

# Density-dependent ARTs Analysis

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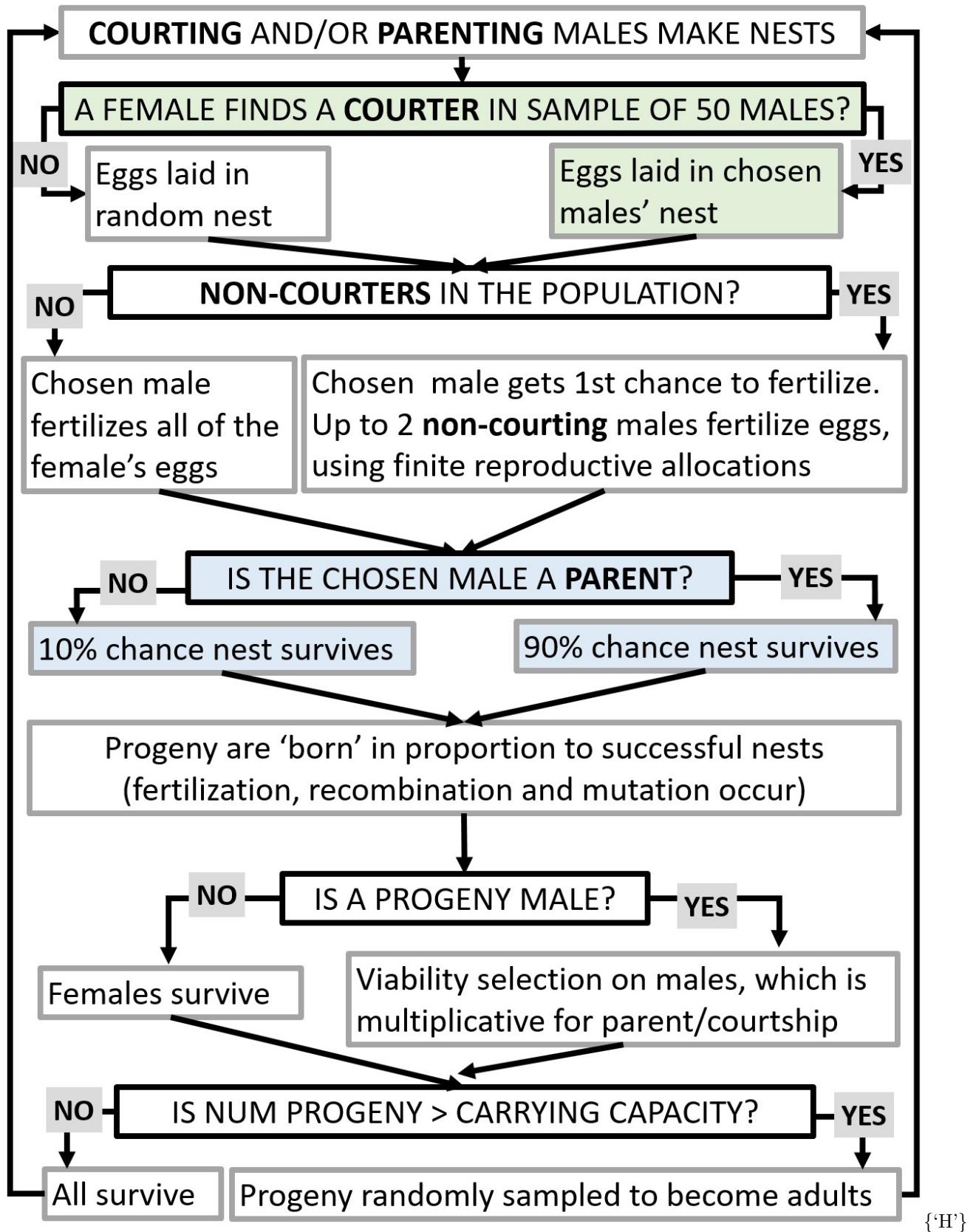
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The purpose of this model is to understand how genetic architectures of alternative reproductive tactics impact their maintenance in populations. I'm using an individual-based simulation model with different selection scenarios, types of alternative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

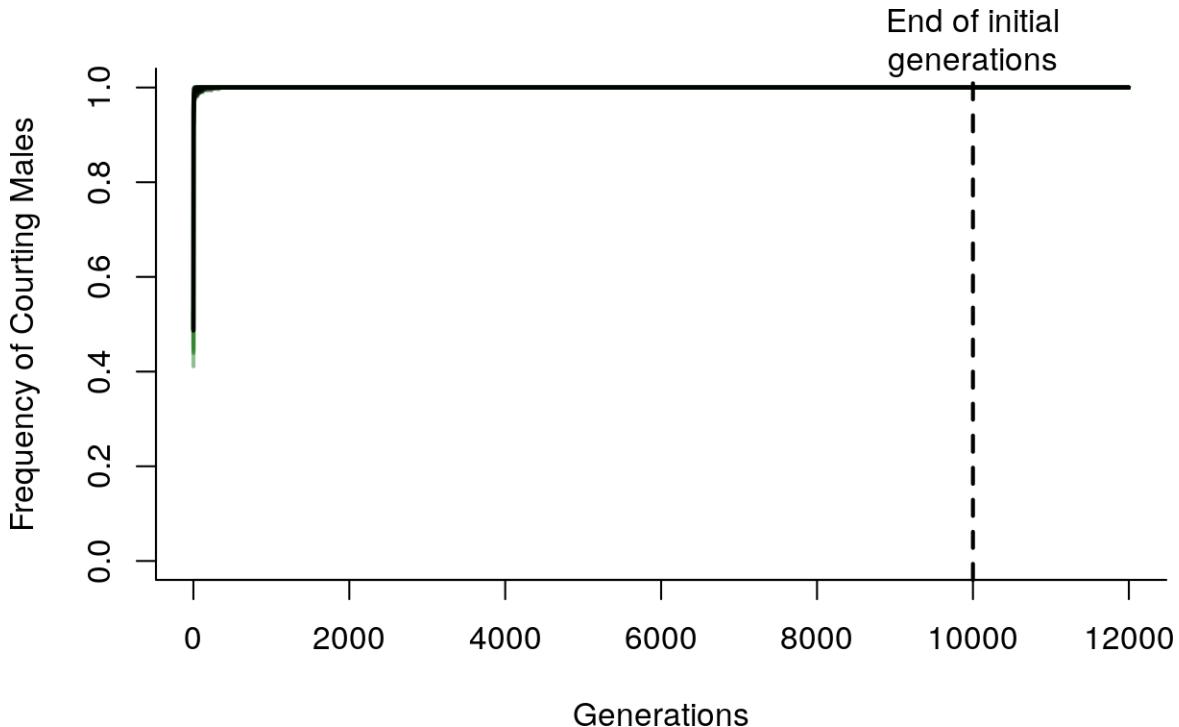


Figure 1: Frequency of the counter morph with unlinked additive genetic variances in all of the replicates

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	1.99192	0
counter_unlinked_1_summary.txt_2	1	2.05785	0
counter_unlinked_1_summary.txt_3	1	2.16558	0
counter_unlinked_1_summary.txt_4	1	2.08632	0
counter_unlinked_2_summary.txt_1	1	2.03055	0
counter_unlinked_2_summary.txt_2	1	1.98805	0
counter_unlinked_2_summary.txt_3	1	1.98606	0
counter_unlinked_2_summary.txt_4	1	1.92100	0
counter_unlinked_3_summary.txt_1	1	1.99200	0
counter_unlinked_3_summary.txt_2	1	1.97222	0
counter_unlinked_3_summary.txt_3	1	1.98802	0
counter_unlinked_3_summary.txt_4	1	2.04303	0
counter_unlinked_4_summary.txt_1	1	1.97813	0
counter_unlinked_4_summary.txt_2	1	2.03049	0
counter_unlinked_4_summary.txt_3	1	2.04938	0
counter_unlinked_4_summary.txt_4	1	2.00000	0
counter_unlinked_5_summary.txt_1	1	1.98807	0
counter_unlinked_5_summary.txt_2	1	1.98020	0
counter_unlinked_5_summary.txt_3	1	2.03666	0
counter_unlinked_5_summary.txt_4	1	1.99203	0

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

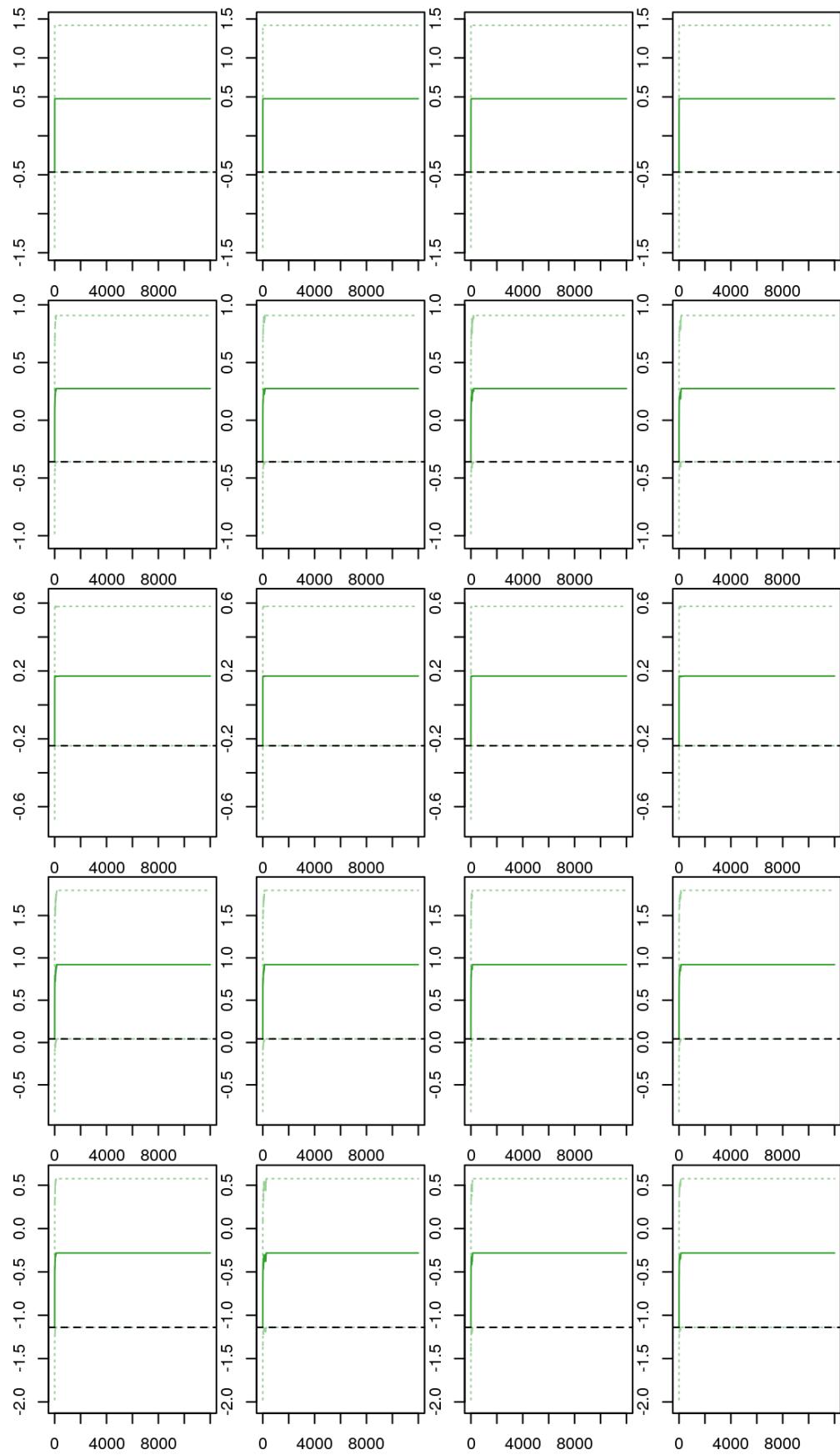


Figure 2: Evolution of courtship trait with unlinked loci. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

### Without viability selection

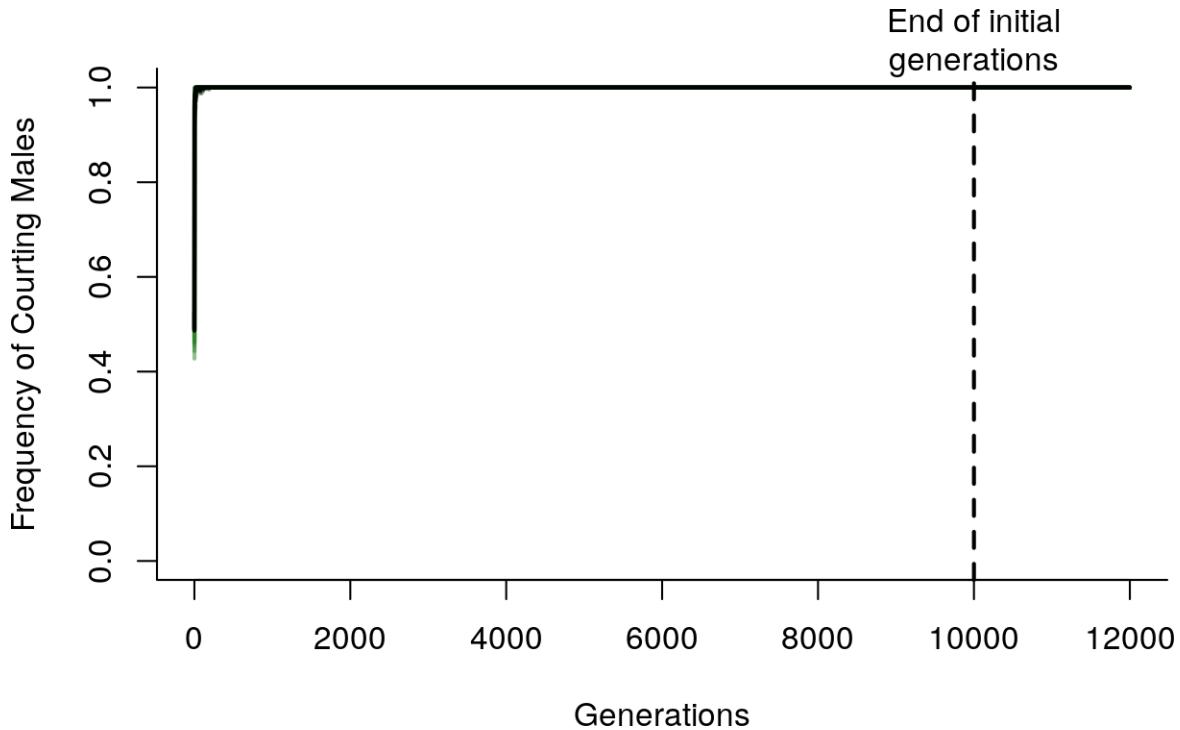


Figure 3: Frequency of the counter morph with unlinked additive genetic variances and without viability selection in all of the replicates

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	1.88679	0
counter_unlinked_novs_1_summary.txt_2	1	2.01207	0
counter_unlinked_novs_1_summary.txt_3	1	2.01613	0
counter_unlinked_novs_1_summary.txt_4	1	2.07900	0
counter_unlinked_novs_2_summary.txt_1	1	1.91939	0
counter_unlinked_novs_2_summary.txt_2	1	1.96850	0
counter_unlinked_novs_2_summary.txt_3	1	2.04499	0
counter_unlinked_novs_2_summary.txt_4	1	1.95695	0
counter_unlinked_novs_3_summary.txt_1	1	2.03252	0
counter_unlinked_novs_3_summary.txt_2	1	1.98807	0
counter_unlinked_novs_3_summary.txt_3	1	1.96078	0
counter_unlinked_novs_3_summary.txt_4	1	2.13220	0
counter_unlinked_novs_4_summary.txt_1	1	2.05339	0
counter_unlinked_novs_4_summary.txt_2	1	1.87617	0
counter_unlinked_novs_4_summary.txt_3	1	2.01613	0
counter_unlinked_novs_4_summary.txt_4	1	1.99203	0
counter_unlinked_novs_5_summary.txt_1	1	1.96850	0

	CourterFreq	CourterW	NonCourterW
courter_unlinked_novs_5_summary.txt_2	1	1.98020	0
courter_unlinked_novs_5_summary.txt_3	1	1.98413	0
courter_unlinked_novs_5_summary.txt_4	1	1.98807	0

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

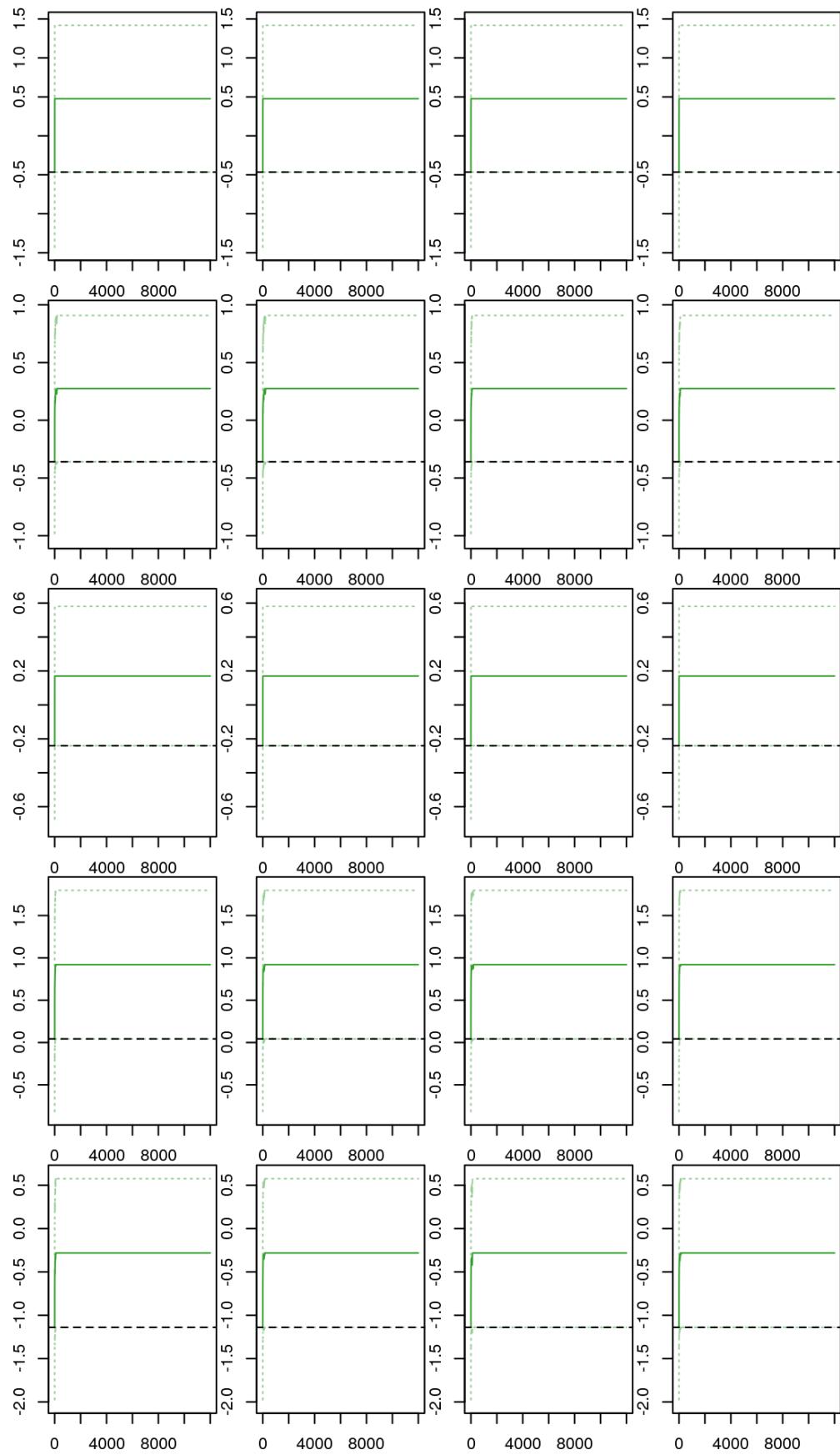


Figure 4: Evolution of courtship trait with unlinked loci and no viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

### 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

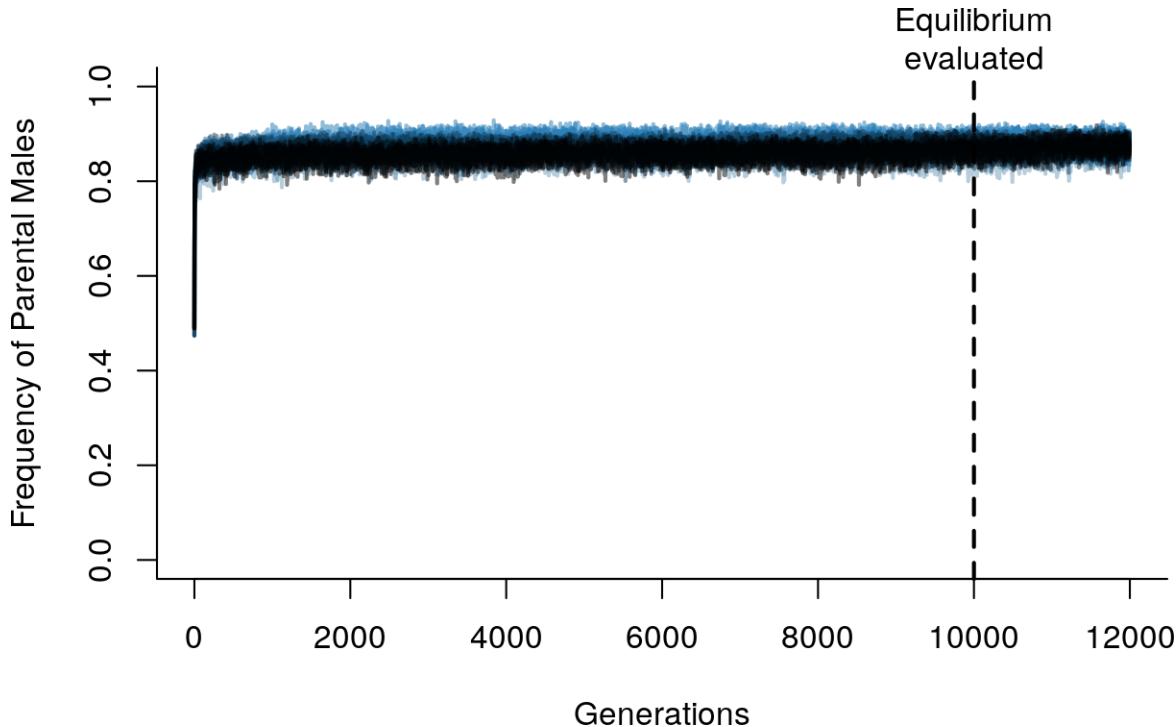


Figure 5: Frequency of parent morph with unlinked loci (each color represents a different replicate)

