**Variation in reproductive success and the effective population size of sex chromosomes**

**General background**

Variation in reproductive success decreases a population’s effective population size. Different sexes will often have differences in their variation in reproductive success. In many species, it is thought that males will have much great variation in reproductive success. With respect to effective population size, this difference between males and females does not typically matter because their genes recombine during breeding allowing them to genetically behave has one population. Sex chromosomes, however, spend a disproportionate amount of time in one sex. This suggests that sex chromosomes could have different effective population sizes from each other. The goal here is to build a spatial explicit model that explores how different parameters influence the effective population size of sex chromosome in a species with UV sex determination (e.g., bryophytes), assuming a simple life history.

**Model design**

*Life history assumptions*

The population has UV sex determination and every individual is either male or female (there are no intersex individuals). All reproduction occurs sexually. We assume that females only mate once per generation and there is no limit to the number of mates that a male can have in a generation. Individuals can only mate with an individual of the other sex that is spatially adjacent to them. There is no mate preference.

*Simulations*

For each run of the simulation (equivalent to one generation of mating), individuals are randomly placed onto a 100 X 100 cell grid. Females mate in a random order. Each female searches the 8 cells adjacent to it for males to mate with. If there is more than one adjacent male, the female randomly selects one of them to mate with. If no males are in the cells adjacent to the female, that female does not mate. An example of the population following one run of the simulation can be seen in figure 1.



**Figure 1.** Example of the population at the end of one run of the simulation. Each cell is a patch that could or could not hold an individual. In the above example, the population size was 6000 and the sex ratio was equal.

We assumed that each mating event within a generation resulted in the same number of offspring. In order to keep population size constant, we adjusted the fecundity so that the mean number of offspring per individual was 2. Therefore, the fecundity *F* was given by **, where *r* is the number of females that mated that generation.

For each run of the simulation, we recorded the total number of offspring per each male and female (females could only have 0 or *F* offspring) and calculated the variance in reproductive success for each sex. The variances in reproductive success were then used to calculate the effective population sizes of the U (females) and V (males) chromosomes, using the following equations, respectively

 ,

where  and  are the realized population sizes and  and  are the variances in reproductive success of females and males, respectively. The effective population size of an autosome is calculated using the equation

 ,

where *N* is the total realized population and  is the variance in reproductive success among the entire population (i.e. males and females).

We ran simulations for a range of population densities and sex ratios. To vary density, we varied the population size while always keeping the arena of a fixed size of 100 X 100 cells. For each parameter set, we ran 100 runs of the simulation.

**Results**

*Population density*

Given our life history assumptions, when the population is sparsely populated, there is large variance in reproductive success because many individuals are not adjacent to potential mates and the few that do find mates have many offspring. Therefore, the effective population size of all chromosomes is lower than the realized population size. As the population becomes more densely populated, the variance in reproductive success decreases more quickly for females than males, leading to differences in the effective population sizes of the U and V chromosomes (Figure 2). This is intuitive, because when the population is densely populated nearly all females will mate once, but some males will have many mates and others will have none. In the densest populations, the effective population size of the U chromosome is about one third that of the V chromosome.



**Figure 2.** The effective population size of an autosome, the U chromosome, and the V chromosome, for different realized population sizes. The arena was always a 100 X 100 cell grid; therefore, larger populations are more densely packed.

*Sex ratio*

The effective population size of all chromosomes is lowest when the sex ratio is male-biased. The effective population size of an autosome and the U chromosome are highest when the sex ratio is female-biased. The effective population size is greatest for the V chromosome when the sex ratio is equal. As the sex ratio becomes more female-biased the difference between the effective population sizes of the U and V chromosomes becomes greatest (Figure 3).



**Figure 3.** The effective population size of an autosome, the U chromosome, and the V chromosome, for different sex ratios. In all simulations the realized population size was held constant at 6000 individuals.

**Comparing data to simulations.**

In general, . Therefore, given the equations above,

 ,

where  is the autosomal mutation rate. Solving for the  gives



Similarly, for the chromosomes U and V, respectively,

 ,

and

 .

Now, if from the data we have the ratio between theta for the U and V chromosomes, , we can solve for the ratio  to determine how different the variances in reproductive success would need to be to explain the results, such that

 .

Similarly, given the ratio  , we can solve for the ratio  , such that

 .

The values of  and  can then be compared to results in the simulations given in figure 4 (same data is in ratioData.csv). This can tell us if the ratio of between thetas could be expected just because of the spatial structure of the population.



**Figure 4.** The ratios between variances in reproductive success of U and V (; black) and U and an autosome (; blue). This data is also shown in ratioData.csv. The patterns plotted here holds for different population and arena sizes. What actually matters in the density of the population (e.g., *N* divided by arena size).

**Example of comparing to data**

Say from the data we get that , , and . I also assume that the mutation rate is the same for all chromosomes at . Unfortunately, we also have to assume a population size, so assume that *N* = 400,000.

*Ratio of V to U*

From the data, we would get that . We can then compare that to the simulation data (figure 4) and see that we would only expect to see that when the density is greater than ~0.25.

*Ratio of U to A*

From the data, we would get that . Comparing this to the simulation results, we would only see this at very low population densities (< 0.05).

*Conclusions*

Considering both the results above, the data probably cannot be explained the population’s spatial structure alone and selection probably played a role. If we assume that there was no selection on the V chromosome, then the population would have to have had a density greater than ~0.25. However,  is smaller than we would expect at that density and thus we would conclude that there was selection on the U chromosome.

Alternatively, we could assume that there was no selection on the U chromosome. In that case, the population would have to have had a density less than 0.05. However,  is smaller than we would expect at that density and thus we would conclude that there was selection on the V chromosome.

So, in sum, if the data looks like this (which it kind of seems like it does) there was likely selection on the U chromosome the V chromosome or both. I do not know if we can tease that apart though.