

HOMWORK 4 ANSWER KEY

(1) The fitness of each genotype is given by:

$$W_{AA} = 1 - 6p(1 - p) + 3(1 - p)^2 \quad (1)$$

$$W_{Aa} = 1 - 2sp(1 - p) \quad (2)$$

$$W_{aa} = 1 - 6p(1 - p) + 3p^2 \quad (3)$$

Assuming $s = 1$, the fitness of each genotype can be plotted as a function of the allele frequency p using the following R code:

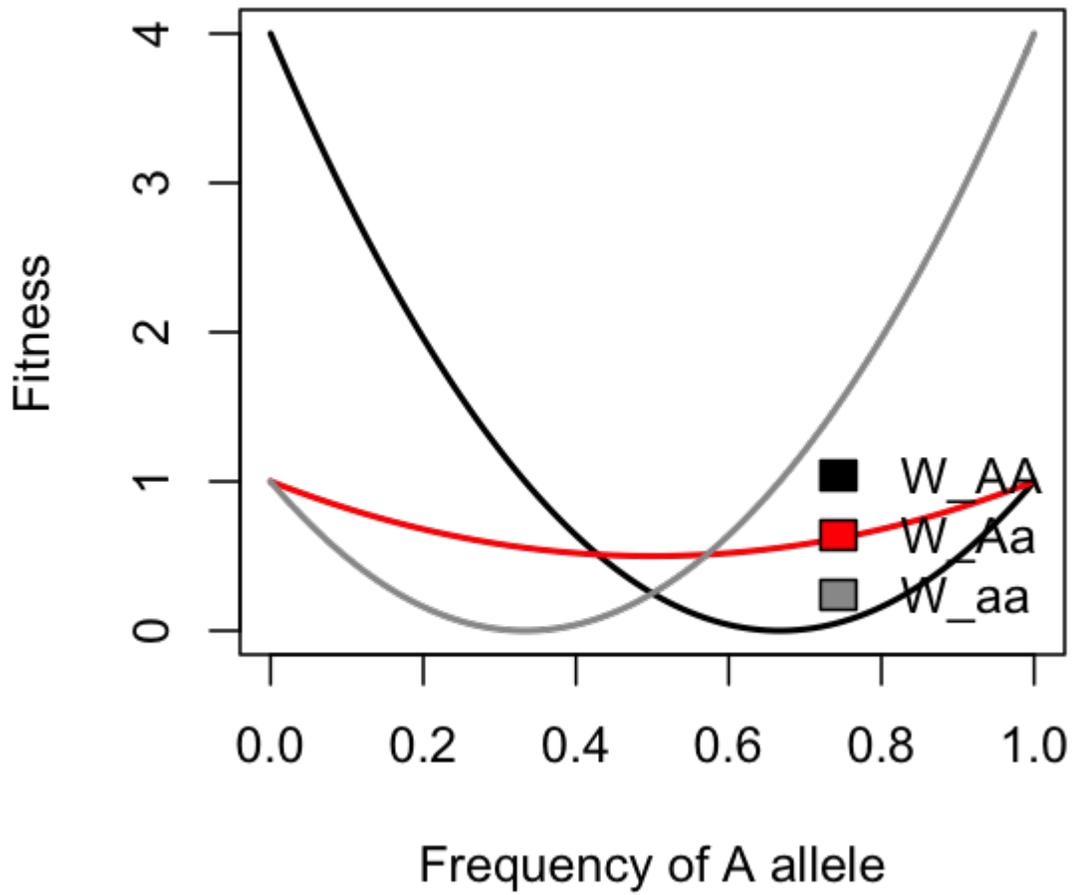
```
W_AA <- function(p) 1-6*p*(1-p) + 3*(1-p)^2
W_Aa <- function(p, s) 1 - 2*s*p*(1-p)
W_aa <- function(p) 1 - 6*p*(1-p) + 3*p^2

p_seq <- seq(0, 1, 0.01)

plot(p_seq, W_AA(p=p_seq), type='l', lwd=2, col='black',
      xlab='Frequency of A allele', ylab='Fitness',
      main='Genotype Fitnesses')
lines(p_seq, W_Aa(p=p_seq, s=1), lwd=2, col='red')
lines(p_seq, W_aa(p=p_seq), lwd=2, col=gray(0.6))
legend(x='bottomright', c('W_AA', 'W_Aa', 'W_aa'),
       fill=c('black', 'red', gray(0.6)), bty='n')
```

