

On the Sympatric Origin of Species: Mercurial Mating in the Quicksilver Model

Peter M. Todd
Department of Psychology
Jordan Hall, Building 420
Stanford University
Stanford, CA 94305
todd@psych.stanford.edu

Geoffrey F. Miller
Department of Psychology
Jordan Hall, Building 420
Stanford University
Stanford, CA 94305
geoffrey@psych.stanford.edu

Abstract

Traditional models of how interbreeding populations split apart into reproductively isolated populations (species) require the intervention of geographic barriers to mating or disruptive selection. We develop an alternate Quicksilver Model of speciation, and show through simulation that sympatric (barrierless) speciation can occur spontaneously, frequently, and robustly even in the absence of external divisive forces given certain broad conditions: (1) individuals have evolvable mate preferences based on degree of similarity to oneself along certain phenotypic dimensions, and (2) individuals compete to match the mate preferences of other individuals, and to have appropriate mate preferences themselves (i.e. sexual selection exists). Our models' success defends the notion of sympatric speciation against charges that it is impossible, implausible, or unlikely. It also offers a new vision of macroevolution based on appreciating the way modest psychological mechanisms of mate choice can have strong emergent effects on macroevolutionary dynamics.

1 SPECIATION IN BIOLOGY

The macroevolutionary record shows two central themes: *diversification* and *discontinuity* (Eldredge, 1989, p.99). Diversification represents the gradual accumulation of various phenotypic adaptations; discontinuity represents disruptions in the smooth continuum of diversity that would be expected from the basic accumulation of adap-

tations. Diversification is readily explained by normal Darwinian processes like natural selection, sexual selection, and genetic drift. But discontinuity remains a problem: why the gaps? Speciation theory is the study of such discontinuity. It seeks to explain why the macroevolutionary record resembles a branching bush with distinct trunks and twigs rather than a homogenous cone of biological diversity.

Mayr (1942, p.120) defined species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Although in macroevolutionary theory species are understood as reproductively isolated populations, in paleontological practice they must often be identified by the empirical criterion of phenotypic similarity. Fortunately for taxonomists, morphological gaps between phenotypically similar groups correlate strongly with reproductive gaps between species. A central question in speciation emerges: does the morphological divergence cause the reproductive divergence, or vice-versa? Or are both caused by something else?

Most theories of speciation answer that both are caused by some external divisive force. These 'cleaver models' propose that some external dividing instrument or force cleaves a population in twain genetically and phenotypically, and then reproductive barriers arise afterwards through genetic drift or through selection against hybridization. In Mayr's (1942) model of *allopatric* speciation, the cleaver is a new geographic barrier arising to separate previously interbreeding populations. In Dobzhansky's (1937) model of *sympatric* speciation, the cleaver is more abstract: it is a low-fitness valley in an adaptive landscape. In both cases, the cleaver models aim to identify a single, simple, deterministic, causal force, external to the speciating population, driving the speciation process.

Since cleaver models form the backbone of contemporary speciation theory, they deserve closer chiropractic scrutiny. In Mayr's (1942) allopatric model, a physical, geo-

graphic barrier arises, like a river shifting course to isolate one population from another. Genetic drift, the founder effect, or disruptive selection then causes the two newly isolated groups to diverge phenotypically, and once enough phenotypic divergence accumulates, the groups can no longer interbreed even without the barrier, and so are recognized as separate species.

Sympatric models are generally analogous, but imagine the barrier to arise in an abstract adaptive landscape (Wright, 1931, 1932) rather than in geographic space. For example, an adaptive landscape might develop two high-fitness 'peaks' (ecotones) separated by a low-fitness 'valley', thereby establishing disruptive selection (Mather, 1953) that drives an original population to diverge towards the separate peaks and thereby to become polymorphic. Dobzhansky (1937) further suggested that after divergence, reproductive isolation evolves through selection against hybridization: since hybrids will usually fall in the lower-fitness 'valley', mechanisms to prevent cross-breeding between the separate populations will tend to evolve. Thus the evolution of reproductive isolation (speciation itself) is viewed as a conservative process of consolidating adaptive change rather than a radical process of differentiation. Vrba (1985) and Futuyama (1987) concur that speciation serves a conservative function, acting like a 'ratchet' in macroevolution: only reproductive isolation allows a newly diverged population to effectively consolidate its adaptive differentiation; otherwise, the parent species will tend to genetically re-absorb it.

