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# Evolutionary wanderlust: Sexual selection with directional mate preferences

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## Abstract

In the pantheon of evolutionary forces, the optimizing Apollonian powers of natural selection are generally assumed to dominate the dark Dionysian dynamics of sexual selection. But this need not be the case, particularly with a class of selective mating mechanisms called ‘directional mate preferences’ (Kirkpatrick, 1987). In previous simulation research, we showed that non-directional assortative mating preferences could cause populations to spontaneously split apart into separate species (Todd & Miller, 1991). In this paper, we show that directional mate preferences can cause populations to wander capriciously through phenotype space, under a strange form of runaway sexual selection, with or without the influence of natural selection pressures. When directional mate preferences are free to evolve, they do not always evolve to point in the direction of natural-selective peaks. Sexual selection can thus take on a life of its own, such that mate preferences within a species become a distinct and important part of the environment to which the species’ phenotypes adapt. These results suggest a broader conception of ‘adaptive behavior’, in which attracting potential mates becomes as important as finding food and avoiding predators. We present a framework for simulating a wide range of directional and non-directional mate preferences, and discuss some practical and scientific applications of simulating sexual selection.

## 1 Overview

The dynamics of evolution and the mechanisms of cognition interact in complex and often surprising ways. For example, once psychological mechanisms of mate choice emerge through natural and sexual selection, they can have profound effects on the further course of evolution. In previous papers (Todd & Miller, 1991; Todd & Miller, submitted), we showed that certain kinds of simple assortative mate preference mechanisms alone are sufficient to result in a sympatric population of simulated organisms splitting apart into distinct species. In this paper, we go one step further to explore a new class of mate choice mechanisms called ‘directional mate preferences’ (Kirkpatrick, 1987). With non-directional mate preferences, one’s ideal mate just has some degree of similarity (or dissimilarity) to one’s own phenotype. With directional mate preferences, one’s ideal mate is some distance away in phenotype space in a particular phenotypic direction (e.g. is much bigger, smarter, or richer than oneself). These two kinds of mate preferences result in very different evolutionary dynamics and make populations move around in phenotype space in very different ways.

In the simulations presented here, genetically coded mate preferences evolve to exploit currently available phenotypes, and phenotypic traits evolve to fulfill currently popular mate preferences. Thus, sexual selection sets up a complex reciprocal interaction between evolving mate preferences and evolving phenotypes. Over the short term, both preferences and phenotypes adapt to each other under strong sexual-selective pressures. But over the long term, the population follows a capricious trajectory through phenotype space that looks a bit like sped-up genetic drift. One might expect that imposing moderate natural selection pressures would eliminate this capricious wandering, but we show that it doesn’t. Even when there are clearly defined natural-selective peaks in an adaptive landscape, a population subject to sexual selection with directional mate preferences will still wander through the landscape, often climbing adaptive peaks but seldom staying there for long. These results provide more evidence for our previous suggestions (Todd & Miller, 1991) that apparently trivial changes in the psychological mechanisms of mate choice can have substantial effects on the evolutionary dynamics of an entire population.

This paper progresses from historical background to simulations methods, simulation results, possible applications, and finally conclusions. An intellectual context for this work is provided in section 2, through a short historical look at sexual selection theory. Section 3 presents our methods for simulating sexual selection with a variety of mate-choice mechanisms. Our results are summarized in section 4, after which section 5 offers some suggestions for how simulations

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of sexual selection might be used in practical applications and in further scientific research. Conclusions about the importance of this line of research are offered in section 6.

## 2 A Brief Review of Sexual Selection Theory

Darwin postulated two kinds of sexual selection: male competition for female mates, and female choice of male mates. Male competition was widely accepted by Victorian biologists as an important, necessary, and general evolutionary process. But the possibility of female choice was almost universally mocked and dismissed, at least until Fisher (1930) proposed his model of 'runaway sexual selection'. In this process, an evolutionary positive-feedback loop gets established between female preferences for certain male traits, and the male traits themselves. As a result, both the elaborateness of the traits and the extermity of the preferences increase at an exponential rate. Fisher's model could account for the wildly exaggerated male traits seen in many species, such as the peacock's plumage, but he did not explain the evolutionary origins of female preferences themselves, nor did he develop formal genetic models of runaway sexual selection. After Huxley (1938) presented many ill-conceived but often-cited arguments against the possibility of female choice and against Fisher's model, both the specific runaway model and the general notion of female choice were left to languish unexamined until quite recently.

