

# To Change Gene Frequencies is to Evolve©

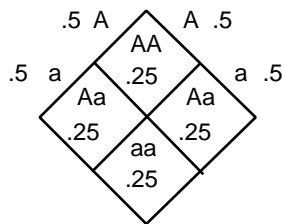
## Background

Population Genetics is sometimes referred to as Hardy-Weinberg Genetics since it begins with the work of two mathematicians, Hardy and Weinberg, whose hypothesis may be summarized as:

- Gene frequencies tend to remain constant from generation to generation IF
- There is no mutation;
  - There is no immigration or emigration;
  - The population remains large;
  - There is no non-random mating; and IF
  - There is no natural selection.

In Mendelian genetics we used the Punnett square to predict the probable offspring of a sexually reproducing pair of parent organisms. With a slight modification we can use the same device to predict the offspring of an entire population whose gene frequencies we know. A population that meets the requirements of Hardy-Weinberg equilibrium above will maintain relatively constant gene frequencies through many generations.

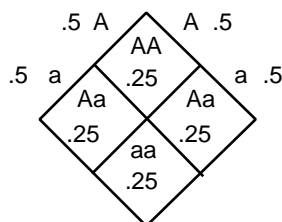
Intuitively it may feel like a dominant allele eventually ought to displace a recessive allele “since it’s dominant,” but such a feeling is based on a misinterpretation of what **dominant** means in the genetic sense. Dominant alleles might better be called **expressive** alleles because they are always expressed—even in heterozygotes—in contrast to recessive alleles that seem to “recede” in heterozygotes and are only expressed when homozygous (or hemizygous for X-linked traits).



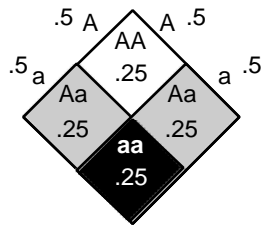
This first square show the predicted outcome of the mating of a pair of individuals heterozygous for an allele that shows simple dominance or a group of individuals in which the frequency of each allele is 0.5 for the entire population. We might imagine them as the descendants of a single pair of heterozygotes who reached an island.

	A	a
AA—>	.25	
Aa—>	.25	.25
aa—>		.25
	.5	.5

This table shows what the individuals of each genotype will contribute to the gene pool, the hypothetical pool of potential gametes. The 25% with the AA genotype produce 25% of the eggs and sperm, all bearing the A allele. Similarly those with the aa genotype produce 25% of the gametes, all with a. The half of the population that is heterozygous (Aa) produces equal numbers of both kinds of gamete.



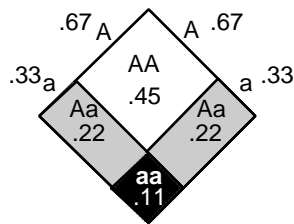
If those gametes produced by the offspring within the first square are used to predict the outcome of the next generation, it is inevitable that the same proportions of the different genotypes will be the result. Provided there are no new mutations, no migration, no natural selection, random mating, and a reasonably large population size (more than 1000).



	A	a
AA	→ .333	
Aa	→ .333	.333
aa	→	.0
	.667	.333

But suppose one genotype suddenly became lethal or caused sterility. Assume that homozygous recessive individuals either die in infancy or produce an individual unable to reproduce. The gene pool from which the next generation will arise will be derived only from individuals with AA or Aa genotypes.

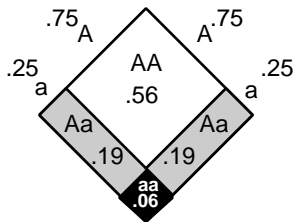
Now the homozygous dominant individuals represent one third of the breeding population and produce 33.3% of all gametes. The heterozygotes constitute two thirds of the breeders and produce two thirds of the gametes, again of both type and in equal numbers.



	A	a
AA	→ .506	
Aa	→ .247	.247
aa	→	.0
	.75	.25

The number of AA individuals will have almost doubled and will be producing 45/89 of the gametes for the next generation (50.1%). There will also be somewhat fewer heterozygotes (44%) born in the next generation, but they will be producing 49% of the gametes. There will be many fewer individuals born with the deleterious homozygous recessive genotype.

