

Sexual Selection, Resource Distribution, and Population Size in Synthetic Sympatric Speciation

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Abstract

Speciation is one of the most fundamental and important processes in evolutionary biology, resulting in the panoply of biological diversity found in the natural world. Speciation likewise has profound implications for artificial life, evolutionary computation, and evolutionary robotics, yet a great many aspects of it remain unexplored. Traditionally, speciation was mainly viewed as taking place allopatrically. More recently, sympatric speciation, which does not require geographic isolation, has been studied. Sympatric speciation raises a number of interesting questions with regard to how and why sympatric populations diverge, some of which we address with a 2x2x2 factorial study that considers the factors of sexual selection, resource distribution, and population size. Our hypotheses were evaluated using a synthetic environment inspired by life on the Galápagos Islands. In particular, the wet and dry season dynamics were modeled to produce the intense selection pressure found there. Our results provide direct evidence for the importance of both female mate choice and resource availability on speciation. They also suggest that the greater stability afforded by larger populations can lead to subpopulations between which gene flow is reduced.

Introduction

We are interested in understanding both “life-as-we-know-it” and “life-as-it-might-be.” The natural world possesses a rich biodiversity brought about through biological evolution, a process we are keenly interested in understanding. Likewise, we are greatly interested in understanding and interpreting the possible mechanisms for the evolution of diversity in synthetic life. In particular, we would like to create environments in which synthetic ecological webs promote the divergence of existing forms into multiple new ones.

In most artificial life and evolutionary computation studies there is a single population, within which all members freely interbreed (typically using a recombination operator known as crossover) or none of which interbreed (typically variation is introduced through different types of mutation) (Bedau, 2003; De Jong, 2006). In nature, by contrast, there are countless population-like units within which there is significant interbreeding yet between which there is little or no breeding. These units are often known as *species* and the

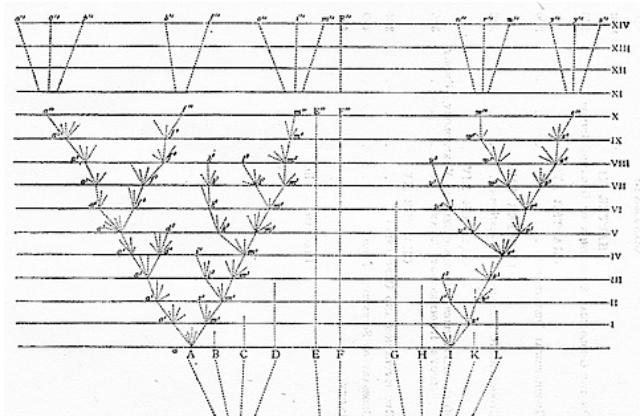


Figure 1: Evolution in action—Darwin’s conceptual diagram of speciation (Darwin, 1859).

division of a single interbreeding population into multiple distinct such populations is known as *speciation*. Species may provide a wealth of diversity in an environment by filling distinct niches. Darwin’s concept of speciation is shown in the only figure he included in his seminal work *On the Origin of Species* (1859) (reproduced here as Figure 1).

Artificial mechanisms could be used to subdivide artificial populations more or less completely, and many such mechanisms have been proposed including crowding (De Jong, 1975), niching (Goldberg, 1989; Horn et al., 1994), tagging (Spears, 1994) imposing a population topology (Sarma, 1998) and using islands (Whitley et al., 1999). All of these approaches have merits for their intended applications but are not entirely appropriate for ours. In particular, none of these allow for new niches to arise based on the behavior (e.g., resource use) of groups within the populations. Other niching approaches (e.g., Tomko et al. 2011) are aimed at evolving a collection of cooperating partial solutions to a problem, rather than evolving independent populations.

Rather than impose upon the algorithm population divisions, or other mechanisms to promote population divisions (Gras et al., 2009; Aspinall and Gras, 2010), we prefer to allow speciation to occur based on interactions between in-

dividuals within an environment where the interactions arise from mechanisms and actions inherently necessary for the individuals' survival and procreation.

