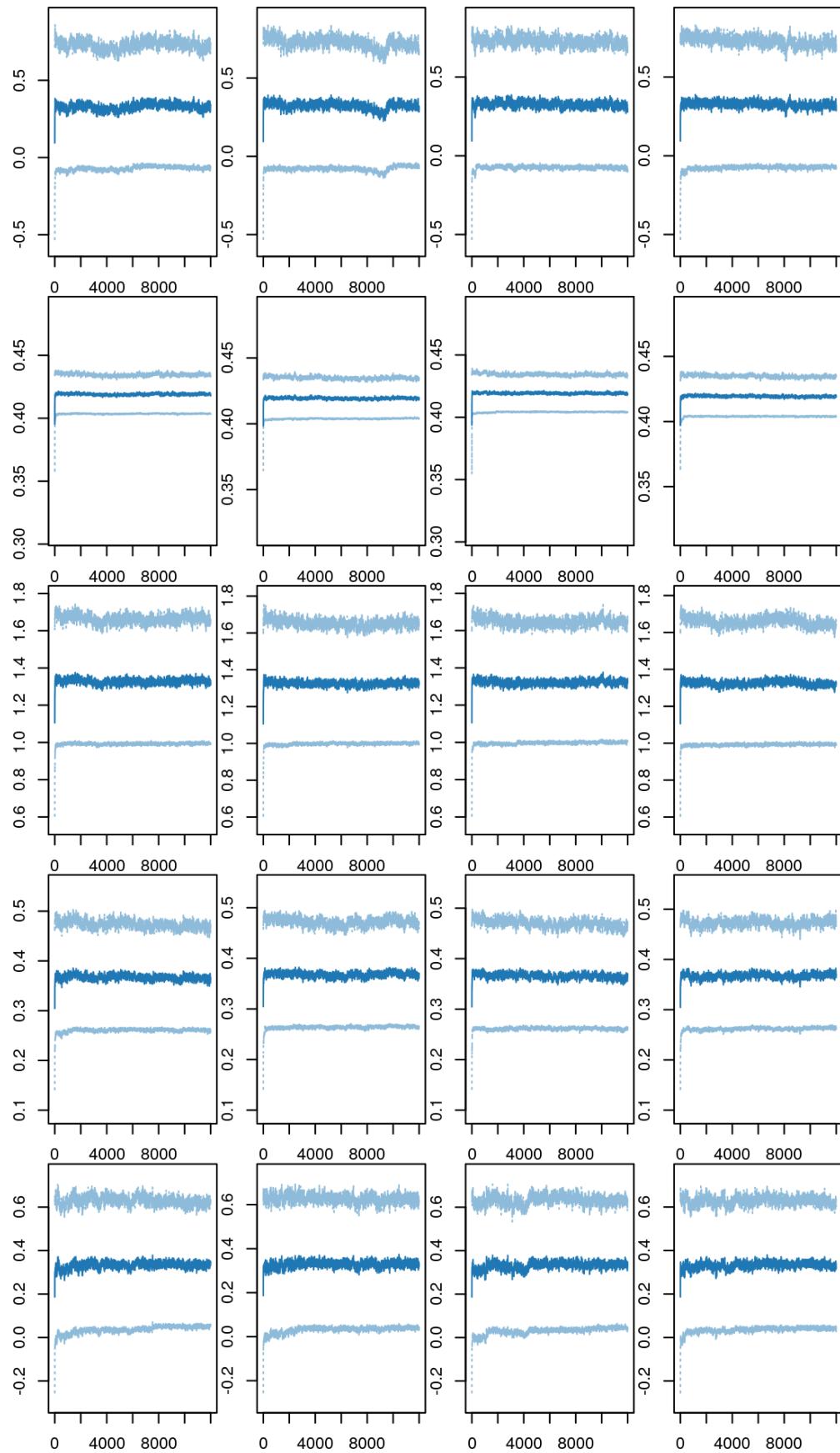


Figure 32: Evolution of parenting trait values with a supergene. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

