Chapter 7

Assortative Mating

7.1 What has Sex got to do with it?

Quite a lot, actually. Evolution is based on the differential survival and reproduction of organisms. Yet, the focus on natural selection and the drama of life and death has tended to eclipse the fact that reproduction is an equally crucial, and potentially shaping, dynamic in evolution (Cronin 1991). After all, survival with no reproduction has the same effect on the genetic composition of the next generation as dying before having the opportunity to reproduce.

Perhaps, given that sexual reproduction defines the boundaries of gene pools, it is not surprising that the dynamics of sex can have an important impact on diversity. Bernstein et al. (1985) point to an important implication of sexual reproduction in addition to the sharing of genes in a gene pool. In order to reproduce sexually, one must find a mate. This may be no problem if a species is quite common and so potential mates abound. However, if the species is rare in an area, it may be quite difficult to locate a potential mate. In other words, sexual reproduction includes a cost for low population density. A superior competitor that arrives in a region either through mutation or migration may still die out if only because the probability of finding a mate is low (Bernstein et al. 1985). All other things being equal, the penalty for low density may tend to kill off the outliers in character or geographical space and so cluster the remaining organisms into discrete bunches. This alone may explain the perception of species as coherent units. The supposition that outliers will be tend to die out rests on the assumption that these outliers tend to be reproductively differentiated from the more common organisms and that this differentiation makes it harder for them to successfully mate.

Andersson (1994, pp. 205–226) reviews the importance of sexual selection in speciation. He finds evidence that "mechanisms of mate recognition, which often seem to be based on sexually selected traits, may be crucial in speciation" (Andersson 1994, p. 223). Specifically, evidence for the importance of sexual selection in diversification comes from the mating behaviors of passerine birds, anurans (frogs), Hawaiian fruit flies and crickets, African cichlid fish, insect pollinated angiosperms (flowering plants), and others. Many of these cases may simply be cases where the organisms are using perceptual cues to selectively mate with similar organisms. That is, cues that facilitate positive assortative mating.

The very existence of sexual reproduction, which was invented about 1 billion[1] years ago (Cowen 1990, p.67), introduces a new dimension to the process of evolution. No longer is it adequate just to survive and accumulate resources. With sexual reproduction, an organism must find and be accepted by a mate. These pressures are every bit as important in the evolution of a lineage as the pressures to avoid predation and find nourishment. Recent models have shown that the evolution of mate preferences can stimulate rapid speciation without any geographic barriers to divide the population (Todd & Miller 1997; 1991). This chapter will examine the extent to which the pressures of mate selection lead to the division of gene pools and the formation of new species.

7.2 Sexual Selection

There are many forms of sexual selection. In general it encompasses all factors that influence the quantity and quality of mating opportunities of organisms. One archetypal arena in which these factors play out is in the choices, or selection, of mates by organisms. However, it is only considered sexual "selection" if the choice of the mates comprises a selective force on the organisms. This means that mate choices lead to differential reproduction due to the expression of genetic differences in the organisms.

Sexual selection has been implicated in the evolution of some of the most glorious exemplars of nature, including most of the spectacular plumage on male birds, most famously the peacock. The power of sexual selection lies in a positive feedback loop. Let us consider two genes. One that encodes a female preference for bright plumage in their mates. The

[1] Give or take half a billion.

other encodes the development of that plumage in the males. Then a male with bright plumage will enjoy an average number of mating opportunities with the females who do not care about plumage, but an additional bonus number of mating opportunities with the choosy females. This explains how the genes for colorful males spread, but not how the females genes for that preference spread. That this was a serious hole in Darwin's theory of sexual selection went largely unnoticed for half a century (Cronin 1991). And so the significance of R. A. Fisher's solution in 1915 was not fully appreciated until quite recently. Cronin quotes a characteristically modest reflection by, perhaps the most brilliant living theoretical biologist, John Maynard Smith:

> "In the extensive publications marking the centenary of the *Origin of Species*, the only explicit treatment of sexual selection was Maynard Smith (1958a); although I did describe a possible mechanism of female choice in *Drosophila subobscura*, it is clear that I had not read or understood Fisher." (Cronin 1991, p.244)

Fisher's solution was to show how selection could indirectly impact preference genes. Given some proportion of choosy females in the population, we know that colorful males have an advantage over their drab brethren. This means that any female that mates with a colorful male will tend to have colorful sons. These sons will pass on to their many offspring the choosy mother's genes as well as their father's colorful genes. Thus a genetic correlation arises, which biologists call linkage disequilibrium, between genes for colorful males and genes for choosy females. The spread of the female preference genes creates an even stronger selective effect benefiting the colorful males and the choosy females. So the spread of both coloration and female preference for coloration leads to a positive feedback loop or "runaway process." The mathematical description of this theory was worked out by Kirkpatrick (Collins & Jefferson 1992, summarize and extend this work). Computational models have been able to elaborate the mathematical version by showing that the predictions are robust to relaxing the simplifications that made the mathematics tractable (Collins & Jefferson 1992). Specifically, Collins and Jefferson showed that the addition of local mate choice, mutations, finite populations, geographic isolation of subpopulations, and diploidy do not qualitatively change the results. Unfortunately, the literature has been more supportive of explanations for the evolution of female mating preferences based on the direct impact of the preference genes upon the female's fitness, and not her offspring's fitness (Kirkpatrick & Ryan 1991).

