

Modelling evolutionary rescue of populations under inbreeding depression

Report of THEE research practical
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Table of contents

ABSTRACT	3
INTRODUCTION	4
METHODS	5
RESULTS	6
CONCLUSION.....	10
ACKNOWLEDGEMENTS	11
AUTHOR CONTRIBUTIONS	11
REFERENCES	11
TABLE OF FIGURES	12
DECLARATION OF AUTHENTICITY	12
APPENDIX	13

Abstract

Populations experiencing inbreeding depression may face extinction when deleterious recessive alleles become fixed or nearly fixed (Robinson et al. 2019). Evolutionary rescue through genetic introgression (introducing individuals carrying alternative alleles) can restore population viability (Aguilar-Gómez et al. 2025). In our research project, we investigate the effectiveness of such interventions depending on both the number of introduced individuals and the timing of their introduction. Here, we develop a stochastic model with non-overlapping generations to simulate an inbred population initially consisting of diploid individuals with a deleterious homozygous genotype aa , where we evaluated how the introduction of individuals with a fitter genotype AA affects population recovery. We show that beyond a relatively small threshold (≈ 8 – 10 introduced individuals), increasing the number of introduced individuals does not substantially increase rescue probability. However, the timing of introduction strongly influences rescue success even beyond this threshold: early introductions enable high rescue probability, while late introductions mostly result in rapid extinction. Our findings highlight that both factors, number of introduced individuals and timing, matters. Early intervention with optimal number of introduced individuals is key to preventing genetic collapse in small, inbred populations.

Introduction

Evolutionary rescue remains an important concept in modern ecology and conservation biology. It describes an increase in population fitness due to the immigration of new alleles (Whiteley et al. 2015). Recently this topic has become more important as many populations face shrinking habitats or increased isolation. With declining population sizes, inbreeding becomes more common. Thus, there is a rise in the risk of inbreeding depression, a reduction in fitness caused by accumulation of deleterious recessive alleles over generations.

A classic example is the Florida Panther (*Puma concolor coryi*). This population is geographically isolated from other cougar populations, which led to severe inbreeding. As a result, more of that population began exhibiting physical and reproductive abnormalities, like a kinked tail and reduced sperm quality. Shortly before becoming extinct, conservationists introduced a small number of females from a genetically diverse Texas cougar population. This successfully increased heterozygosity and reduced the frequency of deleterious alleles which restored population growth. The Florida Panther is therefore considered a textbook example successful conservation efforts to genetically rescue a population suffering from inbreeding depression (Aguilar-Gómez et al. 2025).

Another well-documented case is the Isle Royale wolf (*Canis lupus*) population. They became isolated on an island, resulting in a steady decline in genetic diversity over decades. In the 90s a single male wolf naturally migrated to the island across an ice bridge, which temporarily boosted genetic diversity. This demonstrated the immediate benefits of even a small genetic rescue (Whiteley et al. 2015). However, because no further migration occurred, inbreeding reduced the genetic diversity and fitness, therefore leading again to a concerning decline in population size over the last 20 years. To save the Isle Royale wolf, conservationists recently reintroduced 12 adult wolves from the mainland. The population has started to recover since, and the number of wolves is increasing. This shows how repeated or sustained introductions may be necessary for long-term success (Robinson et al. 2019).

These real-world examples motivated us, to investigate the dynamics beneath evolutionary rescue events and the factors that determine their success.

Thus, our question was: How many individuals must be introduced at time x to rescue an allele of a homozygote population with low fitness?

To explore this question, we used R Studio to simulate population dynamics. The initial population in our model was homozygous for a deleterious recessive allele, leading to reduced fitness and therefore population decline. We then introduced some individuals that were homozygous for the healthy allele and tracked the resulting genotype frequencies over time. By varying parameters like introduction time, fitness level of the hybrid and number of individuals introduced, we could analyse the conditions under which evolutionary rescue occurs. A rescue in this model also includes the possible outcome of a stable population without the allele a , so the only genotype that survived being AA .

Through this modelling approach, we were able to gain insight into how timing and degree of intervention interact to determine whether a declining population can recover. Our

results highlight the importance of intervention size and timing to make a genetic rescue possible.

Methods

Parameters		Default value
N_aa	Initial population size of the genotype aa	100
N_aA	Initial population size of the genotype aA	0
N_AA	Initial population size of the genotype AA	10
r_aa	Fitness of genotype aa (decay rate)	0.2
s_aA	Fitness of genotype aA	1.1
s_AA	Fitness of genotype AA	1.1

Table 1 Parameters and their default value

In this table the most important parameters are presented, what they stand for and the default value that was used if not other specified.