An important recent development in sympatric models is Paterson's (1985) concept of *specific mate recognition systems* (SMRSs: can be pronounced "s'mores" to highlight their sexual-appetitive function). SMRSs are phenotypic mechanisms each species uses to maintain itself as a self-defining reproductive community. A species is thus considered the largest collection of organisms with a shared SMRS. In Paterson's view, sympatric disruption and divergence of these SMRSs themselves (through some unspecified processes) leads to speciation. Eldredge (1989, p.120) emphasizes the potential macroevolutionary significance of SMRSs: "significant adaptive change in sexually reproducing lineages accumulates only in conjunction with occasional disruptions of the SMRSs."

The debate over allopatric versus sympatric speciation continues unabated and unresolved to the present. The debate's importance stems from its implications: if reproductive isolation is an adaptation in itself (as in sympatric theory) rather than a side-effect of drift (as in allopatric theory), then (1) species have more legitimacy as real biological entities because their boundaries are real evolved adaptations rather than by-products of phenotypic divergence, (2) sexual selection becomes almost as important as natural selection in macroevolution, and (3) species selection and macro-selection of lineages for their

ability to speciate (e.g. Vrba, 1980, 1985) become central to macroevolutionary dynamics.

Allopatric speciation appears more immediately plausible, but its frequency and generality might be doubted. Geographic barriers are clearly sufficient to impose reproductive isolation between populations. But to explain the number of similar species that now live sympatrically (in the same geographic area), barriers would have to suddenly arise, persist long enough to allow divergence, and then subside, allowing the divergent groups to live together again (Pimentel, Smith, and Soans, 1967).

Reactions to the possibility of sympatric speciation have ranged from outright denial that it is possible (Mayr, 1942) to hesitant support based on a hunch that it might work (Dobzhansky, 1937). Yet sympatric speciation remains the only mechanism that can hope to explain the real number and diversity of species occupying the same geographic area. Historically, the acceptability of sympatric models has depended on the perceived ability of disruptive selection to generate stable polymorphisms and eventually reproductive isolation. A large number of experiments reviewed by Thoday (1972) show that disruptive selection is sufficient to generate phenotypic divergence even in the face of maximal gene flow between populations (which Mayr, 1963, p.472, saw as the Achilles' heel of sympatric speciation models), and that mechanisms of reproductive isolation would evolve to avoid hybrids and consolidate that divergence. Mathematical models by Maynard Smith (1966) and computer models by Crosby (1970) showed that sympatric speciation could occur when populations choose different micro-habitats, evolve stable polymorphisms through disruptive selection, and then evolve reproductive barriers to avoid hybridization. But, historically, the speciation debate has ground down to a question of whose cleaver is bigger: Mayr's (1942) geographic barriers or Dobzhansky's (1937) fitness valleys. Into the cogs of this debate, which has been churning away for fifty years, we hope to throw a monkey wrench, not just another cleaver.

2 GENETIC ALGORITHM MODELS OF SPECIATION

Most macroevolutionary change occurs just before, during, and after speciation events, not during the relatively gradual selection within stable species. This view is supported by the observed inhomogeneity in rates of morphological change in the fossil record (Eldredge and Gould, 1972). Since the arena of speciation is where much of evolution's adaptive action happens, understanding the dynamics of speciation should be of great importance in developing genetic algorithms capable of modeling complex biological adaptation and of solving difficult real-world problems. Conversely, since much of the ongoing debate in macroevolution centers around the

feasibility of sympatric speciation, and simulation can be of great use in deciding feasibility issues and overcoming arguments from lack of imagination, genetic algorithm models of speciation may help illuminate evolutionary theory itself.

Most speciation work in the genetic algorithms (GA) community has bought into the cleaver model: speciation requires an imposed barrier of some sort, whether concrete (obstacles to migration) or abstract (valleys in the adaptive landscape). Mayr's (1942) allopatric model translates into Grosso's (1985) work on subpopulation formation and migration operators, and into the work of Muhlenbein (1989) and Gorges-Schleuter (1989) on parallel genetic algorithms. Implementing different GA populations on different computer processors is analogous to imposing geographic barriers between biological populations. The migration rules, the distribution of populations over processors, and the fitness landscape itself are all imposed rather than emergent, in accord with the cleaver model.

Dobzhansky's (1937) sympatric model informs most of the other GA work on speciation and niche formation. Goldberg (1989, p.189), for example, reasons that if there are multiple peaks in an adaptive landscape, then speciation will be useful in allowing separate sub-populations to explore those peaks independently, without the cost of repeatedly evaluating low-fitness hybrids between peaks. Sharing functions (Goldberg & Richardson, 1987; Deb & Goldberg, 1989) and crowding functions (De Jong, 1975) can be used to reinforce the disruptive selection emerging in a multi-peaked adaptive landscape, and to insure a reasonable allocation of individuals across different adaptive peaks.