For evolutionary biologists, speciation is one of the most fundamental processes. It is the way biodiversity is generated and a phenomenon that has intrigued biologists since Darwin's time (Darwin, 1859). Traditionally, speciation was mainly viewed as allopatric or geographic speciation. Here species are separated into at least two distinct and geographically isolated units, evolve independently into separate species, then cannot interbreed even if they come into contact again. More recently, another mechanism of speciation has been studied that does not depend on geographic isolation. *Sympatric speciation* occurs when budding species, living together in the same area, split into two or more populations exploiting different niches. For example, in the Galápagos Islands, small populations of finches with different beak sizes (different species) are known to inhabit the islands (Grant and Grant, 1987). With allopatric speciation alone it would be likely that each island would contain a different species of its own but, in fact, different islands contain multiple species living and breeding on them.

The existence and possibility of sympatric speciation processes have long been unclear, but recent theoretical, observational, and experimental studies have made it clear that sympatric speciation is more common than previously thought (Coyne and Orr, 2004). Various mechanisms, such as local abiotic conditions (Tobler et al., 2008; Riesch et al., 2010), can lead to population divergence within a habitat. On the Galápagos, the harsh dry season, in which food abundance drops and the birds forage on increasingly scarce seeds of different sizes, appears to provide one mechanism.

Biologists have identified behavior as an important mechanism causing divergence, in particular female mate preference (Seehausen et al., 1997; Seehausen and van Alphen, 1999; Kraaijeveld et al., 2011). Over the last decade there has been considerable work that provides support for behavior being an important factor in sympatric speciation (Coyne and Orr, 2004). Assortative mating, in which females prefer to mate with males similar to themselves, has been identified as a key element in the development of sympatric speciation (Seehausen and van Alphen, 1999; Kraaijeveld et al., 2011).

The combination of divergent selection (e.g., natural selection during the dry season) and assortative mating acting on the same trait (e.g., beak size) results in a *magic trait*, "a trait subject to divergent selection and a trait contributing to non-random mating that are pleiotropic expressions of the same gene(s)" (Servedio et al., 2011).

By using sympatric speciation, ALife researchers can support multiple species without placing physical barriers in the environment (Yaeger, 1994). In recent work, the need for simpler environments supporting sympatric speciation has been identified (Murdock and Yaeger, 2011). Using assortative mating in agent-based simulations allows for the natu-

ral emergence of diversification and hence speciation. "This common feature suggests that the evolution of biodiversity may be driven not simply by natural-selective adaptation to ecological niches, but by subtle interactions between natural selection and sexual selection" (Todd and Miller, 1997).

Speciation is a very time-consuming process. What is currently poorly understood in evolutionary biology is how often incipient divergence will actually lead to a speciation event and how often the process is aborted. This question has recently been receiving increased attention both theoretically (Bolnick, 2011) and empirically (Vonlanthen et al., 2012). Since the actual process is slow, the true dynamics are difficult to observe or study experimentally, but can be studied in simulations. One of the specific aims of this study was to use an ecological simulator to investigate divergence and speciation under a number of conditions. Our model is based on Galápagos finches but the results are broadly applicable where natural selection and/or mate choice appear.

Hypotheses

The first question we address is whether the existence of differences in the distribution of resources will lead to divergence and speciation. In our simulations we address this by testing two different resource distributions (simulated as seed distributions), bimodal and uniformly random. The second question we address is whether female mate preference will strengthen divergence. Here, we provide two different forms of mate selection, assortative and random. For these different experimental conditions we formed four independent hypotheses:

H₁ For bimodal seeds and assortative mating (BSAM) we expect to find speciation. We reasoned that the bimodal seed distribution provides the environmental structure needed to support two species along with assortative mating which ensures that reproduction produces viable offspring.

H₂ For bimodal seeds and random mating (BSRM) we expect to find directional selection but no speciation. A moderate beak size is rather untenable because there are few moderately sized seeds. We therefore predicted that the population would converge to either small or large beaks, matching either mode of the seed size distribution.