Examination of item 1 shows that the AA genotype's fitness is maximized at $p = 0$, when the frequency of the AA genotype is $p^2 = 0$; the Aa genotype's fitness is maximized at $p = 0$ and $p = 1$, when the frequency of the Aa genotype is $2p(1 - p) = 0$; the aa genotype's fitness is maximized at $p = 1$, when the frequency of the aa genotype is $(1 - p)^2 = 0$. From these observations, it is clear that each genotype has highest fitness when it is uncommon - that is, there is a selective advantage to rarity. Biological examples of situations when it is advantageous to be rare arise when predators form a search image based on the most common traits of prey (by looking different, individuals have lower predation risk), when females prefer to mate with uncommon individuals, or in the presence of disease that quickly adapts to the most common genotype background in the population. The implication of such "negative frequency-dependence" is that evolution will never lead to fixation ($p = 0$ or $p = 1$). As soon as either the A or a allele becomes more common ($p > 0.5$ or $p < 0.5$, respectively), there will be selection favoring individuals carrying the opposite allele.

Genotype Fitnesses



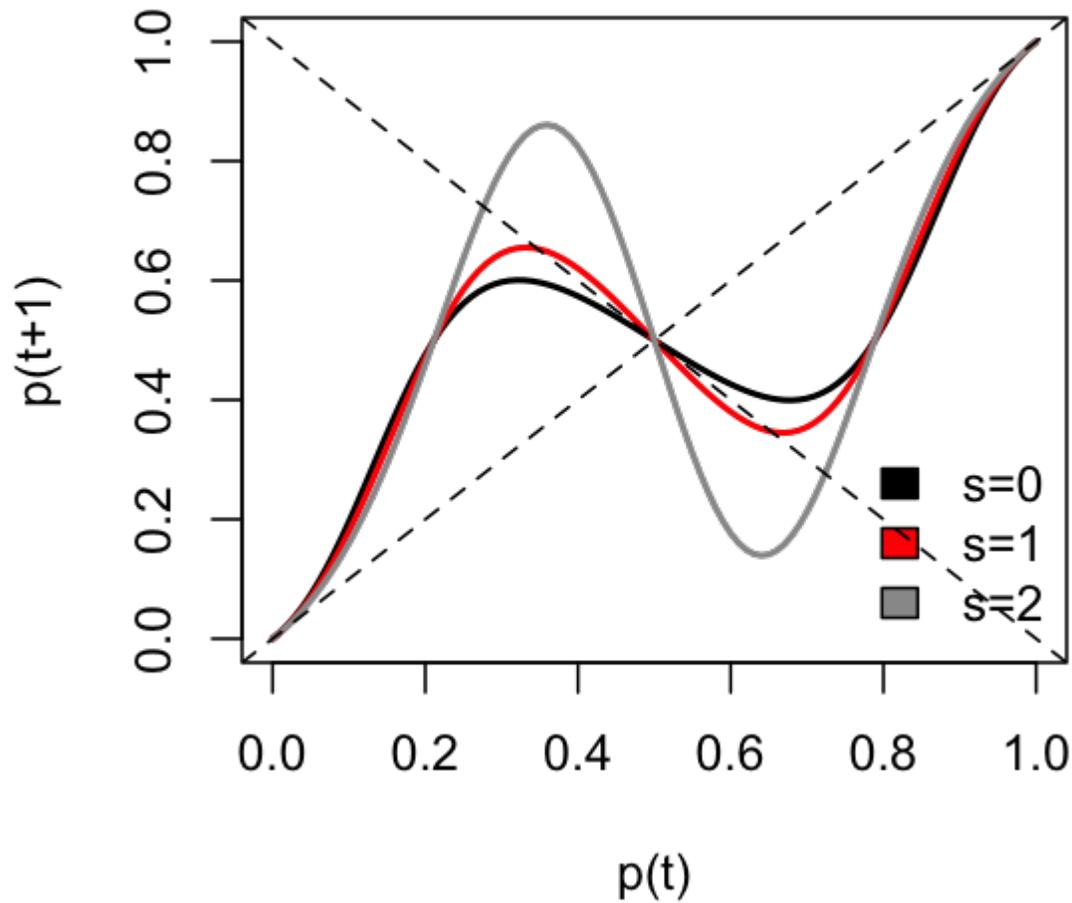
(2) You can plot the recursion equation $p(t+1)$ as a function of $p(t)$ using the code below.

```
## Marginal fitness of the A allele
w_A <- function(p, s) p*W_AA(p) + (1-p)*W_Aa(p,s)
## Mean population fitness
w_bar <- function(p, s) p^2*W_AA(p) + 2*p*(1-p)*W_Aa(p,s) + (1-p)^2*W_aa(p)

## p(t+1) for three different values of s
p_0 <- p_seq * w_A(p_seq, s=0) / w_bar(p_seq, s=0)
p_1 <- p_seq * w_A(p_seq, s=1) / w_bar(p_seq, s=1)
p_2 <- p_seq * w_A(p_seq, s=2) / w_bar(p_seq, s=2)

## Plot on the same axes
plot(p_seq, p_0, type='l', lwd=2, col='black',
      xlab='p(t)', ylab='p(t+1)',
```