In the last 15 years, however, there has been an explosion of work in biology on sexual selection through mate choice. The new population genetics models of O'Donald (1980), Lande (1981), and Kirkpatrick (1982) showed the mathematical feasibility of Fisher's runaway sexual selection process. New behavioral experiments on animals showed that females of many species do exhibit strong preferences for certain male traits (e.g. Andersson, 1982; Catchpole, 1980; Ryan, 1985). New comparative morphology has supported Darwin's (1871) claim that capricious elaboration is the hallmark of sexual selection: Eberhard (1985) argued that the only feasible explanation for the wildly complex and diverse male genitalia of many species is evolution through female preference for certain kinds of genital stimulation. New evolutionary computer simulation models such as those of Collins and Jefferson (1992) confirmed the plausibility, robustness, and power of runaway sexual selection. Once biologists started taking the possibility of female choice seriously, evidence for its existence and significance came quickly and ubiquitously. Cronin (1991) provides a readable, comprehensive, and much more detailed account of this history.

This peculiar historical saga suggests that the scientific neglect of Darwin's process of female choice was due to sexist biases in biology, not to its infeasibility or objective unimportance. What we have, then, is a major evolutionary process that has been neglected in biology until quite recently for demonstrably ideological reasons, and yet has been shown to be widespread, important, and powerful. We suggest that it is time we dust off Darwin's long-neglected theory of sexual selection through mate choice, and use the power of computer simulation to explore its nuances.

In natural selection, the causal flow of evolutionary forces is often one way: organism adapts to environment, but not vice-versa. This makes natural selection easier to study empirically and formally, because one can often specify a stable external set of conditions (e.g. a pre-defined 'fitness function') to which a species adapts. In sexual selection, though, the selective 'environment' itself always evolves. The mate preferences that serve as the selective environment to which sexually selected phenotypic traits adapt, themselves evolve under various forces. Indeed, there is a fierce debate in sexual selection theory between advocates of 'viability indicators', who suggest that mate choice mechanisms always evolve to prefer traits that indicate high natural-selective viability, and advocates of 'arbitrary preferences', who suggest that sometimes preferences are due to intrinsic sensory, perceptual or cognitive biases, such as the greater salience of the large, the colorful, the symmetric, and the novel. This is exactly the sort of debate that can be illuminated best by computer simulation, because it involves such complex interactions between coevolving traits. Just as computer simulation has been important in understanding the dynamics of coevolution between species (e.g. Hillis, 1992; Kauffman & Johnson, 1992), we expect that it will be critical in understanding the reciprocal interactions within a species between mate preferences and sexually selected traits. And as we will show, directional mate preferences *can* often evolve to be quite arbitrary, driving populations away from natural-selective peaks.

## 3 Simulation Methods

To explore the intricacies of sexual selection with directional mate preferences, we modified our previous genetic algorithm method of simulating sexual selection with non-directional preferences (Todd & Miller, 1991). Our general framework for simulating mate preferences is cast within the context of an n-dimensional phenotype space. Every individual in our evolving populations has a particular phenotype, which can be represented as a particular location in that space. Each individual also has associated with it its own genetically determined probability-of-mating (POM) function. This function is defined across the entire phenotype space, determining not only the phenotypic location of an individual's ideal mate, but also willingness to mate with non-ideal mates. The individual's POM function assigns to every phenotypic location, and thus every potential mate, a certain probability-of-mating, which can be represented as a height in the $n+1$st dimension. This probability represents the individual's willingness to mate with some prospective paramour: a zero probability indicates total disdain and disinterest, while a probability of one indicates wild, unquenchable, obsessive lust (or its simulated equivalent). Sexual selection is then driven by the topography of evolved POM functions interacting with the evolved frequency distribution of available mates in phenotype space.

To make the phenotype space easy to visualize, we restrict it to two dimensions in these simulations. Each individual thus embodies, and has preferences for, just two phenotypic traits, and can be represented as a particular (x,y) location in phenotype space. Individual phenotypes and ideal mate preferences can thus be displayed together in the same plot. We furthermore use a toroidal phenotype space, plotted as a square with its opposite edges effectively connected, just to avoid edge effects. It is important to remember that positions in this abstract 2-D phenotype space are not spatial locations in some simulated world, and that phenotypic separation between individuals does not imply geographic separation. Mate preferences permitting, it is as easy for two individuals far apart in phenotype space to meet and mate as for two individuals close together in that space.