A persistent question though has been how to allow reproductive isolation itself to evolve. Perry (1984) simply pre-defined a set of *external schemata*, that identify each individual as belonging to a particular reproductively isolated community: the species and niches are essentially fixed in advance. Deb and Goldberg (1989) developed a phenotypic mating restriction scheme such that individuals within a certain threshold distance in phenotype space were allowed to mate and individuals outside that distance were not. The threshold distance must be pre-set by the experimenter according to the structure of the adaptive landscape, again in accord with a cleaver model.

So far, very little GA research has allowed individuals to evolve their mating preferences themselves – to decide for themselves how much reproductive isolation they 'want'. The only example we know is Booker's (1985) use of evolvable mating templates. These genetic templates are matched against the functional (phenotype-encoding) portions of other individual's genotypes to determine who mates with whom. Booker's mating templates are essentially SMRSs that specify a particular genotypic ideal that each individual would like to mate

with. Different sub-populations can in principle evolve different templates, hence different SMRSs, and thus evolve into distinct species. But for reasons discussed in later sections, we believe that mating templates defined in terms of absolute genotypic or phenotypic preferences are unlikely to promote speciation.

3 THE QUICKSILVER MODEL

In this paper we advance a view of speciation profoundly different from the cleaver models that underlie most current speciation theory in biology and GA research. We were inspired by three converging observations. First, the widespread existence of 'sibling species' (phenotypically very similar species occupying the same geographic area and perhaps even the same econiche) suggests that in many cases reproductive isolation can evolve *before* geographic barriers to mating or disruptive selection on phenotypic attributes. Sibling species are difficult to explain under any existing allopatric or sympatric model. Second, our previous experience with neural networks, artificial life, and genetic algorithms (e.g. Miller, Todd, & Hegde, 1989; Miller & Todd 1990; Todd & Miller 1991a, 1991b) led us to consider whether speciation might occur as a kind of spontaneous, emergent phenomenon. Third, we had an intuition that the evolution of psychological mechanisms to assess potential mates might in itself substantially increase the likelihood and alter the dynamics of speciation. We believe it is crucial for the fields of psychology, cognitive science, and even artificial life to recognize that evolution constructed all existing psychological adaptations and behavioral repertoires (Miller & Todd, 1990). But we are also intrigued by instances where psychological and behavioral phenomena can have profound reciprocal influences on evolutionary dynamics (as in sexual selection itself, and in the Baldwin effect: see Hinton & Nowlan, 1985).

Our speciation model derives metaphoric inspiration from the behavior of mercury ("quicksilver") shaken gently on a flat plate: sometimes large cohesive blobs will split into separate smaller blobs. The mercury's behavior depends on two opposing forces: the random shaking forces that tend to jostle blobs apart, and the cohesive, surface-tension forces that tend to keep blobs intact. In our metaphor, the flat plate represents a fitness landscape defined over a space of possible phenotypes (in this case, a simple 2-D space). The shaking force represents the random effects of mutation (and to some extent the disruptive effects of crossover), and the cohesive force represents mate-choice preferences evolved to favor phenotypically somewhat similar mates. The Quicksilver Model suggests that, given some reasonable balance between these forces of mutation and mate-choice, spontaneous sympatric speciation can and will occur. Note that no cleavers are required: no physical barriers intercede to limit mating, and the fitness landscape has no to-

pography leading to disruptive selection. Sometimes speciation just happens.

Since most of the arguments against spontaneous sympatric speciation were essentially arguments from failure of imagination, we endeavored to develop a genetic algorithm simulation model to demonstrate the feasibility of sympatric speciation under the following conditions: (1) no geographic barriers, (2) no disruptive selection pressures (a 'flat' adaptive landscape), and (3) no pre-defined assortative mating preferences or SMRSs. Paterson's (1985) SMRS concept did seem to offer an alternate to clever models of speciation, but we wondered exactly how and why SMRSs might be disrupted spontaneously in a way capable of accounting for sibling species.

Our key observation was that although mate preferences can always be *represented* as probability-of-mating distributions over a phenotype space, they need not be *defined* directly in terms of phenotypic coordinates. Booker's (1985) mating templates represent a kind of mate preference defined directly in phenotypic coordinates: what we call a *space-relative mate preference*. But Deb and Goldberg's (1989) threshold mating distance represents a fundamentally different kind of mate preference, defined relative to the individual's current position in phenotype space. This we call an *individual-relative mate preference*. Space-relative and individual-relative mate preferences have very different implications for speciation and macroevolutionary dynamics.