Recursion for different s values



```

main='Recursion for different s values')
lines(p_seq, p_1, lwd=2, col='red')
lines(p_seq, p_2, lwd=2, col=gray(0.6))
legend(x='bottomright', c('s=0', 's=1', 's=2'),
      fill=c('black', 'red', gray(0.6)), bty='n')
## Add the 1-1 line
abline(0, 1, lty=2)
## Also add a negative 1-1 line to assess whether
## the slope at p=0.5 is less than -1
abline(1, -1, lty=2)

```

There are three equilibria for each value of s : $p = 0$, $p = 0.5$, and $p = 1$. To assess the stability of each equilibrium, you can simply look at the slope of the recursion. If the slope of the recursion is between -1 and 1 , the equilibrium is stable; if it is greater than 1 or less

than -1 , the equilibrium is unstable. Moreover, if the slope is negative, there will be oscillations in the allele frequency through time. Based on item 2, the recursions have slope greater than 1 at $p = 0$ and $p = 1$, indicating that these two equilibria are both unstable. (Actually, the slope is exactly equal to 1 ; however, any initial starting allele frequency greater than $p = 0$ or less than $p = 1$ (no matter how small the difference from the equilibrium) will eventually move away, so it is reasonable to characterize both of these equilibria as unstable.) The slope of the recursion at $p = 0.5$ depends on the value of s . When $s = 0$, the recursion has a slope greater than -1 , so the equilibrium is stable; for $s = 1$ and $s = 2$, the recursion has a slope less than -1 , so the equilibrium is unstable.

- (3) To simulate the change in allele frequency through time, you can use the following code. The subsequent figures confirm our predictions from (2): when $s = 0$, the $p = 0.5$ is stable; when $s = 1$, the $p = 0.5$ equilibrium is unstable, giving rise to a 2-cycle; when $s = 2$, the $p = 0.5$ equilibrium is unstable, giving rise to chaotic dynamics.