In the work described here, the POM function always has a conical shape, such that probability-of-mating peaks at some point in phenotype-space and falls off linearly until it hits zero at some radial distance away from that point. Thus if we plotted an individual's POM function in three dimensions, it would look like a conical mountain poking up from the two-dimensional plane of phenotypes. A whole population's mate preferences could be represented as an overlapping set of such conical mountains. Across a whole population, if one summed the heights of every individual's POM function for every point in phenotype space, one would obtain a whole complicated mountain range of mating probabilities. Those individuals who are lucky enough to have phenotypes perched at a high elevation in this mountain range will be sought after by many other individuals wishing to mate with them. This abstract mountain range formed from individuals' POM functions is literally the environment to which individuals adapt through sexual selection.

But because POM functions are determined by genes which can evolve, this apparently stable mountain range of sexual preferences is actually, at a longer time scale, more like a storm-tossed ocean with wave-peaks rising and falling as generations go by. Mate preferences evolve because individuals with POM functions that peak in deserted, mate-poor regions of phenotype space will tend to die virgins. In contrast, individuals with POM functions that peak in densely populated regions of phenotype space will find a plethora of acceptable mates, and will likely have more offspring. So the peaks of POM functions will generally evolve towards the peaks in the current frequency distribution of individuals across phenotype space (i.e. the preferences will evolve to exploit the available phenotypes). And sexual selection will drive the peaks in that population frequency distribution itself to evolve towards the peaks of the POM functions (i.e. the phenotypes will evolve to fulfill the preferences).

One might expect both sorts of peaks to converge on one another and thereby reach a stable equilibrium. But this need not happen for two reasons. First, with small populations especially, sampling error (genetic drift) operating on all genes can keep mate preferences and phenotypic traits from converging perfectly onto one another, and thereby maintain the sexual-selective tension between them that drives the population's movement through phtnotype space. Second, with directional preferences, a given individual's POM peak can be forced to be some distance away from the individual's own location. In this case, the POM mountain range obtained by summing together POM functions across individuals could never completely coincide with the population's frequency distribution peaks, and the two would endlessly chase each other across phenotype space in a futile attempt at mutual satisfaction. The dynamics of sexual selection thus depend critically on the way POM functions are defined and genetically determined. We now explore some of the possibilities.

To begin with, each individual has its own *sexual reference position* (SRP) somewhere in the phenotype space. This SRP can determined in one of four ways, depending on the model of sexual selection being explored: (1) with "individual-relative preferences", the SRP is identical to the individual's own phenotype-location; (2) with "parent-relative preferences" (which can result from sexual imprinting at a young age), the SRP is the phenotype of a parent; (3) with "population-relative preferences", the SRP is the average of all phenotypes in the population or some specified sub-population; (4) with "space-relative preferences", the SRP is some absolute position in phenotype-space. To illustrate this somewhat whimsically: in humans, individual-relative preferences correspond to narcissism, parent-relative preferences correspond to an Oedipus or Electra complex, population-relative preferences to sexual conformism, and space-relative preferences to romantic idealism. We concentrate here on parent-relative preferences because they are better-documented in the biological literature, but we have discussed the other three types elsewhere (Todd & Miller, 1991; Todd & Miller, submitted).

Given a particular SRP, the peak of the cone-shaped POM function can be determined in two general ways. First, the POM peak could simply be centered on the SRP itself to yield *non-directional* preferences. We showed in previous work (Todd & Miller, 1991) that such non-directional assortative mate preferences can result in spontaneous sympatric speciation. Second, individuals can have *directional* preferences, in which the POM function is offset some distance away from the SRP in a particular direction, with both distance and direction parameters genetically specified. These directional preferences can be plotted as *mate preference vectors* in phenotype space, originating at the SRP and ending at the center of the POM function. Directional preferences are of interest primarily because they can facilitate runaway sexual selection (Kirkpatrick, 1987), and because they seem quite common in nature. Many species probably use a combination of non-directional preferences for some phenotypic dimensions and directional preferences for others. We focus here on the effects of directional preferences.