H₃ For uniform seeds and assortative mating (USAM) we may find speciation. There was no clear prediction on what the outcome would be but speciation seemed possible, because assortative sexual selection could drive the speciation process despite the fact that there were no clear environmental niches to occupy.

H₄ For uniform seeds and random mating (USR) we do not expect to find speciation. Since there were no resource niches around which species could form and no sexual selection to drive speciation, we predicted no speciation.

The third question we address is whether population size will affect speciation. Since we do not directly control population size for the finches, this question was addressed by

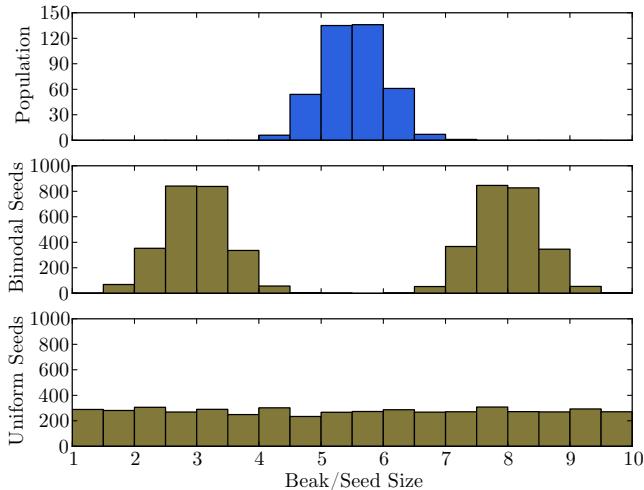


Figure 2: An illustration of the initial population beak size (top) and seed size distributions for the 1x seeds case (middle and bottom for bimodal and uniform random seeds, respectively).

varying the number of seeds provided at the start of the dry season. We had two seed conditions, low and moderate, where the moderate condition had ten times as many seeds as the low condition. This led to a fifth hypothesis:

H₅ For a moderate increase in the number of seeds we expect to see a corresponding increase in population size and a greater stability in all four cases. We predicted that, even with the increased stability, we would not see differences with respect to the presence or absence of speciation in any of the four cases.

These three questions, with two conditions tested for each question, resulted in our 2x2x2 factorial study.

Methods

To test these hypotheses, we developed an artificial island—a square region 100 x 100 units, containing two types of simulated objects: birds and seeds. The birds have the following individual properties: age, beak size, energy level, and gender. The seeds have a specific energy, location, and size. The birds have two additional constraints—a maximum energy capacity of two units and a lifespan of four years. Using this island, we conducted numerous repetitions for each of the four experimental conditions for up to 1000 generations. A repetition can end before 1000 generations if complete extinction occurs. At each generation of a run (a particular repetition) we logged data related to the individuals and the seeds; in particular, we recorded the following data for each individual: age, beak size, energy, gender, and mating count. In addition we recorded a unique identifier for new offspring along with the identifiers of the parents. The data recorded for each seed includes energy and location.

Two different seed distributions are used to model the

available food resources as shown in Figure 2. The bimodal seed distribution (means 3 and 8, variance 0.5) represents an environment that contains two distinct seed sizes with a limited amount of variation. Conversely, the uniform seed distribution (1 to 10) models an environment in which there is no distinction with regard to abundance for any given seed size. The initial population size for each experimental run was 400 individuals possessing moderately sized beaks (mean 5.5, variance 0.5) as shown in Figure 2. The initial population had a 1:1 sex ratio.

The extended dry season on the Galápagos Islands is modeled as an interval lasting 100 days. On each day the individuals search the island looking for seeds. As each day passes there are fewer and fewer seeds on the island—the seeds are present at the beginning of the dry season and are gradually consumed by the individuals. For the small population condition, we started the dry season with 5,000 seeds. For the moderate population condition, we started with ten times as many. These conditions are therefore called the 1x and 10x seed conditions. We conducted 48 repetitions for each of the four seed/mating combinations using the 1x seed condition and 24 repetitions for the 10x seed condition.