Paterson's (1985) and Eldredge's (1989) assumption that sympatric speciation would require a split in a population's SMRS would thus hold true only if each individual's mate preferences happen to be space-relative. For spontaneous sympatric speciation to happen with space-relative mate preferences through something analogous to the Quicksilver Model, the frequency distribution of actual phenotypes and the frequency distribution of mate preferences would have to both jostle (through mutation and crossover) into the same bimodal form at the same time. This seems an extremely unlikely event.

But if a populations' mate preferences are individual-relative, sub-populations that are splitting apart can retain exactly the same mate preferences. This makes the Quicksilver model more plausible because speciation requires only that the frequency distribution of actual phenotypes go temporarily bimodal; the frequency distribution of mate preferences need not change at all. So we postulated that individual-relative mate preferences could generate the cohesive forces needed in the Quicksilver model of speciation. The remainder of this paper demonstrates that indeed freely evolvable individual-relative mate preferences, in conjunction with sexual competition for mates, promotes fast, robust, consistent, and spontaneous sympatric speciation.

4 IMPLEMENTING THE QUICK-SILVER MODEL IN A GA

To demonstrate the feasibility of our Quicksilver Model, we devised a very simple GA scenario which we hoped still had enough richness to allow sympatric speciation. Each genotype includes just three genes: two genes coding for phenotypic attributes, and one gene coding for a mating preference. Using just two phenotypic genes makes visualization and representation easy: the phenotype of each individual can be represented as a single x,y point on a 2-D plot, and the phenotype frequency distribution of an entire population can be represented as a set of points in the same space. In this case, we interpret phenotype space as a 1x1 toroid (where the top edge connects to the bottom, and left edge to right). It is imperative to remember that positions in this abstract 2-D phenotype space are not spatial locations in physical space, and that separation in this space cannot be interpreted allopatrically. Mate preferences permitting, it is as easy for two individuals far apart in phenotype space to mate as for two individuals close in this space.

All of the genes are Gray-coded. For the two phenotypic genes corresponding to x and y positions, Gray-coding has the nice property of making each edge of the phenotype-space just one mutation away from the corresponding opposite (and toroidally connected) edge; for example with four bits, 0000, which codes for 0.0, is one mutation away from 1000, which codes for the identical 1.0. The Gray-code representation is thus smooth in our toroidal phenotype space (which normal binary coding would not be), eliminating center-biasing and edge effects.

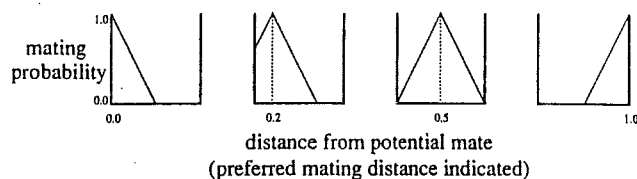


Figure 1: Mating Probability Function

In addition to the two phenotypic genes, every genotype includes one gene specifying a preferred mating distance, which in turn determines an individual-relative mate preference. We determined the general shape of a mate preference function: the single-peaked "triangular" function shown in Figure 1. This function maps relative phenotypic distance between the individual and some potential mate on to a probability that the individual would actually choose to indulge in this mating opportunity. The peak of this function represents the individual's preferred mating distance, and mating probabilities fall off linearly with equal slopes on both sides of this peak.

(The lower probability of mating with another individual closer than one's ideal can be thought of as an 'incest taboo'; the lower probability of mating with another farther than one's ideal can be thought of as 'xenophobia'.) Hence, different genetically encoded preferred mating distances essentially "slide" this triangular function back and forth, as can be seen in Figure 1, often yielding distances where the chance of mating is reduced to zero. By squaring this probability function, or raising it to a higher power, we can sharpen its peak and tighten up the preferred range of acceptable mating distances – we square the function for the simulations presented here (though the model is robust with respect to the peakiness of the function).

Implementing sexual selection with mating preferences is fairly straightforward. To create the next generation, a "mom" individual is first picked from the old population using normal roulette-wheel selection based on scaled fitness. Since our fitness landscape is flat, this amounts to uniform random sampling. Since it takes two to tango, a "dad" is next selected from the population using the same kind of selection. (Of course, individuals do not have a sex per se; how each individual is picked determines whether it plays the mom or dad role in each mating.) The phenotypic distance between the mom and the dad is computed (using the Euclidean metric in the 2-D toroidal phenotype space), and each individual computes its probability of mating with the other based on this mutual distance and its individual mate preference function. The two probabilities are likely to be different (mom might want dad more than the reverse), so they are multiplied together to yield a single probability that this pair will mate. Multiplying the two probabilities gives equal weight to each individual's choice in the matter, and mating happens only if both want to. Given this product of both their mating probabilities, a die is thrown, and if their number comes up, the pair gets to mate, and they are crossed over and their offspring put in the next population. If mating fails, then a new dad is chosen at random (with replacement), and the process is repeated, until the initially-selected mom finds a mate. Once the mom mates, a new mom is picked randomly (with replacement), and the search for a suitable dad begins again. This continues until the next generation is filled. (If a mom cannot find a suitable mate after five times through the population, she is deemed hopelessly picky, and a new mom is chosen.)