The genotypes in this simulation encode the elements just described in the following way. Two genes determine the individual's phenotypic traits. Two genes determine the direction in phenotype space along which the POM function is offset from the SRP, and one gene determines the distance in phenotype space by which the POM function is offset from the SRP. Together, these three genes determine the individual's mate preference vector. Finally, one gene determines the width of the base of the POM function: the wider the base, the less steeply the POM function slopes off from its peak down to zero probability, and the less 'picky' the individual is about its potential mates in terms of the area in phenotype space that its POM function covers. The resulting binary genotype for each individual is about 120 bits long.

The population size is fixed in these simulations (as it is in most genetic algorithms); here we use 100 individuals. To create the next generation of individuals, we use the following sexual selection method (an earlier version of which was described in greater detail in Todd & Miller, 1991). First, one individual is selected to play the role of "mom" and another is selected to play the role of a potential "dad" – these are temporary gender roles, not genetically determined sexes. Both mom and dad are selected probabilistically according to whatever *natural* selection fitness function has been imposed over phenotype space, or at random if there is no natural selection at work. Next, mom's POM function is constructed based on her *directional* preferences, and dad's is constructed based on his *non-directional* preferences (i.e. by centering his POM function on his SRP). We do not use the directional preferences of both individuals, because, for complicated theoretical reasons, this has been found to make it almost impossible for any individual to find mates in our simulations. Other possible methods for determining directional preferences may not have this trouble, but powerful directional selection still results even with this asymmetric scheme.

Next, mom's probability of mating with dad is determined, given her POM function and his phenotype, and dad's probability of mating with mom is determined, given his POM function and her phenotype. These two probabilities are multiplied (representing mutual consent) to yield an overall probability of mating, a die is thrown, and if the parents are lucky then two new offspring are created and put into the next generation. The offspring are made by applying 2-point crossover to the two parental bit-string genotypes, and then mutating the resulting children slightly (mutation rate .01 per bit). If the mom and dad prove unlucky, failing to meet each others' preferences, a new dad is chosen and tried again with the same mom. This continues until a successful match is found for this mom, or until she has proven too finicky (our criterion is going through 500 failed mating attempts). The entire mating process is repeated until the next generation is filled (that is, until 50 successful matings have occurred, each yielding two new offspring).

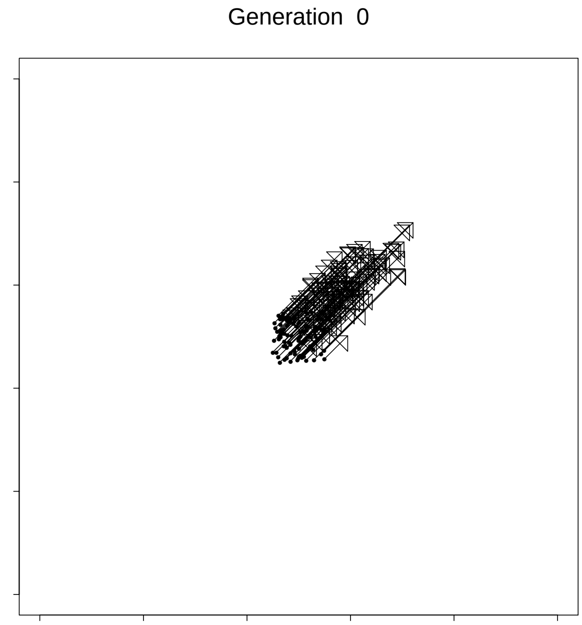

Figure 1. The initial population, clustered in the middle of phenotype space with preferences pointing NE.

It is important to remember just what is evolving in this population. The phenotypic locations of individuals will change from generation to generation, evolving in response to sexual selection pressures exerted by the mate preferences of the population as a whole, and to any natural selection pressures present. The preferences themselves also evolve from generation to generation, tracking the locations of the individuals (i.e. potential mates) in the population. For the simulations in this paper, we specified a small minimum length for the directional preference vectors to ensure that they wouldn't devolve to be effectively non-directional; and we used a (small) fixed width for the POM functions to keep overly indiscriminate individuals who'll mate with anything from evolving. But the phenotypes and the direction of the preference vectors are always free to evolve, even when we preset their initial values in the first generation; and these are the genes of most interest here, as we will now see.