Model Structure

We modelled a diploid population that started off with only the homozygous genotype aa. At time of introduction (represented mathematically by reducing N_{aa} as a proxy for time), a specified number of AA individuals were added to the population.

Individuals then reproduced in non-overlapping-generations, where the number of offspring for each genotype was drawn from a Poisson-distribution. After reproduction, alleles were pooled and the genotype frequencies for the next generation were assigned according to Hardy-Weinberg proportions.

This created a population with three genotypes: aa, aA and AA.

- aa individuals reproduce with rate $(1 - r_{aa})$, representing reduced fitness due to inbreeding depression.
- aA and AA individuals reproduce with rates s_{aA} and s_{AA} , representing hybrid vigor and healthy genotype fitness, respectively.

After simulating the population dynamics with the initial parameters, we used different values for parameter N_{aa} , N_{AA} and s_{aA} , to evaluate the influence those have on the model. We simulated 100 –1000 independent replicate populations per parameter set.

We evaluated:

1. Rescue probability: proportion of replicates in which the final population size exceeded the initial population size.
2. Allele frequency outcomes: final frequency of allele *a* among rescued populations.
3. Effects of introduction timing: modeled using reduced initial N_{aa} to represent later phases of decline.

Simulations were performed in R using the functions *simulate_gen* and *simulate_pop*, which iteratively applied genotype-based reproduction and Hardy-Weinberg reconstitution until either extinction or rescue occurred.

Results

Number of introduced individuals

Figure 1 shows that the rescue probability is increasing sharply with increasing number of introduced AA individuals, but only up to a certain threshold. Over 100 simulations, introducing 8–10 individuals was sufficient to consistently achieve $\geq 80\%$ rescue probability. Beyond this point, introducing additional individuals does not substantially increase the rescue probability any further. This outcome only answers our question partially (i.e. optimal number of introduced individuals), but since we are interested in *i)* rescuing the original gene pool of our starting population (a rescue in this model also includes the possible outcome of a population being rescued but only containing AA individuals, i.e. allele *a* is lost; see Appendix Figure 6) and *ii)* the time when we have to introduce the healthy homozygous individuals (AA). To be able to answer our question and include the mentioned points *i)* and *ii)*, we further investigate in the frequency of allele *a*.

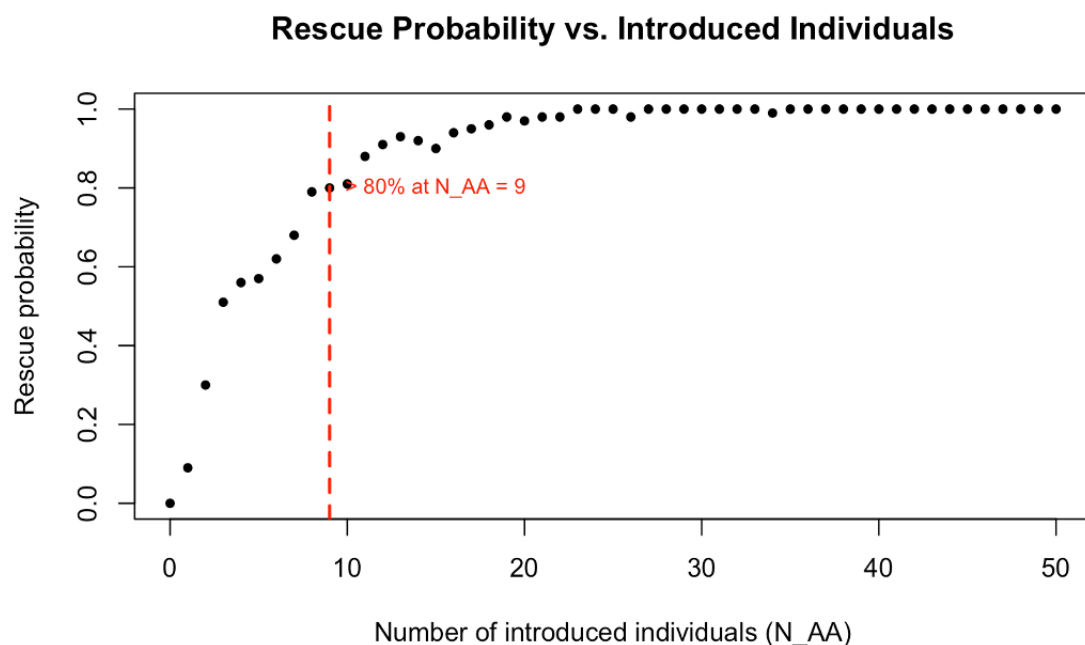


Figure 1 Rescue Probability vs. Number of Introduced Individuals

This figure shows the rescue probability of the population (on the y-axis) as a function of the number of introduced healthy homozygous individuals (N_{AA}) (on the x-axis). Each point represents the proportion of successful rescues across 100 replicates, where a rescue is defined as the final population size reaching or surpassing the initial population size at the end of a simulation. The rescue probability increases sharply within the first ten introduced individuals, reaching approximately 80% success rate at $N_{AA} \approx 9$. This value is indicated by the dashed red line. Beyond this threshold, additional introductions lead to a rescue probability that approaches saturation near 100%. The parameters were set to the default values as mentioned in table 1.