This moms-sample-dads scheme is unbiased in the sense that, although it enforces sexual selection, it does tend to preserve the frequency distribution of phenotypes from one generation to the next. It allows different phenotypically-separate and reproductively-isolated clusters to maintain their relative numeric proportions, by tending to pick mating pairs in just those proportions. This is important in promoting speciation. In contrast to our scheme, a random-pair-sampling scheme in which a mom and a dad are picked independently and randomly

at each step, and thrown back if they didn't like each other, will bias the next generation's frequency distribution of phenotypes towards currently more common phenotypes. Smaller, reproductively-isolated phenotypic clusters would be at a great disadvantage, because there would be a much smaller probability of choosing both parents from the same small cluster simultaneously, so potential new species would be eliminated prematurely.

We use traditional bit-wise mutation and two-point crossover, which seemed sufficient to generate the mercurial jostling required in the Quicksilver model. Mutation rate should be high enough to shake things around (to produce the quicksilver effect), so we typically used a value of 0.01. The crossover rate is 1.0 – the mom and dad always cross over – because the very use of sexual selection implies that sexual reproduction will be employed. To allow fairly fine-grained structure to emerge in the phenotype space, we typically use 15 bits to encode each phenotype gene, and 30 bits for the preferred mating distance gene, yielding a total genotype length of 60 bits. Population size is usually 100.

Since speciation is the process of an existing reproductive community diverging out into the surrounding phenotype space, it would be inappropriate here to start out with a random initial population uniformly distributed throughout phenotype space (the default for most GA applications). Instead, we give the initial population some elbow room to branch out into by starting them out as a small random cluster in the middle of a much larger space of potential phenotypes. Initial x and y phenotype genes were constrained to be in a range from 0.45 to 0.55, and the initial preferred mating distances were constrained to be in a range from 0.0 to 0.1. This initial population (and all later generations) can be graphically displayed in a 1x1 grid with a dot at each x,y phenotypic position, surrounded by a circle of radius equal to the individual's preferred mating distance. Figure 2 shows such a representation for Generation 0, with the centered square of initial phenotypic positions, surrounded by the overlapping halos of their preferred mating distances.

5 RESULTS

With this instantiation of the Quicksilver Model in a GA, speciation is immediate and obvious, as can be seen in the progression of generations shown in Figure 2. After 10 generations, several "outpost" individuals have been shaken loose from the central blob, but no outlying phenotypic region has built up enough concentration of individuals to keep from being reabsorbed for long. The preferred mating distances of some individuals in the central blob have in fact grown to recapture a few of the errant individuals, as can be seen particularly in the circles extending to the left of the center. By 20 generations, though, a new species can be seen in the blobs above and below the original central one (these two new blobs represent just one new species, because of the