Without viability selection

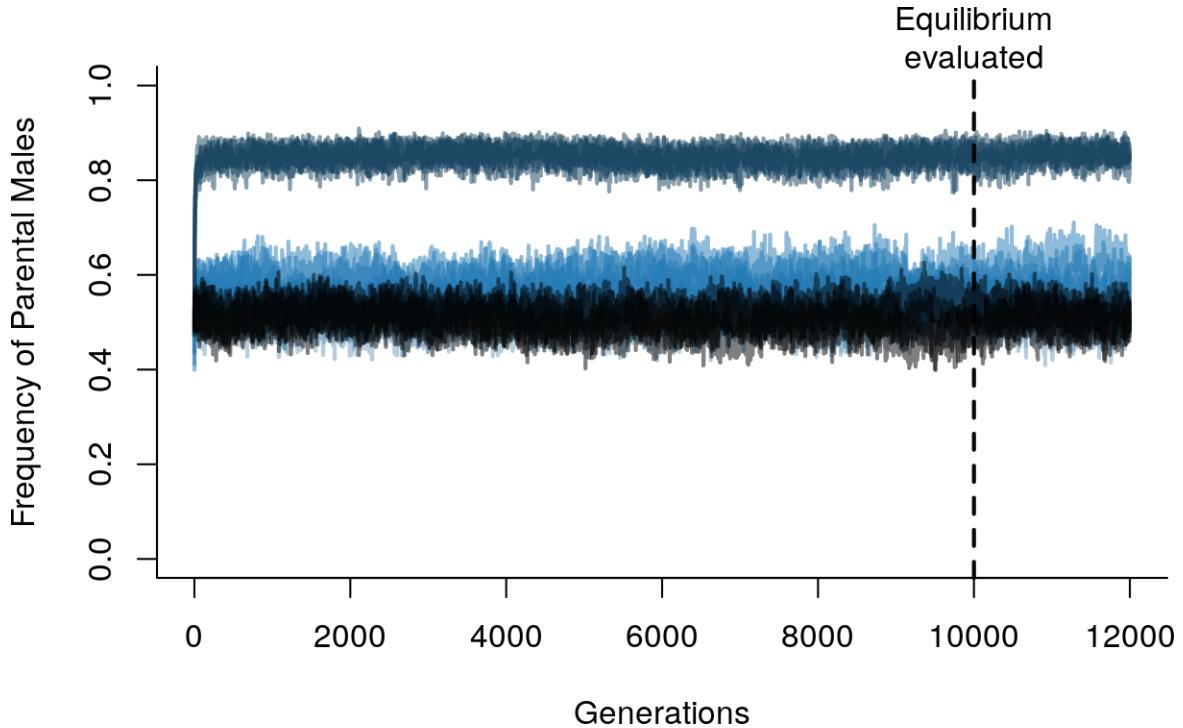


Figure 33: Frequency of parent morph with supergenes without viability selection (each color represents a different replicate)

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

	ParentFreq	ParentW	NonParentW
parent_supergene_novs_1_summary.txt_1	0.531828	1.59459	0.451754
parent_supergene_novs_1_summary.txt_2	0.506198	1.46939	0.263598
parent_supergene_novs_1_summary.txt_3	0.515528	1.48594	0.256410
parent_supergene_novs_1_summary.txt_4	0.528046	1.49451	0.397541
parent_supergene_novs_2_summary.txt_1	0.628231	1.45253	0.347594
parent_supergene_novs_2_summary.txt_2	0.500000	1.36515	0.331950
parent_supergene_novs_2_summary.txt_3	0.545455	1.61364	0.404545
parent_supergene_novs_2_summary.txt_4	0.586538	1.56721	0.297674
parent_supergene_novs_3_summary.txt_1	0.853707	1.60094	0.630137
parent_supergene_novs_3_summary.txt_2	0.852772	1.50897	0.311688
parent_supergene_novs_3_summary.txt_3	0.852823	1.55083	0.863014
parent_supergene_novs_3_summary.txt_4	0.824242	1.58824	0.643678
parent_supergene_novs_4_summary.txt_1	0.516194	1.51765	0.255230
parent_supergene_novs_4_summary.txt_2	0.486141	1.49561	0.344398
parent_supergene_novs_4_summary.txt_3	0.486869	1.31535	0.374016
parent_supergene_novs_4_summary.txt_4	0.501002	1.47390	0.280000
parent_supergene_novs_5_summary.txt_1	0.849130	1.47836	0.692308
parent_supergene_novs_5_summary.txt_2	0.833652	1.58716	0.758621
parent_supergene_novs_5_summary.txt_3	0.822266	1.54632	0.428571
parent_supergene_novs_5_summary.txt_4	0.817460	1.57039	0.782609

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.