Frequency of allele *a*

Figure 2 seems to illustrate that the allele frequency gets higher with increasing number of introduced individuals. But this positive correlation vanishes if we remove the extinction events of the *a* allele from the population from our plot, as it is shown in Figure 3. The reason why we exclude the extinction events is to observe if there is an effect on the allele frequency when we increase the number of introduced individuals further than the optimal threshold (Figure 1) (i.e. we are not interested in a number of introduced individuals below 8). Since after this threshold the rescue probability is $\geq 80\%$ and rapidly increasing to 100%, we can exclude mentioned extinction events and use this approach to show that there is no “significant” (or no strong positive) effect on the allele frequency of *a* by increasing the number of introduced individuals any further than the threshold.

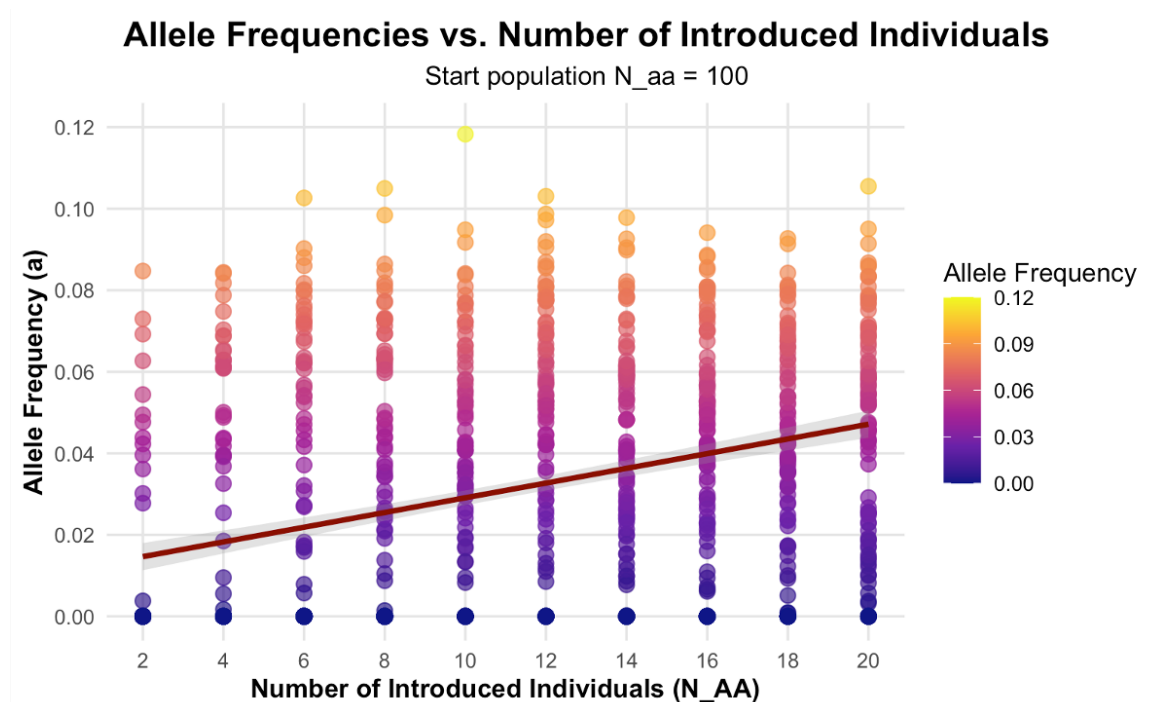


Figure 2 Allele Frequencies vs. Number of Introduced Individuals with *a* Extinction Events

This figure shows the frequency of allele *a* of the total population (y-axes) as a function of the number of introduced healthy homozygous individuals (N_{AA}) (x-axes). The initial population (N_{aa}) is fixed at 100 individuals. Each point represents the proportion of the allele frequency after one simulation and for each number of introduced individuals (2-20) 100 replicates are performed. Allele frequency of *a* is indicated with different color intensity. Rescue is defined the same way as stated in the caption of Figure 1. The fitted regression trend (red line) shows a positive correlation between increasing number of introduced individuals and *a* frequency. It is important to notice that this illustration includes all *a* extinction events (i.e. where rescue of *a* has failed) which affect the regression line. Not mentioned parameters are set to default values, see table 1.