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	0.874510	1.66816	0.656250
parent_unlinked_1_summary.txt_2	0.873106	1.61822	0.731343
parent_unlinked_1_summary.txt_3	0.852823	1.63593	0.712329
parent_unlinked_1_summary.txt_4	0.886869	1.61048	1.035710
parent_unlinked_2_summary.txt_1	0.876953	1.59688	0.460317
parent_unlinked_2_summary.txt_2	0.894841	1.64967	0.867925
parent_unlinked_2_summary.txt_3	0.897590	1.65996	0.921569
parent_unlinked_2_summary.txt_4	0.903093	1.77854	1.063830
parent_unlinked_3_summary.txt_1	0.867220	1.71770	1.046880
parent_unlinked_3_summary.txt_2	0.890000	1.65843	0.727273
parent_unlinked_3_summary.txt_3	0.863158	1.66341	0.800000
parent_unlinked_3_summary.txt_4	0.885214	1.74286	0.711864
parent_unlinked_4_summary.txt_1	0.877712	1.57753	0.854839
parent_unlinked_4_summary.txt_2	0.864341	1.49552	0.885714

	ParentFreq	ParentW	NonParentW
parent_unlinked_4_summary.txt_3	0.877953	1.72646	0.870968
parent_unlinked_4_summary.txt_4	0.874755	1.58613	0.625000
parent_unlinked_5_summary.txt_1	0.568228	1.56989	0.231132
parent_unlinked_5_summary.txt_2	0.545082	1.47744	0.288288
parent_unlinked_5_summary.txt_3	0.600000	1.59933	0.358586
parent_unlinked_5_summary.txt_4	0.543825	1.44689	0.358079

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

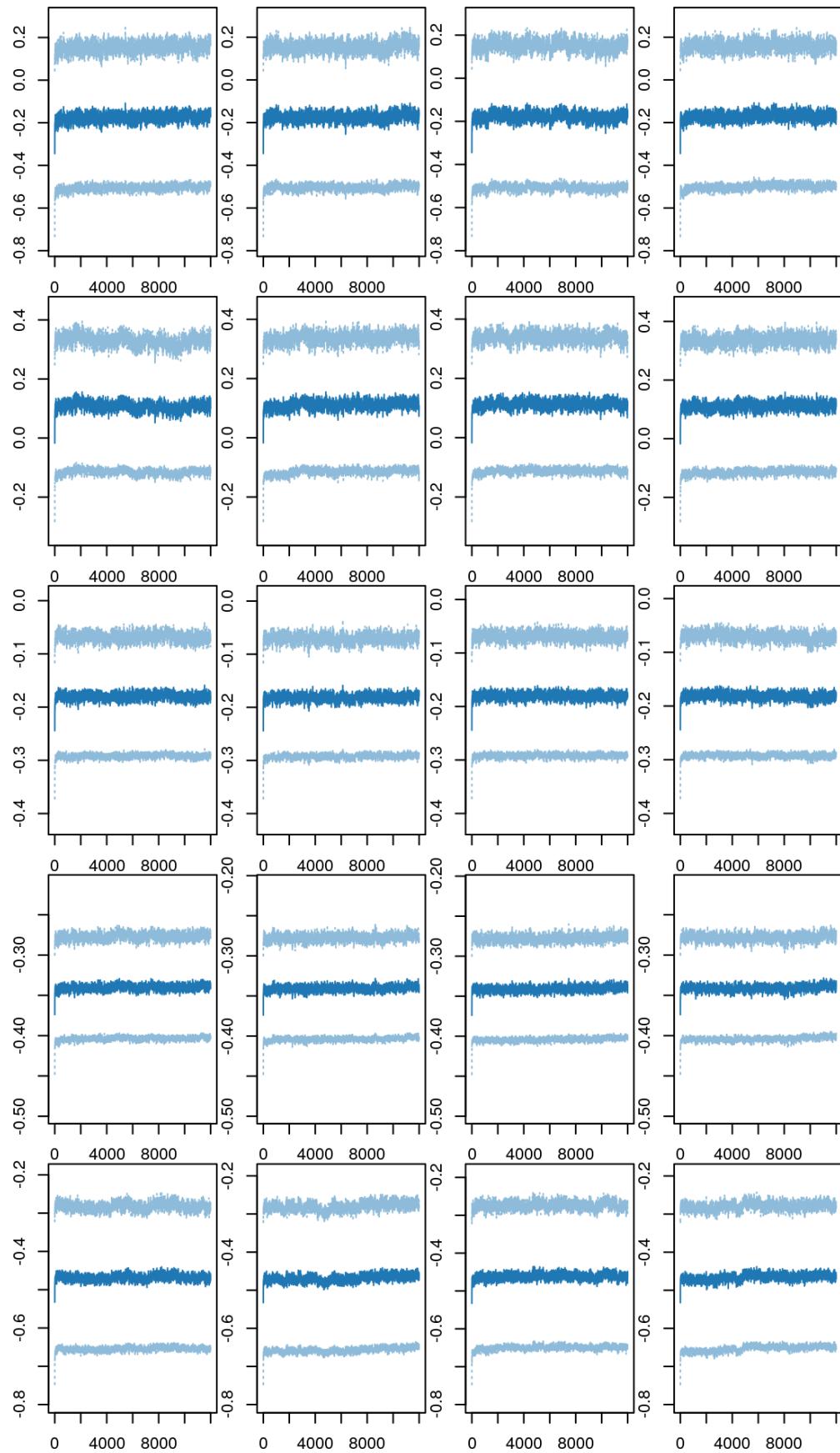


Figure 6: Evolution of parenting trait values with additive genetic variation. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

### Without viability selection

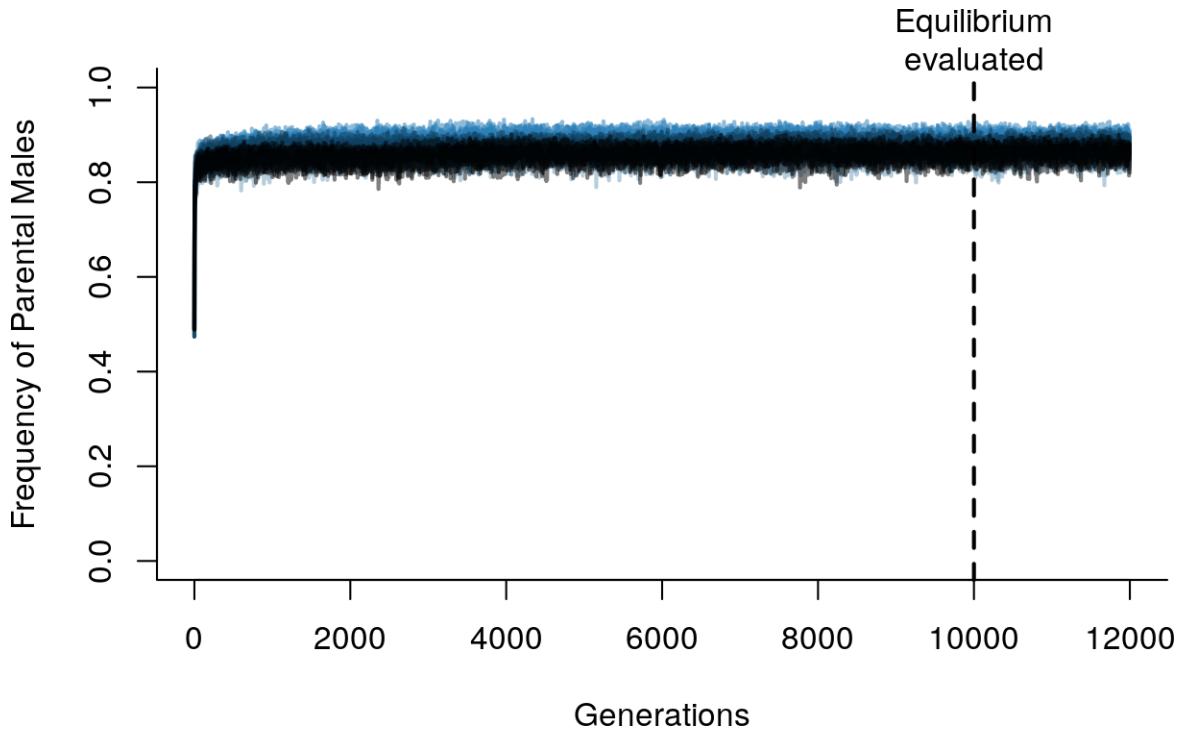


Figure 7: Frequency of parent morph with unlinked loci without viability selection for all replicates

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	0.842857	1.64891	0.766234
parent_unlinked_novs_1_summary.txt_2	0.860000	1.63256	0.600000
parent_unlinked_novs_1_summary.txt_3	0.861804	1.60134	0.652778
parent_unlinked_novs_1_summary.txt_4	0.870000	1.65057	0.969231
parent_unlinked_novs_2_summary.txt_1	0.890873	1.65256	0.545455
parent_unlinked_novs_2_summary.txt_2	0.878543	1.68203	0.633333
parent_unlinked_novs_2_summary.txt_3	0.892784	1.75289	0.615385
parent_unlinked_novs_2_summary.txt_4	0.884462	1.62162	0.741379
parent_unlinked_novs_3_summary.txt_1	0.885892	1.67681	1.036360
parent_unlinked_novs_3_summary.txt_2	0.888660	1.73550	0.648148
parent_unlinked_novs_3_summary.txt_3	0.878788	1.75172	0.616667
parent_unlinked_novs_3_summary.txt_4	0.879079	1.57205	0.730159
parent_unlinked_novs_4_summary.txt_1	0.860421	1.56889	0.452055
parent_unlinked_novs_4_summary.txt_2	0.862934	1.63311	0.464789
parent_unlinked_novs_4_summary.txt_3	0.837500	1.74876	0.512821
parent_unlinked_novs_4_summary.txt_4	0.867769	1.83333	0.781250
parent_unlinked_novs_5_summary.txt_1	0.543825	1.48352	0.213974
parent_unlinked_novs_5_summary.txt_2	0.609312	1.54817	0.202073
parent_unlinked_novs_5_summary.txt_3	0.532946	1.47273	0.236515
parent_unlinked_novs_5_summary.txt_4	0.522917	1.35458	0.362445

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

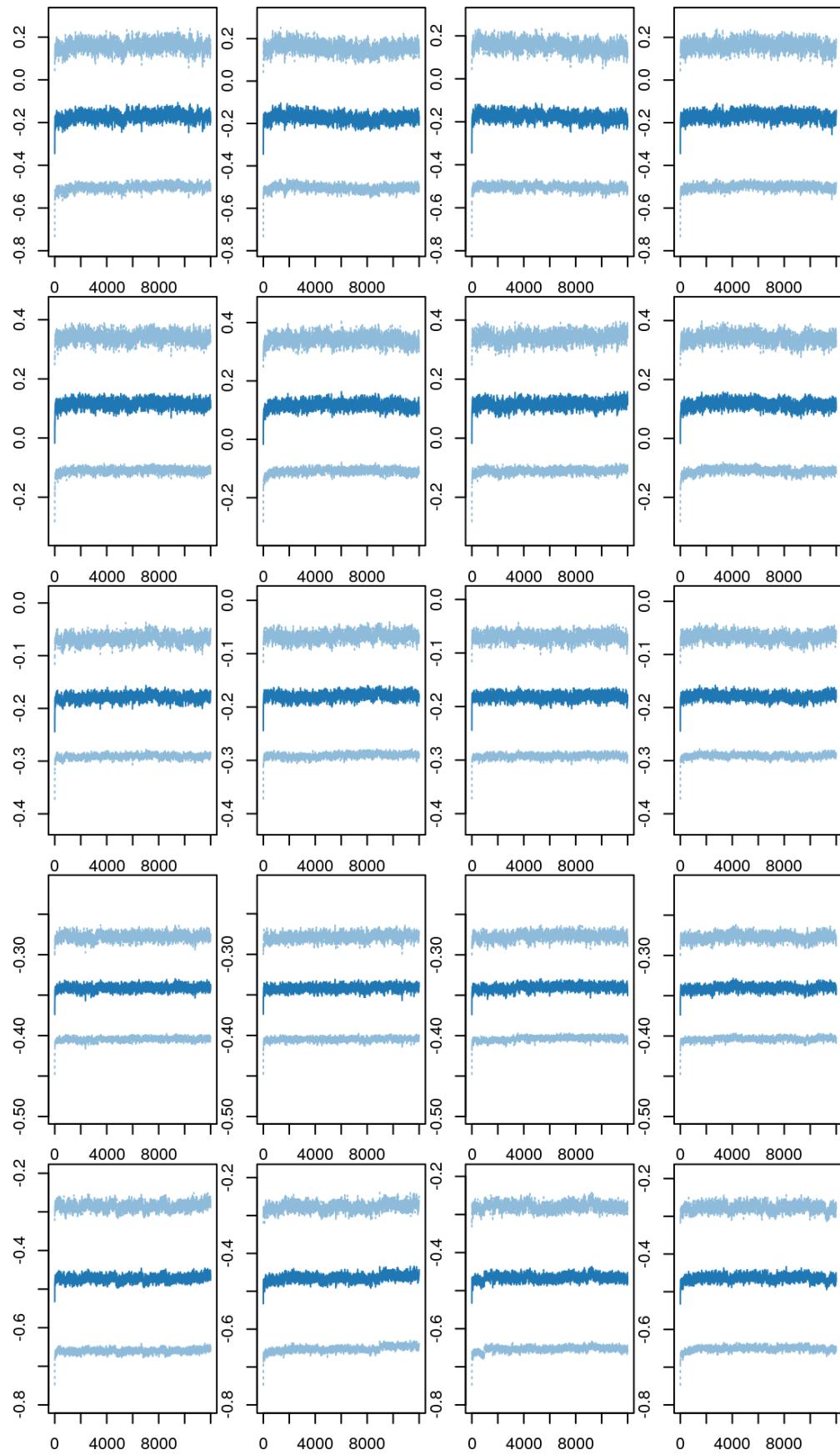
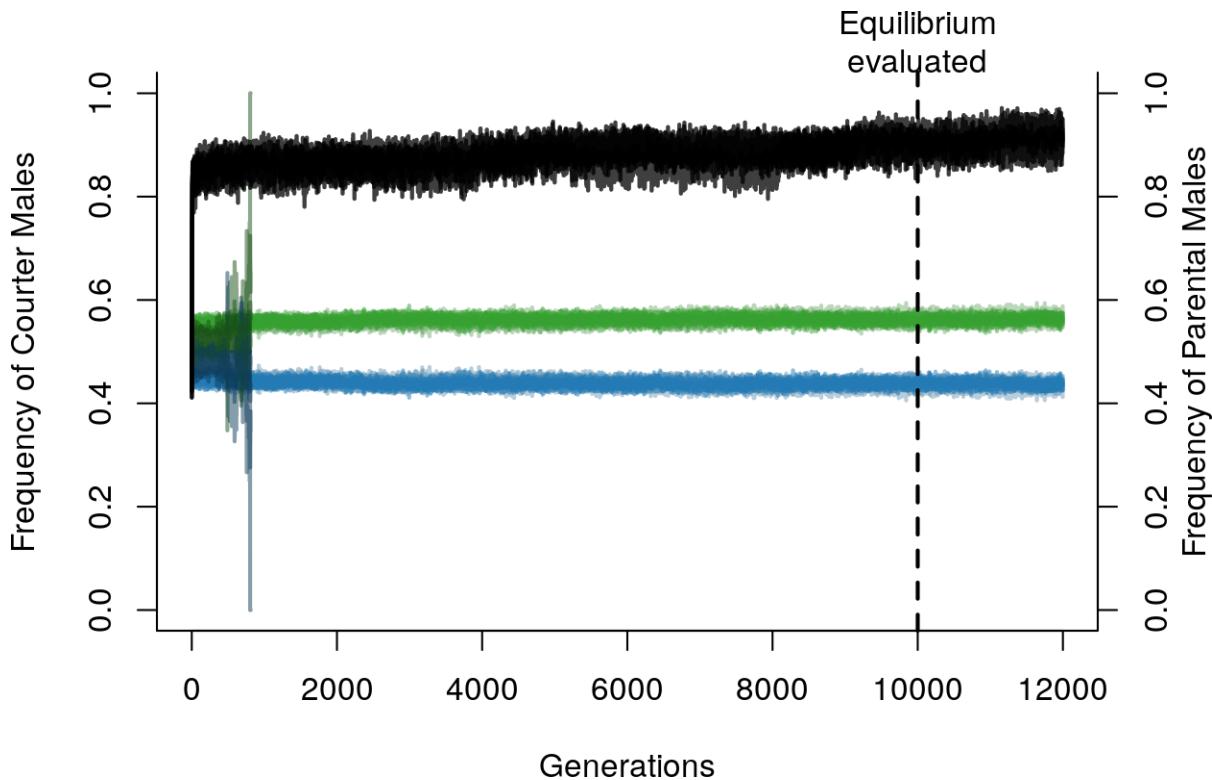


Figure 8: Evolution of parenting trait values with additive genetic variation and no viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

## 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.

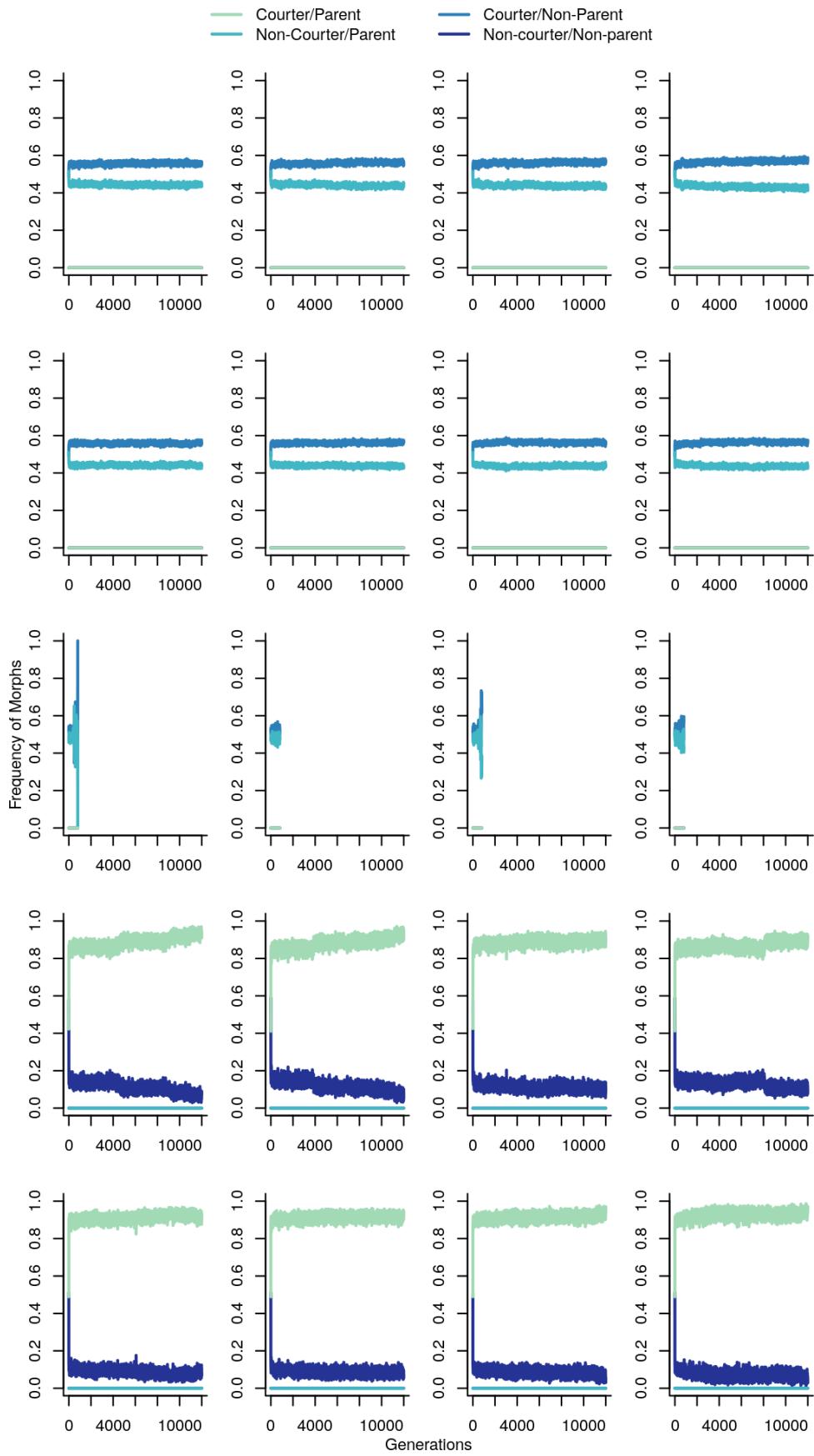


Figure 9: Frequency of the 4 morphs in each rep with unlinked genetic variation

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	Par
parent-courter_unlinked_1_summary.txt_1	11999	Pop0	940	460	480	1000	0
parent-courter_unlinked_1_summary.txt_2	11999	Pop1	942	461	481	1000	0
parent-courter_unlinked_1_summary.txt_3	11999	Pop2	908	461	447	1000	0
parent-courter_unlinked_1_summary.txt_4	11999	Pop3	923	464	459	1000	0
parent-courter_unlinked_2_summary.txt_1	11999	Pop0	1000	524	476	1000	0
parent-courter_unlinked_2_summary.txt_2	11999	Pop1	1000	527	473	1000	0
parent-courter_unlinked_2_summary.txt_3	11999	Pop2	1000	513	487	1000	0
parent-courter_unlinked_2_summary.txt_4	11999	Pop3	1000	527	473	1000	0
parent-courter_unlinked_3_summary.txt_1	811	Pop0	4	2	2	7	-0
parent-courter_unlinked_3_summary.txt_2	811	Pop1	720	362	358	759	-0
parent-courter_unlinked_3_summary.txt_3	811	Pop2	51	26	25	68	-0
parent-courter_unlinked_3_summary.txt_4	811	Pop3	295	135	160	303	-0
parent-courter_unlinked_4_summary.txt_1	11999	Pop0	940	461	479	1000	-0
parent-courter_unlinked_4_summary.txt_2	11999	Pop1	956	475	481	1000	-0
parent-courter_unlinked_4_summary.txt_3	11999	Pop2	961	456	505	1000	-0
parent-courter_unlinked_4_summary.txt_4	11999	Pop3	976	496	480	1000	-0
parent-courter_unlinked_5_summary.txt_1	11999	Pop0	975	458	517	1000	0
parent-courter_unlinked_5_summary.txt_2	11999	Pop1	976	495	481	1000	0
parent-courter_unlinked_5_summary.txt_3	11999	Pop2	963	487	476	1000	0
parent-courter_unlinked_5_summary.txt_4	11999	Pop3	939	465	474	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.