During each day of natural selection the individuals feed in random order—only one feeding attempt per day. To simulate the feeding process, an individual first picks a random region, 10x10 units in size, to search. In this region the individual will look for seeds that are compatible with its beak size. An individual can consume seeds plus or minus one unit from its beak size. For example, an individual with a beak size of 4.2 can only select seeds within the range of 3.2 to 5.2. From these acceptable seeds, an individual selects one seed at random and consumes all of its energy. The exact amount of energy contained in each seed varies randomly from zero to two units (uniformly random). The cost for search is 0.1 units of energy—considerably less than the energy gained from an average seed. Note that the energy level of an individual is decreased even if no seed is consumed. After accounting for the cost for searching, the energy level of the individual is examined and if it falls below zero that individual is removed from the population. At the end of 100 days, the dry season ends and a season of abundance begins, during which all individuals who survived the dry season's harsh natural selection process may attempt to mate and produce offspring. The first step in this process is sexual selection.

During sexual selection all females are allowed to select a male and produce offspring. In this simulation the female can show two possible mating behaviors—assortative or random mating—as determined by the experimental conditions of the run. For assortative mating, the female is choosy with respect to the mate she selects—she will only choose a male that is plus or minus one unit from her own beak size. If there is more than one acceptable mate, the female chooses one of those males at random. To limit the influence of a sin-

gle male, and to account for the limited energy males have for courting females, males are only allowed to mate five times per breeding season. For random mating, a female selects one of the males in the population at random. Note that random mating is just a special case of assortative mating where the acceptable beak size is large enough to encompass all males for any given female.

During the reproduction phase, the female mates with the selected male and produces an offspring. This offspring has a beak size that is the average of its parents' plus a small amount of random mutation in the form of Gaussian noise (mean 0, variance 0.2). The gender of the new offspring is determined randomly and the energy level is set to zero.

After reproduction the age of each individual in the population is incremented by one and individuals older than four are removed. The remaining seeds are removed and a new supply of seeds is added—a new dry season begins.

Results

The data is presented in a series of what we have termed *phenogenealogic trees*, which illustrate evolution in action. The trees show each individual in the population plotted with respect to beak size and generation. We connect each individual to its parents using lines forming a tree. A marker is drawn for all the individuals in a given generation. Females are represented as circles, males as squares. Two different colors are used to represent individuals who survived natural selection (blue/dark) and individuals that perished (green/light). Individuals who perish during natural selection are superimposed on individuals who survived.

1x Seeds

The phenogenealogic trees for BSAM, USAM, BSRM, and USRM Run 1 are shown in Figure 3a–3d as prototypical examples. The average initial population sizes (generation 1, after natural selection) for the bimodal random seed and uniform random seed cases are 11.1 and 5.82 respectively. The average final population sizes (generation 1000, after natural selection) for BSAM, USAM, BSRM, and USRM are 43.5, 41.31, 26.0, and 18.4 respectively. When extinction occurred, it was more often due to a lack of females than a lack of males, since a single male can mate with up to five females in a single breeding season, resulting in five new offspring, whereas a single female can only produce a single offspring regardless of her mating activities.

BSAM: It is clear that once divergence occurs no interbreeding takes place between the two branches. The populations for the left and right branches have an average beak size of three and eight and remain stable up to 1000 generations. Stability here refers to the fact that the populations do not go extinct. Such speciation was observed in 31 out of 48 repetitions. In the other 17 repetitions, one of the two populations went extinct primarily due to the lack of females. In

13 of these cases, branch extinction took place before generation 10. Complete extinction did not occur in any of the repetitions.

USAM: The defining characteristic for USAM with small populations is the repeated branching and merging—with more branching than merging. Here, populations are not fixed entities; when a population goes extinct another population moves in to fill the niche. Boundary effects appear to be present in that populations do not occupy the lower and upper size limits of the food supply. The same pattern is repeated throughout each repetition—significant die-off in the center of a given population followed by divergence and/or possible extinction. For example, just after generation 400 the branch with an average beak size near 3.0 splits into two populations which then merge back together a few generations later. Stability of new branches is not guaranteed. For example, the branch with an average beak size near 2.25 goes extinct just after generation 200. This is most likely due to a sex ratio imbalance, which is a result of small population sizes. Also, something akin to a genetic drift component is present which causes a random wobble in each subpopulation. We identified the number of populations in the final generation of each repetition. In a single repetition we found one population, in five repetitions we found two populations, in 19 repetitions we found three populations, and in 10 repetitions we found four populations. The remaining 13 repetitions ended in complete extinction.