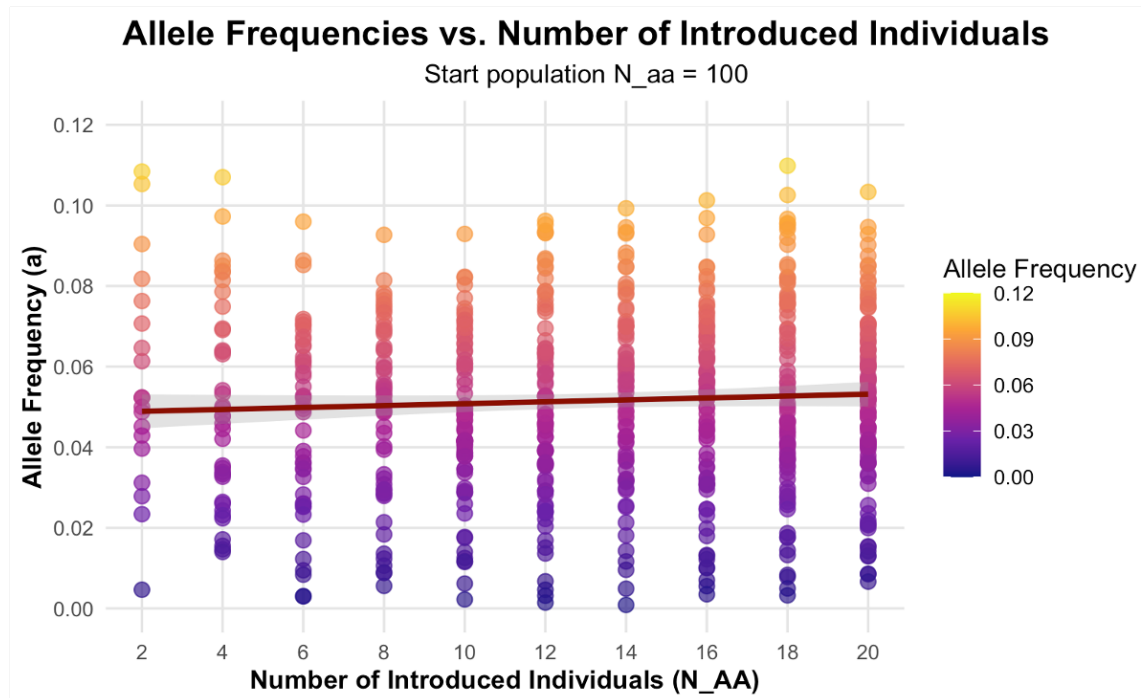


Figure 3 Allele Frequencies vs. Number of Introduced Individuals without a Extinction Events

This figure again shows the frequency of allele a of the total population (y-axes) as a function of the number of introduced healthy homozygous individuals (N_{AA}) (x-axes). The initial population (N_{aa}) is fixed at 100 individuals. Each point represents the proportion of the allele frequency after one simulation and for each number of introduced individuals (2-20) 100 replicates are performed. Allele frequency of a is indicated with different color intensity. Rescue is defined the same way as stated in the caption of Figure 1. The fitted regression trend (red line) now doesn't show the same positive correlation as seen in Figure 2, instead it is nearly horizontal. Here it is important to notice that this illustration excludes all a extinction events (i.e. where rescue of a has failed) which affect the regression line. Not mentioned parameters are set to default values, see table 1.

Timing of Introduction

In Figure 4 we can observe the effect of the time, i.e. when we introduce healthy homozygous individuals (N_{AA}), on the frequency of allele a when the population gets successfully rescued. The timing of the intervention had an effect on the allele frequency as well as for the rescue probability. Early introductions, where the initial population remained relatively large, resulted in higher allele frequencies and in high rescue probability. This effect is even stronger visualized in Figure 8 (see Appendix), when intervention was carried out with small introduction numbers. In contrast late intervention often resulted in failed rescue and smaller allele frequencies. This can be explained by the fact that small initial population sizes are more prone to extinction just by chance (i.e. deleterious effect of being homozygous for allele a can act stronger on small population sizes).