# 4 Simulation Results

## 4.1 Sexual Selection Alone

To understand the basic effects of directional mate preferences on the course of evolution, our initial simulations used

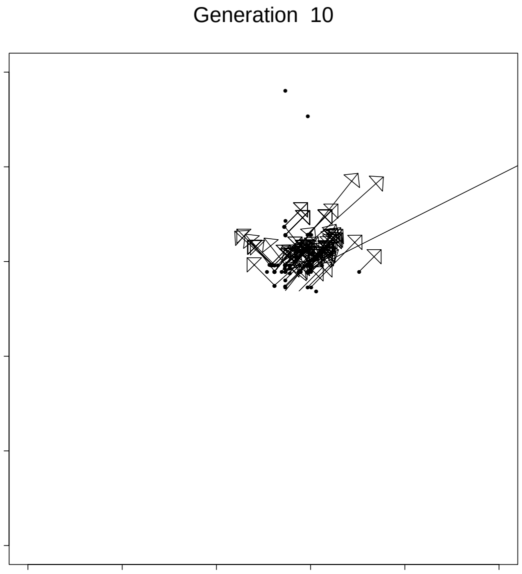

Figure 2. The population after 10 generations, now shifted NE and with some diversity of preferences.

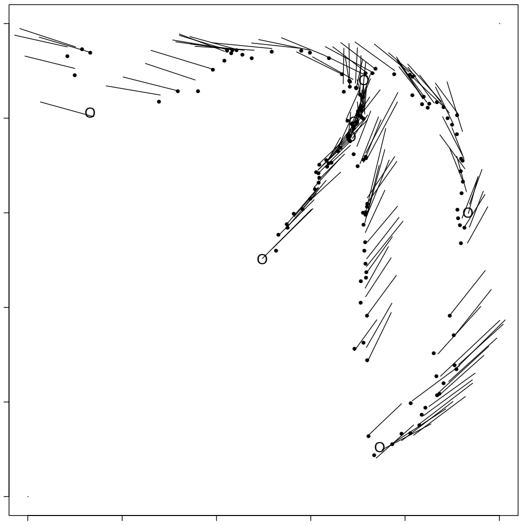

Figure 3. Sexual selection alone over 300 generations, showing population average phenotype and directional mate preference every two generations.

sexual selection alone without natural selection. Thus, every individual has an equal chance of being picked as a potential parent, so only their success at choosing mates and at being chosen determines their reproductive ability. Our initial population was clustered in the center of phenotype space, with all of their directional mate preferences pointing to the upper-right corner of this abstract space. To simplify our discussion, we will use compass-point terminology, and call this corner of abstract phenotype space the "northeast" (NE), This initial population of 100 individuals at generation 0 is shown in Figure 1. Each individual's phenotypic location is shown as a dot, and each individual's directional mate preference is shown as an arrow-vector. The mate preference vector originates at the individual's SRP (which in this parent-less first generation is just the phenotypic location of the individual itself) and extends in a genetically determined direction for a genetically determined distance.

The NE-pointing vectors shown here mean that every individual would prefer to mate with another who has a higher x-value (e.g. bigger antennae) and a higher y-value (e.g. greener wings) on their phenotypic traits than did their parent (their SRP). But remember that only the "mom" in each mating pair *expresses* this directional preference; the preference vectors for everyone are displayed because we can't know ahead of time who will play a mom-role and who will play a dad-role during mating. For clarity, we do not display each individual's cone-shaped POM function here, but these are simply centered at the arrowhead-end of the preference vector when the individual plays the mom-role, or at the SRP end of the vector for the dad-role. The conical 3-D POM functions would project down onto this 2-D space as circles, with radii in these simulations about half the length of the average preference vector.

After starting these initial individuals in the center of phenotype-space, we turn them loose, letting both phenotypes and preferences evolve freely, and see where sexual selection takes the population over successive generations. Since every individual's mate preference vector pointed NE, we expected the population as a whole to move initially in that direction. As we see in Figure 2, showing the population at generation 10, this is exactly what happens: most individuals have evolved higher values on both of their phenotypic traits, so are now closer to the NE corner of phenotype-space. (Note that in this plot there are some dots not connected to arrows, and some arrows not connected to dots – this is because each dot shows an individual's own phenotypic location, while each associated arrow shows that individual's preference vector, which originates at its SRP, a parental phenotypic location.) Moreover, most of the preference vectors still point NE. But because they are free to evolve, a few have started to diverge, mutating to point NW instead; one (extending off the E edge of phenotype space) has mutated to a much larger magnitude. But overall, the population is still headed in the same direction, with the phenotypes evolving to match the preferences, and the preferences evolving to match the phenotypes.