If this canonical form of sexual selection is the ornate arch of a Gothic cathedral, then simple assortative mating is an arch from Stonehenge. It is a general, and often non-directional, form of selection. Assortative mating arises from organisms pairing up in non-random ways. These non-random pairings may be the result of some structuring of the population (e.g., sedentary organisms will tend to mate with their neighbors) or from some form of mate choice. The famous Hardy-Weinberg equilibrium[2] for the proportion of homozygous and heterozygous individuals in a population is based on the assumption of random mating. This assumption is patently false in our species for many of the characters that humans most readily perceive (Hartl & Clark 1997). That is, mating is only random with respect to certain characteristics or loci, not others. In fact, biologists routinely check for non-random mating with respect to a locus by looking for deviations from the Hardy-Weinberg equilibrium.

Non-random mating with respect to a locus is also called assortative mating. It comes in two flavors, positive and negative[3]. Positive assortative mating is the tendency to mate with individuals with similar characteristics or alleles. This tends to lead to an excess of homozygotes in comparison to Hardy-Weinberg equilibrium. Humans exhibit positive assortative mating with respect to many characters, including height and hair color (Hartl & Clark 1997). In contrast, negative assortative mating is the tendency to mate with dissimilar individuals and so it tends to lead to an excess of heterozygotes. An extreme form of this is found in many plants which prevent fertilization by pollen that carry the same alleles as the plant at "self-incompatibility" loci. They select for pollen from plants that are different from them at these loci.

Todd and Miller (1997) introduced mating preference genes to an evolutionary model and

[2] In an almost apologetic letter to *Science* in 1908, the mathematician Godfrey Hardy pointed out the following phenomenon (developed by Weinberg independently in the same year). If the proportion of one allele (A) in a population is p, and the proportion of the other allele at that locus (a) is $q = 1 - p$, then you can expect to get p^2 of the AA homozygotes in the next generation, along with $2pq$ of the Aa heterozygotes, and q^2 of the aa homozygotes. This is easiest to see by considering the gametes, the sperm and eggs, that will combine to form the next generation. We know that on average p of the sperm will carry the A allele while p of the eggs will also carry the A allele. So the chance of an A-sperm coming together with an A-egg is just $p \times p$. The same reasoning can deduce the proportions of Aa heterozygotes and aa homozygotes, with a note that some of the pq heterozygotes are formed by the union of an A-sperm and an a-egg, while other pq heterozygotes are formed by the union of an a-sperm and an A-egg. This results in $2pq$ heterozygotes.

[3] Positive and negative assortative mating are also sometimes called assortative and disassortative mating.

found that populations tended to speciate sympatrically. More specifically, a subpopulation would converge on a particular phenotype as well as a preference for that phenotype in a mate. Different subpopulations converged on different preferences. So the subpopulations naturally formed reproductively isolated gene pools. However, because phenotypes were only specified by two loci, the preferred phenotypes in the subpopulations often drifted towards each other and the gene pools of those subpopulations merged. Would the same dynamic of spontaneous sympatric speciation play out in an ecological model with many loci?

Assortative mating was implemented in the model by choosing a random location in the array of organisms and inspecting the first eight potential mates after that point. A potential mate is a live organism in the same patch whose reproductive chromosome is at most one bit different from the organism initiating the mating. The best of the eight potential mates was then selected for mating, where "best" was interpreted differently for negative and positive assortative mating. For positive assortative mating, "best" meant the closest match of the chromosomes of the two mates. For negative assortative mating, "best" meant the greatest mismatch. In the case of a tie, the first of the top ranked mates was chosen. The particular chromosomes that were used to determine similarity differed across the experiments. This is a simplified version of Todd and Miller's (1997) sexual selection in that the phenotype and the preference are encoded in the same genes.

Does this form of assortative mating constitute a kind of sexual selection? An organism will differentially gain mating opportunities based on its genotype (which is identical to its phenotype). Given a population's genotypes and the form of assortative mating, we can predict which genotypes will leave more copies of themselves in the next generation. So it is selection in that sense. However, over long time scales, there are no particular characters that are specifically being selected. We would not expect to see a peacock's tail evolve under assortative mating.

The only form of positive feedback possible under assortative mating, is the convergence of subpopulations into homogeneous mating pools with positive assortative mating. If we consider genotype space for a moment, any clusters of similar organisms will tend to all mate with each other, while isolated outliers will be forced to mate with relatively distinct organisms. So the clusters of similarity will grow, fed by the assimilation of the outliers. This is not the kind of runaway process we expect from positive feedback. There is a clear limit to the process once the populations become completely homogeneous. Whether or not this limit is reached will depend on factors like the mutation rate and whether or not the homogeneous subpopulations can grow large enough that the individuals can easily find each other when it comes time to mate.

7.3 Assortative Mating and Speciation

How might assortative mating affect speciation? It has long been recognized that positive assortative mating facilitates a sort of disruptive selection (Andersson 1994). Under positive assortative mating, a population will soon sort itself into a set of relatively homogeneous subpopulations in which individuals prefer to mate with other individuals of their subpopulation to the exclusion of mating with outsiders. Note that positive assortative mating in the model, and often in nature, does not create isolated gene pools in and of itself. If an organism in the model cannot find a similar mate, it will mate with a dissimilar organism. Given such, slightly porous, behavioral reproductive isolation we might expect the reproductive chromosomes of the subpopulations to drift apart. Analogous to geographical isolation, positive assortative mating should separate the subpopulations, allowing them to diverge[4] and eventually become species in their own right. So we should expect positive assortative mating to boost speciation rates.

Conversely, negative assortative mating should tend to bind populations together, and prevent them from forming isolated subpopulations. Any new mutant will instantly become "popular" and the mutation will tend to be mixed with the other genes, rather than forming a distinct subpopulation. This should suppress speciation.