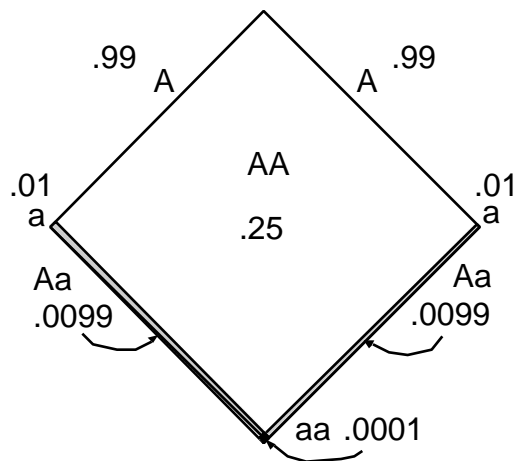
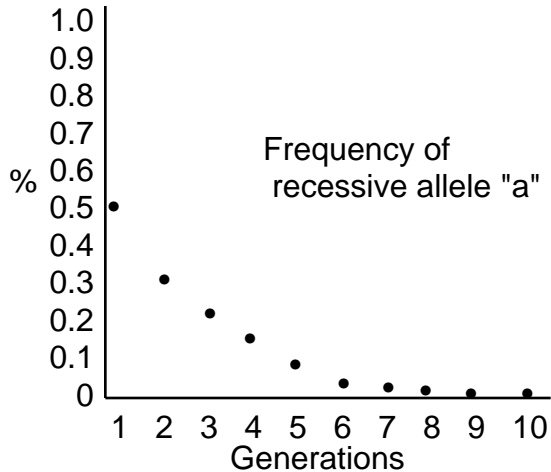
Here the 45% who have AA constitute 45/89 of the breeding population (50.56%). The 44% who are heterozygotes will produce 49.44% of the gametes, again of both kinds (A and a) and in equal numbers.



Extending the progression for another generation we would see a further increase of the AA genotype and continued declines of both the Aa and aa genotypes. More simply put, the gene frequency of A is increasing and the gene frequency of a is decreasing. The table of gene frequencies for this cross was calculated in the same tedious fashion as previously.

A graph of the frequency of the recessive allele *a* over several generations would show that, after an initial sharp drop, it would continue to decline but never completely disappear.

Consider how differently things would go if it were the dominant allele *A* that suddenly became lethal or produced sterility.



In this square, which might represent a much later generation of the same population—or the current human population in the U.S.A. with respect to the recessive trait, phenylketonuria—it can be seen that the deleterious homozygous condition appears only once in 10,000 births. Is the recessive allele all but gone? Not while it is carried by a heterozygous 2% of the population.

At relatively minor cost to a population it can carry a hidden reservoir of diversity in

the form of recessives currently selected against, but which may one day have great survival value—like the light morph of the Pepper Moth. The calculations used in this example assume the most severe possible selection. Every individual with the lethal genotype was prevented from reproducing. The resulting change in gene frequencies was dramatic. But suppose a beneficial variation only conferred a slight or moderated advantage in survival or in reproductive success. In that case only some fraction of the individuals with the deleterious trait would be kept from participating in the production of each succeeding generation. The *Evolve* software lets us model such slight advantages while assuming most of the computational drudgery. And much more.

The mathematics involved is fairly basic and may be the first opportunity to use the “square of a binomial” since beginning algebra. If we let “*p*” represent the frequency of the dominant allele of a gene and “*q*” represent the frequency of the recessive, then the sum of *p* and *q* in the gene pool must be 100% ( $p + q = 1.0$ ). You can think of a gene pool as consisting of all the sperm and all the eggs that can potentially meet in fertilization.) The product of sperm meeting egg is a new diploid individual with a genotype consisting of two alleles. The mathematical product of all the sperm ( $p + q$ ) and all the eggs ( $p + q$ ) must also equal one, or  $(p + q)^2 = p^2 + 2pq + q^2 = 1.0$ , where  $p^2$  is the frequency of the homozygous dominant genotype in the population,  $2pq$  is the frequency of the heterozygotes, and  $q^2$  is the frequency of the homozygous recessive genotype. Hardy-Weinberg Equilibrium is reached when *p* and *q* do not change from one generation to the next. If either *p* or *q* increases (and the other one necessarily decreases), then we say that the gene frequencies have changed and a small step in the evolution of the population has been taken.

Instead of using letters like A and a—or even the more generic p and q—Evolve uses the two symbols • and . The *Evolve* software let us model such slight advantages while assuming most of the computational drudgery. And much more.

Although p and q can be used to represent the frequencies of two codominant alleles instead of a simple dominant and recessive, the designers of Evolve chose an even more flexible approach. Neither of the symbols • and . is necessarily dominant, recessive or codominant, since these attributes are determined by how the Natural Selection parameters are set: if heterozygotes resemble the •• homozygotes in their ability to survive and reproduce, then clearly • is being expressed and is dominant; if heterozygotes are different from both homozygotes, then both • and . are being expressed and likely (co)dominant.

Even if your instructor demonstrated some of the Evolve scenarios, you should probably explore all of them yourself. Use the program to find answers to questions like:

1. Given a population with dominant and recessive alleles present in equal frequencies and a moderate advantage to the dominant phenotype in survival and reproduction, how long would it take to eliminate the recessive phenotype? And the recessive allele altogether?
2. Assuming the same conditions as in the previous question, except with the same moderate advantage to the recessive phenotype, how long would it take to eliminate the dominant phenotype? And the dominant allele altogether?
3. Which would have a greater impact on a population in which all genotypes have a survival rate of 22.0 and a reproductive rate of 5: an increasing the survival rate by 3 or increasing the reproductive rate by 3?