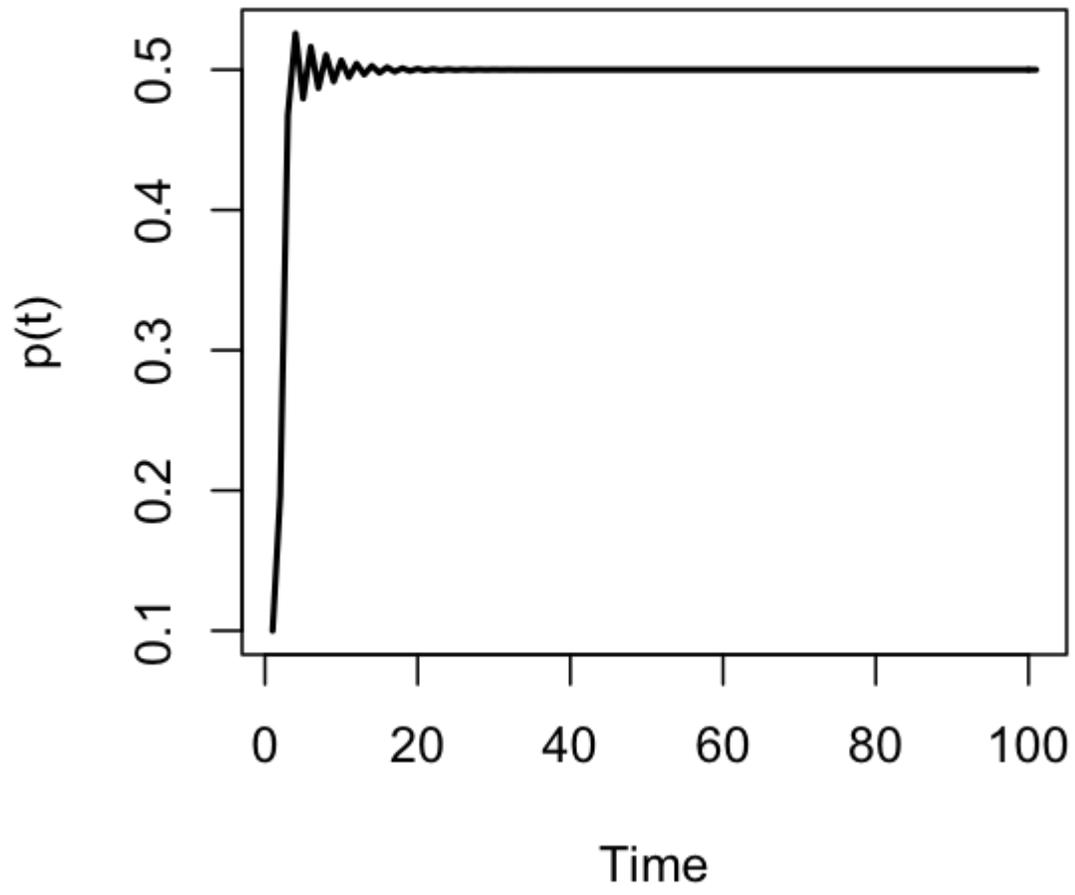
```
## Function to calculate allele frequency change through time
freq_dep_model <- function(s, p0, T) {
  ## Vector to store allele frequencies through time
  p_vec <- vector(mode='numeric', length=T+1)
  p_vec[1] <- p0
  for (i in 1:T)
    p_vec[i+1] <- p_vec[i]*w_A(p_vec[i],s)/w_bar(p_vec[i],s)
  return(p_vec)
}
freq_dep_0 <- freq_dep_model(s=0, p0=0.1, T=100)
freq_dep_1 <- freq_dep_model(s=1, p0=0.1, T=100)
freq_dep_2 <- freq_dep_model(s=2, p0=0.1, T=100)

plot(1:101, freq_dep_0, type='l', lwd=2,
     xlab='Time', ylab='p(t)',
     main='Frequency of A when s=0')
plot(1:101, freq_dep_1, type='l', lwd=2,
     xlab='Time', ylab='p(t)',
     main='Frequency of A when s=0')
plot(1:101, freq_dep_2, type='l', lwd=2,
     xlab='Time', ylab='p(t)',
     main='Frequency of A when s=0')
```