In all the following cases the baseline for comparison is the original random mating data presented in Chapter 5 with the matching level of migratory barriers and habitat heterogeneity. With no migratory barriers and a homogeneous environment there was a baseline average of 2.5 species living at the end of 5000 time steps and a speciation rate of 0.0425 speciation events per time step. However, random mating in a heterogeneous environment with 0.99 barriers resulted in an average of 11.83 species and 0.1195 speciation events per time step. As before, a heterogeneous environment means an average of 10.3 bits

[4] Divergence will occur mainly in the characters that are not being selected through assortative mating, given appropriate conditions for divergence. These conditions include either divergence selection or small enough populations that genetic drift can play an important role in the population's evolution.

different between the habitat bit patterns of any two patches.

7.3.1 Selection on Predation Resistance Characters

Two forms of assortative mating were examined: selection on a mate's predation resistance chromosome and selection on a mate's reproductive chromosome. The degree of similarity between mates was based on a count of the number of bits that differed between the relevant chromosomes of the two mates.

Negative Assortative Mating

Under negative assortative mating based on predation resistance characters, an organism would choose, from up to 8 potential mates, the organism that had the least similar predation resistance chromosome. Offspring were then generated in the normal way, their chromosomes being determined by two point crossover between the parental chromosomes, along with possible point mutations. Under a homogeneous environment with no migratory barriers, negative assortative mating based on predation resistance characters resulted in only 1.5 species and 0.0160 speciation events per time step. Both of these values are significantly below the equivalent measurements of the random mating condition ($p < 0.001$ in a two-sided T-test). Similarly, under 0.99 migratory barriers and a heterogeneous environment, this form of negative assortment resulted in 5.18 species and 0.0615 speciation events per time step. Again, these are significantly below the results for random mating ($p < 0.001$). A heterogeneous environment with 0.95 migratory barriers produced an average of 3.98 species and a speciation rate of 0.04988. Both of these are below the values observed under random mating in a heterogeneous environment with 0.95 barriers ($p < 0.001$).

Positive Assortative Mating

Positive assortative mating on predation resistance chromosomes is analogous to negative assortment, except that mates are chosen out of the 8 random suitors so as to maximize the number of bits that match between the organism's predation resistance chromosome and that of its suitor. Under a homogeneous environment and no migratory barriers, this led to the survival of 3.09 species and a speciation rate of 0.0608. With a heterogeneous environment and 0.99 barriers, these statistics rose to a whopping 44.27 species and 0.7127 speciation events per time step. All of these are significantly higher than the corresponding values under random mating ($p < 0.01$ in the first case, and $p < 0.001$ in the other three). A heterogeneous environment with 0.95 migratory barriers similarly led to an average of 16.76 species and a 0.3874 speciation rate ($p < 0.001$).

7.3.2 Selection on Reproductive Characters

Sexual selection on the predation resistance chromosome is tantamount to choosing a mate based on its predation characteristics. It is also reasonable to consider the selection of a mate based on its reproductive characters like a mating dance or secondary sexual displays. Because reproductive isolation is based on these characteristics, assortative mating in reference to them should have an impact on speciation dynamics. An initial hypothesis might suggest that, like assortative mating on predation resistance, negative assortative mating should tend to glue species together. In contrast, we might expect positive assortative mating to fragment populations and thus boost speciation rates.

Negative Assortative Mating

Negative assortative mating on reproductive characters was implemented in a similar fashion to assortative mating on predation resistance characters. The only difference is that a potential mate can have at most a one bit difference in its reproductive chromosome compared to the chromosome of the initiating organism. So negative assortative mating means looking at eight potential mates and taking the first one that has a different reproductive chromosome. If none of the eight had a different reproductive gene, the first potential mate was chosen. The reproductive chromosome of the offspring was identical to the reproductive chromosome of one of the parents, assuming no mutation. The offspring had a 50/50 chance of matching a particular parent's reproductive chromosome.

In a homogeneous environment with no migratory barriers, negative assortment on reproductive characters led to an average of 2.24 species. This is significantly below the 2.5 species generated by the random mating condition ($p < 0.05$). Similarly, negative assortment led to a speciation rate of 0.0148, significantly below 0.0425 for random mating ($p < 0.001$). However, the situation reversed when the model was run with 0.99 barriers to migration and environmental heterogeneity. Under these conditions, negative assortative mating on reproductive genotypes leads to an astonishing average of 29.42 species and a speciation rate of 0.2732. These are both significantly *greater* ($p < 0.001$) than the corresponding values, 11.83 and 0.1195, for random mating. Similarly, in a heterogeneous environment with 0.95 migratory barriers, negative assortment on reproductive characters produces a significant ($p < 0.001$) increase in the number of species (17.22) and the speciation rate (0.2260).

Positive Assortative Mating

As before, positive assortative mating was the opposite of negative assortative mating on reproductive characters. The initiating organism looked for an exact match with its reproductive chromosome amongst the eight potential mates. If none was to be found, it accepted the first potential mate with a one bit difference.

In a homogeneous environment with no reproductive barriers, positive assortative mating based on reproductive characters resulted in an average of 2.2 species and a speciation rate of 0.0148 species per time step. These are both significantly lower than the random mating condition ($p < 0.05$ and $p < 0.001$ respectively). Yet, when the organisms are evolving in a heterogeneous environment with 0.99 migratory barriers between patches, the biodiversity rises to 30.00 species and the speciation rate rockets to 0.2765 species per time step. A heterogeneous environment with 0.95 migratory barriers results in a biodiversity of 15.26 species and a speciation rate of 0.2338. All of these are statistically significant ($p < 0.001$).