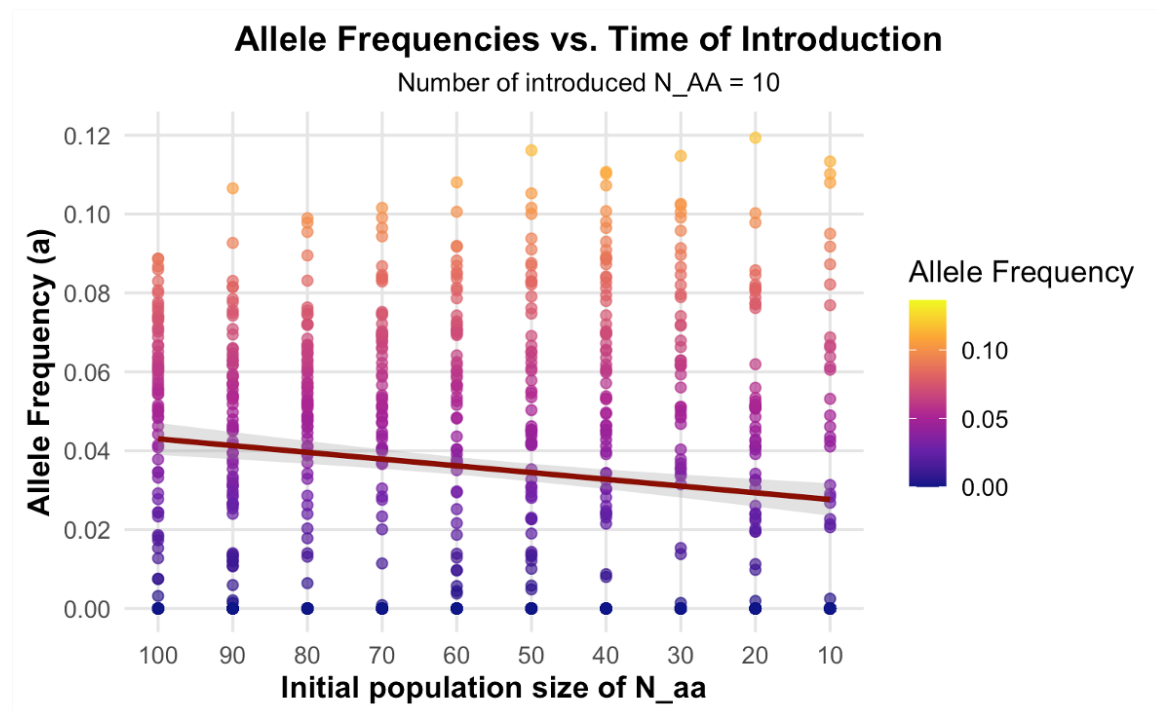


Figure 4 Allele Frequencies vs. Time of Introduction

This figure shows the frequency of allele a of the total population (y-axes) as a function of the initial population size of the deleterious homozygous genotype (N_{aa}) (x-axes). The number of introduced individuals (N_{AA}) is fixed at 10 individuals. The initial population size is used as a proxy for time, i.e. the smaller the initial population size the further time has passed (since the initial population is declining over time). Each point represents the proportion of the allele frequency after one simulation and for each initial population size (100-10) 100 replicates are performed. Allele frequency of a is indicated with different color intensity. Rescue is defined the same way as stated in the caption of Figure 1. The fitted regression trend (red line) shows a negative correlation between a frequency and time, i.e. the allele frequencies of a are declining over time. It is also important to notice that with ongoing time more a extinction events occur, indicated with fewer points occurring in the plot the more time has passed. Not mentioned parameters are set to default values, see table 1.

Conclusion

Our model demonstrates that successful evolutionary rescue in inbred depressed populations depends on both factors, the absolute number of introduced individuals of a homozygous healthy population and the timing of the intervention. But timing seems to play a superior role after knowing the crucial number (rescue $\geq 80\%$) of introduced individuals. Introducing 8-10 Individuals lead to a rescue probability of over 80 percent and by introducing this fixed number of individuals the only way to improve the allele frequency of a is to act early on, i.e. early introductions are far more effective than late ones. The findings therefore do answer our research question: How many individuals (8-10) must be introduced at time x (*Early interventions*) to rescue an allele of a homozygote population with low fitness? Our model therefore provides a simple but informative framework to guide management of genetically compromised populations in deciding *how many* and *when* to introduce individuals to prevent extinction.

These results also align with documented conservation cases such as the Florida panther (Aguilar-Gómez et al. 2025) and Isle Royale wolves (Robinson et al. 2019), where delayed interventions limited the scope of successful recovery of these populations.