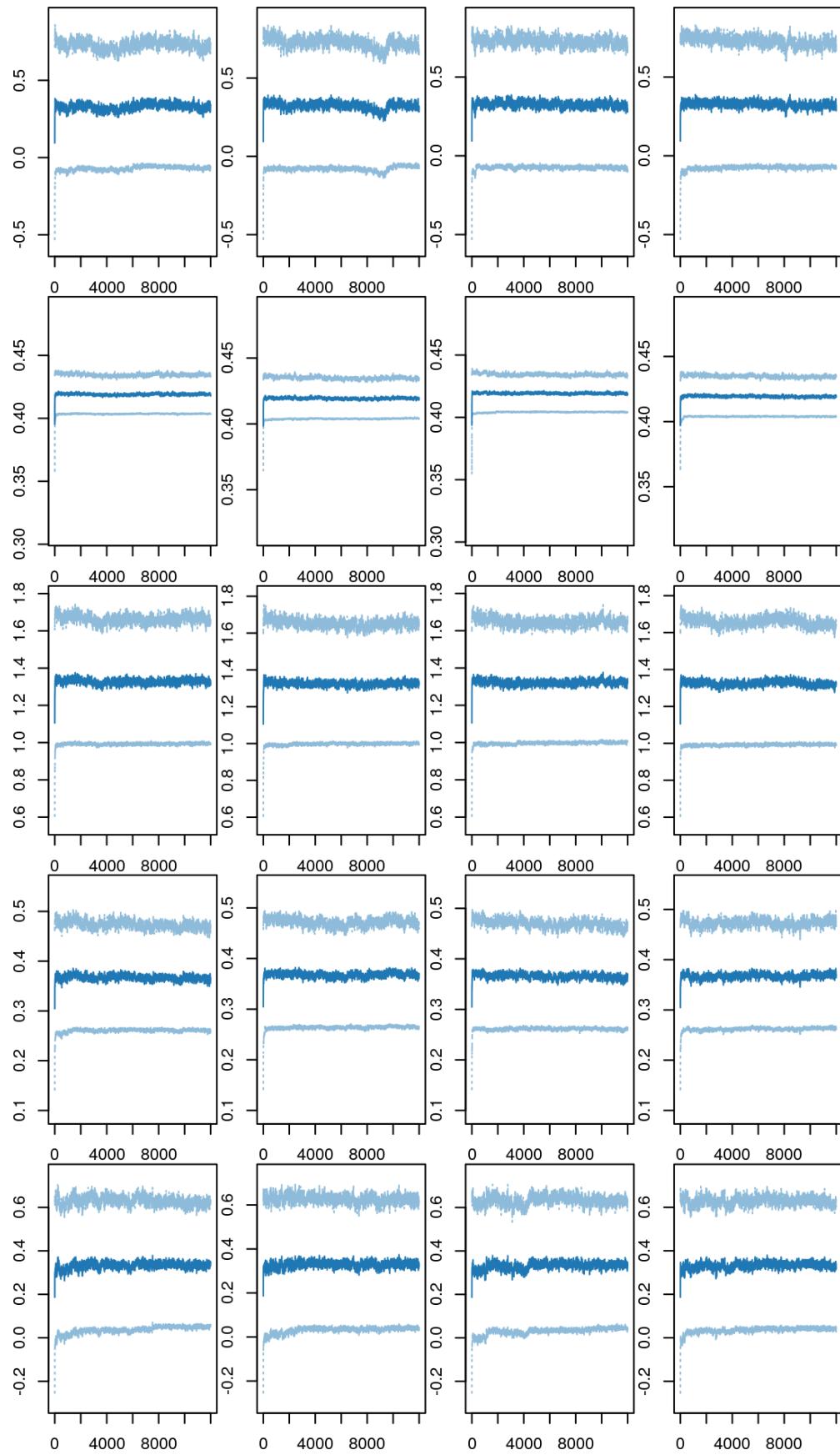


Figure 34: Evolution of parenting trait values with a supergene without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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.