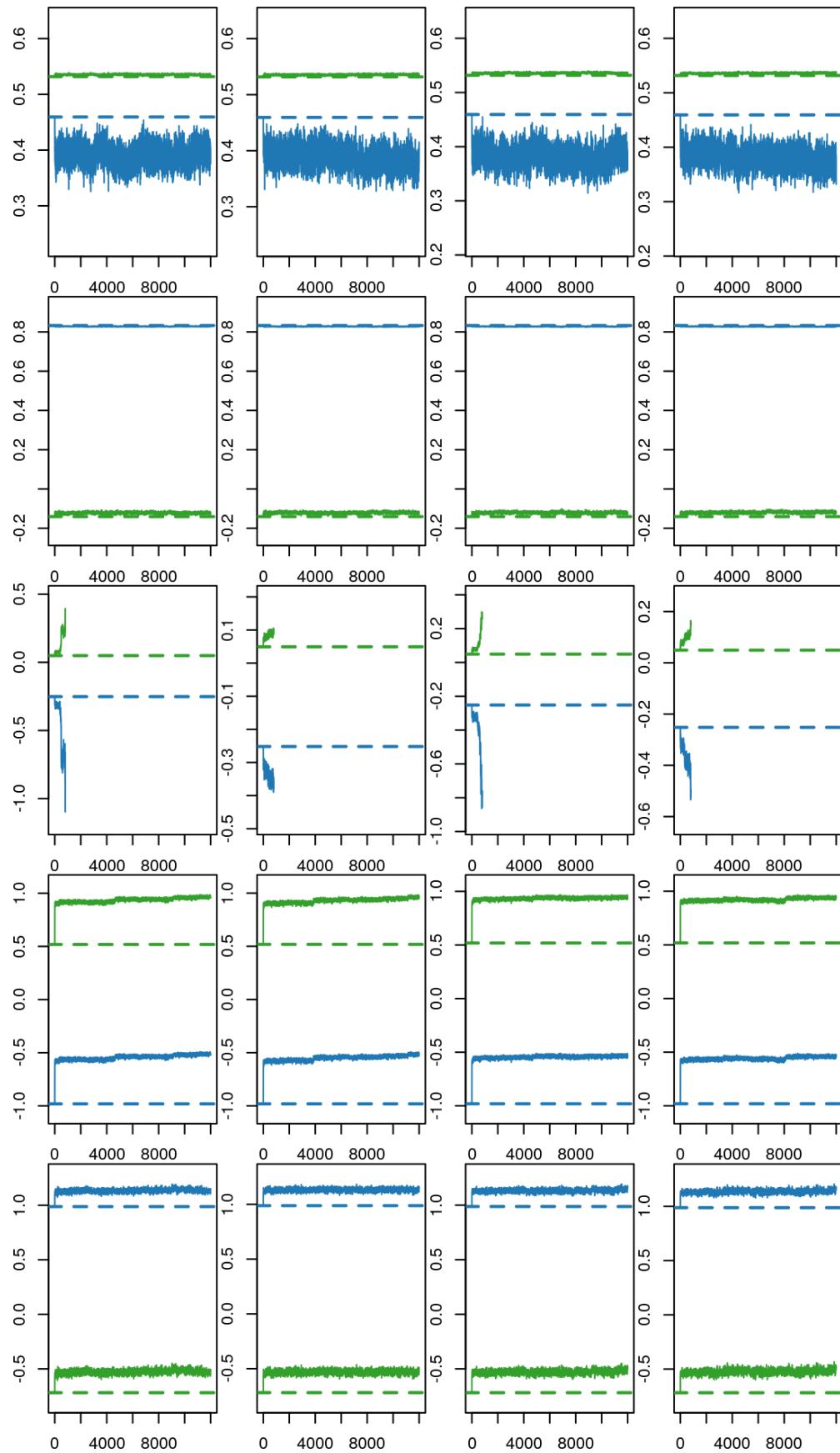
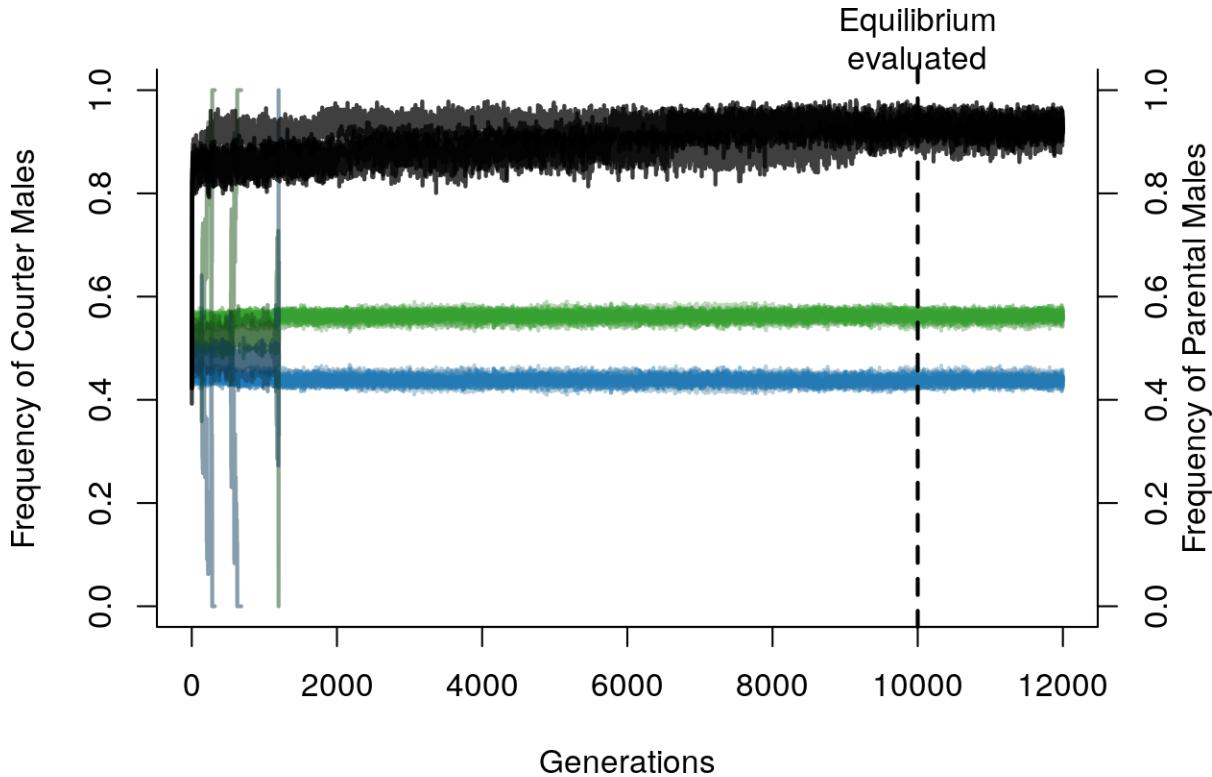


Figure 10: Evolution of the counter and parenting trait values in each rep with unlinked genetic variation. Dotted line shows the thresholds determining if males become courters (green) or parents (blue)

### 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.

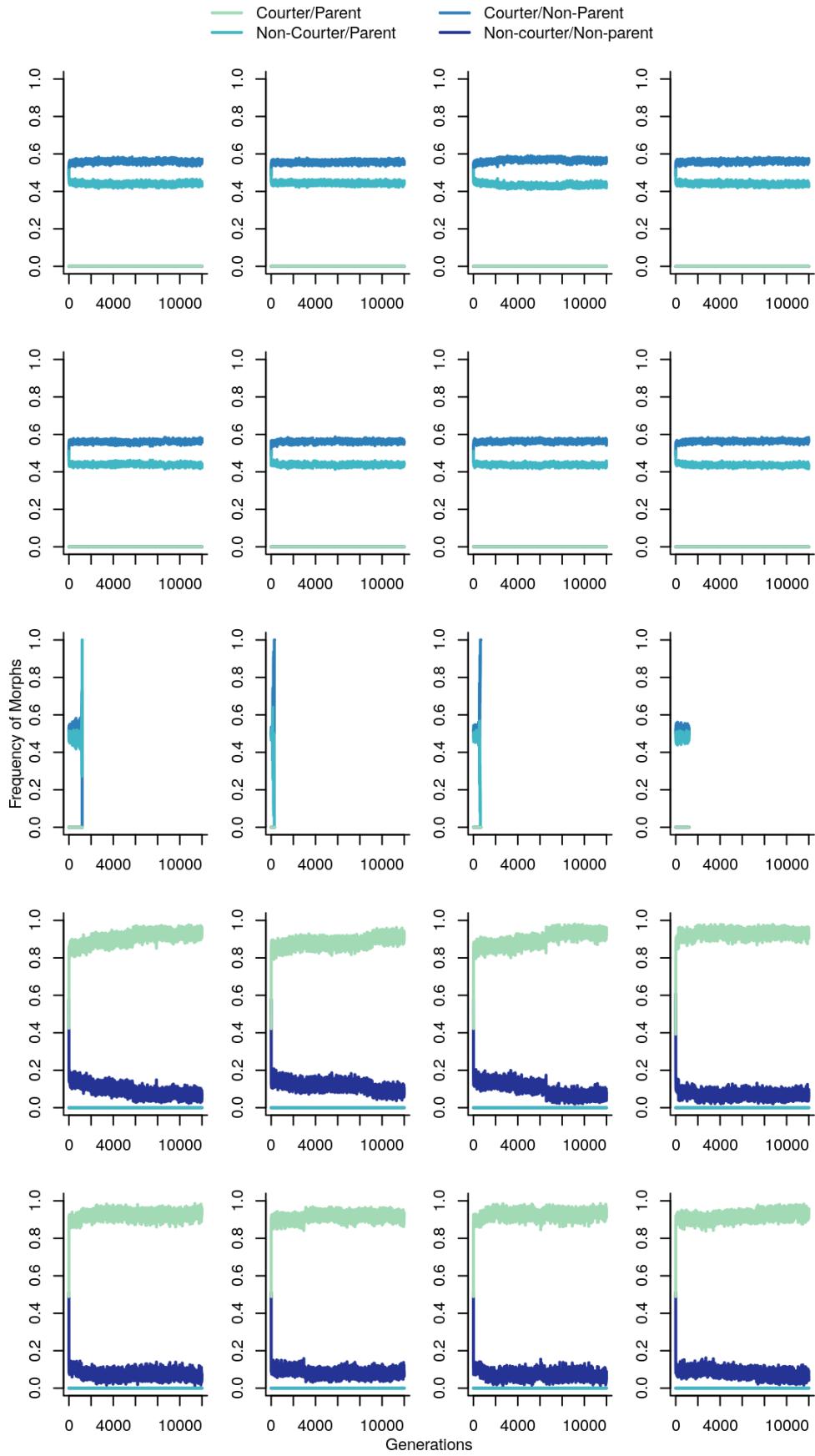


Figure 11: Frequency of the 4 morphs in each rep with unlinked genetic variation and no viability selection

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_unlinked_novs_1_summary.txt_1	11999	Pop0	939	471	468	1000
parent-courter_unlinked_novs_1_summary.txt_2	11999	Pop1	944	460	484	994
parent-courter_unlinked_novs_1_summary.txt_3	11999	Pop2	936	451	485	1000
parent-courter_unlinked_novs_1_summary.txt_4	11999	Pop3	943	458	485	1000
parent-courter_unlinked_novs_2_summary.txt_1	11999	Pop0	1000	523	477	1000
parent-courter_unlinked_novs_2_summary.txt_2	11999	Pop1	1000	522	478	1000
parent-courter_unlinked_novs_2_summary.txt_3	11999	Pop2	1000	520	480	1000
parent-courter_unlinked_novs_2_summary.txt_4	11999	Pop3	1000	526	474	1000
parent-courter_unlinked_novs_3_summary.txt_1	1203	Pop0	4	3	1	4
parent-courter_unlinked_novs_3_summary.txt_2	317	Pop1	4	4	0	0
parent-courter_unlinked_novs_3_summary.txt_3	680	Pop2	4	4	0	0
parent-courter_unlinked_novs_3_summary.txt_4	1203	Pop3	962	495	467	1000
parent-courter_unlinked_novs_4_summary.txt_1	11999	Pop0	945	470	475	1000
parent-courter_unlinked_novs_4_summary.txt_2	11999	Pop1	972	492	480	1000
parent-courter_unlinked_novs_4_summary.txt_3	11999	Pop2	949	447	502	1000
parent-courter_unlinked_novs_4_summary.txt_4	11999	Pop3	946	456	490	1000
parent-courter_unlinked_novs_5_summary.txt_1	11999	Pop0	939	496	443	1000
parent-courter_unlinked_novs_5_summary.txt_2	11999	Pop1	977	474	503	1000
parent-courter_unlinked_novs_5_summary.txt_3	11999	Pop2	968	481	487	1000
parent-courter_unlinked_novs_5_summary.txt_4	11999	Pop3	947	475	472	1000

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

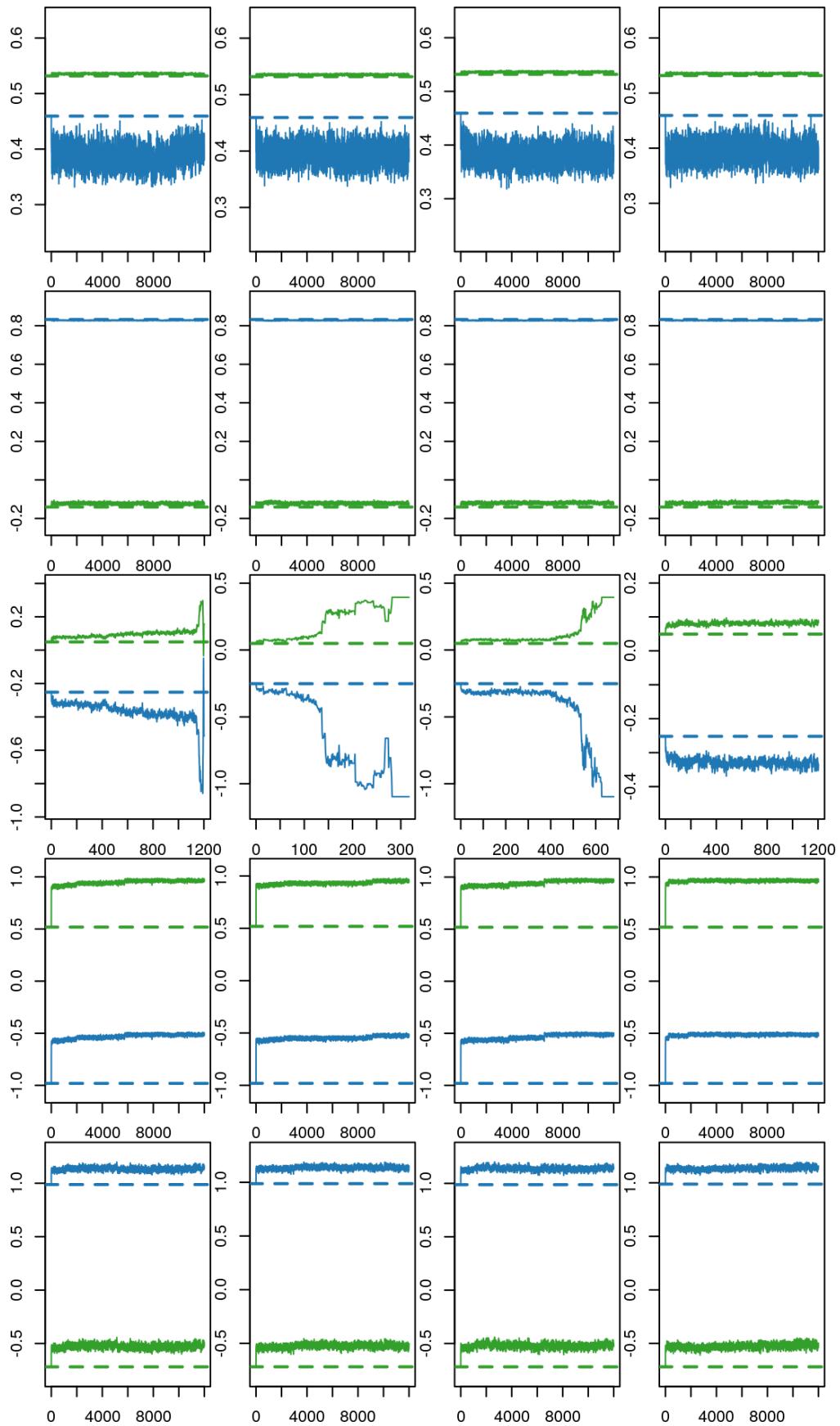


Figure 12: Evolution of the courtier and parenting trait values in each rep with unlinked genetic variation and without viability selection. Green represents courtship trait values and blue represents parental trait values, and the dotted lines are the thresholds

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

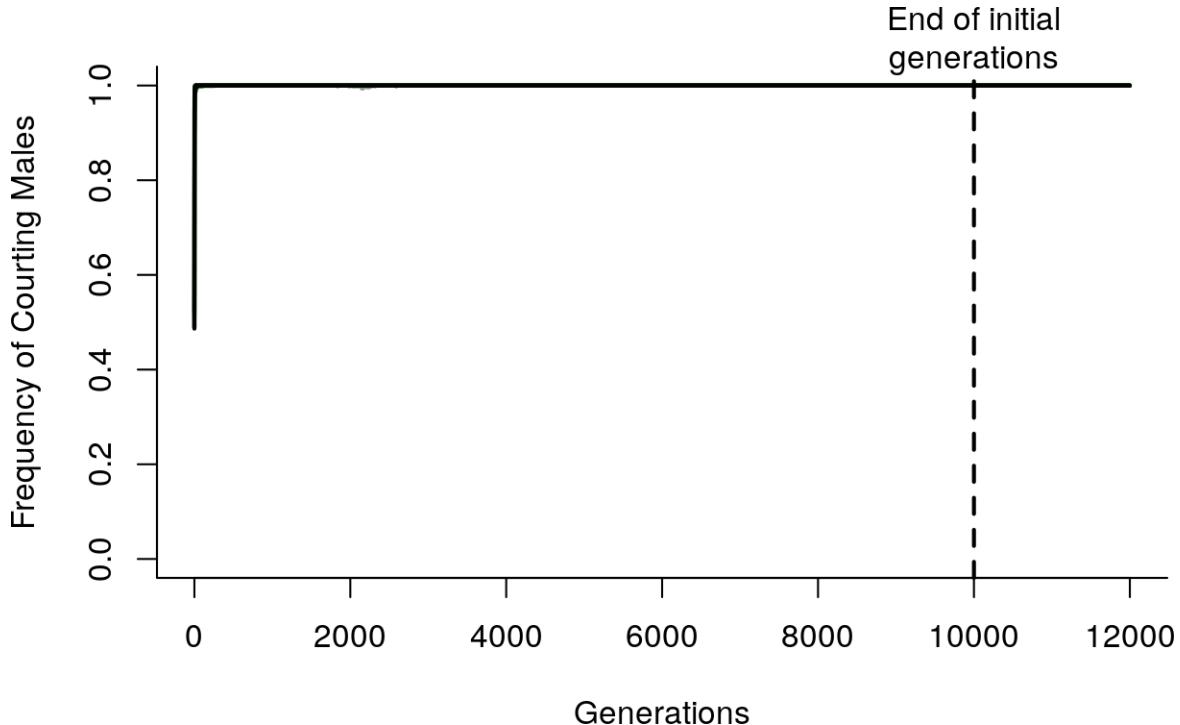


Figure 13: Frequency of the counter morph with linked QTLs (each color represents a different replicate)

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	1.93922	0

	CounterFreq	CounterW	NonCounterW
courter_linked_1_summary.txt_2	1	1.96443	0
courter_linked_1_summary.txt_3	1	1.95481	0
courter_linked_1_summary.txt_4	1	2.02227	0
courter_linked_2_summary.txt_1	1	2.04499	0
courter_linked_2_summary.txt_2	1	1.93424	0
courter_linked_2_summary.txt_3	1	2.10970	0
courter_linked_2_summary.txt_4	1	2.04918	0
courter_linked_3_summary.txt_1	1	1.92678	0
courter_linked_3_summary.txt_2	1	2.08333	0
courter_linked_3_summary.txt_3	1	1.94553	0
courter_linked_3_summary.txt_4	1	2.06186	0
courter_linked_4_summary.txt_1	1	1.96634	0
courter_linked_4_summary.txt_2	1	2.03049	0
courter_linked_4_summary.txt_3	1	2.11253	0
courter_linked_4_summary.txt_4	1	1.97624	0
courter_linked_5_summary.txt_1	1	2.12766	0
courter_linked_5_summary.txt_2	1	1.98020	0
courter_linked_5_summary.txt_3	1	1.94932	0
courter_linked_5_summary.txt_4	1	2.00401	0

Every replicate has the courtship trait go to fixation.