BSRM: The results are very similar to the BSAM case except that only one population is supported. A single population with an average beak size of three is clearly stable up to generation 1000. As is the case for BSAM the high amount of variability in the individuals is clearly visible. The convergence to a single population with an average beak size of three or eight is a defining feature for BSRM. In 41 of the repetitions a single population, centered on one of the two distinct seed sizes, is present in the final generation. In the remaining seven repetitions, there is complete extinction by generation 1000. In three of these cases, complete extinction took place before generation 10.

USRN: The defining characteristic for USRN is a single population, stable up to generation 1000 with a central green/light band indicating a large die-off in the center of the population. Also, there is no branching as seen in the USAM case. Wobble in the average population beak size, a result of a process akin to genetic drift, is clearly visible. In 13 repetitions the population went extinct before generation 1000. In six of the cases, complete extinction takes place before generation 10, due to the lack of males (three cases) or females (three cases) in the population. In the seven remaining repetitions (after generation 10) the population went extinct entirely due to the lack of females.

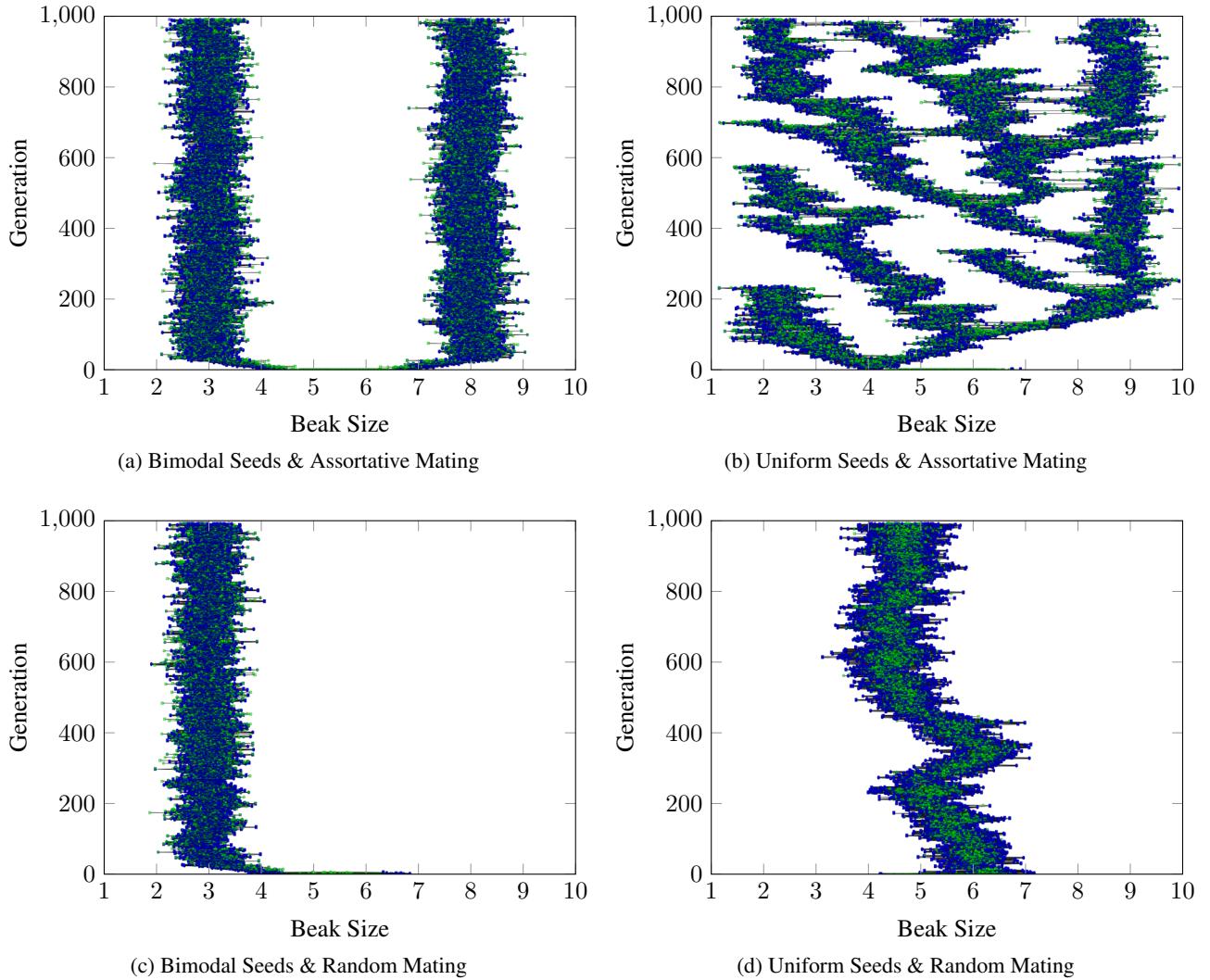