This NE migration of population phenotypes continues for 50 generations, as we can see in the "time-lapse" view of generation 0 to 300 shown in Figure 3. Here we have plotted a dot at the average phenotype of the entire population every two generations (or a circle to mark every 50th generation), and a line segment to show the population average preference vector. After starting in the center of phenotype space (the central circle) with NE preferences, the population marches steadily upwards in that direction, with its preference average continuing to point that way. In general the population average evolves in the direction that the average preference vector points, and the average preference vector evolves to point in the direction that the population is heading. This pattern seems to be violated after generation 50, when the population reaches the end of its first NE run; the population average phenotype then moves straight S (down), while the preferences continue to point NNE. But this is an artifact of how the population average is determined given the toroidal wrap-around of our phenotype space. The population has actually moved off the top edge of phenotype space, and reappeared at the bottom; but the phenotype averages don't take this into account, and so seem to move S. In fact, the phenotype/preference coupling is still working all along. We can see this in SE corner after generation 150, when once again the population heads NE, following the NE-pointing preference vectors.

But this feedback coupling between phenotypes and preferences is somewhat noisy and inaccurate, due to the noisy, stochastic nature of the evolutionary process (e.g. genetic drift due to selectional sampling error with small populations). This evolutionary noise can affect both phenotypes and preferences, weakening the reciprocal interaction between them. The population can drift in phenotype space, meaning that new preferences must evolve to ensure that individuals will find mates. Perhaps even more importantly, the direction of the preference vectors can drift, as we saw in Figure 2. This starts to happen noticeably around generation 200, in the middle of the E edge of phenotype space. Preference vectors which before had pointed NE, now begin to slowly shift, pointing more and more straight N, which in turn causes the phenotypes to evolve in that direction. The preference vectors continue to swing counter-clockwise around the compass dial, pointing more and more westerly: first NW, and then, after generation 250, straight W. The population follows (or maybe leads?) this trend, curving around the N (top) edge of phenotype space until it ends up in the NW corner at generation 300.

The coupling between preferences and phenotypes under sexual selection ensures that neither will shift too rapidly, and changes in one will force congruent changes in the other. This can result in a kind of evolutionary hysteresis, wherein the population's movement through phenotype space has a sort of momentum represented by the average mate preference vector. The interplay between this momentum effect, which drives the population in a consistent direction, and the genetic drift effects, which change the population's direction, result in the unique type of evolutionary trajectory shown in Figure 3. If we let the simulation keep running and allowed the population to evolve further (which we have done many times), it would continue wandering about in phenotype space, powered by directional mate preferences that impose strong sexual selection from generation to generation, but with nothing to guarantee a consistent direction or ultimate goal for the population's movement.

This simulation shows the capricious nature of directional sexual selection, and the way in which it can drive a population along a rapid but winding trajectory through phenotype space. In a flat fitness landscape (no natural selection), with directional mate preferences initialized to point in some direction but free to evolve in any direction thereafter, the short-term evolution is 'adaptive': phenotypic traits adapt to the current mate preferences, and mate preferences adapt to the current phenotypic traits, yielding effective sexual selection. But the long-term course of evolution is continuously capricious: neither phenotypic traits nor mate preferences ever settle down to a stable, optimal, equilibrium, because there is no stable 'adaptive landscape' external to the population. Rather, the two play catch-up with each other, engaged in a kind of arms-race that neither preferences nor traits can ever win, but which keeps them running quixotically across phenotype space. Directional mate preferences thus can indeed lead to runaway sexual selection, but the direction in which evolution runs cannot be predicted.

## 4.2 Sexual and Natural Selection Combined

What happens when we introduce natural selection into our model, to operate simultaneously with sexual selection? Whereas the population in the previous simulation wandered capriciously through phenotype space, one might expect that imposing some stern natural-selective fitness function would bring an end to all that sexual-selective rambling, and force the population responsibly upwards to some adaptive peak. But with directional mate preferences at play, the population's wanderlust can be surprisingly robust.