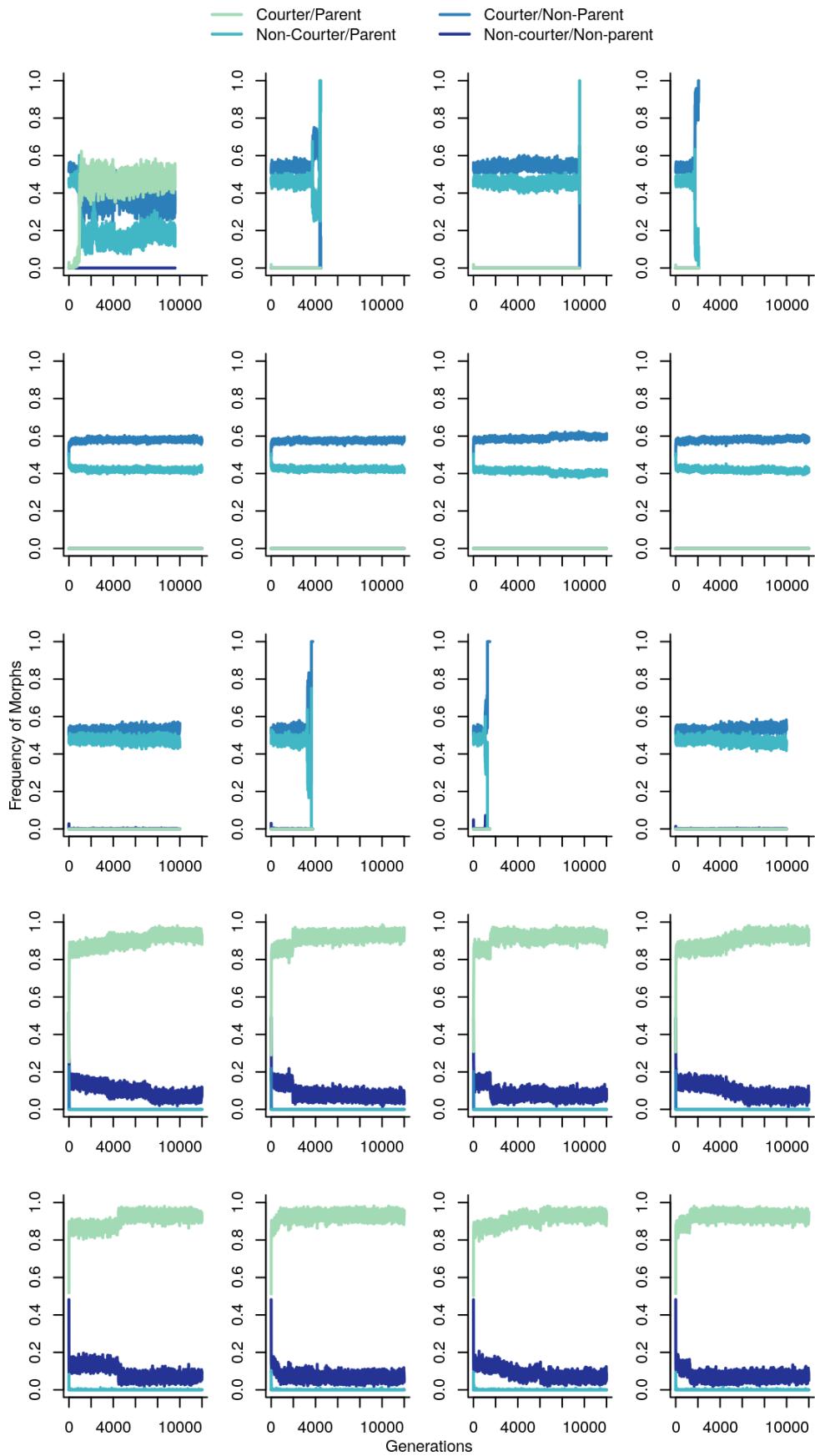


Figure 35: Frequency of the 4 morphs in each rep with supergenes

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	Par
parent-courter_supergene_1_summary.txt_1	9577	Pop0	657	336	321	939	
parent-courter_supergene_1_summary.txt_2	4470	Pop1	4	4	0	0	
parent-courter_supergene_1_summary.txt_3	9576	Pop2	8	3	5	4	
parent-courter_supergene_1_summary.txt_4	2074	Pop3	4	4	0	0	
parent-courter_supergene_2_summary.txt_1	11999	Pop0	942	454	488	1000	
parent-courter_supergene_2_summary.txt_2	11999	Pop1	944	467	477	1000	
parent-courter_supergene_2_summary.txt_3	11999	Pop2	908	452	456	1000	
parent-courter_supergene_2_summary.txt_4	11999	Pop3	936	460	476	1000	
parent-courter_supergene_3_summary.txt_1	10000	Pop0	757	388	369	845	
parent-courter_supergene_3_summary.txt_2	3749	Pop1	4	4	0	0	
parent-courter_supergene_3_summary.txt_3	1473	Pop2	4	4	0	0	
parent-courter_supergene_3_summary.txt_4	9999	Pop3	741	381	360	818	
parent-courter_supergene_4_summary.txt_1	11999	Pop0	939	456	483	1000	
parent-courter_supergene_4_summary.txt_2	11999	Pop1	944	479	465	1000	
parent-courter_supergene_4_summary.txt_3	11999	Pop2	935	468	467	1000	
parent-courter_supergene_4_summary.txt_4	11999	Pop3	938	460	478	1000	
parent-courter_supergene_5_summary.txt_1	11999	Pop0	951	465	486	1000	
parent-courter_supergene_5_summary.txt_2	11999	Pop1	942	489	453	1000	
parent-courter_supergene_5_summary.txt_3	11999	Pop2	952	521	431	996	
parent-courter_supergene_5_summary.txt_4	11999	Pop3	959	497	462	1000	

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a courter. 6 of those reps with variation went extinct before 10000 generations.