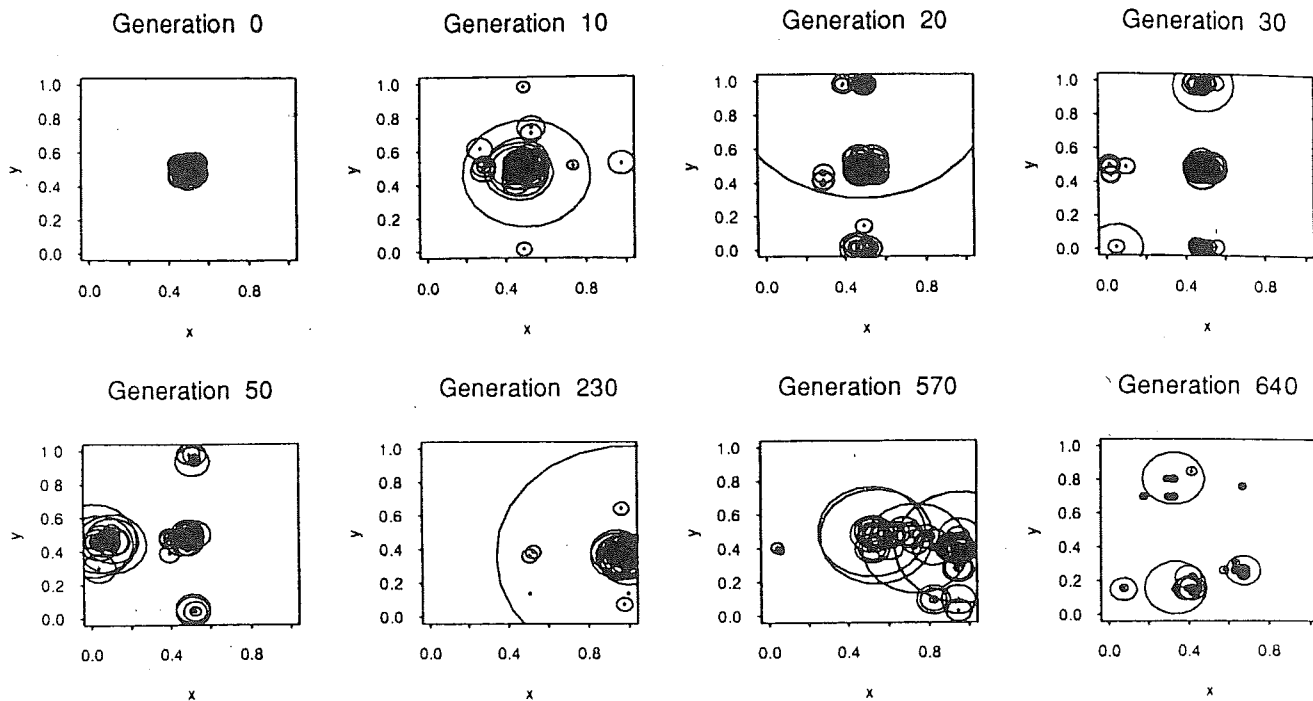


Figure 2: Sympatric Speciation Over Successive Generations

wraparound in this toroidal phenotype space). These individuals are far enough away from the ones in the center, and tightly enough clustered in phenotypes and mate preferences, to achieve reproductive isolation from the original species. Thus, this new species keeps from being directly reabsorbed by the original species, and it remains stable for many generations.

After 30 generations, the nascent uprising of a new species can be seen in the middle left edge of the space ($x=0.0$), "hopeful monsters" flung to this new phenotypic position and seeking others with similar inclinations; by 50 generations, this reproductively isolated subpopulation has grown significantly, at the expense of the second species. The species in the center hangs on for a long while, losing and recapturing individuals in a stochastic manner, with the advantage of having started out with the greatest number of members. But by 230 generations, even this founding population has dwindled to nothingness, being replaced by another single species in yet a new region of phenotype space.

About the messiest the population ever gets is shown at generation 570, where two relatively densely-populated regions of phenotype space are bridged by a succession of hybrids, and several individuals have larger preferred mating distances to take advantage of this spread. But by 640 generations, the preferred mating distances have again shrunk to highly selective values, and tight phenotypic clusters are evident. These shifting patterns of species formation, growth, dwindling, death, and rebirth are played out endlessly as the generations march on.

The fact that species come and go in this model, splitting and recombining, should not be seen as a drawback. In more complex biological systems, once speciation has been achieved through sexual isolation via mate preferences, divergent evolution of other phenotypic aspects (niche preference, identifying calls, mating apparatus, etc.) can serve to consolidate the species differences and prevent them from recombining. Removing the GA restriction used here of fixed population size will also serve to allow multiple species to coexist for longer, since growth of one will no longer automatically require the demise of another. Furthermore, the frequent emergence of new species relatively distant from already-existing ones, rather than a gradual budding and drifting apart, can be interpreted as an artifact of the particular scale we are witnessing the phenotypic changes on. If we "zoomed back" and took in a much larger range of phenotype space, it is entirely possible that the formation of new species would have just this sort of budding-and-splitting look.

But at this phenotype-space scale, other interesting features emerge. In particular, we often see a sort of "sexual dimorphism" *within* species, where two (or sometimes more) subgroups within a species will each cluster tightly together, but will only mate with members from the *other* subgroup. This can be seen most clearly here in Figure 2 at generation 20 in the small group of individuals just to the left of the central blob. The individuals in the lower tiny cluster all have their preferred mating distances evolved so that they coincide exactly with the po-

sition of the members of the upper tiny cluster, and vice versa. The resulting "interlocking rings" structure can commonly be seen in these simulations, arising as a geometrically stable configuration. Interestingly, the separate "sexes" never diverge and become their own independent species; but we are looking for instances in which these sexually dimorphic species may divide across sex-lines to form new species (half the "males" and "females" go to one new species, the rest to another).