Figure 3: An illustration of the four combinations for the small population condition (5,000 seeds). (a) For the bimodal seeds and assortative mating combination, two populations are clearly present. (b) In the uniform seeds and assortative mating case, there is considerable branching and some merging. (c) When the mating behavior is changed from assortative to random mating, only one of the niches is exploited. (d) The chaotic branching found in (b) is reduced to a single population. Here there is significant die-off near the center of the population during each generation but divergence does not occur because mating is random within the whole population.

10x Seeds

The phenogenealogic trees for the 10x seed case are shown in Figure 4. The overall results are the same as the 1x seed case except for the USAM combination. In all combinations the population sizes were larger due to increased food resource and therefore more stable (there were no complete extinctions before generation 1000). The average initial population size (generation 1, after natural selection) for the bimodal and uniform seed cases are 49.9 and 139 respectively. The average final population size (generation 1000, after natural selection) for BSAM, USAM,

BSRM, and USRM are 541, 546, 280, and 208 respectively. For USAM (Figure 4b), the chaotic branching and merging found in the corresponding 1x case is absent. Instead, four populations are formed around generation 100 and remain stable up to generation 1000. A significant amount of interbreeding takes place between the adjacent branches.

Discussion

In this study we demonstrated the usefulness of our framework and its overall utility when applied to the finch studies of the Galápagos Islands. By focusing on one phenotypic