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

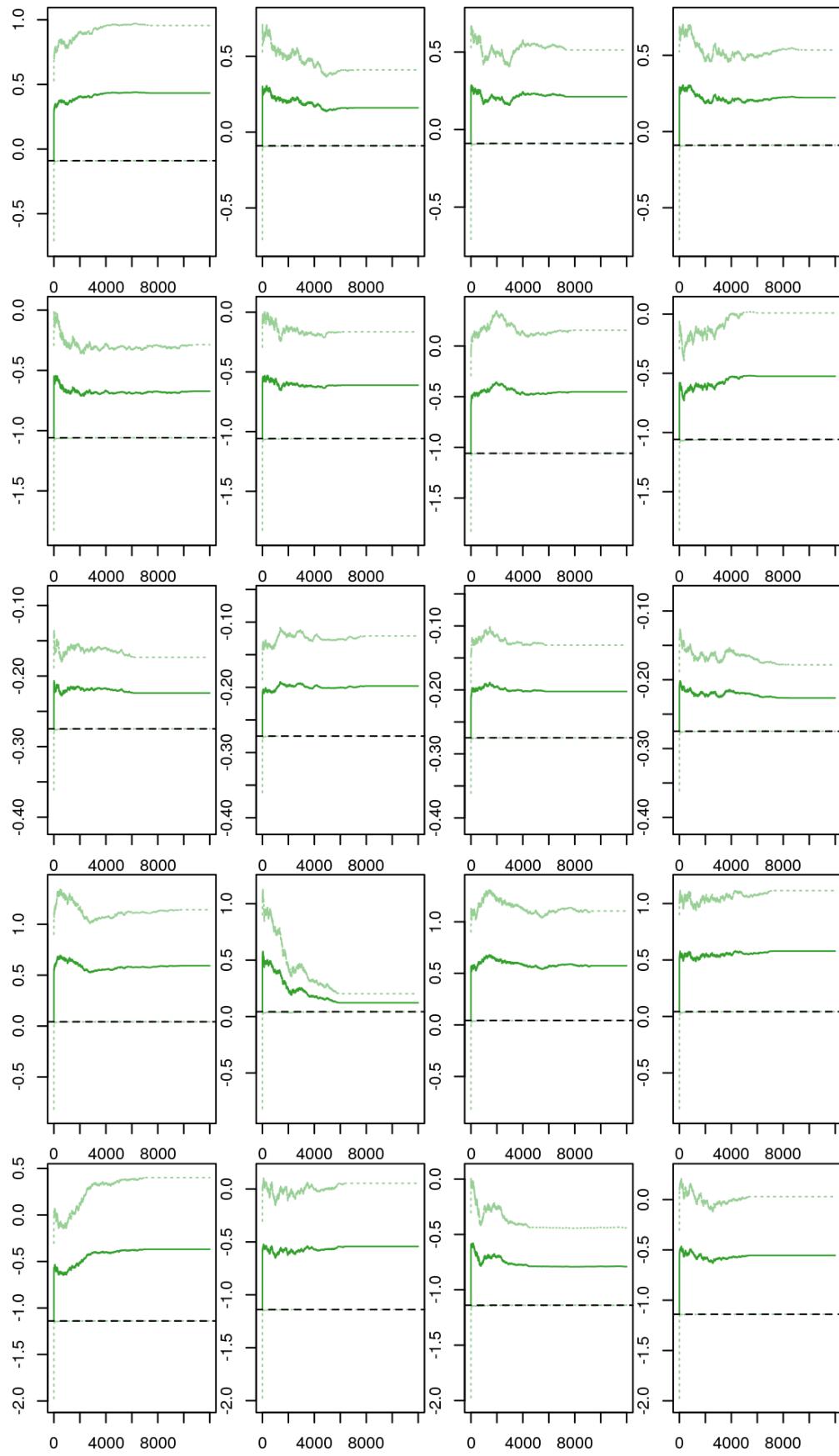


Figure 14: Evolution of courtship trait with linked loci. Green dotted lines are the standard deviations of the traits and the black dotted line is the threshold

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

#### Without viability selection

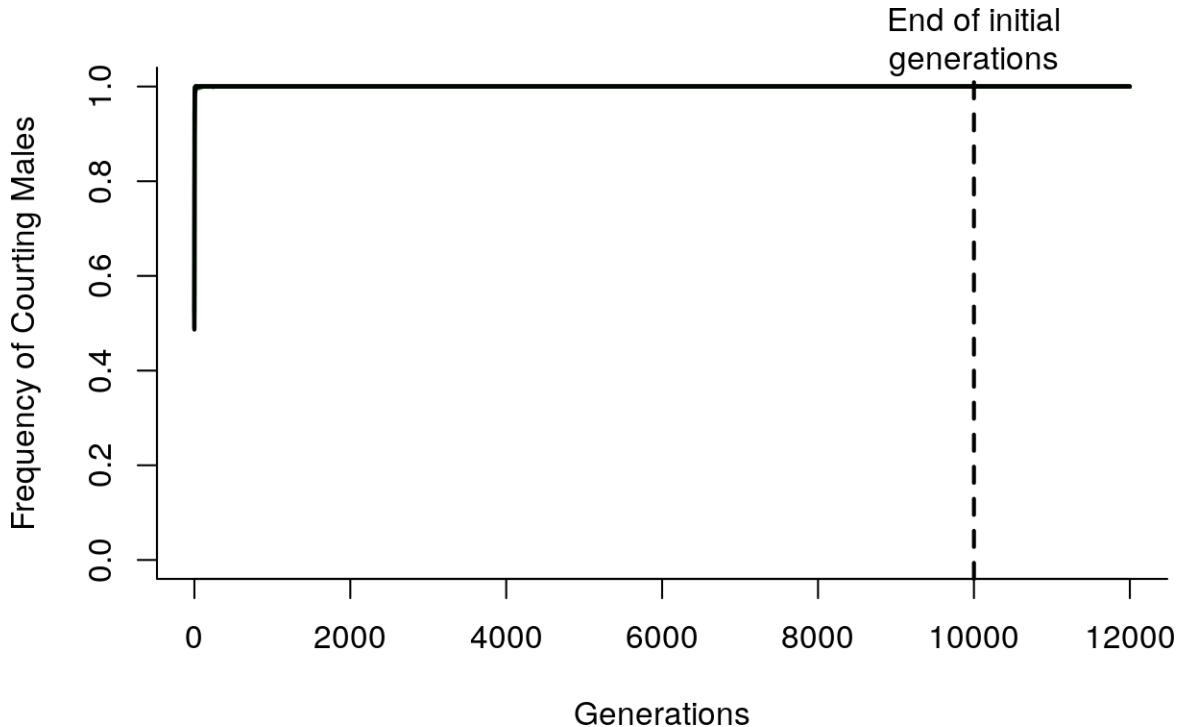


Figure 15: Frequency of the courtship trait with linked QTLs and no viability selection (each color represents a different replicate)

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	2.06186	0
counter_linked_novs_1_summary.txt_2	1	2.01613	0
counter_linked_novs_1_summary.txt_3	1	2.05339	0
counter_linked_novs_1_summary.txt_4	1	2.00803	0
counter_linked_novs_2_summary.txt_1	1	1.99203	0
counter_linked_novs_2_summary.txt_2	1	1.99601	0
counter_linked_novs_2_summary.txt_3	1	1.97239	0
counter_linked_novs_2_summary.txt_4	1	2.00401	0
counter_linked_novs_3_summary.txt_1	1	1.90114	0
counter_linked_novs_3_summary.txt_2	1	2.10970	0
counter_linked_novs_3_summary.txt_3	1	2.06186	0
counter_linked_novs_3_summary.txt_4	1	1.96078	0
counter_linked_novs_4_summary.txt_1	1	1.95695	0

	CourterFreq	CourterW	NonCourterW
courter_linked_novs_4_summary.txt_2	1	1.95695	0
courter_linked_novs_4_summary.txt_3	1	2.06612	0
courter_linked_novs_4_summary.txt_4	1	2.01613	0
courter_linked_novs_5_summary.txt_1	1	2.02840	0
courter_linked_novs_5_summary.txt_2	1	2.10526	0
courter_linked_novs_5_summary.txt_3	1	1.91939	0
courter_linked_novs_5_summary.txt_4	1	2.07469	0

Every rep has the courtship trait go to fixation.

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

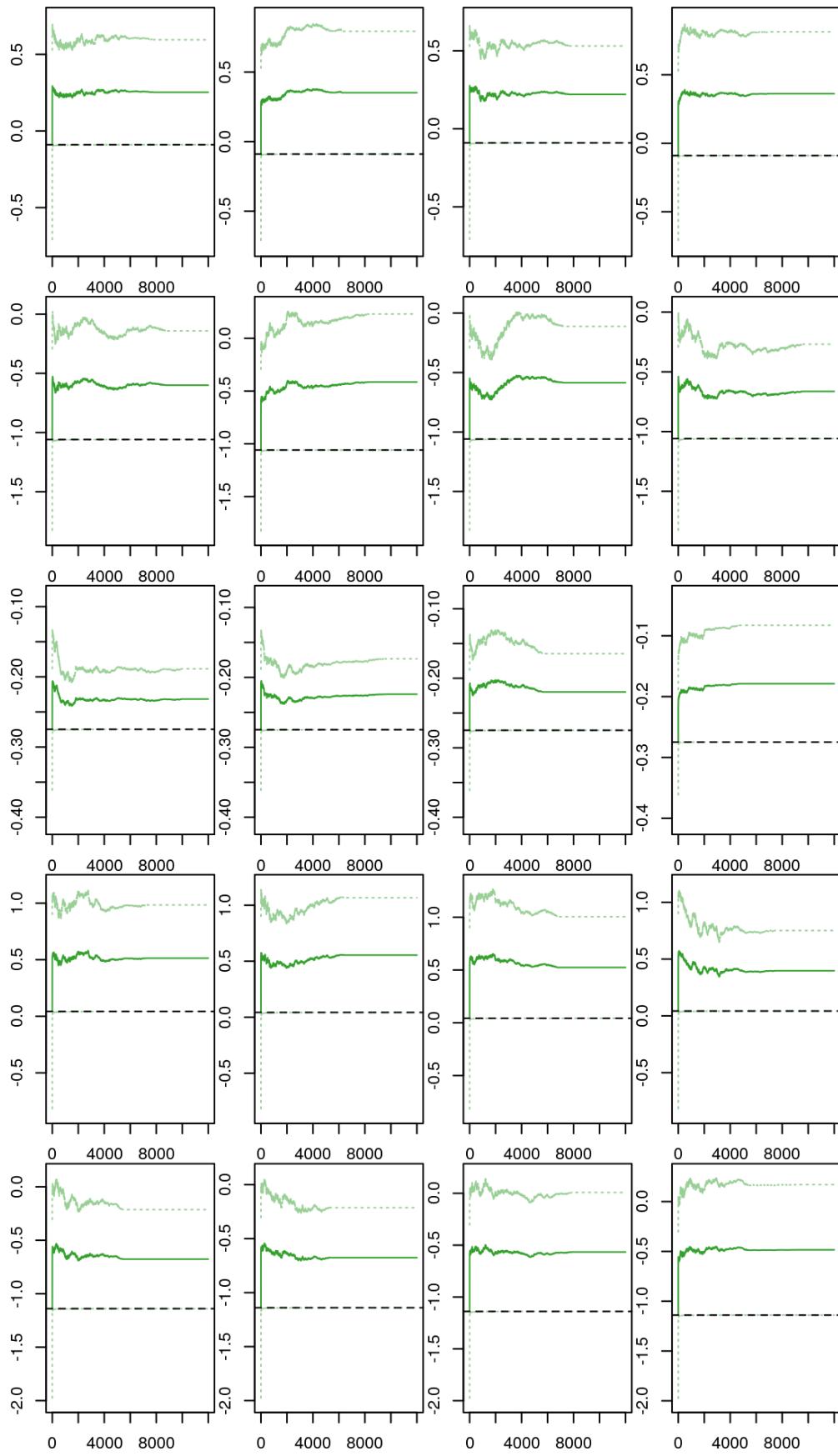


Figure 16: Evolution of courtship trait with linked loci and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

### Parental trait

#### With viability selection

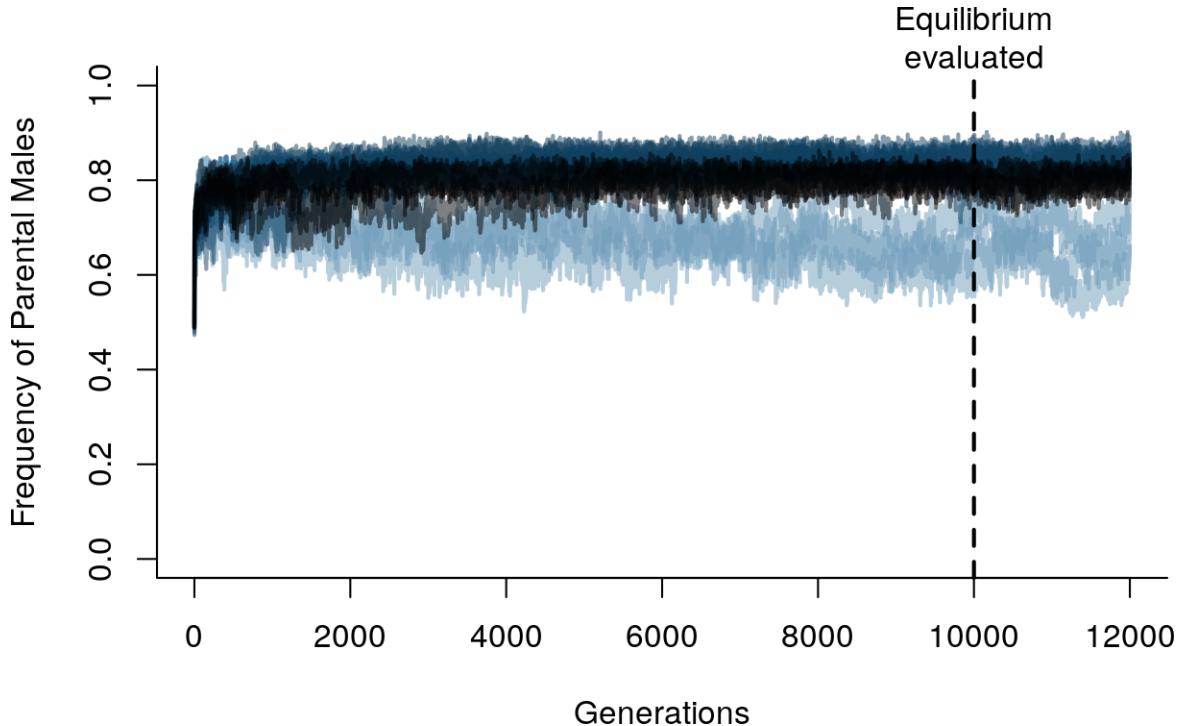


Figure 17: Frequency of parent morph with linked QTLs (each color represents a different replicate)

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	0.685934	1.48876	0.263804
parent_linked_1_summary.txt_2	0.641176	1.46789	0.322404
parent_linked_1_summary.txt_3	0.745283	1.46701	0.382353
parent_linked_1_summary.txt_4	0.661538	1.47093	0.284091
parent_linked_2_summary.txt_1	0.818004	1.56459	0.645161
parent_linked_2_summary.txt_2	0.821721	1.74314	0.643678
parent_linked_2_summary.txt_3	0.843496	1.64096	0.623377
parent_linked_2_summary.txt_4	0.835938	1.67523	0.464286
parent_linked_3_summary.txt_1	0.851852	1.61353	0.708333
parent_linked_3_summary.txt_2	0.838966	1.53791	0.753086
parent_linked_3_summary.txt_3	0.851485	1.56512	0.520000
parent_linked_3_summary.txt_4	0.875752	1.70938	1.000000
parent_linked_4_summary.txt_1	0.821918	1.70238	0.494505
parent_linked_4_summary.txt_2	0.796443	1.64764	0.330097
parent_linked_4_summary.txt_3	0.825843	1.56689	0.591398

	ParentFreq	ParentW	NonParentW
parent_linked_4_summary.txt_4	0.803150	1.59314	0.740000
parent_linked_5_summary.txt_1	0.822835	1.64354	0.622222
parent_linked_5_summary.txt_2	0.859073	1.54157	0.739726
parent_linked_5_summary.txt_3	0.839921	1.60706	0.790123
parent_linked_5_summary.txt_4	0.866538	1.56920	0.652174

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:

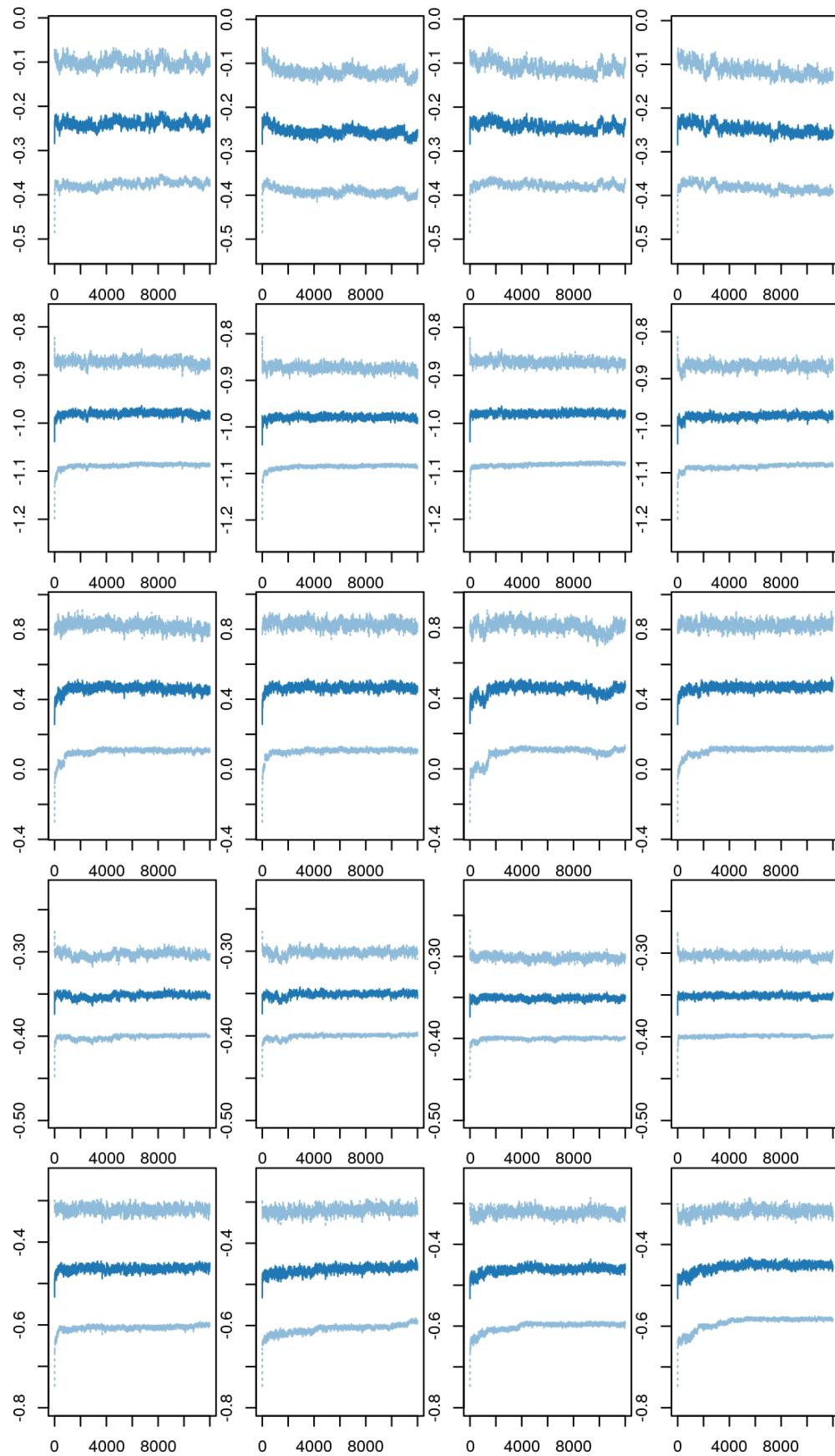


Figure 18: Evolution of parenting trait values with linked QTLs. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