These speciation results are remarkably robust across parameter changes. A wide variety of mutation rates all yielded more or less messy but similar speciation, with larger mutation rates resulting in greater cluster spread and hence correspondingly larger preferred mating distances to exploit that spread. Different crossover rates seem merely to affect the amount of speciation (that is, the ease and frequency with which new species form); even in the absence of crossover, speciation still occurs, though at a slower rate, since mutation must then provide all of the scattering and jiggling forces. Different population sizes similarly just affect the amount of speciation, in ways that we are continuing to characterize. The length of the genes used also has effects we are investigating; we hope that by increasing the length of the preferred mating distance gene, relative to the length of the phenotype-component genes, we will be able to alter the rate of preference evolution with respect to phenotype evolution. In this way we hope to make it easier or harder for the preferred mating distances to change to track diverging phenotype clusters, and thus correspondingly harder or easier for new species to break away. Over the ranges we have investigated so far (from 1:2 ratio to 2:1), though, we have not found significant effects.

In work to be described more fully elsewhere, we have applied the Quicksilver Model to non-flat fitness landscapes, to investigate its ability to guard against low-fitness hybrids and increase speed of convergence. Our evolvable mating distances generally performed at least as well as traditional search without sexual selection, and populations often converged faster on an adaptive peak and stayed perched at the peak more steadily. Without crowding or sharing functions, however, separate species did not generally form on the different peaks. We intend to extend these comparisons to more complex GA-deceptive problems and see whether a more robust sexual selection scheme can be found that allows speciation to separate adaptive peaks without crowding or sharing functions.

6 CONCLUSIONS

Spontaneous sympatric speciation is easier than most biologists think. According to our Quicksilver Model, if a population's SMRS is composed of individual-relative mate preferences evolved for phenotypically similar individuals (cohesiveness), spontaneous sympatric speciation requires only that the phenotype frequency distribution it-

self change through mutation and crossover (jostling). These results support the feasibility of sympatric speciation in real biological systems, help clarify the longstanding debate between Mayr and Dobzhansky, and offer the possibility of developing a deeper understanding of sexual selection itself. Our results also point towards the potential for a more general class of genetic algorithms capable of navigating adaptively through very complex fitness landscapes.

We have already developed a general theory of mate preference schemes, including a method for representing how natural-selective and sexual-selective fitness landscapes interact with each other and with evolving mating preferences, which will appear elsewhere. In future work, we hope to show that if populations are allowed to evolve different kinds of mate preferences for different phenotypic dimensions, then populations will tend to evolve space-relative mate preferences along those phenotypic dimensions that have stable natural-selective fitness peaks, but will evolve individual-relative mate preferences along those dimensions with more unstable fitness peaks. Next, we intend to develop a very large macro-evolutionary simulation with natural-selective and sexual-selective pressures that tend to select lineages for their ability to speciate; perhaps speciation ability can be understood as a population-level 'adaptation' instantiated in the mate preferences of individuals in the population. Finally, as evolutionary psychologists, we will apply the theory to human mate selection and sexual attraction, by (1) analyzing the adaptive landscapes underlying different classes of phenotypic cues, (2) based on that analysis, predicting which phenotypic cues would be expected to be judged according to space-relative, population-relative, or individual-relative mate preferences, and (3) testing those predictions experimentally. If successful, this would be the first general theoretical framework for making sense of how human sexual attraction works.

Natural selection and sexual selection are the twin engines that drive the evolution of complex adaptations. Although GA simulations of natural selection are beginning to enter their maturity, GA simulations of sexual selection are only now beginning to gestate. Since sexual selection logically depends on evolvable mate preferences, we hope our Quicksilver Model of spontaneous sympatric speciation is taken as more than just another footnote to the debate on allopatric versus sympatric speciation. We hope it inspires other researchers to explore the rich, surprising, and illuminating dynamics that can emerge when we let our bit-strings evolve their own mate preferences.

References

- Booker, L.B. (1985). Improving the performance of genetic algorithms in classifier systems. In *Proc. of an Int'l Conf. on Genetic Algorithms*