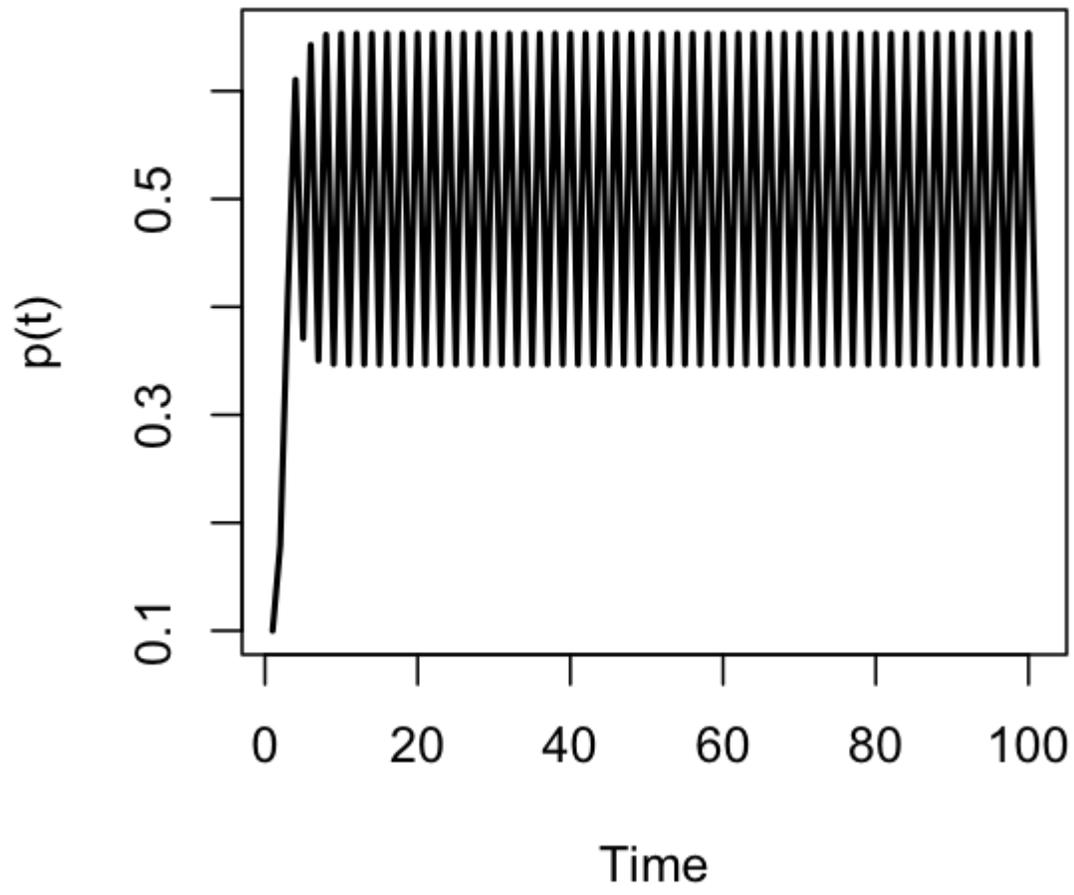
Grading rubric: Question (1) was worth 4 points. Two marks were awarded for correctly plotting the fitnesses, identifying the p value where genotype fitness was maximized, and the genotype frequency at this p value. Two marks were also awarded for the discussion of evolution and fixation. **However, this question was worded too ambiguously.** I awarded full marks to anyone who attempted the question.

Question (2) and (3) were combined into 3 2-point questions, one for each value of s . Full marks were awarded for correct plots, correct identification of equilibria, and correct characterization of stability. By far, the most common way to lose marks on this question was to misidentify the $p = 0.5$ equilibrium as stable for all s values. Two marks were lost if this mistake was made because the answers between (2) and (3) were not consistent: in (2), $p = 0.5$ was identified as stable, but (3) clearly shows unstable dynamics. Only half a point was lost for an incorrect but consistent set of plots.

Frequency of A when $s=0$



Frequency of A when $s=1$



Frequency of A when $s=2$