7.3.3 Summary of the Results

Figures 7-1 and 7-2 summarize the results. The influence of the different kinds of assortative mating on species diversity (Figure 7-1) and speciation rates (Figure 7-2) have been normalized by the results for random mating. In all cases, the influence of assortative mating is statistically significant at the $p < 0.05$ level, as indicated by the red bars in the figures.

As one might guess from Figure 7-1, biodiversities under positive and negative assortative mating on reproductive characters are statistically indistinguishable. The same is true for speciation rates in Figure 7-2. When there are no migratory barriers and a homogeneous environment, both conditions lead to significantly less speciation than the random mating case and lower biodiversity. However, with 0.95 barriers to migration and habitat heterogeneity across patches, both conditions lead to higher speciation rates and biodiversity relative to random mating. Yet, both conditions remained statistically indistinguishable.

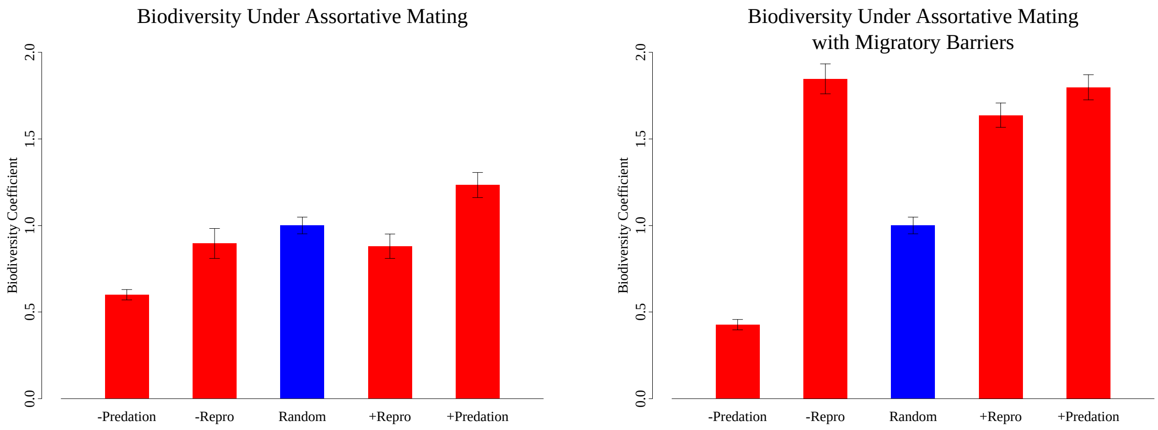

Figure 7-1: The effects of assortative mating on species diversity in a homogeneous environment with no migratory barriers (left) and in a heterogeneous environment with 0.95 migratory barriers (right). "Repro" stands for either positive (+Repro) or negative (−Repro) assortative mating on reproductive characters. "Predation" indicates either positive (+Predation) or negative (−Predation) assortative mating on predation resistance characters. Red bars indicate statistically significant effects that distinguish assortative mating from the baseline of random mating. The effects of each condition have been normalized against the baseline value. For example, under a heterogeneous environment with 0.95 migratory barriers (right hand bar chart) positive assortment on predation resistance characters increases biodiversity by a factor of 1.8.

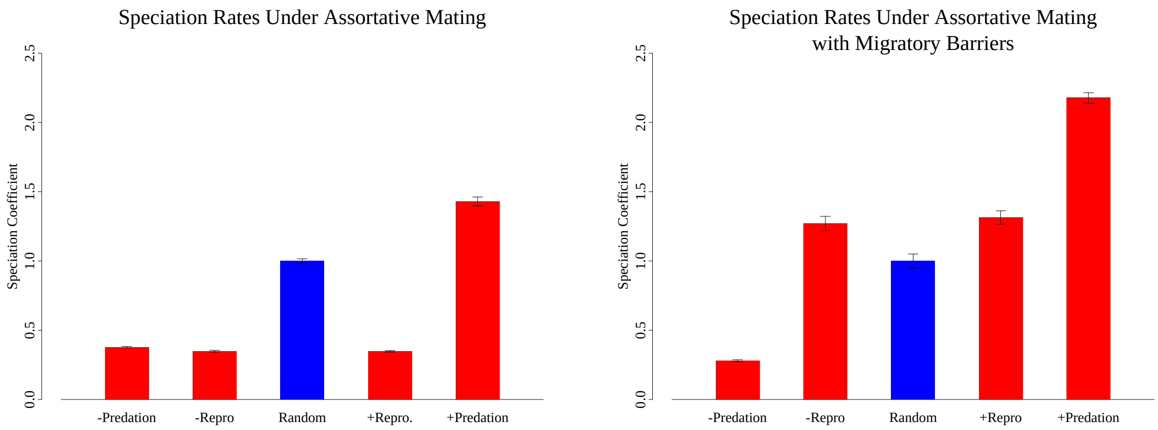

Figure 7-2: The effects of assortative mating on speciation rates in a homogeneous environment with no migratory barriers (left) and in a heterogeneous environment with 0.95 migratory barriers (right). Again, red bars indicate statistically significant effects that distinguish assortative mating from the baseline of random mating. The effects of each condition have been normalized against the baseline value.

The same is true for 0.99 migratory barriers in a heterogeneous environment.