- and their Applications, pp. 80-92.
- Crosby, J.L. (1970) The evolution of genetic discontinuity: Computer models of the selection of barriers to interbreeding between subspecies. *Heredity*, 25: 253-297.
- De Jong, K.A. (1975) An analysis of the behavior of a class of genetic adaptive systems. (Doctoral dissertation, Univ. of Michigan). *Dissertation Abstracts International*, 36(10): 5140B.
- Deb, K. & Goldberg, D.E. (1989) An investigation of niche and species formation in genetic function optimization. In J.D. Schaffer (Ed.), *Proc. of the Third Int'l Conf. on Genetic Algorithms*. San Mateo, CA: Morgan Kaufmann. pp. 42-50.
- Dobzhansky, T. (1937). *Genetics and the origin of species*. (Reprinted 1982). New York: Columbia University Press.
- Eldredge, N. (1989). *Macroevolutionary dynamics: Species, niches, and adaptive peaks*. New York: McGraw-Hill.
- Eldredge, N., & Gould, S.J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T.J.M. Schopf (Ed.), *Models in paleobiology*. San Francisco: Freeman, Cooper. pp. 82-115.
- Futuyama, D.J. (1987). On the role of species in anagenesis. *American Naturalist* 130: 465-473.
- Goldberg, D.E. (1989). *Genetic algorithms in search, optimization, and machine learning*. Reading, MA: Addison-Wesley.
- Goldberg, D.E., & Richardson, J. (1987) Genetic algorithms with sharing for multimodal function optimization. *Genetic algorithms and their applications: Proc. of the Second Int'l Conf. on Genetic Algorithms*, pp. 41-49.
- Gorges-Schleuter, M. (1989) ASPARAGOS: An asynchronous parallel genetic optimization strategy. In *Proc. of the Third Int'l Conf. on Genetic Algorithms*, pp. 422-427.
- Grefenstette, J.J. (1987). *A user's guide to GENESIS* (Tech. Rep.). Washington, DC: Naval Research Laboratory, Navy Center for Applied Research in Artificial Intelligence.
- Grosso, P.B. (1985) Computer simulation of genetic adaptation: Parallel subcomponent interaction in a multilocus model. (Doctoral dissertation, Univ. of Michigan.)
- Hinton, G.E., & Nowlan, S.J. How learning guides evolution. *Complex systems*, 1: 495-502.
- Mather, K. (1953) The genetical structure of populations. *Symp. Soc. exp. Biology*, 7: 66-95.
- Maynard Smith, J. (1966) Sympatric speciation. *American Naturalist*, 100(916): 637-650.
- Mayr, E. (1942). *Systematics and the origin of species*. (Reprinted 1982). New York: Columbia University Press.
- Mayr, E. (1963) *Animal species and evolution*. Cambridge, MA: Harvard U. Press.
- Miller, G.F., & Todd, P.M. (1990). Exploring adaptive agency I: Theory and methods for simulating the evolution of learning. In D.S. Touretzky, J.L. Elman, T.J. Sejnowski, & G.E. Hinton (Eds.), *Proc. of the 1990 Connectionist Models Summer School*. San Mateo, CA: Morgan Kaufmann. pp. 65-80.
- Miller, G.F., Todd, P.M., & Hegde, S.U. (1989). Designing neural networks using genetic algorithms. In *Proc. of the Third Int'l Conf. on Genetic Algorithms*, pp. 379-384.
- Muhlenbein, H. (1989) Parallel genetic algorithms, population genetics, and combinatorial optimization. In *Proc. of the Third Int'l Conf. on Genetic Algorithms*, pp. 416-421.
- Paterson, H.E.H. (1985). The recognition concept of species. In E.S. Vrba (Ed.), *Species and Speciation*. Transvaal Museum Monograph 4, pp. 21-29.
- Perry, Z.A. (1984) Experimental study of speciation in ecological niche theory using genetic algorithms. (Doctoral dissertation, Univ. of Michigan.) *Dissertation Abstracts International*, 45(12): 3870B.
- Pimental, D., Smith, G.J.C., & Soans, J. (1967) A population model of sympatric speciation. *American Naturalist* 101(922): 493-504.
- Thoday, J.M. (1972) Disruptive selection. *Proc. of the Royal Soc. of London B*, 182: 109-143.
- Todd, P.M., & Miller, G.F. (1991a). Exploring adaptive agency II: Simulating the evolution of associative learning. In S.W. Wilson & J.-A. Meyer (Eds.), *From animals to animats: Proceedings of the First Int'l Conf. on Simulation of Adaptive Behavior*. Cambridge, MA: MIT Press/Bradford Books. pp. 306-315.
- Todd, P.M., & Miller, G.F. (1991b). Exploring adaptive agency III: Simulating the evolution of habituation and sensitization. In *Proc. of the First Int'l Conf. on Parallel Problem Solving from Nature*. Berlin: Springer-Verlag.
- Vrba, E.S. (1980). Evolution, species, and fossils: How does life evolve? *S. Afr. J. Sci.*, 76: 61-84.
- Vrba, E.S. (1985). Environment and evolution: Alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science*, 81: 229-236.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16: 97-159.
- Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proc. of the Sixth Int'l Congress on Genetics*, 356-366.