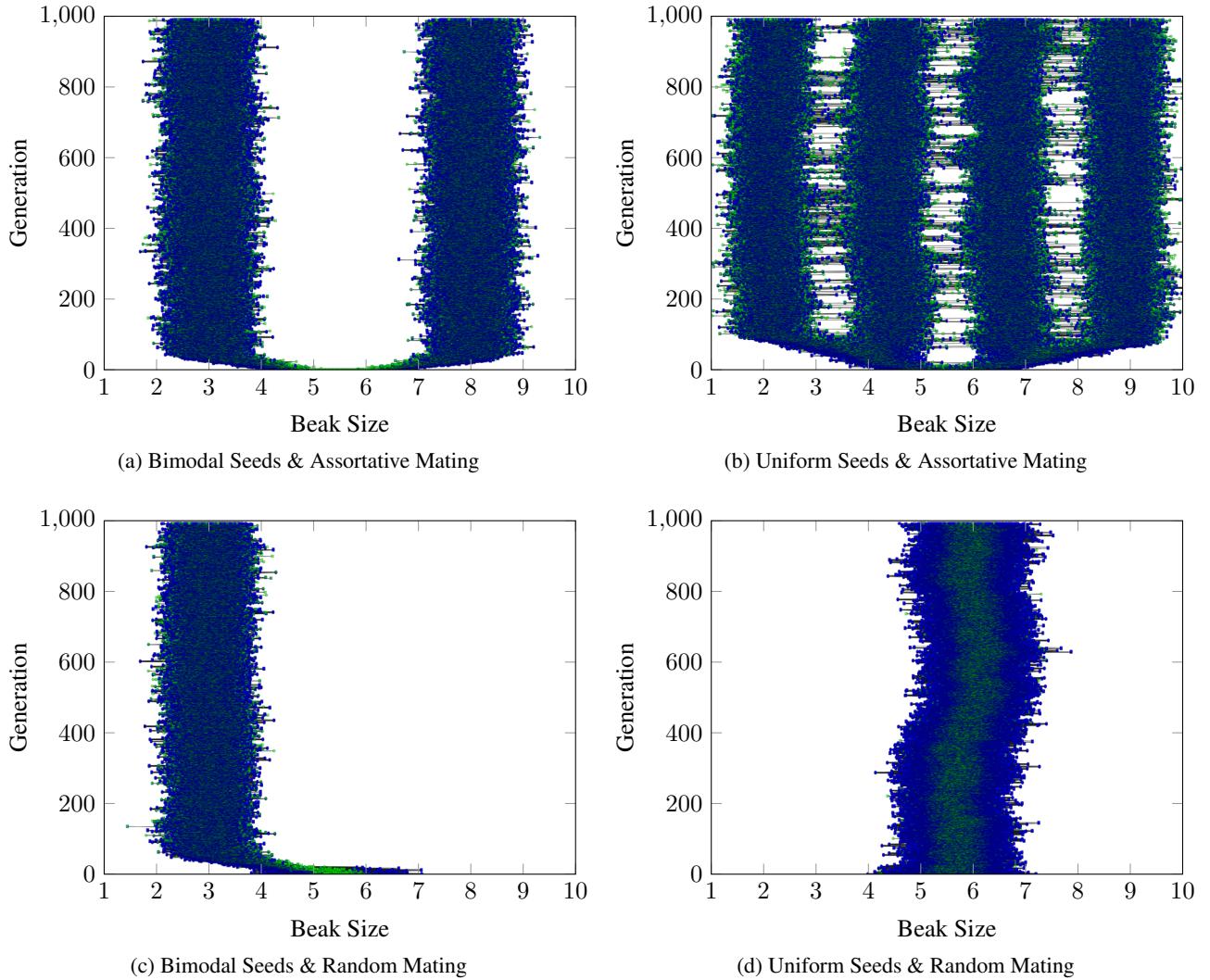


Figure 4: An illustration of the four combinations for the moderate population condition (50,000 seeds). In all four cases the increased population size is clearly visible. (a) For the bimodal seeds and assortative mating combination there is qualitatively no change from the 1x case. (b) The results for uniform seeds and assortative mating are substantially different from the 1x case. The intricate branching patterns have been replaced by four stable populations. (c) The bimodal seeds and random mating combination is qualitatively similar to the corresponding 1x case. (d) Likewise, the uniform seeds and random mating results are similar to the 1x counterpart except for a decreased drift-like component.

trait we have shown how a highly variable trait along with the process of natural selection and sexual selection can lead to speciation and therefore diversity.

We addressed interesting questions related to mate choice in our ecological simulation. The first question regarding the ability of the population to track resources was addressed. We found that our simulated bird populations evolved specialized beaks for the food resources available. The second question regarding the role of female mate preferences was addressed. We found that sexual selection based on assortative mating was necessary for speciation in our simulations.

Our results showed no divergence for the USRM combination, generally maintaining one lineage that did not shift much in expression of the trait over time. Similarly, BSRM generally led to a single species but with a shift of the mean beak size. These results may be surprising from a biological perspective because they leave substantial resources unused. However, they reflect the restrictions put on the experiments. For example, because the simulated finches are not allowed to evolve assortative mating in the random mating conditions, that mechanism for speciation is removed and ecological niches are left unfilled.