Assortative mating based on predation resistance characters has the predicted effects. Negative assortative mating depresses speciation rates and the resulting species diversity. Positive assortative mating stimulates speciation and the maintenance of diversity. The presence of more species in the positive assortative mating condition does not necessarily indicate the colonization of more niches. It may result from the same number of "successful" species surrounded by a plethora of young species that are quickly dying out. If this were the case, a histogram of the population sizes of the species would show many small, a few large, and a very few medium sized species populations. However the histograms in Figure 7-3 show that the high diversity of the positive assortative mating spans all possible population sizes.

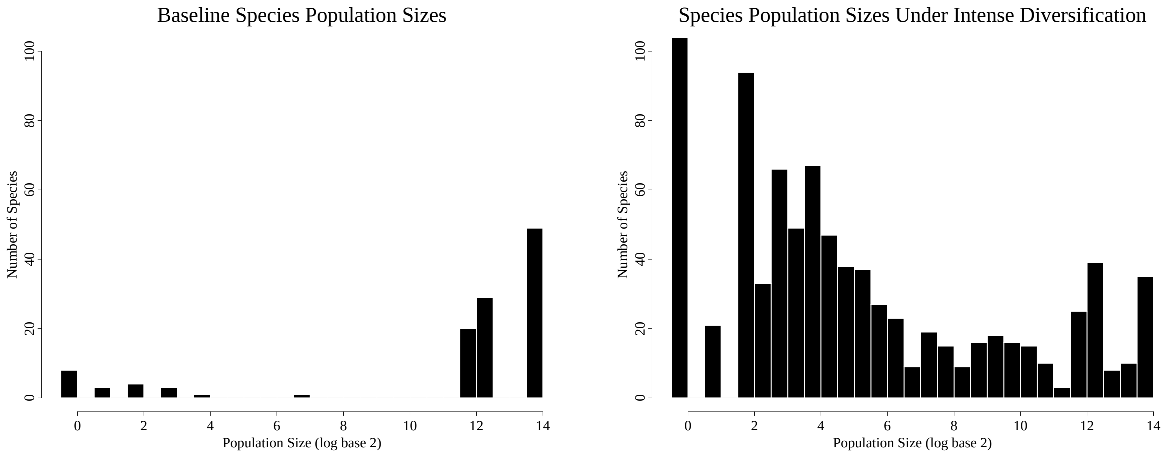

Figure 7-3: The distribution of species population sizes for both the baseline "vanilla" conditions (left) and strongly diversifying conditions (right) summed over 49 trials. Population sizes have been scaled logarithmically. The right histogram is based on running the model with positive assortative mating based on predation resistance characters in a heterogeneous habitat with 0.95 migratory barriers. The baseline condition, with random mating, no migratory barriers and a homogeneous environment produces a bimodal distribution. Typically an extremely large species is accompanied by a few very rare species. In contrast, the intense diversification condition leads to a distribution that spans all the possible population sizes.

7.4 Discussion

Why should positive and negative assortative mating based on reproductive characters behave similarly? And why should they interact so dramatically with habitat heterogeneity and migratory barriers?

To understand the dynamics of speciation we must examine the graph components that represent species. The growth and fragmentation dynamics of these graphs are complicated due to the underlying population interactions that generate the graphs (see Appendix A for a discussion of some related open problems). However, a few things can be deduced about the effects of assortative mating when selection is based on the reproductive genotypes.

7.4.1 Negative Assortative Mating on the Hypercube

First, consider the simple case of a "populous" node, where many organisms share the same reproductive genotype. If a mutation in the offspring of one of these organisms creates a new node, what are the expected dynamics of the population on this two node graph? It is perhaps easiest to see the effects of negative assortative mating. If all the organisms are trying to mate with different reproductive genotypes, then many of the organisms in the populous node will mate with the mutant with the new genotype. Half of these matings will produce organisms with the rare genotype, and half with the populous genotype. Similarly, the new genotype organism will mate with an organism that has the common genotype. The end result is a net flow from the populous to the rare genotype. It is clear that this flow will continue until the two genotypes reach an equal popularity. This is a stable equilibrium because any perturbation will stimulate a new flow from the more populous genotype to the less populous genotype. However, the story does not end there.

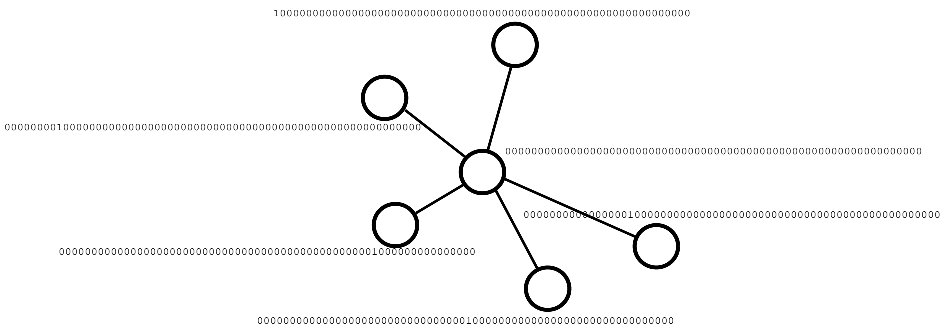

Figure 7-4: A star graph of reproductive genotypes. Each node has been labeled with a representative 64-bit genotype. The presence of a node indicates that an organism exists with that genotype. So the appearance and disappearance of nodes is determined by the underlying population dynamics of the organisms that have those reproductive chromosomes.