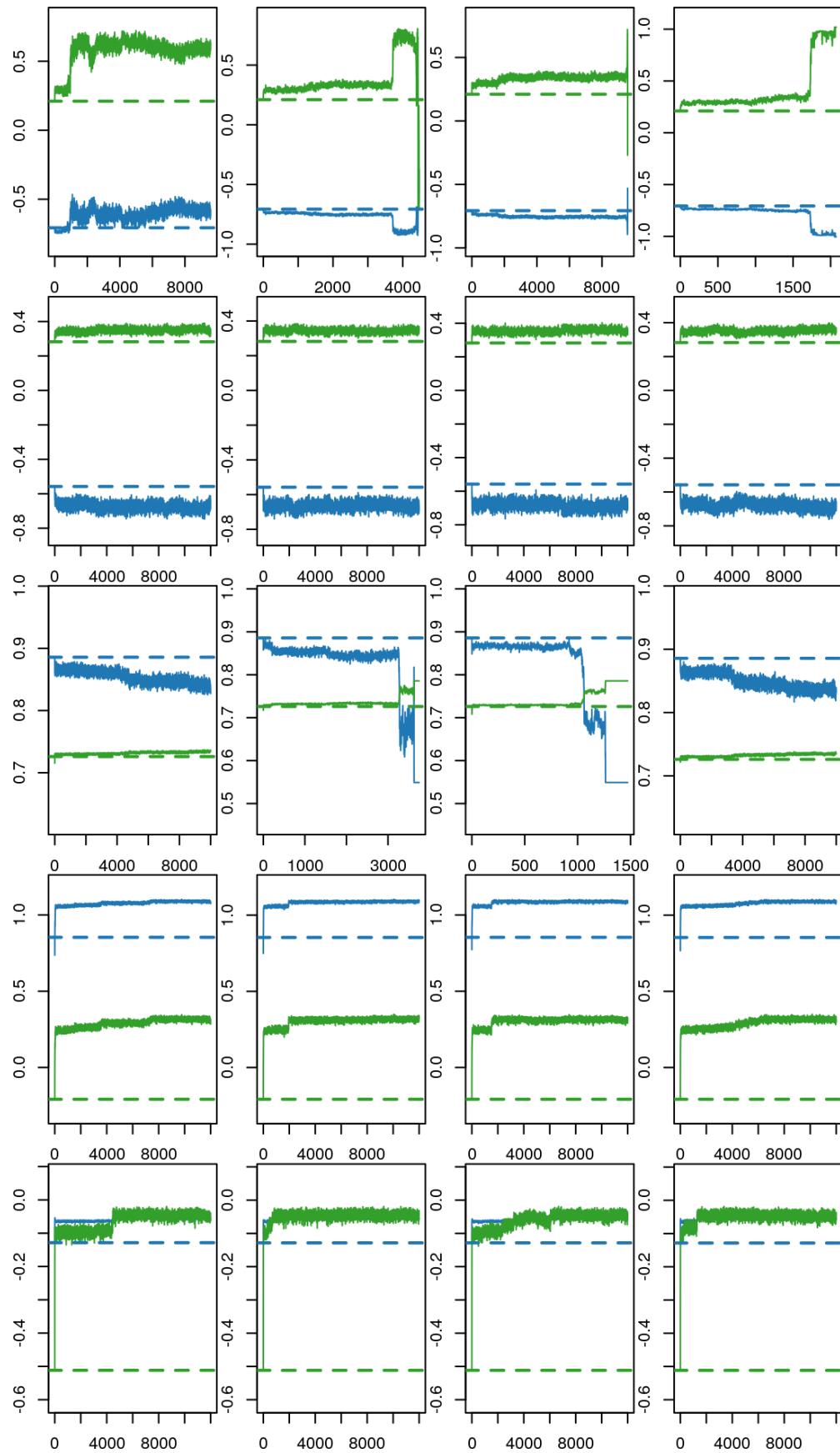


Figure 36: Evolution of the counter and parenting trait values in each rep with a supergene
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Without viability selection