More interestingly, we found very rapid divergence in BSAM. Very quickly two populations evolved tracking the two available seed sizes. This rapid divergence was accentuated by assortative mating. The most interesting case is when assortative mating is combined with uniform random seeds (USAM). We hypothesized that we might see something akin to speciation supporting a given number of populations. This was supported by the data we collected. However, we did not anticipate the diverse branching and less frequent merging seen across the beak/seed range for the 1x seeds case. We observed long term stability in these new populations, remaining distinct for fifty generations or more. Nonetheless, the observed patterns are characterized by significant interplay between lineages, multiple lineages going extinct, and overall the most complex trees. The case was quite different for USAM in the 10x seed case. In this case, we observed rapid divergence but, rather than the complex splitting and merging patterns seen in the 1x seed case, the resulting four populations in the 10x case stayed quite stable, maintaining consistent means and avoiding extinction, but were not entirely distinct from one another with frequent hybridization observed.

In our study, the interplay of natural selection and sexual selection leads to speciation. Natural selection causes the initial die-off in the center of the beak size distribution, increasing the variance and essentially forming two new populations, and selection keeps them apart. Under conditions with more resources (10x seeds) we observed wider populations overall, but the qualitative patterns we found were very similar to the 1x seeds case. One important difference though was that in USAM four apparent lineages were supported, which appear distinct in the trees (Fig. 4b), but are connected by massive hybridization, suppressing true speciation. It appears that the more relaxed ecological conditions used here do not favor complete divergence whereas harsher conditions and smaller population sizes do.

Our results are important to biologists because they show how deceptive viewing speciation phenomena over a limited time can be: if one had a study lasting 200 generations in our USAM example, one would conclude that speciation has occurred and produced three distinct lineages. Without major changes in ecology, however, this situation changes drastically and eventually leads to four distinct lineages after 1000 generations. One interpretation of this finding is that early stages of divergence are more labile than currently thought and can collapse again for many generations. Our finding is in agreement with other recent work on sticklebacks (Bolnick, 2011) and whitefish (Vonlanthen et al., 2012).

Overall, our findings are congruent with earlier empirical studies that indicated an important role of female choice (Seehausen and van Alphen, 1999; Boake, 2000; Boughman, 2001; Bleay and Sinervo, 2007; The Marie Curie SPECIATION Network, 2011). It is also noteworthy that sexual selection using beak size has been implicated in other finches,

too (Slabbekoorn and Smith, 2000).

Interestingly, small population size is of great importance in our simulations and generally favors divergence (but also leads to random extinctions). The finch populations on which we are basing our simulations have small population sizes so there is a biological basis for this discussion. Therefore, our simulation results may have an impact on biologists studying small populations sizes in general (Grant and Grant, 2011). The possibility of extinction is always a concern with small population sizes and is of particular importance in the study of speciation.

More investigation is needed but larger population sizes may affect the outcome for BSRM. If larger population sizes are tested—at least two orders of magnitude larger than our smallest case—we might see two populations supported. We saw some hints of support for this in our 10x case.

Our study provides key insights to the ALife community. By coupling natural selection and sexual selection by using so-called magic traits (Servedio et al., 2011), we demonstrated how population diversity can be generated and maintained. In this work, we did not focus too much on how to identify species. Instead, we produced a synthetic environment in which clustering and hence speciation was an emergent property of our system. Although we validated our framework using the finch studies of the Galápagos Islands, the results could be applied broadly where natural selection and/or sexual selection operate. We find the interplay between these two selection methods to be a tantalizing prospect for the evolution of meaningful diversity.

Future Work

We believe that this research can be extended in a number of important ways. We made a significant contribution in the qualitative analysis of the data with our phenogenealogic tree. We would like to extend this work to a quantitative analysis of the phenomena observed. One possibility is the automatic identification of different species (Murdock and Yaeger, 2011). Manually identifying the different species in a given population is a tedious process and especially difficult when the subpopulations are not well defined. With this new capability we could gather new statistics for each population, such as size and gender ratio, which may be useful in predicting extinctions.

Although we have used key principles from biology in the design of our simulation, we are interested in validating our results with actual finch data. Given that our framework employs an agent-based model, it is well-suited to incorporating empirically measurable parameters.

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