Consider the dynamics of a star graph, a graph with one central node and many neighbors, but with no connections between the neighbors, as shown in Figure 7-4. Recall from Section 4.3 that in a random graph in a subcritical state, the largest component will tend not to have cycles (Gavrilets & Gravner 1997). A star graph is thus a reasonable archetype to analyze[5]. Each of the satellite, or leaf, nodes has only one neighbor, and so all of the organisms in the leaf nodes will choose to mate with the organisms of the central node. In contrast, organisms in the central node will tend to mate with organisms from all the neighboring nodes. If there are a total of m organisms in the leaf nodes, then approximately $m/2$ organisms will flow into the central node every generation. In contrast, if there are n organisms in the central node, it will tend to distribute $n/2$ organisms evenly across its neighboring nodes. It is clear that this balances out when $n = m$, or when the number of organisms in the central node equals the sum of all the organisms in its neighboring nodes. So with negative assortative mating, the equilibrium distributes the population across the nodes of a component in proportion to the number of neighbors a node has. The result is that the leaf nodes have the fewest organisms and so are the most susceptible to dying out. However, a species only splits if a non-leaf node dies. Furthermore, the flow of organisms into a node when its population is pushed below equilibrium, acts as a buffer against the disconnection of a component. If a non-leaf node starts to become rare, all of its neighbors will begin contributing individuals to that node, boosting it back up again. In particular, the neighbors with genes that are ecologically successful are the most likely to contribute to the endangered node. So that node will be infused with relatively successful ecological chromosomes. In sum, due to the low populations in the leaves and the buffering effects in the non-leaves, we should expect speciation events to be suppressed by negative assortative mating. We will leave the discussion of the interaction between migratory barriers, environmental heterogeneity, and negative assortative mating until later.

7.4.2 Positive Assortative Mating on the Hypercube

Now consider the case of positive assortative mating. As before we will start with a single populous node and a new mutant neighbor node with only one organism. The organisms in the populous node will only mate with themselves, while the new mutant will not be able to find a similar mate and so will also mate with an organism in the populous node. The result

[5]Although a star graph is probably not a realistic representation of the mating relationships in a real species. See Section 4.5.

of this mating is that there is only a 50% chance that a new organism will enter the mutant node. Even if the mutant node's population grows a little, since the organisms of this node will be relatively rare, there is still a good chance that they will not find each other when they scan over eight potential mates in their patch. So positive assortative mating biases against the growth of new mutant nodes, and many will tend to get reabsorbed by the populous nodes. Liou and Price (1993) found the same dynamic in their model of positive assortative mating. The rarer population tended to go extinct.

This dynamic remains the same in a star graph. If a mutant node ever does grow to a point where the constituent organisms can find each other as mates, the dynamics of the populous node and the new node will be relatively independent. Each will rise and fall on the merits of the ecological chromosomes in their constituent organisms as well as the chance events of death through competition for space. Thus positive assortative mating is also biased against the survival of leaf nodes, and so depresses speciation, but for completely different reasons as compared to the bias of negative assortative mating.

7.4.3 Random Mating on the Hypercube

Finally, consider the dynamics of random mating on a two node graph. If there are n organisms in the first node and m in the second, we can derive the population sizes of the next generation as:

$$n' = n\frac{n}{n+m} + \frac{n}{2}\left(\frac{m}{n+m}\right) + \frac{m}{2}\left(\frac{n}{n+m}\right) \tag{7.1}$$

$$= n \tag{7.2}$$

$$m' = m\frac{m}{n+m} + \frac{m}{2}\left(\frac{n}{n+m}\right) + \frac{n}{2}\left(\frac{m}{n+m}\right) \tag{7.3}$$

$$= m \tag{7.4}$$

The first term in Equation 7.1 corresponds to the number of matings between organisms in the populous node. The second term, $\frac{n}{2}\left(\frac{m}{n+m}\right)$ is the number of organisms contributed to the populous node from matings between nodes, initiated by organisms with the common genotype. Finally, the last term is the number of organisms contributed by matings between nodes that were initiated by organisms with the mutant genotype. The result $n' = n$ means that, despite the interbreeding, the population sizes of the two nodes should remain the same. This does not hold for the star graph case. If we call the population size of the central node n and the populations of the leaf nodes m_i, then

$$n' = n\frac{n}{n + \sum_i m_i} + \frac{n}{2}\left(\frac{\sum_i m_i}{n + \sum_i m_i}\right) + \sum_i \frac{m_i}{2}\left(\frac{n}{n + m_i}\right) \tag{7.5}$$

and since

$$\sum_i \frac{m_i}{2}\left(\frac{n}{n + m_i}\right) > \frac{n}{2}\left(\frac{\sum_i m_i}{n + \sum_i m_i}\right) \tag{7.6}$$

we get

$$n' > n \tag{7.7}$$

So there is a tendency, though a weak one, for the less populous nodes to get absorbed by their neighbors. This tendency is not nearly as strong as it is in positive assortative mating. Nor does random mating produce the kind of buffering effects against node death that negative assortative mating exhibits. Thus, random mating, stuck half way between either extreme, ends up exhibiting higher speciation than either positive or negative assortative mating.

7.4.4 Migratory Barriers and Habitat Heterogeneity

Why, then, does the relationship between random and assortative mating reverse under high migratory barriers and habitat heterogeneity? The complexities of the underlying dynamics mitigate against a full analysis. However, a few hypotheses may be laid on the table. For a start, negative assortative mating is generally thought to boost variation within a population (Cronin 1991, p.237). Since variation is the meat upon which selection feeds, this ought to interact well with disruptive selection pressures, speeding a subpopulation along to a new adaptive "peak." In contrast, positive assortative mating ought to increase the variation between populations. This may interact well with selection pressures that differ between populations.