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

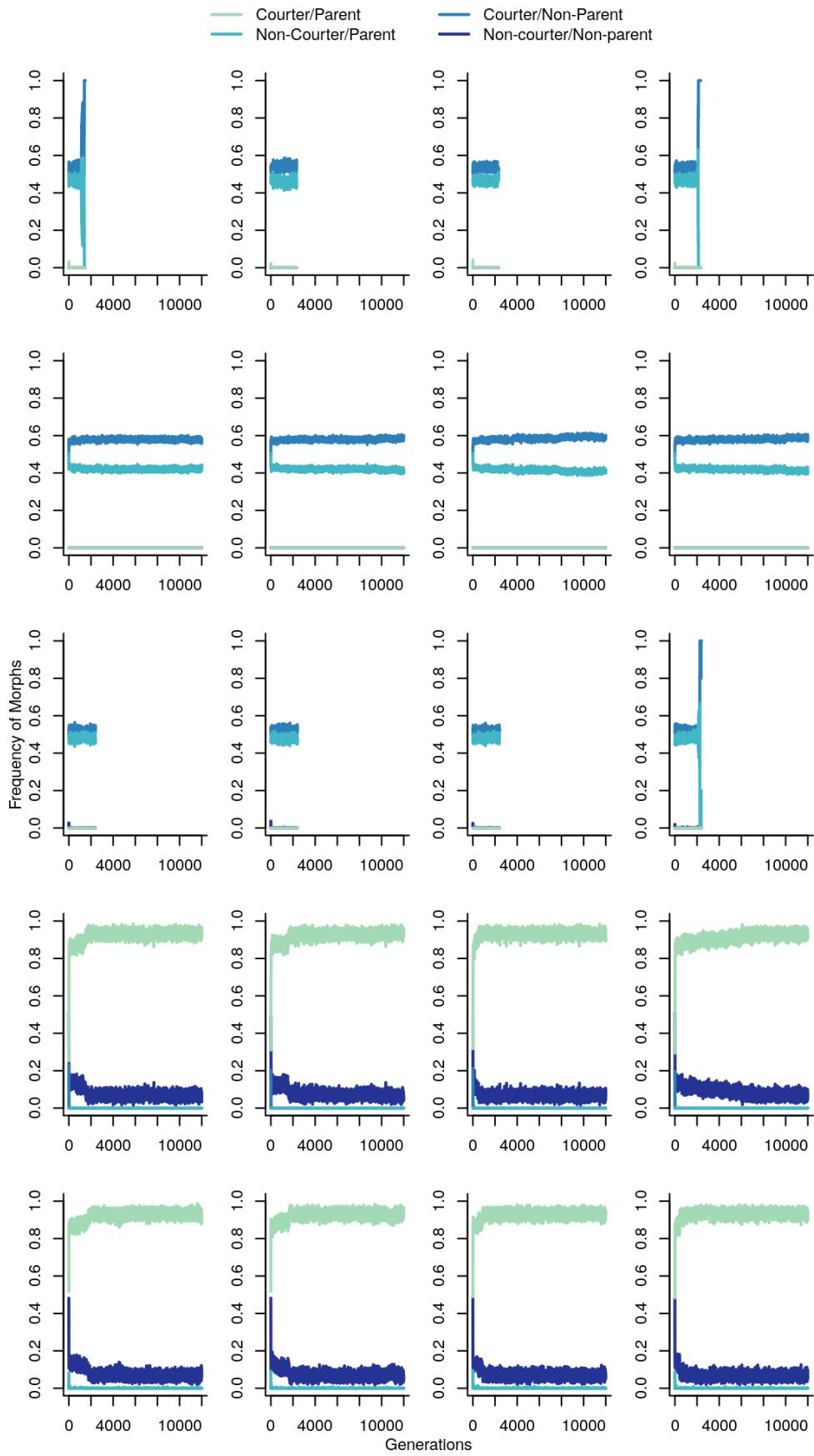


Figure 37: Frequency of the 4 morphs in each rep with supergenes without viability selection

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_supergene_novs_1_summary.txt_1	1483	Pop0	4	4	0	0
parent-courter_supergene_novs_1_summary.txt_2	2334	Pop1	744	386	358	841
parent-courter_supergene_novs_1_summary.txt_3	2334	Pop2	758	378	380	771
parent-courter_supergene_novs_1_summary.txt_4	2333	Pop3	4	1	3	4
parent-courter_supergene_novs_2_summary.txt_1	11999	Pop0	948	458	490	1000
parent-courter_supergene_novs_2_summary.txt_2	11999	Pop1	936	456	480	1000
parent-courter_supergene_novs_2_summary.txt_3	11999	Pop2	945	474	471	1000
parent-courter_supergene_novs_2_summary.txt_4	11999	Pop3	930	454	476	1000
parent-courter_supergene_novs_3_summary.txt_1	2409	Pop0	966	499	467	1000
parent-courter_supergene_novs_3_summary.txt_2	2409	Pop1	968	501	467	1000
parent-courter_supergene_novs_3_summary.txt_3	2409	Pop2	976	504	472	1000
parent-courter_supergene_novs_3_summary.txt_4	2408	Pop3	7	1	6	4
parent-courter_supergene_novs_4_summary.txt_1	11999	Pop0	942	483	459	1000
parent-courter_supergene_novs_4_summary.txt_2	11999	Pop1	938	473	465	1000
parent-courter_supergene_novs_4_summary.txt_3	11999	Pop2	949	474	475	1000
parent-courter_supergene_novs_4_summary.txt_4	11999	Pop3	951	458	493	1000
parent-courter_supergene_novs_5_summary.txt_1	11999	Pop0	936	458	478	1000
parent-courter_supergene_novs_5_summary.txt_2	11999	Pop1	949	480	469	1000
parent-courter_supergene_novs_5_summary.txt_3	11999	Pop2	942	471	471	1000
parent-courter_supergene_novs_5_summary.txt_4	11999	Pop3	944	472	472	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.