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

### Without viability selection

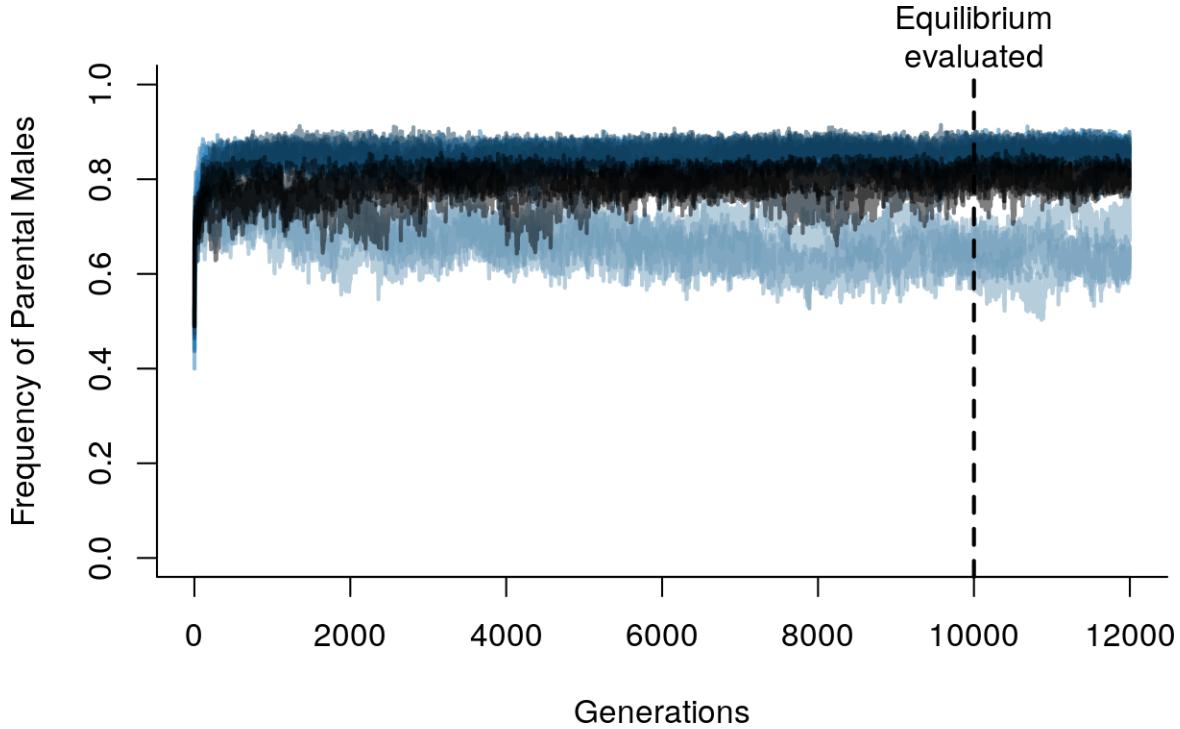


Figure 19: Frequency of parent morph with linked QTLs without viability selection (each color represents a different replicate)

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	0.609375	1.39744	0.405000
parent_linked_novs_1_summary.txt_2	0.658252	1.53687	0.318182
parent_linked_novs_1_summary.txt_3	0.626459	1.45652	0.265625
parent_linked_novs_1_summary.txt_4	0.693032	1.45109	0.447853
parent_linked_novs_2_summary.txt_1	0.822176	1.80662	0.623529
parent_linked_novs_2_summary.txt_2	0.848671	1.75422	0.540541
parent_linked_novs_2_summary.txt_3	0.866397	1.63551	0.590909
parent_linked_novs_2_summary.txt_4	0.865878	1.52847	0.676471
parent_linked_novs_3_summary.txt_1	0.849095	1.65166	0.613333
parent_linked_novs_3_summary.txt_2	0.848723	1.61343	0.584416
parent_linked_novs_3_summary.txt_3	0.872727	1.73380	0.730159
parent_linked_novs_3_summary.txt_4	0.866667	1.64569	0.636364
parent_linked_novs_4_summary.txt_1	0.812890	1.71100	0.566667
parent_linked_novs_4_summary.txt_2	0.792157	1.59901	0.528302

	ParentFreq	ParentW	NonParentW
parent_linked_novs_4_summary.txt_3	0.812500	1.62019	0.552083
parent_linked_novs_4_summary.txt_4	0.787190	1.61155	0.786408
parent_linked_novs_5_summary.txt_1	0.850299	1.61033	0.680000
parent_linked_novs_5_summary.txt_2	0.841270	1.65330	0.725000
parent_linked_novs_5_summary.txt_3	0.855102	1.67780	0.732394
parent_linked_novs_5_summary.txt_4	0.837891	1.61772	0.734940

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:

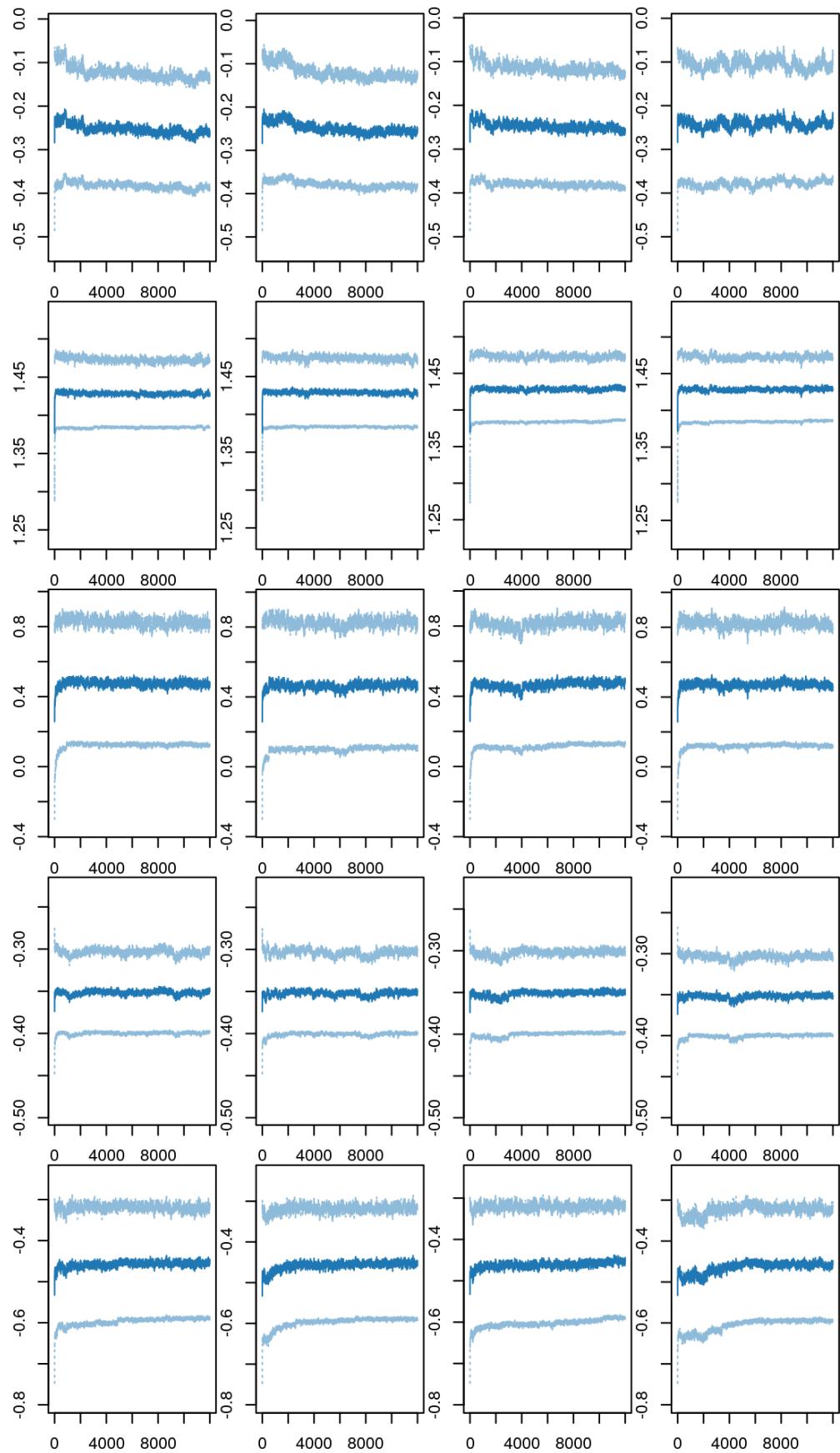


Figure 20: Evolution of parenting trait values with linked QTLs and without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

## 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

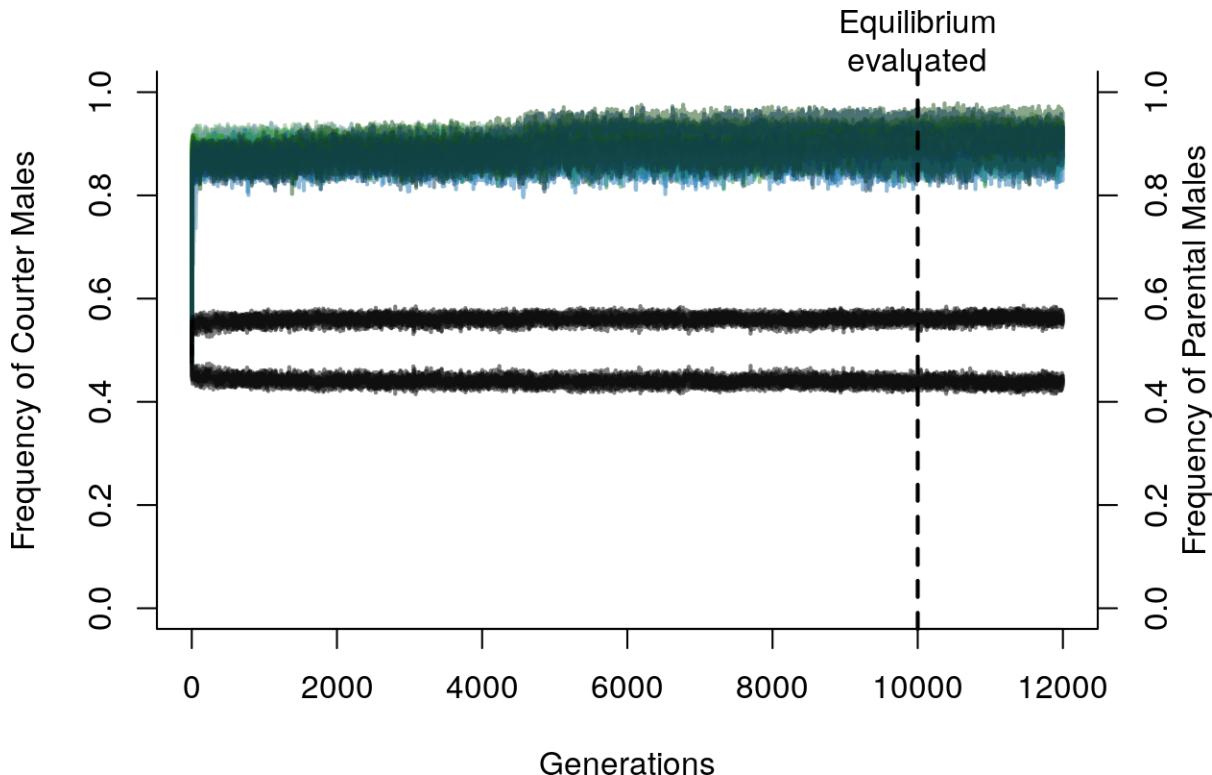


Figure 21: Frequency of the two morphs with linked QTLs (counter = green, parent = blue)

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

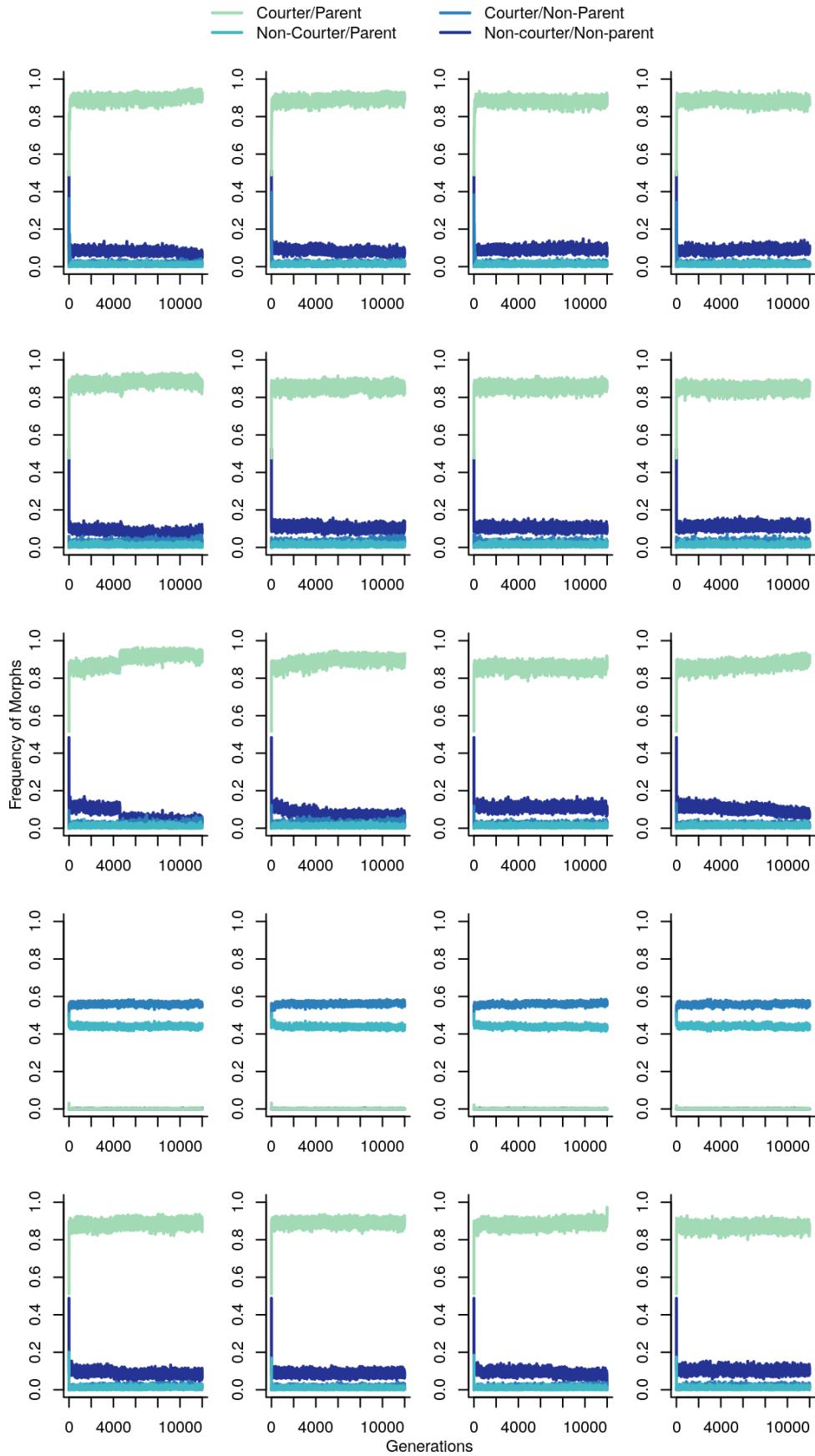


Figure 22: Frequency of the 4 morphs in each rep with linked QTLs

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	986	488	498	1000	0.36
parent-courter_linked_1_summary.txt_2	11999	Pop1	1000	519	481	1000	0.36
parent-courter_linked_1_summary.txt_3	11999	Pop2	987	487	500	1000	0.36
parent-courter_linked_1_summary.txt_4	11999	Pop3	1000	518	482	1000	0.36
parent-courter_linked_2_summary.txt_1	11999	Pop0	990	501	489	1000	-1.25
parent-courter_linked_2_summary.txt_2	11999	Pop1	1000	529	471	1000	-1.25
parent-courter_linked_2_summary.txt_3	11999	Pop2	1000	494	506	1000	-1.25
parent-courter_linked_2_summary.txt_4	11999	Pop3	1000	515	485	1000	-1.25
parent-courter_linked_3_summary.txt_1	11999	Pop0	957	492	465	1000	-0.72
parent-courter_linked_3_summary.txt_2	11999	Pop1	973	486	487	1000	-0.72
parent-courter_linked_3_summary.txt_3	11999	Pop2	985	505	480	1000	-0.72
parent-courter_linked_3_summary.txt_4	11999	Pop3	983	509	474	1000	-0.72
parent-courter_linked_4_summary.txt_1	11999	Pop0	1000	523	477	1000	-0.04
parent-courter_linked_4_summary.txt_2	11999	Pop1	1000	522	478	1000	-0.04
parent-courter_linked_4_summary.txt_3	11999	Pop2	1000	534	466	1000	-0.04
parent-courter_linked_4_summary.txt_4	11999	Pop3	1000	528	472	1000	-0.04
parent-courter_linked_5_summary.txt_1	11999	Pop0	982	494	488	1000	-1.00
parent-courter_linked_5_summary.txt_2	11999	Pop1	1000	481	519	1000	-1.00
parent-courter_linked_5_summary.txt_3	11999	Pop2	953	476	477	1000	-1.00
parent-courter_linked_5_summary.txt_4	11999	Pop3	995	475	520	1000	-1.00

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:

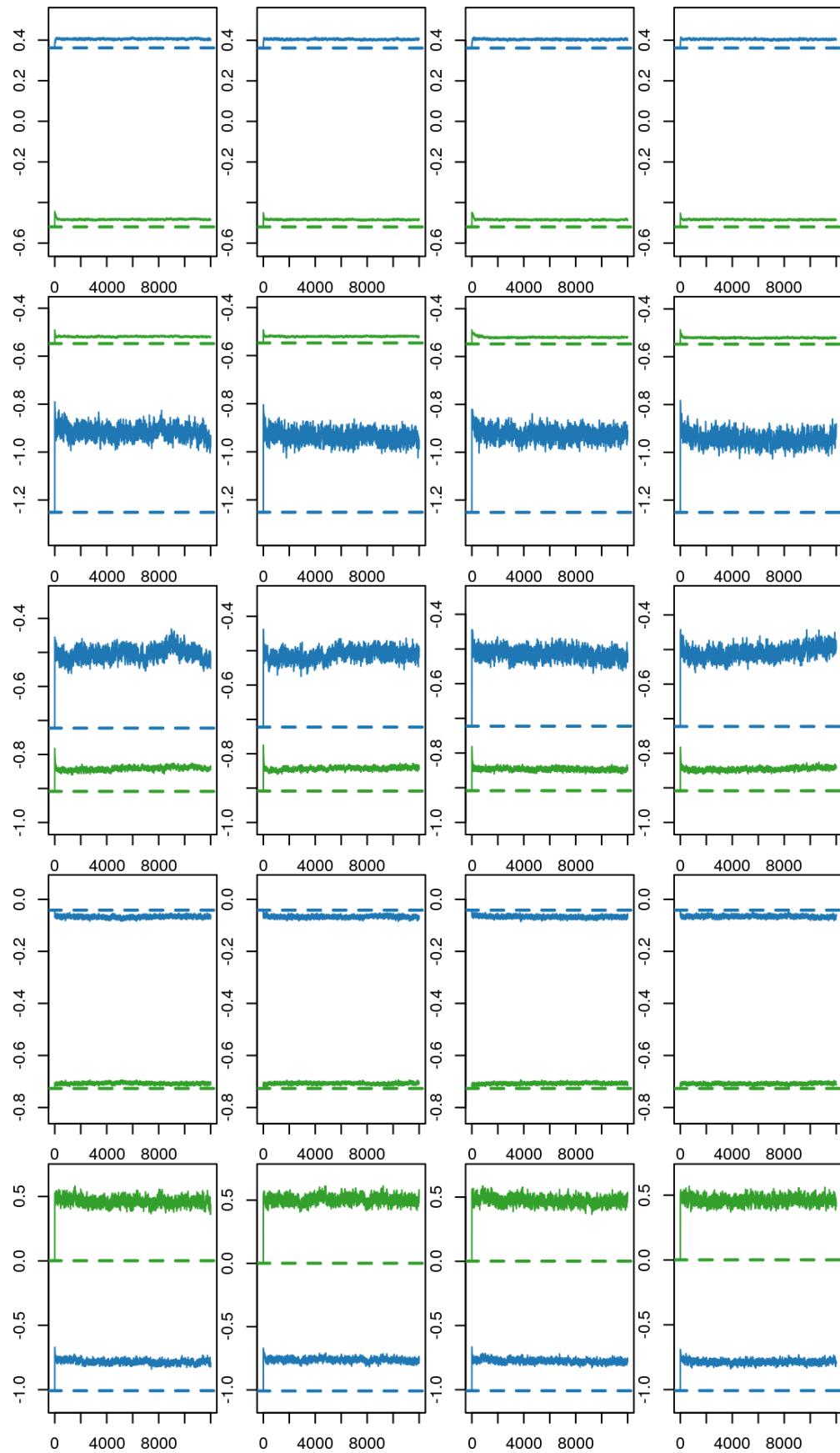


Figure 23: Evolution of the counter and parenting trait values in each rep with linked genetic variation