Despite these positive findings our model comes with some limitations. For one we asked ourselves if we can consider it an evolutionary rescue if there is no genetic component of the original population left. Therefore, we decided to focus on the allele frequency of a , which the initial individuals were homozygous for. The results show that allele a does not disappear entirely but instead stabilizes at moderate frequencies at 3-10% of the total gene pool. The relatively low abundance of allele a can be explained by the strong deleterious effect when being homozygous for allele a ($r_{aa} = 0.2$). If we weaken the effect of this deleterious allele the a frequency is increasing strongly. On the other hand, these low frequencies are also consistent with the outcomes in the Florida panther, where ancestral genotypes persisted post-introgression. Additionally, a higher fitness of the heterozygous Aa has a positive effect on the rescue of the allele a . The effect of varying fitness values for heterozygous individuals is illustrated in Figure 7 in the appendix.

Furthermore, some other limitations come along due to the model being very simplified, i.e. we are missing some more complex population structures. Parents die of after reproduction, which means there are no overlapping generations. We also did not include different life stages; therefore, every individual can immediately reproduce. Other factors we could have implemented to make it more realistic and projectable to nature are environmental factors, e.g. habitat degradation or climate change, or density dependence, e.g. negative/positive density dependence, carrying capacity. In further research we would clearly investigate how a carrying capacity and adjusting some parameter settings, e.g. effect of overdominance in hybrids, would influence our model and the outcomes of it.

Acknowledgements

At this point we like to thank our supervisor Claudia Bank and all the assistants namely, Franziska Andrea Brenninger, Russell Jackman Jasper, Ana-Hermina Ghenu, and Julio Antonio Ayala Lopez for all the support they provided to use during this research practical. The provided base R-code and the short lecture inputs they presented helped us to improve our skills with tools like R-Studio, GitHub and to optimize our general workflow in scientific research. They always had an open ear for all our problems and were very patient when some frustration occurred. So, for all these mentioned reasons and many more: Thank you all!

Author contributions

- Abstract: PG
- Introduction: IN
- Methods: PG, IN
- Results: PG
- Discussion: PG, IN
- Revision: PG, IN
- PPP: PG, IN
- Readme: PG
- Code: PG, IN

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Table of figures

Table 1 Parameters and their default value	5
Figure 1 Rescue Probability vs. Number of Introduced Individuals	6
Figure 2 Allele Frequencies vs. Number of Introduced Individuals with <i>a</i> Extinction Events	7
Figure 3 Allele Frequencies vs. Number of Introduced Individuals without <i>a</i> Extinction Events	8
Figure 4 Allele Frequencies vs. Time of Introduction	9
Figure 5 Lifecycle of our model	13
Figure 6 Possible outcomes of one population simulation	13
Figure 7 Multiple populations with changing parameters	14
Figure 8 Allele Frequencies vs. Time of Introduction (varying N_{AA})	14

Declaration of Authenticity

We hereby declare that we have written this report independently and that all sources used have been appropriately cited. Artificial intelligence tools (ChatGTP by OpenAI) and DeepL were used to refine the language and improve readability. We also used ChatGTP during the development of our R code to help us with troubleshooting and the structure of the methods chapter.

Appendix

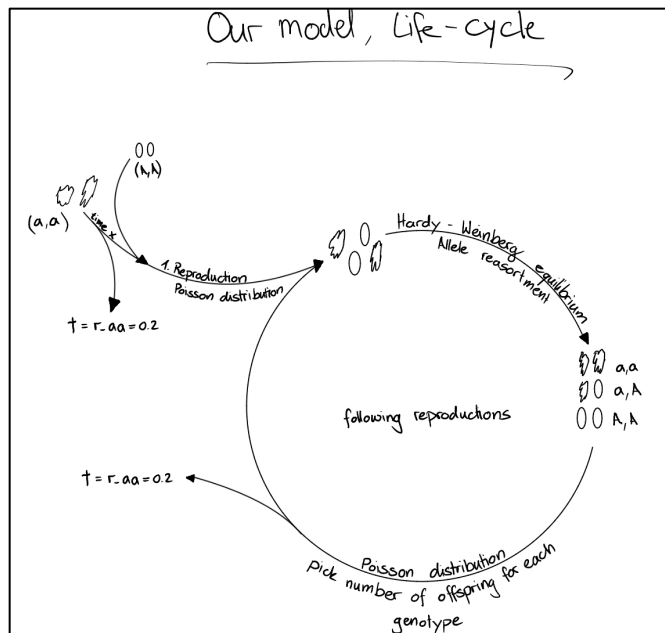


Figure 5 Lifecycle of our model

This is an illustration of every step that happens in our code during one lifecycle. We start with aa individuals, which decline with a decay rate r_{aa} . After time X (we use amount of aa as a proxy for time) we introduce a small amount of AA individuals after which we draw the number of offspring for each genotype from a Poisson distribution. Using the Hardy-Weinberg equilibrium, we reassort the alleles that were in the gene pool to the three different genotypes possible. Once more we use a Poisson distribution to generate the number of offspring for each genotype, where genotype aa declines with r_{aa} and the cycle continues.