To investigate the interplay between natural and sexual selection, we constructed a single-peaked natural-selective fitness function as follows: phenotypes in the SW (lower left) corner are given the highest fitness, those in the NE are given the lowest, and the fitness of those in between falls off linearly from SW to NE. Thus, the isofitness contours in this landscape are just straight lines running diagonally from NW to SE. If a standard genetic algorithm were run in this fitness space, its population would sprint up these isofitness contours, heading S and W, and would quickly end up clustered at the peak in the SW corner. But in our simulations, these natural-selective fitnesses simply influence the probability of an individual being chosen as a potential parent; that individual's final reproductive success will also depend on sexual selection. Thus, there is an ever-shifting sexual-selective landscape overlaid on the fixed natural-selective fitness function; their combination determines actual final fitness.

To see what happens when sexual selection forces are in direct opposition to natural selection, we again initialized a starting population in the center of phenotype-space with

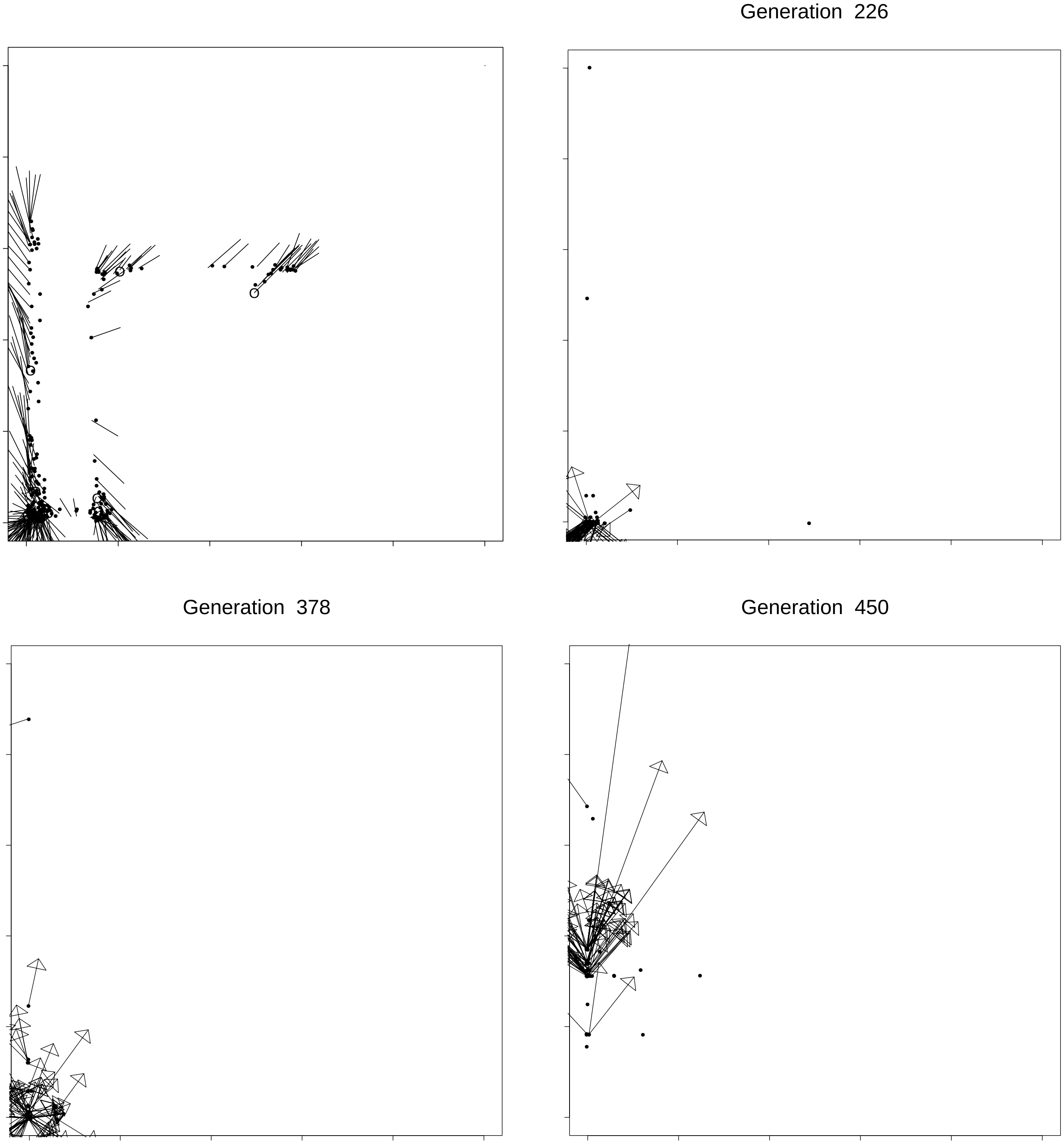

Figure 4. a. Sexual selection and natural selection initially pointing in opposite directions, plotted for 500 generations. b. The population clustered at the natural-selective fitness peak at generation 226, with SW directional preferences. c. The population still clustered near the fitness peak at generation 378, with varied directional preferences. d. The population shifted in position significantly by sexual selection at generation 450, with N directional preferences.

preference vectors pointing NE, away from the SW direction of the natural-selective fitness peak. Moms and dads are now sampled from the population according to their natural-selective fitness, but they still will only get to mate and have offspring if they each meet the other's mate preference. The population's movement under the influence of both selective forces is shown over 500 generations in Figure 4a.

At first, sexual selection seems to dominate. The population starts heading NE in the direction of the mate preference vectors, just as it did in the previous run with sexual selection alone. But after about a dozen generations, this movement has stopped. The population then dithers around a bit, but finally succumbs to the pull of natural selection, and starts heading straight W, obliquely up the fitness function's slope, despite the preferences vectors continuing to