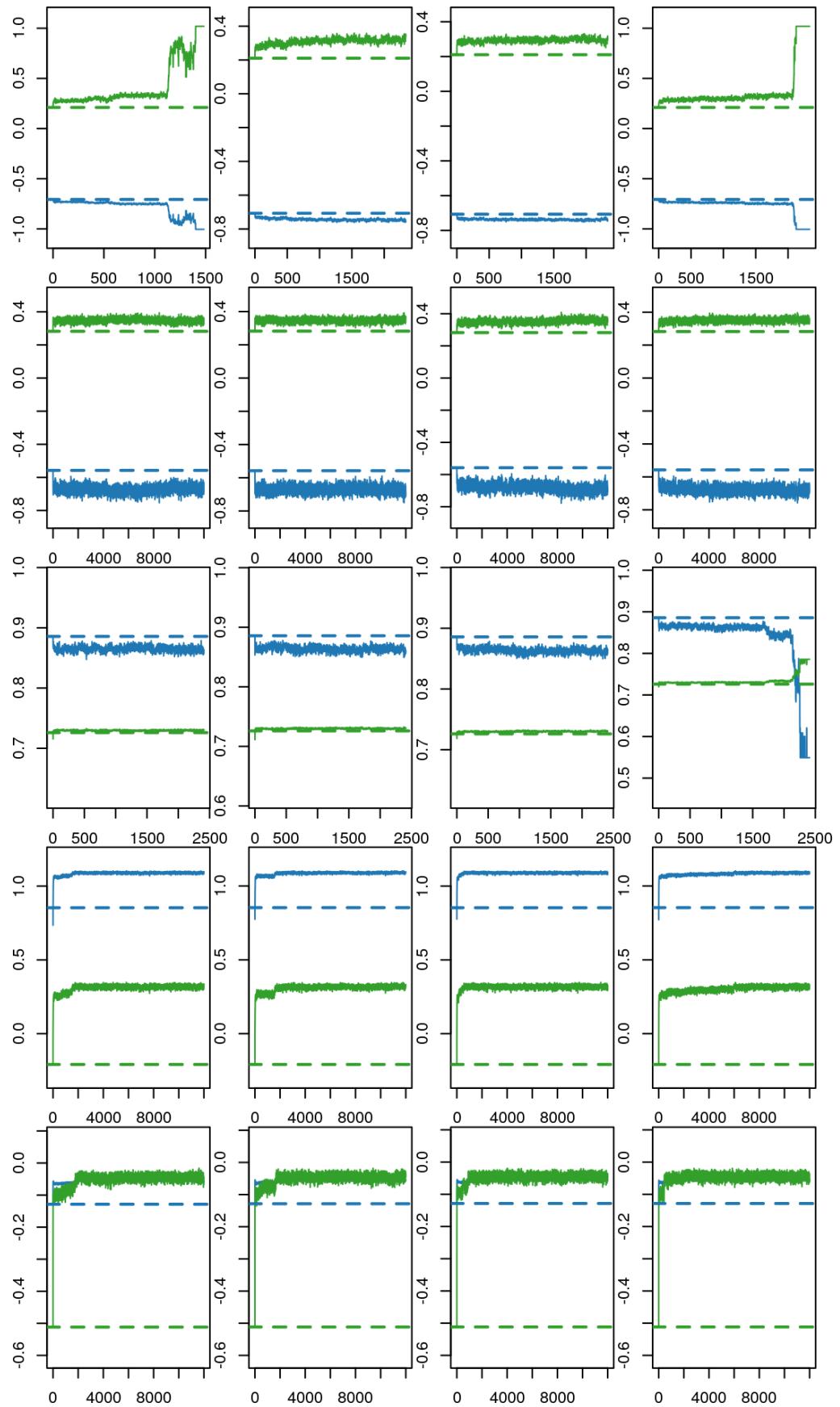


Figure 38: Evolution of the counter and parenting trait values in each rep with a supergene without viability selection

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.