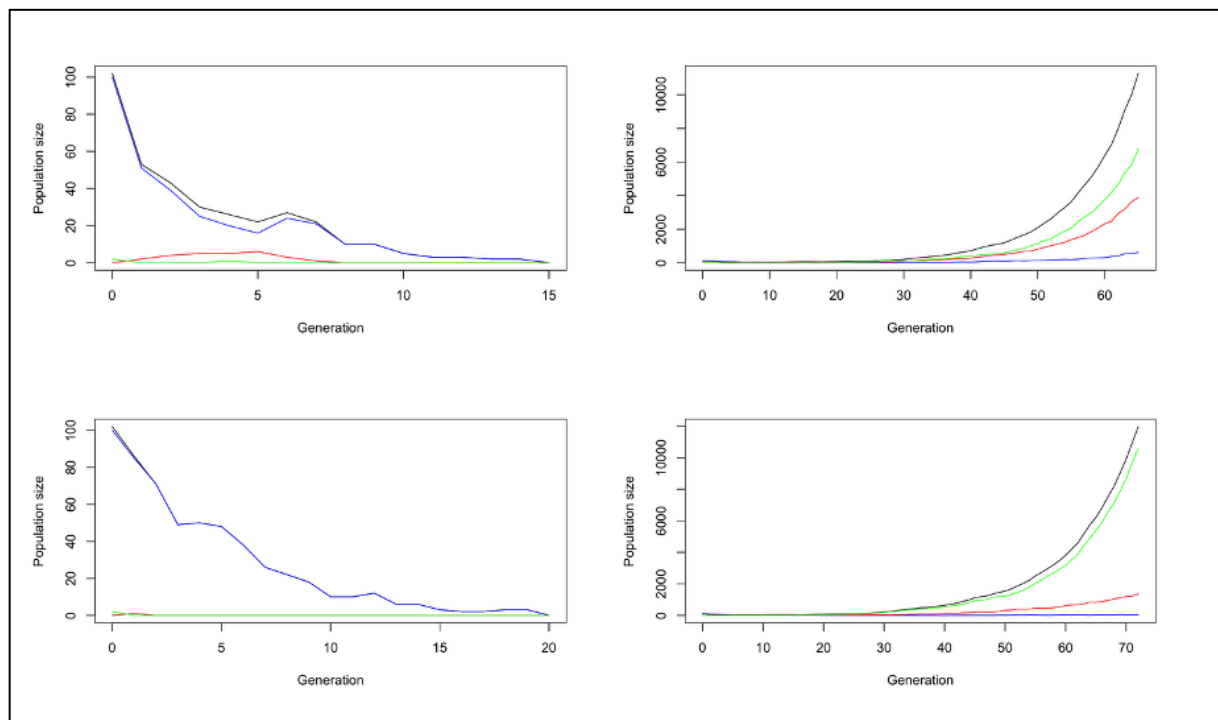


Figure 6 Possible outcomes of one population simulation

This graph shows different outcomes of the simulation of one population. The lines represent the amount of the different genotypes (black = total amount; blue = aa; red = aA; green = AA) that are present. On the x-axis you can see the time in generations, note that the four graphs all were run for a different period. The y-axis represents the population size. The values were set to the default values.