### Without viability selection

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

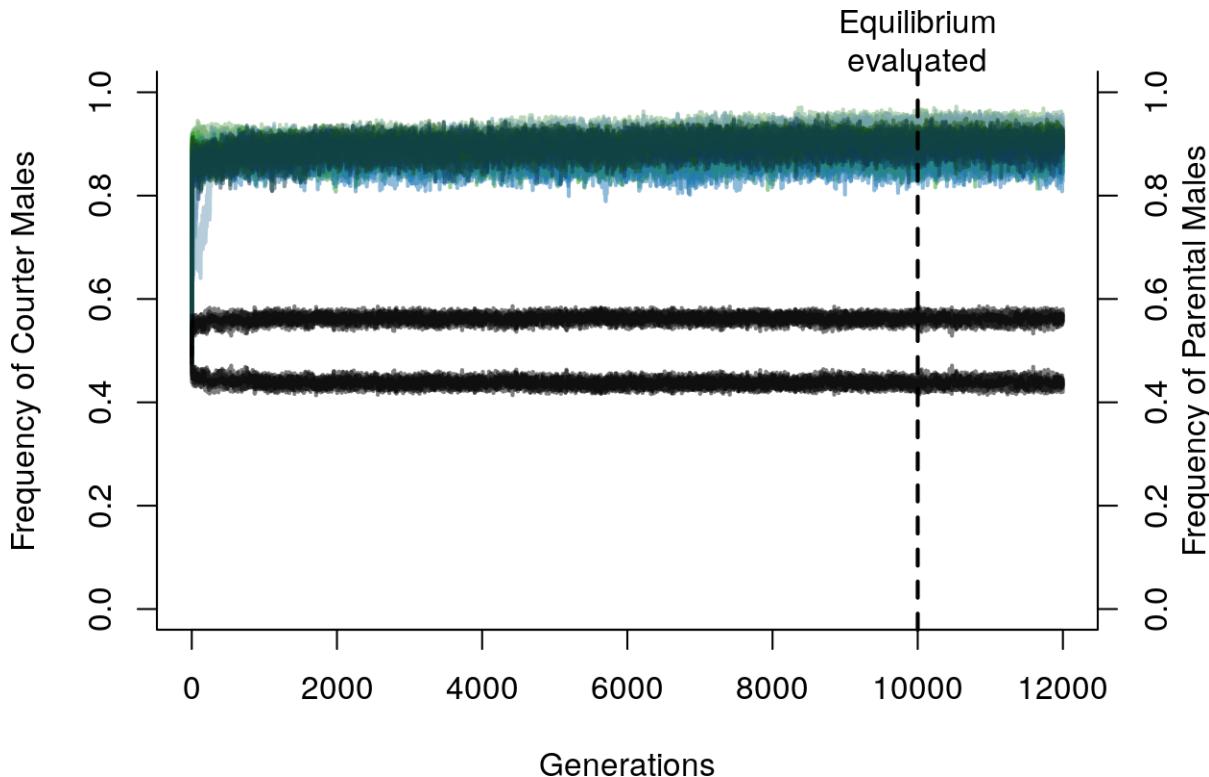


Figure 24: Frequency of the two morphs with linked QTLs and without viability selection (courter = green, parent = blue)

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

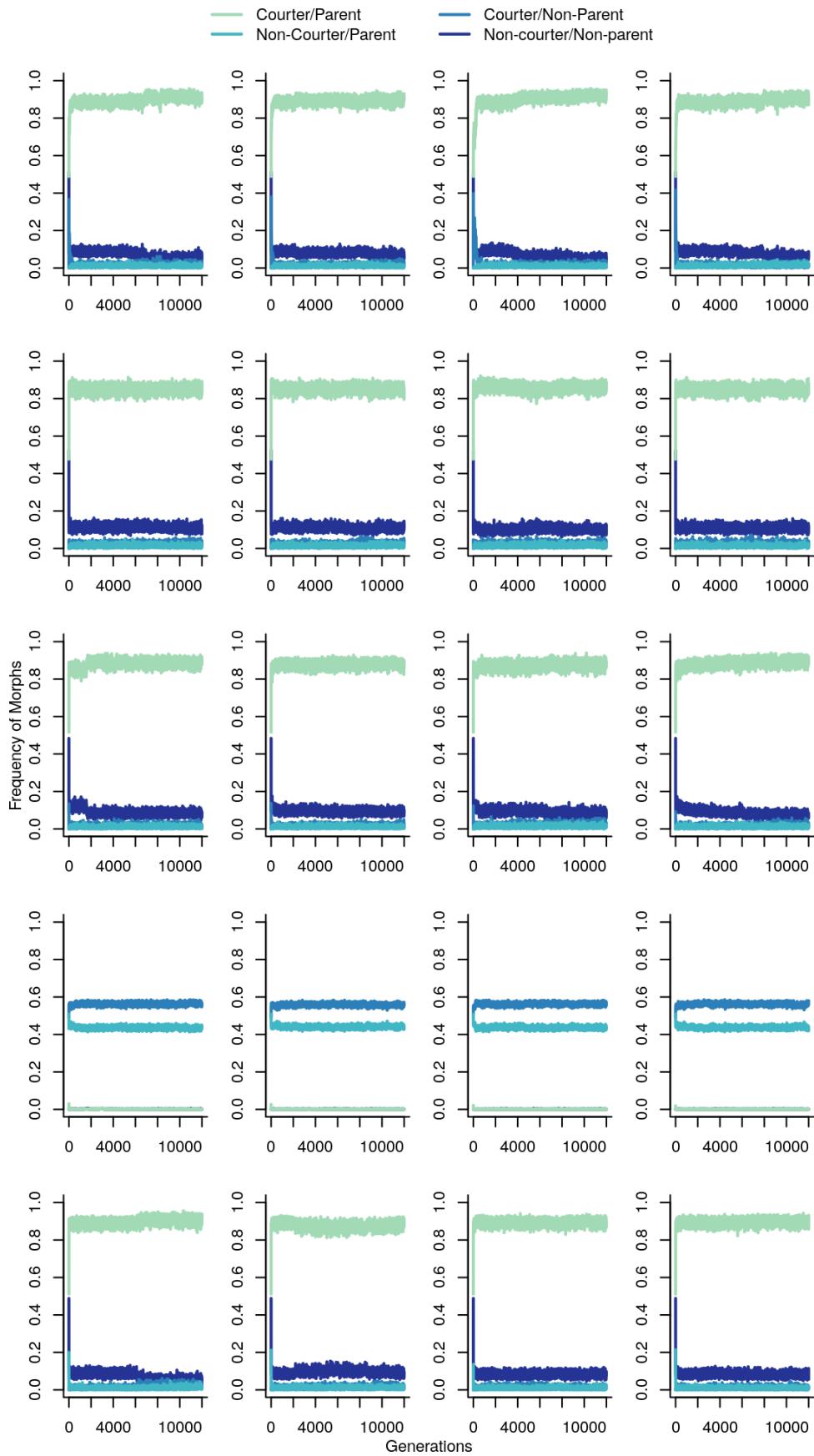


Figure 25: Frequency of the 4 morphs in each rep with linked QTLs without viability selection

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	968	484	484	1000	
parent-courter_linked_novs_1_summary.txt_2	11999	Pop1	992	505	487	1000	
parent-courter_linked_novs_1_summary.txt_3	11999	Pop2	974	479	495	1000	
parent-courter_linked_novs_1_summary.txt_4	11999	Pop3	983	519	464	1000	
parent-courter_linked_novs_2_summary.txt_1	11999	Pop0	1000	476	524	1000	
parent-courter_linked_novs_2_summary.txt_2	11999	Pop1	1000	493	507	1000	
parent-courter_linked_novs_2_summary.txt_3	11999	Pop2	999	494	505	1000	
parent-courter_linked_novs_2_summary.txt_4	11999	Pop3	997	504	493	1000	
parent-courter_linked_novs_3_summary.txt_1	11999	Pop0	984	515	469	1000	
parent-courter_linked_novs_3_summary.txt_2	11999	Pop1	997	476	521	1000	
parent-courter_linked_novs_3_summary.txt_3	11999	Pop2	979	500	479	1000	
parent-courter_linked_novs_3_summary.txt_4	11999	Pop3	983	481	502	1000	
parent-courter_linked_novs_4_summary.txt_1	11999	Pop0	1000	522	478	1000	
parent-courter_linked_novs_4_summary.txt_2	11999	Pop1	1000	542	458	1000	
parent-courter_linked_novs_4_summary.txt_3	11999	Pop2	1000	526	474	1000	
parent-courter_linked_novs_4_summary.txt_4	11999	Pop3	1000	526	474	1000	
parent-courter_linked_novs_5_summary.txt_1	11999	Pop0	967	497	470	1000	
parent-courter_linked_novs_5_summary.txt_2	11999	Pop1	996	502	494	1000	
parent-courter_linked_novs_5_summary.txt_3	11999	Pop2	1000	508	492	1000	
parent-courter_linked_novs_5_summary.txt_4	11999	Pop3	1000	499	501	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:

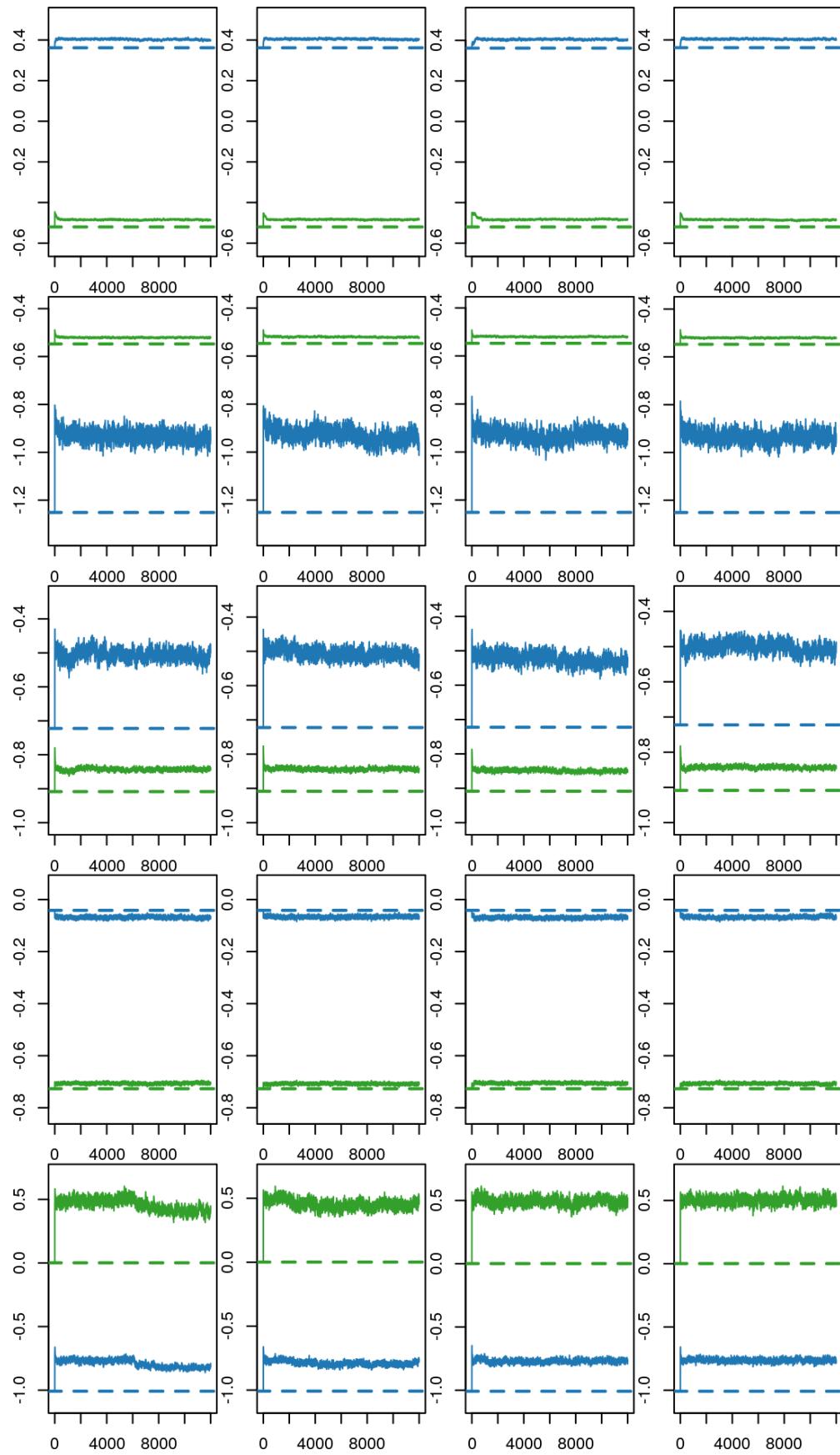


Figure 26: Evolution of the counter and parenting trait values in each rep with linked genetic variation and no viability selection

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

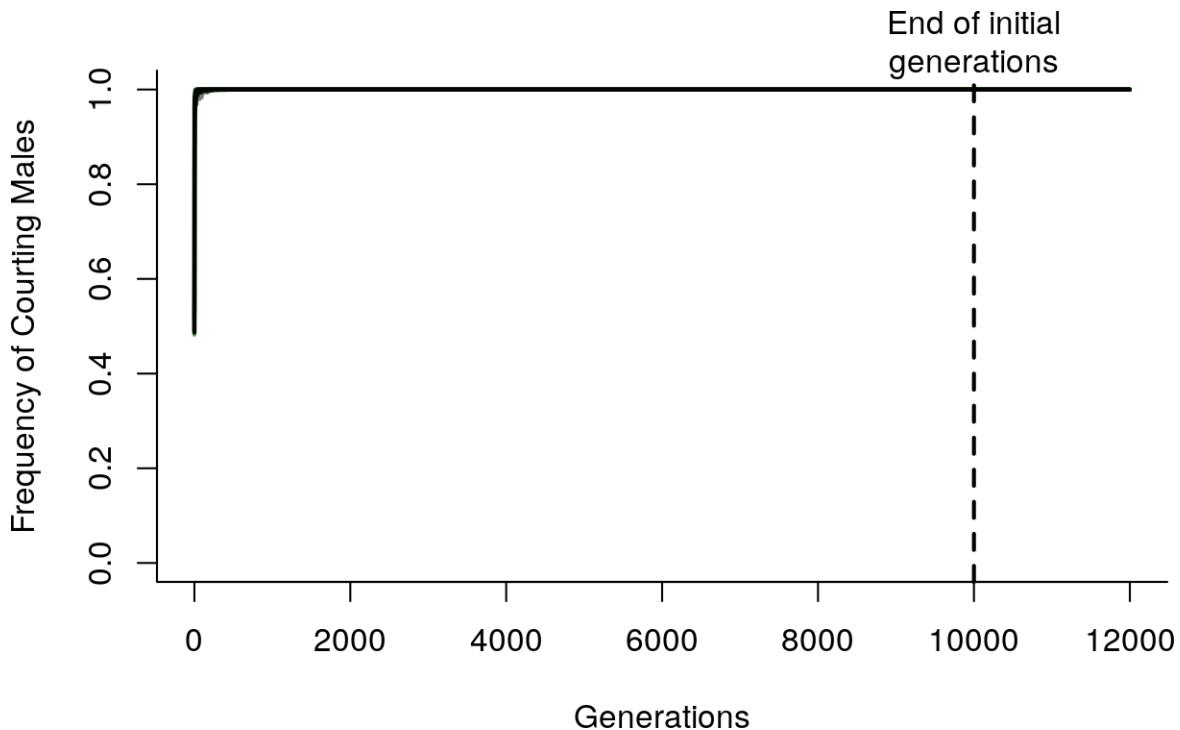


Figure 27: Frequency of the courter morph with supergenes (each color represents a different replicate)

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	2.02028	0
courter_supergene_1_summary.txt_2	1	1.89524	0
courter_supergene_1_summary.txt_3	1	1.94922	0
courter_supergene_1_summary.txt_4	1	1.99799	0
courter_supergene_2_summary.txt_1	1	2.04499	0
courter_supergene_2_summary.txt_2	1	2.01613	0
courter_supergene_2_summary.txt_3	1	1.96464	0

	CounterFreq	CounterW	NonCounterW
courter_supergene_2_summary.txt_4	1	1.96850	0
courter_supergene_3_summary.txt_1	1	2.01215	0
courter_supergene_3_summary.txt_2	1	2.03469	0
courter_supergene_3_summary.txt_3	1	1.96838	0
courter_supergene_3_summary.txt_4	1	2.09684	0
courter_supergene_4_summary.txt_1	1	2.03696	0
courter_supergene_4_summary.txt_2	1	1.90249	0
courter_supergene_4_summary.txt_3	1	1.96238	0
courter_supergene_4_summary.txt_4	1	2.07307	0
courter_supergene_5_summary.txt_1	1	2.08333	0
courter_supergene_5_summary.txt_2	1	1.92308	0
courter_supergene_5_summary.txt_3	1	2.03252	0
courter_supergene_5_summary.txt_4	1	1.90840	0

Looking at the evolution of the trait values:

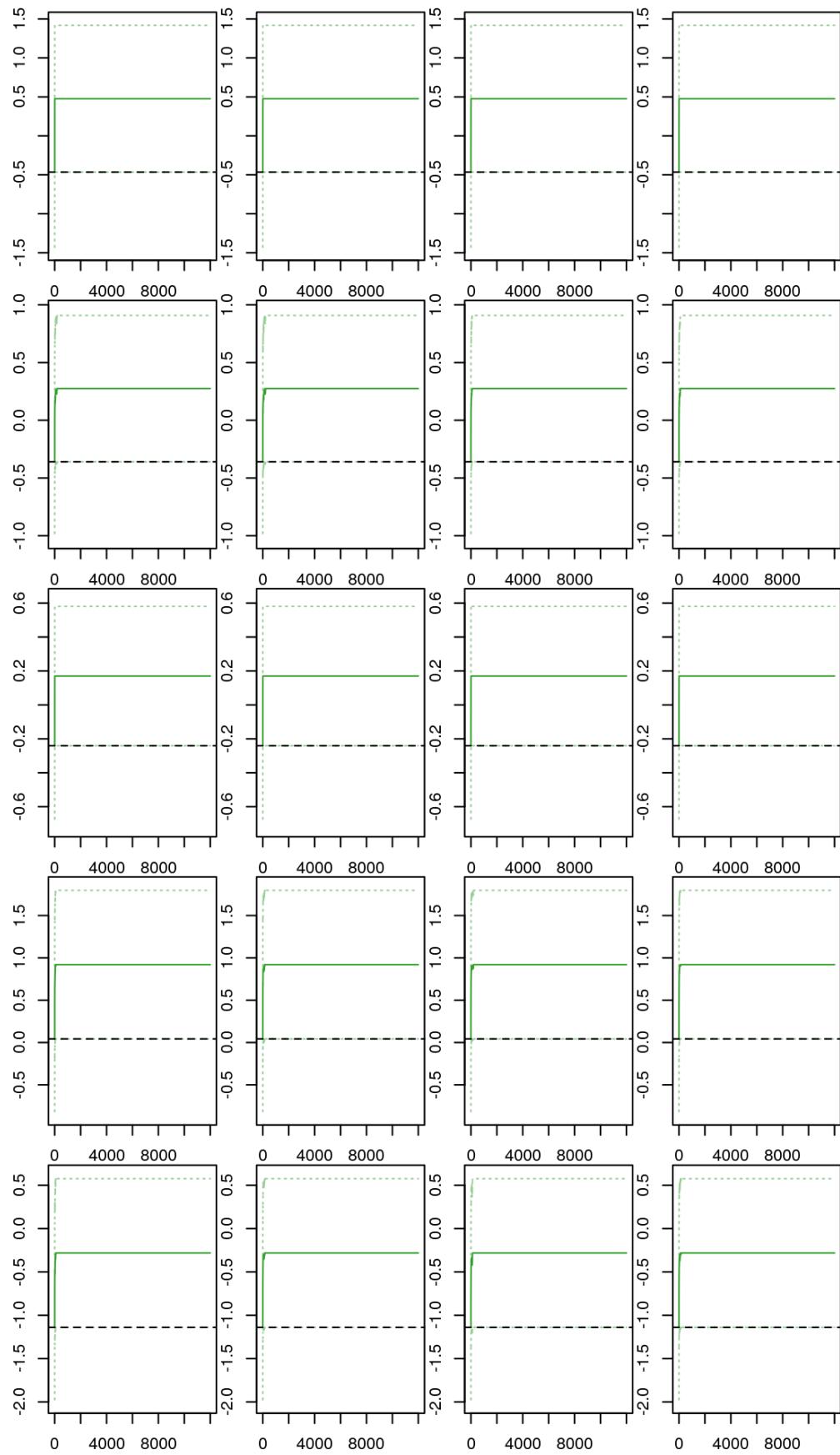


Figure 28: Evolution of courtship trait with a supergene. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