The effect of high migratory barriers is the divide the total population that we have been describing by the reproductive graphs, into 16 subpopulations which are nearly independent. A speciation event can be caused by any one of these subpopulations evolving to a state in which its reproductive graph is disconnected from the reproductive graph represented by the agglomeration of the other 15 subpopulations. Furthermore, since each subpopulation experiences a significantly different habitat as compared to the others, selection becomes a disruptive force. This is clearly illustrated in the random mating case when comparing the speciation rate under a homogeneous environment with no barriers (0.0425) to a heterogeneous environment with 0.99 barriers (0.1195). Is there any reason to suspect that both positive and negative assortative mating should interact with this sort of disruptive selection?

In both positive and negative assortative mating, the interaction with habitat heterogeneity and migratory barriers probably depends on the fate of "rare" mutant nodes in the total population's reproductive graph. A node that represents few organisms in the total population, may have a local majority within its patch. Purely by the variance of the sampling that divides the total population into 16 subpopulations, it may occasionally be the case that within a patch a "mutant" node's population will out number its neighbor node's population. This is made all the more likely because of the different pressures in the patches. Ecological chromosomes that help their organisms in one patch will often hinder their organisms in another patch. So a "mutant" node with a small population that has relatively good ecological chromosomes for its patch may well outgrow the population in a neighboring node that has more constituent individuals in the total population. Once a "rare" node outnumbers its neighbors, the dynamics of both negative or positive assortative mating will work in its favor. It will tend to spawn more satellite, leaf nodes and so become the center of its own star graph. Its satellite nodes will tend to contribute more organisms to it than it gives up to them. In short, it becomes the center of an isolated reproductive graph in its patch. Thus, the patch's reproductive graph dynamics are effectively separated from the total population and given the pressures of selection, it is likely to drift apart from the reproductive graphs in the other patches.

7.5 Conclusions and Implications

There are three important conclusions from these experiments. First, assortative mating has dramatic effects on speciation rates and diversity levels. Second, the nature of those effects depends on what characters organisms are using to select their mates. If the selected characters do not interact with reproductive barriers, except through the assortative mating, then positive assortment dramatically boosts speciation while negative assortment suppresses it. The importance of positive assortative mating for diversification in the model matches evidence that mate choice based on ecological characters has promoted the rapid diversification of three-spined stickleback fish (Schluter 1996). If the selected characters influence reproductive barriers through channels independent of mating preferences, then we are faced with the third and by far the strangest conclusion. The effects of assortative mating on reproductive characters changes depending on the relative isolation and degree of disruptive selection on subpopulations. If the organisms are evolving under homogeneous conditions as one large population, then assortment by reproductive characters depresses speciation regardless of whether the assortment is positive or negative. However, if subpopulations are isolated and experience different habitats, then both forms of assortment dramatically boost speciation relative to random mating. Notice that these conclusions make no reference to the cost of wasting a mating attempt on an incompatible mate. There is no obvious force of natural selection in the traditional sense of the struggle for survival. It is rather a dynamic of the sexual selection in the model and its interaction with the genes that control characters for reproductive isolation.

The results carry implications for systematists and paleobiologists looking for explanations for the explosive radiation of a group. When searching for a "key innovation" that allowed the group to diversify, one should look for characters that allowed or affected mate choice, as well as characters that stimulated geographical isolation of subpopulations. Angiosperm (flowering plant) evolution may provide a particularly interesting test case. The evolution of pollination by animals (usually insects) acts as a form of positive assortative mating. Those plants that share similar attractive features for a pollinator will tend to pollinate each other. There is some evidence that animal pollination indeed boosted diversification in angiosperms (Eriksson & Bremer 1992). Whether or not the effects on diversity of animal pollination is analogous to positive assortative mating is debatable.

There is some reason to think that the degree of positive assortative mating should reduce or at least stabilize over time, due to coevolution with parasites. The more homogenous the hosts, the easier it is for parasites to evolve strategies for exploiting the host population. A mutation in a parasite that gives it an advantage in its utilization of its current host will tend to help it and its offspring exploit the other hosts in a homogeneous population. In fact, one of the theories for the origin and maintenance of sexual reproduction is based on the idea that sexual reproduction helps to maintain genetic variation in a population (Hamilton et al. 1990). These same pressures should tend to reduce the prevalence of extreme forms of positive assortative mating. Particularly positive assortative mating based on characters that relate to an immune system.

The vulnerability of homogenous populations to parasitism is part of the reasoning that Brown (1997) uses to suggest that there is selection for maximizing heterozygosity in offspring. Brown also cites developmental stability, and attractiveness (based on an organism's symmetry) as further benefits of heterozygosity. He predicts that various forms of negative assortative mating should be prevalent across all sexual species (Brown 1997). If it is true that negative assortative mating is widespread, the model would suggest that in most cases this has depressed speciation. The only exception being in cases where a species is fragmented into relatively isolated populations experiencing a variety of selective pressures. In this case, if assortment is based on characters that are independently involved in reproductive isolation, selection for heterozygosity may actually stimulate speciation.

The results also have implications for computer science, in the design of evolutionary algorithms. The field of evolutionary algorithms is characterized by the attempt to evolve solutions to a given problem through successive applications of mutation, crossover (sexual reproduction), and selection of the best individuals in the current population of solutions (Goldberg 1989; Mitchell 1996; Banzhaf et al. 1998). One common problem in our attempts to evolve solutions to complex problems, is premature convergence. Often, the entire population of solutions becomes homogenized, with all the members representing small variations on one solution that is only locally, and not globally, optimal. When a population loses variation, selection is useless. Without variation it is impossible to say one solution is better than another. There is no way to shuffle genes between individuals through sexual reproduction to produce new variations. Ideally, we would like the population to maintain genetic diversity such that a broader area of the solution space may be searched and thereby raise the probability of discovering the global optimum. A few studies have shown that the performance of a genetic algorithm improves with the prohibition of mating between similar (Eshelman & Schaffer 1991) or related (Craighurst & Martin 1995) solutions. This fits well with the intuition that negative assortative mating boosts genetic variation within a population.