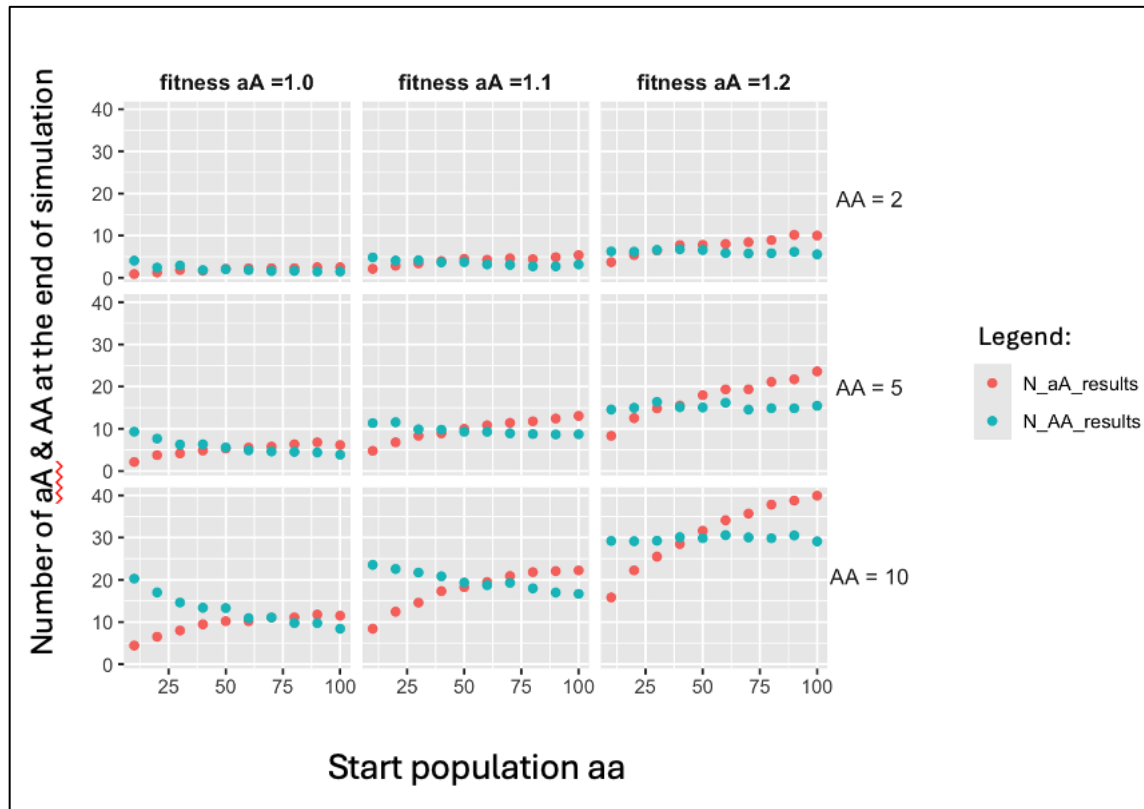


Figure 7 Multiple populations with changing parameters

This graph shows the mean of multiple populations with changing parameters. The dots represent the frequency of the genotypes aA and AA in the population at the end of each simulation. The x-axis shows the population size of aa at the beginning of the simulations, the y-axis the frequency of aA and AA. We altered the parameters for the population size of the genotype aa (10 till 100), the number of the genotype AA that was introduced (2,5,10) and the fitness of the hybrids (1.0, 1.1, 1.2). Each combination was 1000 times replicated and the mean of the frequencies of aA and AA then calculated.

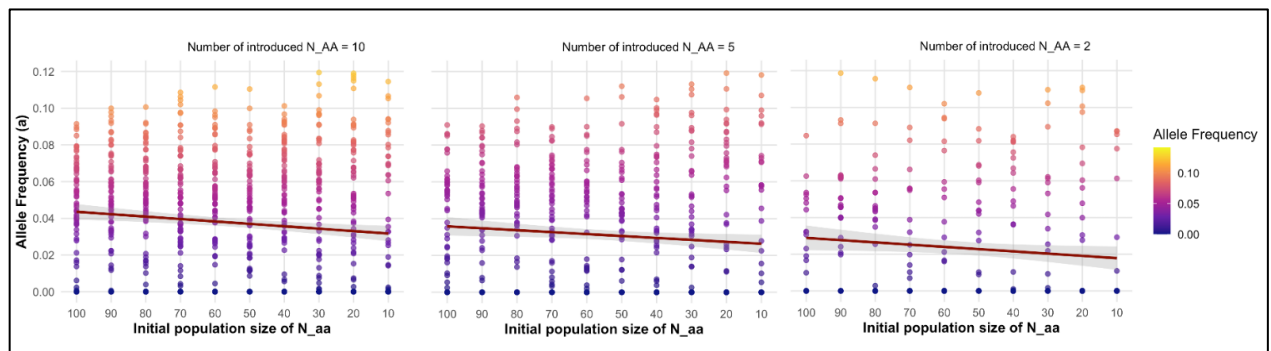


Figure 8 Allele Frequencies vs. Time of Introduction (varying N_{AA})

This figure shows the frequency of allele *a* of the total population (y-axes) as a function of the initial population size of the deleterious homozygous genotype (N_{aa}) (x-axes). The number of introduced individuals (N_{AA}) varies from 10, 5, and 2 individuals. The initial population size is used as a proxy for time, i.e. the smaller the initial population size the further time has passed (since the initial population is declining over time). Each point represents the proportion of the allele frequency after one simulation and for each initial population size (100-10) 100 replicates are performed. Allele frequency of *a* is indicated with different color intensity. Rescue is defined the same way as stated in the caption of Figure 1. The fitted regression trend (red line) shows a negative correlation between *a* frequency and time, i.e. the allele frequencies of *a* are declining over time. It is also important to notice that with ongoing time more *a* extinction events occur, indicated with fewer points occurring in the plot the more time has passed. Not mentioned parameters are set to default values, see table 1.