### Without viability selection

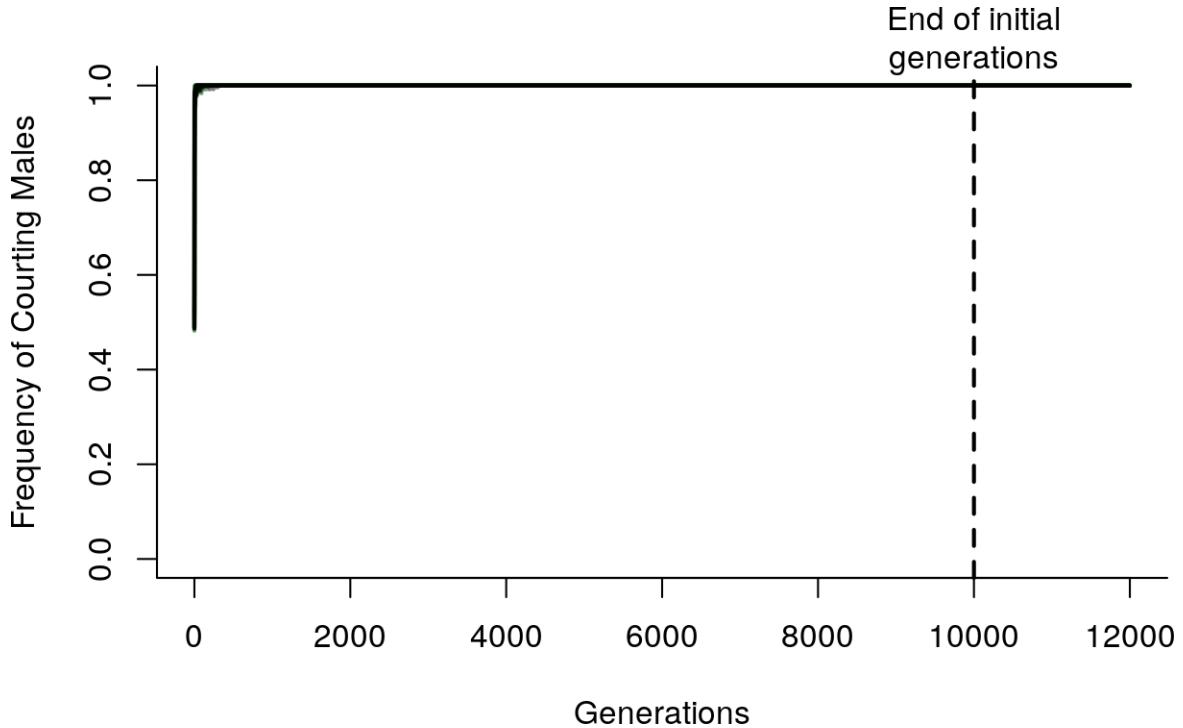


Figure 29: Frequency of the counter morph with supergenes without viability selection (each color represents a different replicate)

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	1.87970	0
counter_supergene_novs_1_summary.txt_2	1	1.96078	0
counter_supergene_novs_1_summary.txt_3	1	2.14133	0
counter_supergene_novs_1_summary.txt_4	1	2.10526	0
counter_supergene_novs_2_summary.txt_1	1	1.97628	0
counter_supergene_novs_2_summary.txt_2	1	1.94175	0
counter_supergene_novs_2_summary.txt_3	1	1.89394	0
counter_supergene_novs_2_summary.txt_4	1	1.99601	0
counter_supergene_novs_3_summary.txt_1	1	1.94932	0
counter_supergene_novs_3_summary.txt_2	1	2.04918	0
counter_supergene_novs_3_summary.txt_3	1	2.00803	0
counter_supergene_novs_3_summary.txt_4	1	1.95312	0
counter_supergene_novs_4_summary.txt_1	1	1.96078	0
counter_supergene_novs_4_summary.txt_2	1	2.07469	0
counter_supergene_novs_4_summary.txt_3	1	2.02429	0
counter_supergene_novs_4_summary.txt_4	1	1.96078	0
counter_supergene_novs_5_summary.txt_1	1	2.03252	0
counter_supergene_novs_5_summary.txt_2	1	2.03666	0
counter_supergene_novs_5_summary.txt_3	1	2.03252	0

	CourterFreq	CourterW	NonCourterW
courter_supergene_novs_5_summary.txt_4	1	2.08768	0

Looking at the evolution of the trait values:

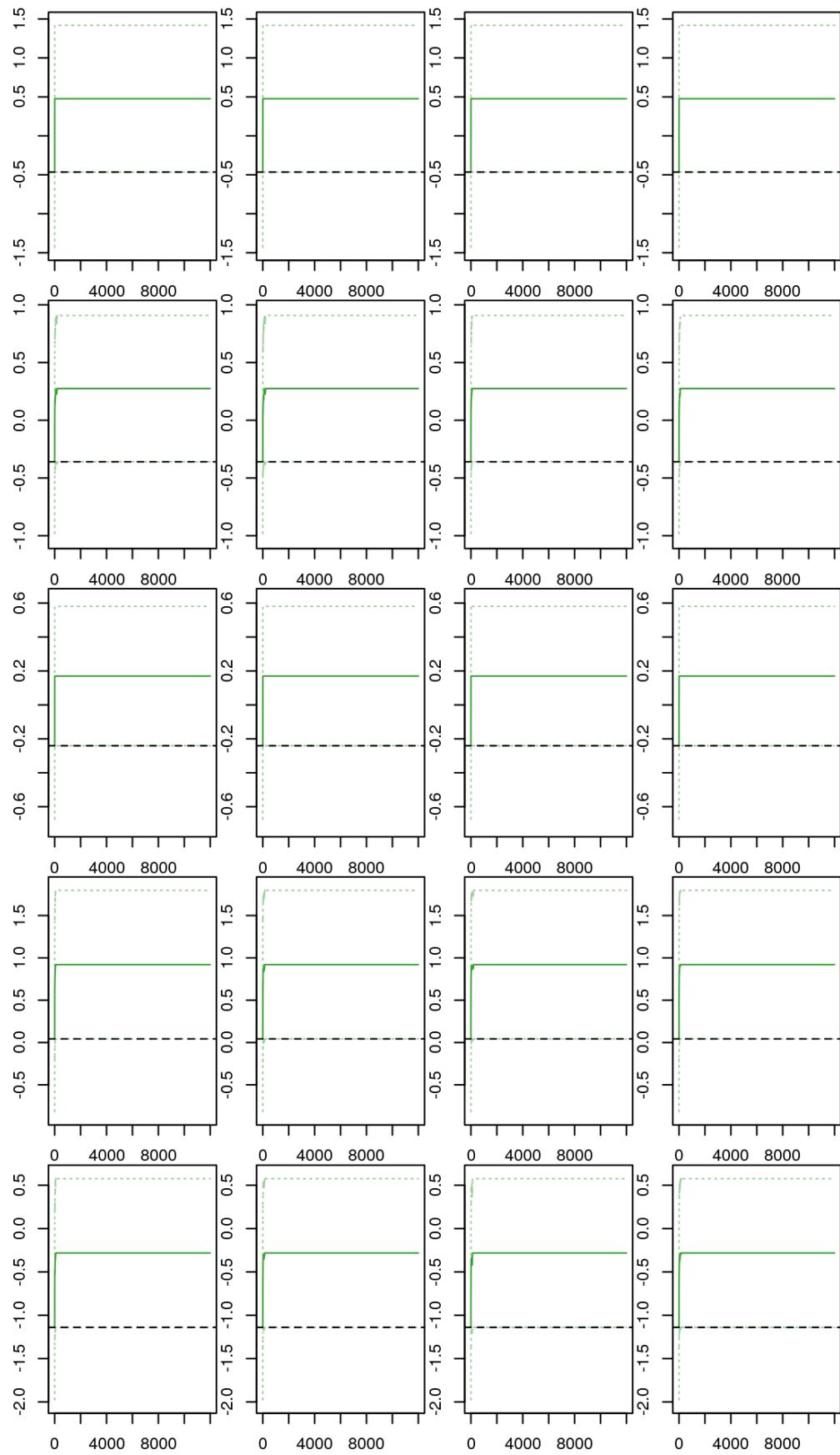


Figure 30: Evolution of courtship trait with a supergene and without viability selection. Green dotted lines are the standard deviations around the mean and the black dotted line is the threshold

**Parental trait**

**With viability selection**

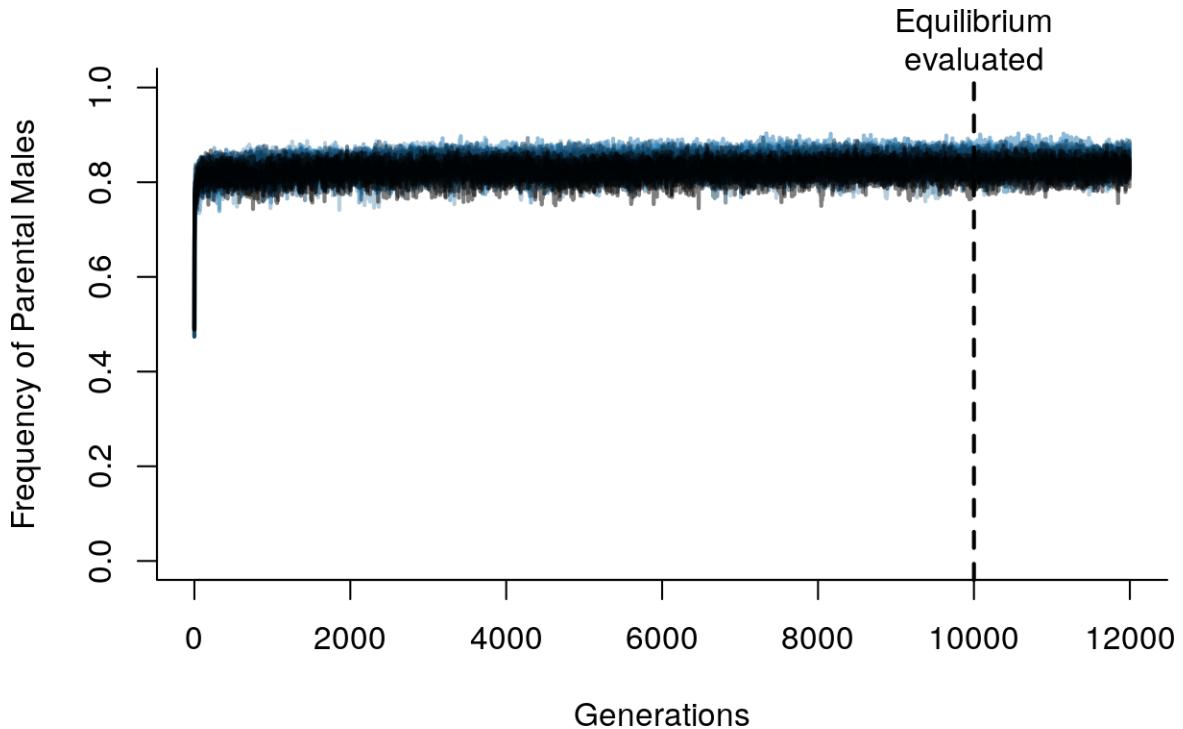


Figure 31: Frequency of parent morph with supergenes (each color represents a different replicate)

Table 15: Frequency of parents with supergenes in final generation

	ParentFreq	ParentW	NonParentW
parent_supergene_1_summary.txt_1	0.848249	1.61697	0.692308
parent_supergene_1_summary.txt_2	0.878788	1.71724	0.633333
parent_supergene_1_summary.txt_3	0.851923	1.49436	0.597403
parent_supergene_1_summary.txt_4	0.852697	1.70316	0.647887
parent_supergene_2_summary.txt_1	0.849687	1.67813	0.972222
parent_supergene_2_summary.txt_2	0.827801	1.74185	0.638554
parent_supergene_2_summary.txt_3	0.869565	1.70476	0.841270
parent_supergene_2_summary.txt_4	0.849287	1.69544	0.540541
parent_supergene_3_summary.txt_1	0.862745	1.66818	0.700000
parent_supergene_3_summary.txt_2	0.847525	1.56542	0.844156
parent_supergene_3_summary.txt_3	0.826638	1.70844	0.634146
parent_supergene_3_summary.txt_4	0.837302	1.55213	0.487805
parent_supergene_4_summary.txt_1	0.826772	1.60714	0.420455
parent_supergene_4_summary.txt_2	0.823770	1.62438	0.813953
parent_supergene_4_summary.txt_3	0.807322	1.60382	0.460000
parent_supergene_4_summary.txt_4	0.829026	1.56595	0.383721
parent_supergene_5_summary.txt_1	0.474950	1.39662	0.320611
parent_supergene_5_summary.txt_2	0.491194	1.50996	0.223077
parent_supergene_5_summary.txt_3	0.521830	1.57371	0.330435
parent_supergene_5_summary.txt_4	0.531062	1.61887	0.277778

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.

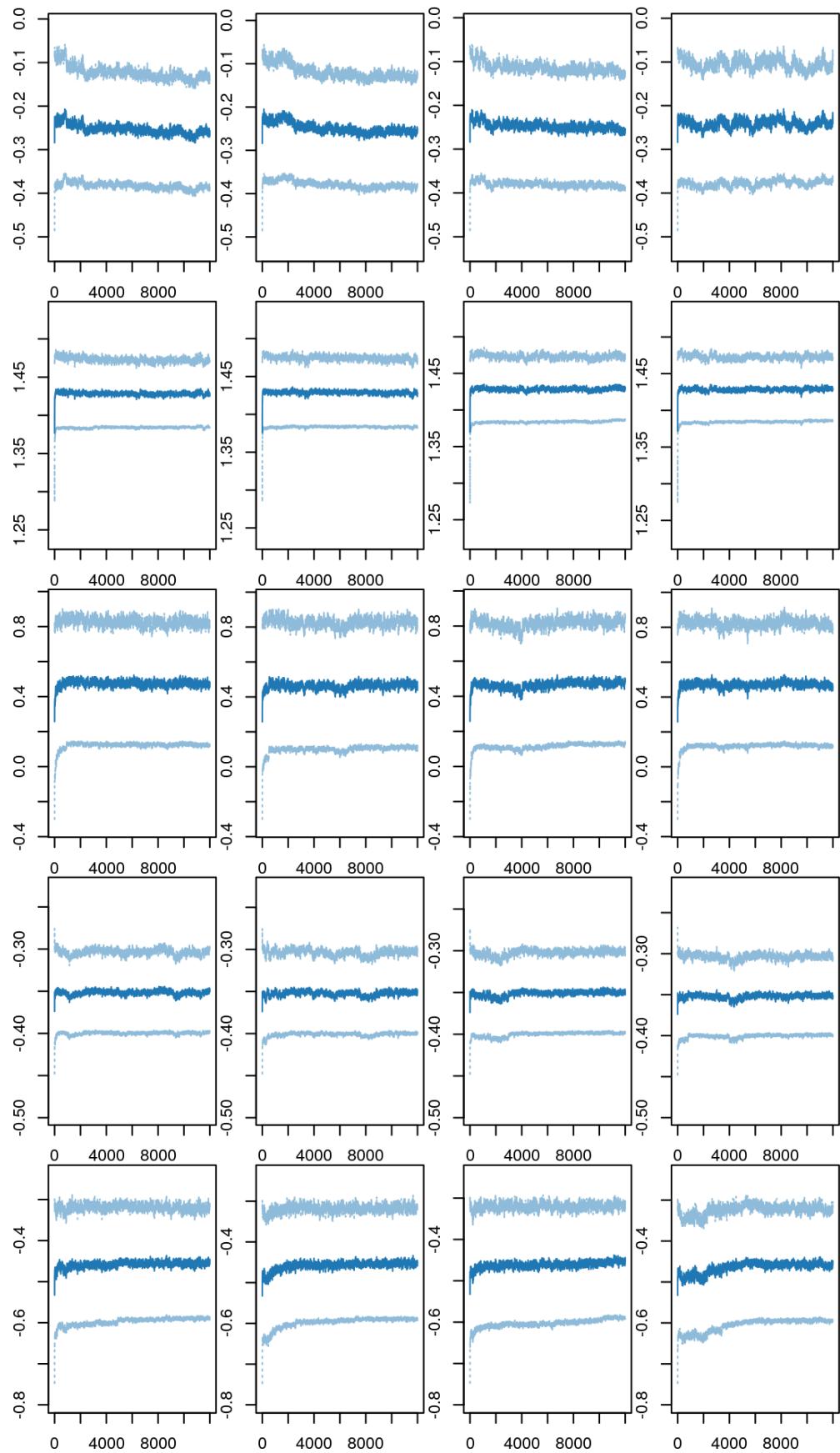


Figure 32: Evolution of parenting trait values with a supergene. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

### Without viability selection

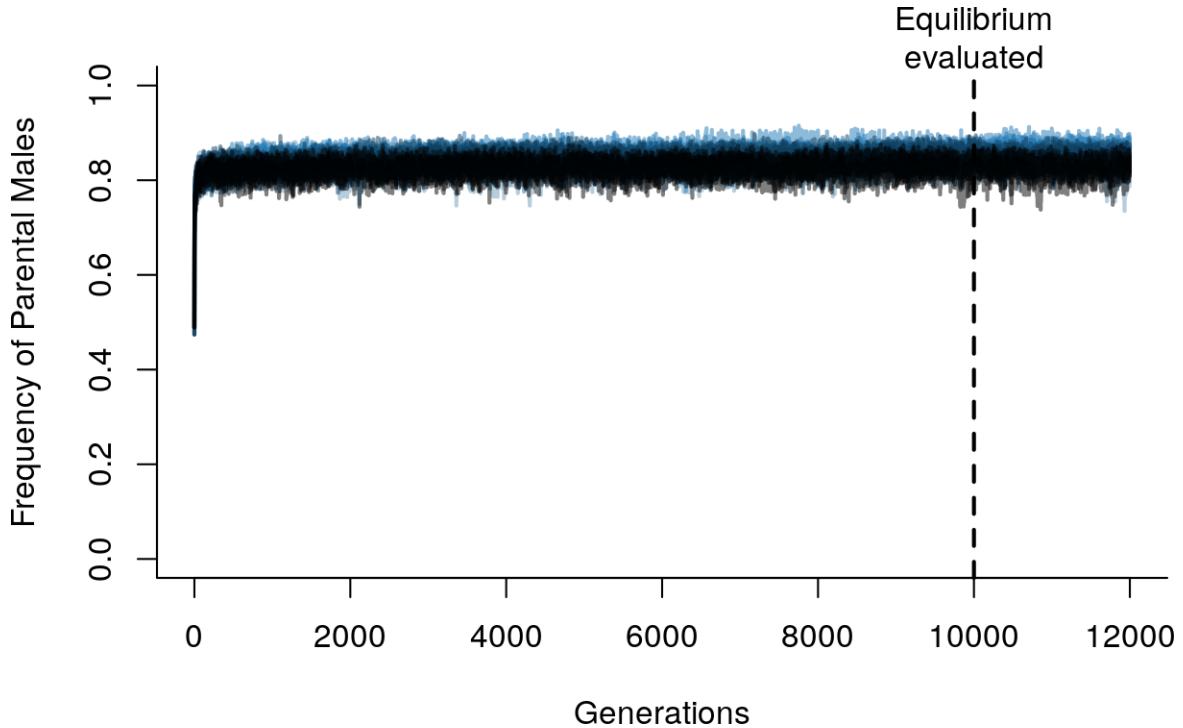


Figure 33: Frequency of parent morph with supergenes without viability selection (each color represents a different replicate)

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

	ParentFreq	ParentW	NonParentW
parent_supergene_novs_1_summary.txt_1	0.806911	1.65239	0.778947
parent_supergene_novs_1_summary.txt_2	0.850312	1.79951	0.527778
parent_supergene_novs_1_summary.txt_3	0.852071	1.62500	0.680000
parent_supergene_novs_1_summary.txt_4	0.886148	1.56745	0.800000
parent_supergene_novs_2_summary.txt_1	0.876543	1.76291	0.866667
parent_supergene_novs_2_summary.txt_2	0.835590	1.56481	0.717647
parent_supergene_novs_2_summary.txt_3	0.877670	1.67257	0.650794
parent_supergene_novs_2_summary.txt_4	0.853119	1.54245	0.739726
parent_supergene_novs_3_summary.txt_1	0.876289	1.75765	0.850000
parent_supergene_novs_3_summary.txt_2	0.868263	1.68046	0.575758
parent_supergene_novs_3_summary.txt_3	0.820116	1.54009	0.473118
parent_supergene_novs_3_summary.txt_4	0.854582	1.65035	0.712329
parent_supergene_novs_4_summary.txt_1	0.844860	1.52212	0.771084
parent_supergene_novs_4_summary.txt_2	0.813780	1.36384	0.670000
parent_supergene_novs_4_summary.txt_3	0.809339	1.54567	0.591837
parent_supergene_novs_4_summary.txt_4	0.830116	1.61860	0.477273
parent_supergene_novs_5_summary.txt_1	0.537549	1.33088	0.324786
parent_supergene_novs_5_summary.txt_2	0.529532	1.52308	0.333333
parent_supergene_novs_5_summary.txt_3	0.496842	1.49576	0.280335
parent_supergene_novs_5_summary.txt_4	0.468379	1.33333	0.234201

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.