The opposite effect, positive assortative mating, has also been explored and shown to be effective (Deb & Goldberg 1989; Booker 1985). If similar solutions preferentially mate, then the population should fracture into subpopulations (Todd & Miller 1991). In a genetic algorithm, this can be exploited to maintain subpopulations on multiple fitness peaks. A simple implementation of this positive assortative mating would be to choose a few potential mates for a solution and then select the mate with the fewest bits different from that solution (i.e., the shortest Hamming distance). Deb and Goldberg (1989) used both negative assortative and positive assortative mating to improve the performance of a GA on a fitness landscape with many peaks. Negative assortative mating was a side effect of their "sharing" scheme which reduces a solutions fitness if there are similar solutions in the population. Since mating is a probabilistic function of the fitness values, this encourages solutions to mate with dissimilar solutions. They also introduced explicit positive assortative mating to fracture the population by selecting similar solutions for mating from the population. They refer to these subpopulations as "species."

7.5.1 Towards an Experimental Test of the Predictions

These interactions between the characters for mate selection, population structure and habitats seem hopelessly complicated. With this in mind, I will conclude with the description of an experimental test of the model's predictions. A potential test of the hypotheses rests on the behavior of *Wolbachia* bacteria (Werren 1997). Members of the *Wolbachia* genus infect the reproductive tissues of arthropods. They have the surprising effect that males infected with a particular strain of *Wolbachia* can only successfully fertilize females that are also infected with that same strain. So, hosts that are infected with different strains of *Wolbachia* will appear to be members of different species until they are treated with antibiotics and demonstrate that they can, in fact, successfully reproduce. It seems that the *Wolbachia* in the male host alters the sperm of its host. These deformed sperm are incapable of fertilizing an uninfected female[6]. However, if an egg contains the same strain of *Wolbachia*, the bacteria seems to "rescue" the deformed sperm, allowing it to combine with the egg and form a viable zygote. Given their effects on reproductive isolation, it is perhaps not surprising that *Wolbachia* has been implicated in the rapid speciation of some taxa (Giordano et al. 1997; Rousset & Solignac 1995; Hurst & Schilthuizen 1998) and are found in two of the most

[6]A zygote forms but typically does not survive past the first few cell divisions. The mechanisms for this failure are still being worked out (Werren 1997).

specios groups, insects and mites (Giordano et al. 1997).

The restriction to mating between organisms infected with the same strain of *Wolbachia* may be sufficiently similar to positive assortative mating to allow a test of the model. In this case, the "character" being selected by the hosts is the type of sperm or eggs in their potential mates. This suggests that populations infected with a variety of strains of *Wolbachia* may be evolving under conditions similar to positive assortative mating on reproductive characters. The model predicts that subpopulations should evolve reproductive isolation relative to each other if they are geographically segregated and experience somewhat different selective pressures. Paradoxically, the model also predicts that if the population is kept in one large homogenous environment, it should resist reproductive segregation relative to a randomly mating, uninfected population. This can be tested with population cages of *Drosophila* fruit flies.

The fruit flies carrying the different strains of Wolbachia should also carry genetic markers for easy identification. Typically these include characters like red or white eye color mutations. The experiment requires at least four conditions. In the first control condition, flies carrying the markers but free of *Wolbachia* infection would be kept in one large, homogeneous cage. This corresponds to the "vanilla" condition in the model. The second condition would separate uninfected flies into a system of cages with some form of low level migration between populations. Each cage would have different food sources and environmental conditions so as to provide a heterogeneous environment with migration barriers. Both these conditions, lacking *Wolbachia* infection, should exhibit random mating. The two experimental conditions would be the same as the controls except that all populations would have a mixture of infections of the different *Wolbachia* strains, each associated with a genetic marker. The populations would be allowed to evolve for a sufficient amount of time such that mutations might introduce other forms of reproductive isolation, besides the *Wolbachia* infections. Some mutagen might be added to speed up this process. At any time we could check for incipient speciation by treating the infected flies with antibiotics and then testing for hybrid viability in crosses between flies with different genetic markers. The prediction is that flies that evolved under the heterogeneous environment along with *Wolbachia* infections should demonstrate more reproductive isolation than flies that had not been infected. These uninfected flies should, in turn, demonstrate more reproductive isolation than the infected flies that were kept in a homogeneous environment.

Note that I have turned the traditional speciation experiment on its head. The typical speciation experiment enforces some degree of post-zygotic barrier, such as killing the hybrid offspring between two populations. It then looks for the evolution of positive assortative mating in the resulting subpopulations (Rice & Hostert 1993). I am suggesting enforcing the pre-zygotic barriers, and then, after removing the pre-zygotic barrier with antibiotics, testing for the evolution of post-zygotic barriers.

A weakness of this design is the ambiguity in the analogy between *Wolbachia* infection and positive assortative mating based on reproductive characters. If it is more analogous to positive assortative mating on non-reproductive characters, then the infected flies raised in the homogeneous environment should demonstrate more reproductive isolation than the uninfected flies. However, they should still demonstrate less isolation than the uninfected flies raised in the homogeneous environment with high migratory barriers. The attraction of using *Wolbachia* is that mate "choice" can be manipulated by the application of antibiotics.