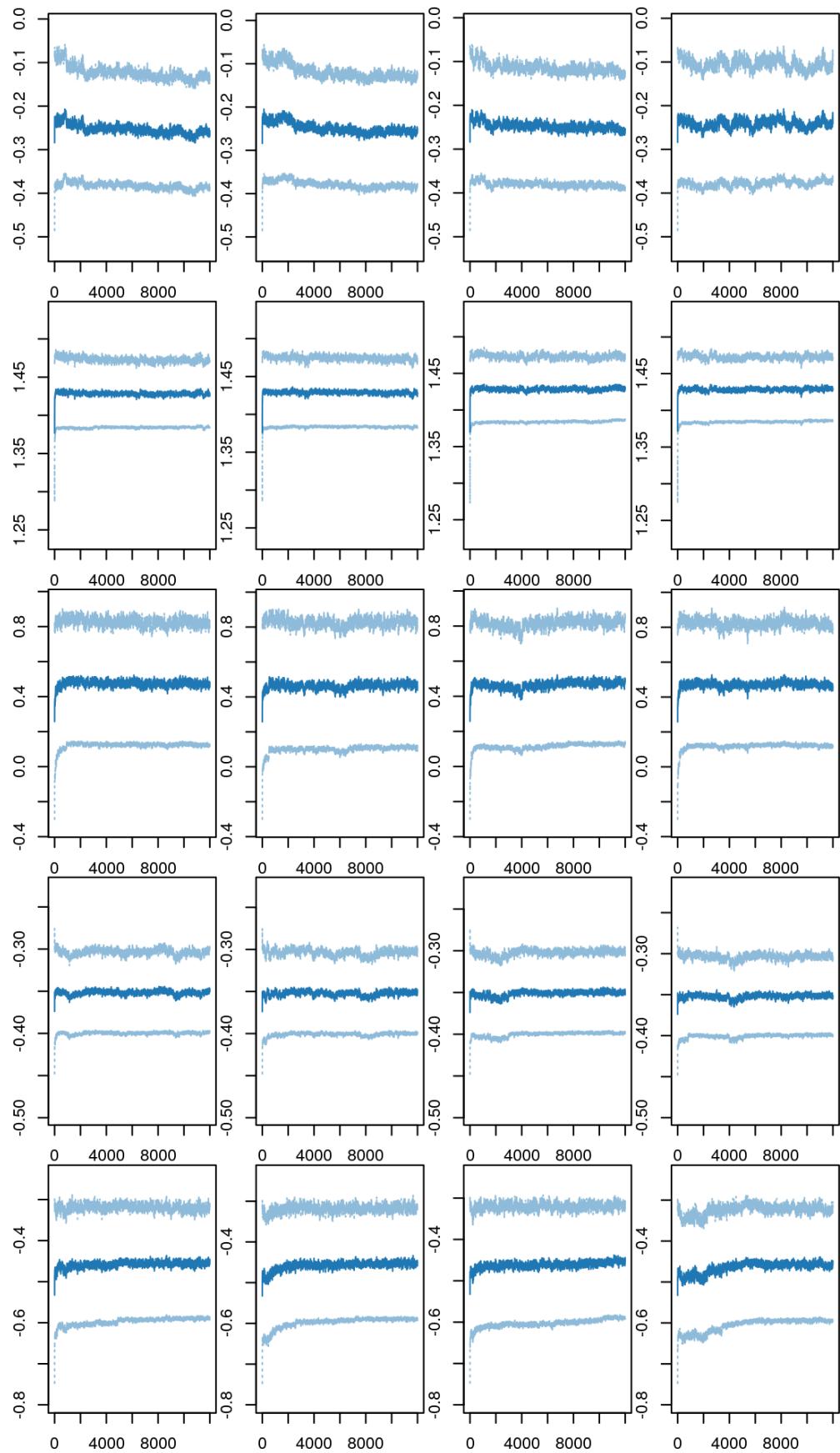


Figure 34: Evolution of parenting trait values with a supergene without viability selection. Blue dotted lines are the standard deviations around the mean and the black dotted line is the threshold

## 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.

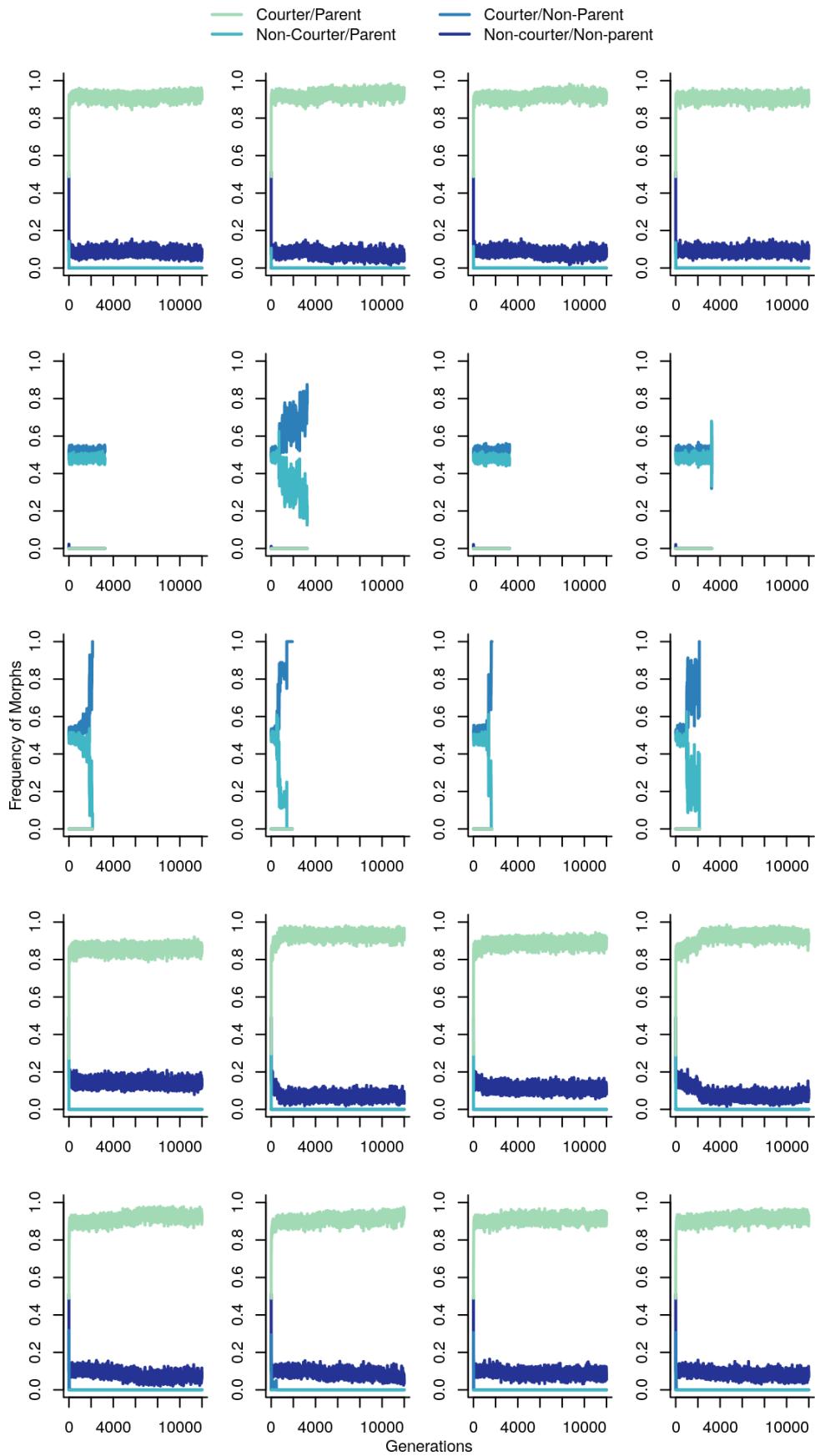


Figure 35: Frequency of the 4 morphs in each rep with supergenes

	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny	Par
parent-courter_supergene_1_summary.txt_1	11999	Pop0	950	475	475	1000	
parent-courter_supergene_1_summary.txt_2	11999	Pop1	944	464	480	1000	
parent-courter_supergene_1_summary.txt_3	11999	Pop2	959	481	478	1000	
parent-courter_supergene_1_summary.txt_4	11999	Pop3	987	489	498	1000	
parent-courter_supergene_2_summary.txt_1	3254	Pop0	999	530	469	1000	
parent-courter_supergene_2_summary.txt_2	3254	Pop1	34	19	15	54	
parent-courter_supergene_2_summary.txt_3	3254	Pop2	992	526	466	1000	
parent-courter_supergene_2_summary.txt_4	3253	Pop3	8	2	6	4	
parent-courter_supergene_3_summary.txt_1	2133	Pop0	7	6	1	4	
parent-courter_supergene_3_summary.txt_2	1910	Pop1	4	4	0	0	
parent-courter_supergene_3_summary.txt_3	1668	Pop2	4	4	0	0	
parent-courter_supergene_3_summary.txt_4	2132	Pop3	7	1	6	4	
parent-courter_supergene_4_summary.txt_1	11999	Pop0	1000	526	474	1000	
parent-courter_supergene_4_summary.txt_2	11999	Pop1	944	469	475	1000	
parent-courter_supergene_4_summary.txt_3	11999	Pop2	970	479	491	1000	
parent-courter_supergene_4_summary.txt_4	11999	Pop3	947	477	470	1000	
parent-courter_supergene_5_summary.txt_1	11999	Pop0	951	470	481	1000	
parent-courter_supergene_5_summary.txt_2	11999	Pop1	959	467	492	1000	
parent-courter_supergene_5_summary.txt_3	11999	Pop2	971	492	479	1000	
parent-courter_supergene_5_summary.txt_4	11999	Pop3	967	474	493	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.

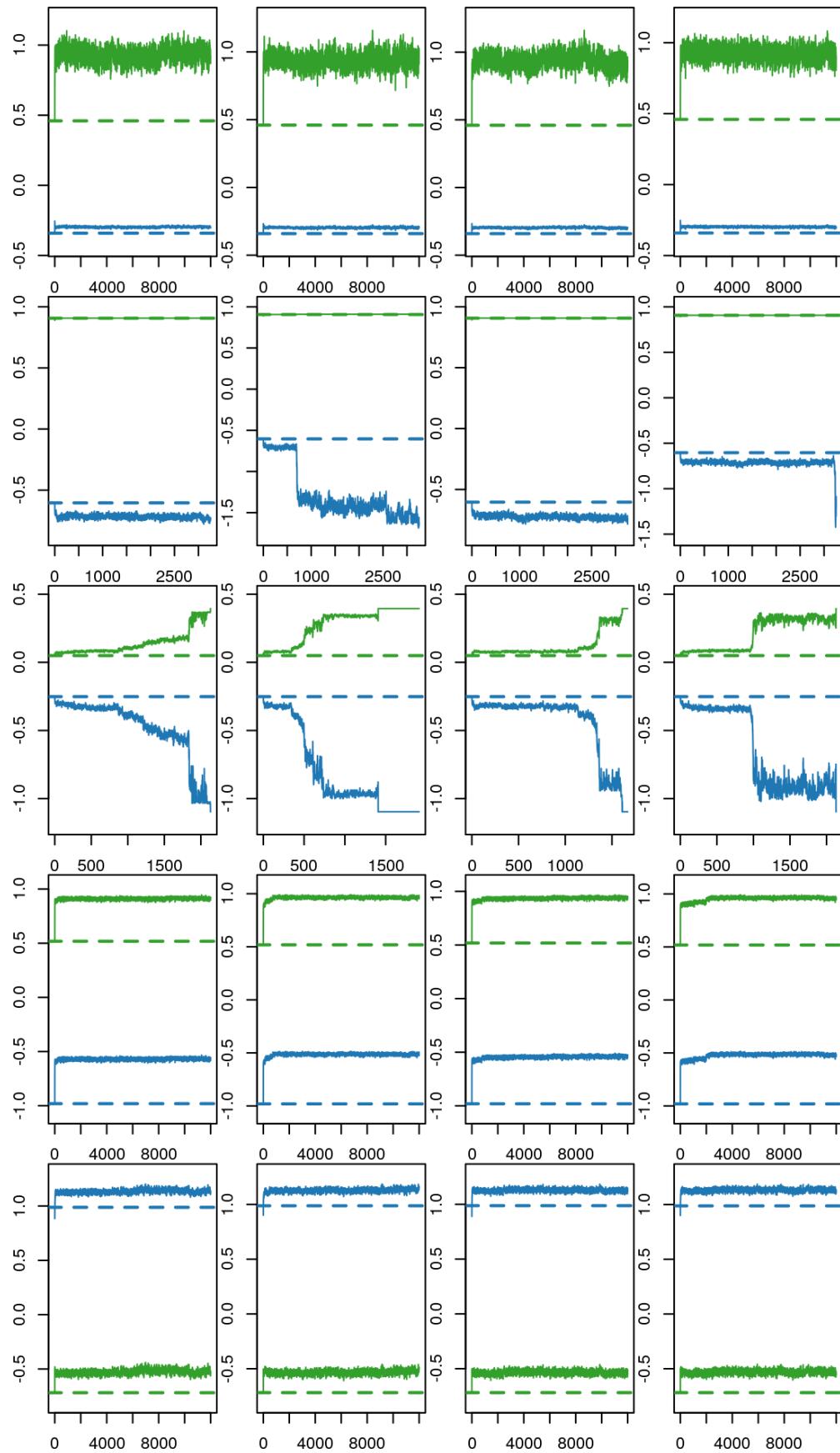


Figure 36: Evolution of the counter and parenting trait values in each rep with a supergene  
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### **Without viability selection**

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

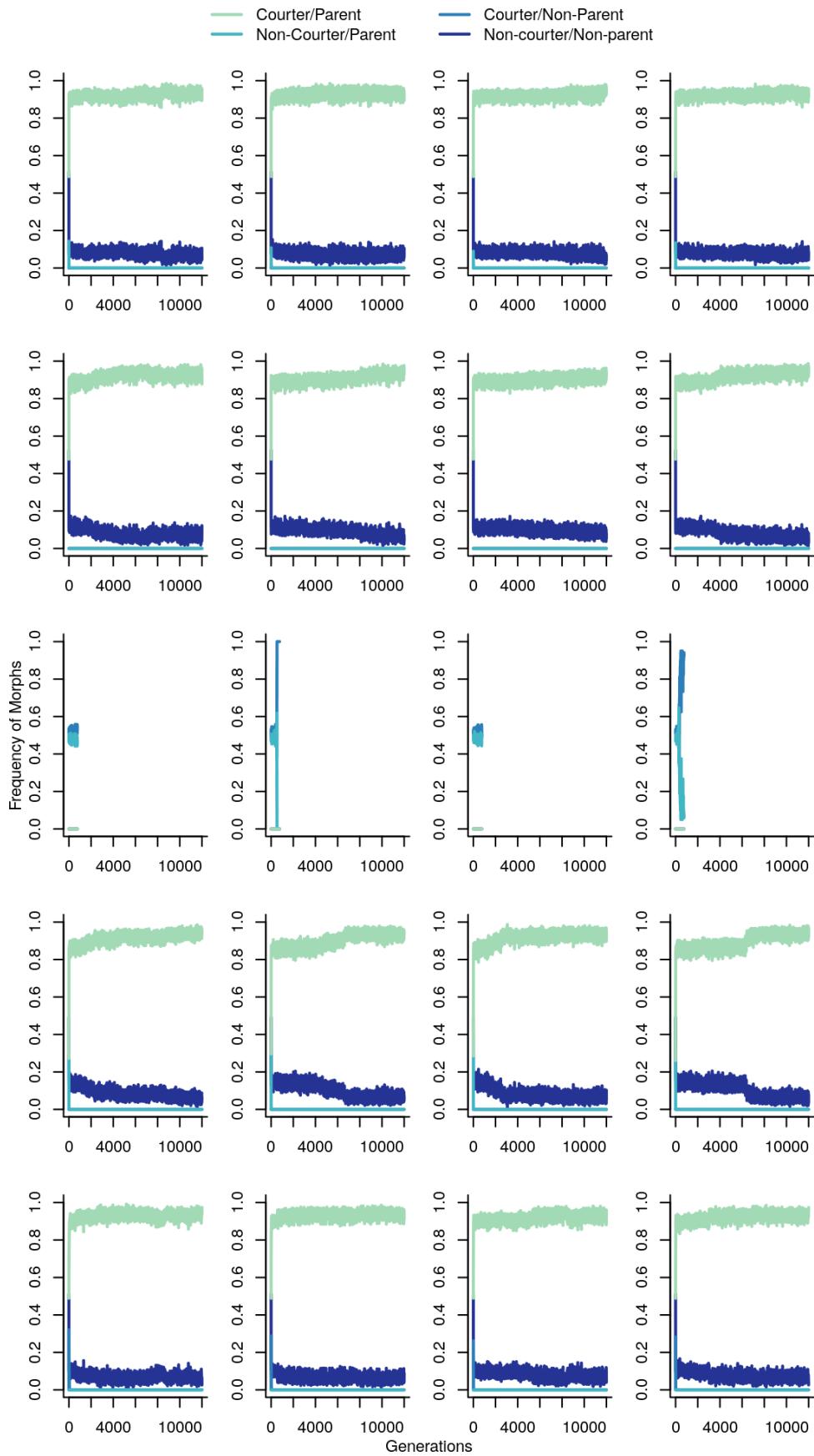


Figure 37: Frequency of the 4 morphs in each rep with supergenes without viability selection  
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	Generation	Pop	PopSize	NumMal	NumFem	NumProgeny
parent-courter_supergene_novs_1_summary.txt_1	11999	Pop0	951	458	493	1000
parent-courter_supergene_novs_1_summary.txt_2	11999	Pop1	958	484	474	1000
parent-courter_supergene_novs_1_summary.txt_3	11999	Pop2	953	470	483	1000
parent-courter_supergene_novs_1_summary.txt_4	11999	Pop3	959	506	453	1000
parent-courter_supergene_novs_2_summary.txt_1	11999	Pop0	943	459	484	1000
parent-courter_supergene_novs_2_summary.txt_2	11999	Pop1	922	447	475	1000
parent-courter_supergene_novs_2_summary.txt_3	11999	Pop2	961	483	478	1000
parent-courter_supergene_novs_2_summary.txt_4	11999	Pop3	953	475	478	1000
parent-courter_supergene_novs_3_summary.txt_1	765	Pop0	989	498	491	1000
parent-courter_supergene_novs_3_summary.txt_2	764	Pop1	7	1	6	4
parent-courter_supergene_novs_3_summary.txt_3	764	Pop2	946	479	467	963
parent-courter_supergene_novs_3_summary.txt_4	764	Pop3	32	15	17	53
parent-courter_supergene_novs_4_summary.txt_1	11999	Pop0	955	475	480	1000
parent-courter_supergene_novs_4_summary.txt_2	11999	Pop1	941	493	448	992
parent-courter_supergene_novs_4_summary.txt_3	11999	Pop2	948	477	471	1000
parent-courter_supergene_novs_4_summary.txt_4	11999	Pop3	956	456	500	1000
parent-courter_supergene_novs_5_summary.txt_1	11999	Pop0	953	477	476	1000
parent-courter_supergene_novs_5_summary.txt_2	11999	Pop1	951	504	447	1000
parent-courter_supergene_novs_5_summary.txt_3	11999	Pop2	943	484	459	1000
parent-courter_supergene_novs_5_summary.txt_4	11999	Pop3	954	468	486	1000

Multiple morphs are maintained in 20 of the 20 replicates, and those morphs contain either a parent or a counter. 4 of those reps with variation went extinct before 10000 generations.

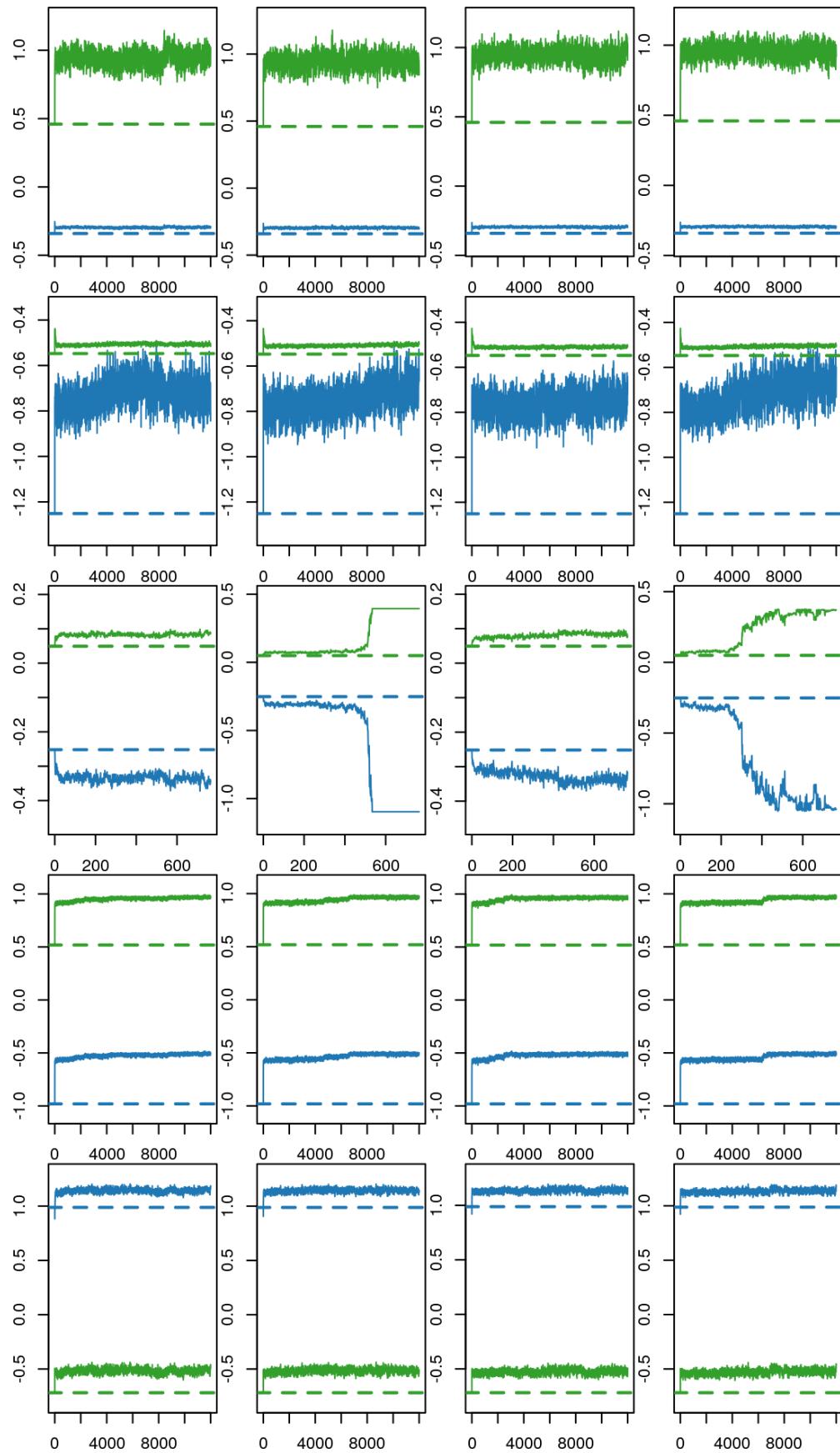


Figure 38: Evolution of the counter and parenting trait values in each rep with a supergene without viability selection

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.