point NE. After 50 generations, the population does a switch-back, changing direction to heads straight S up the fitness function slope. At this point, the preference vectors try to catch up with the phenotypic movement, shifting to point more southward, and the population hovers at a high-fitness point slightly E of the peak for several generations. Finally the population closes in on the peak in the SW corner. The preferences then swing around to point SW, reflecting the fitness landscape and reinforcing its selective pressures, so that high-fitness mates are also sexually preferred. And there the population stays, generation after generation.

But this appearance of happy optimality does not last forever. For the dark forces of sexual selection, first reigning, then overthrown, and then joining ranks with natural selection, remain powerful and capricious. And they reassert their command over the population after about 150 generations. For a while, all is well at the fitness peak – the individuals in the population remain clustered there, and their preference vectors continue to point predominately SW, as shown for generation 226 in Figure 4b. But by generation 378, in Figure 4c, the preference vectors escape the magnetic pull of the fitness function and no longer point towards its peak. They now point in all directions, with many starting to point northward. The mate preference vectors continue to drift about in different directions until a general northward consensus is reached, around generation 400. Wanderlust returns: sexual selection entices the population towards the north, away from the natural-selective peak. By generation 450, in Figure 4d, the population has moved significantly northwards, and this progress continues over many generations, as Figure 4a showed.

If we ran this simulation further, we would see a continual battle between homesickness and wanderlust, with natural selection pulling the population towards its comfortable home on the fitness peak, and sexual selection compelling the population to wander through the wilderness of phenotype space under the momentum of the directional mate preferences. Of course, one of these forces could be made stronger, so that it alone controls the population's path. But we believe that in nature as in this simulation, the two are often balanced in a tenuous tug-of-war, with both affecting the course of evolution.

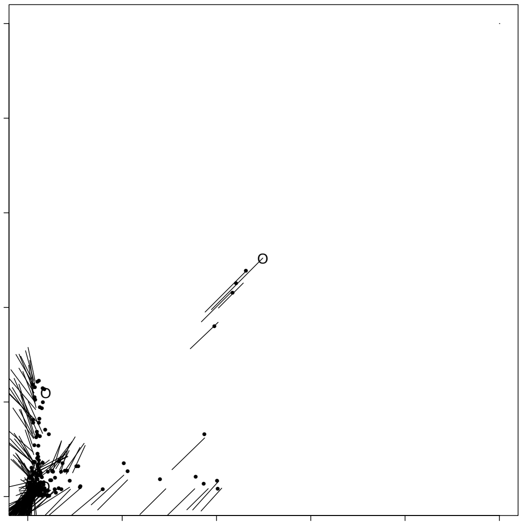

Figure 5. Sexual selection and natural selection initially pointing in the same direction, plotted for 500 generations.

We next explored the effect of pointing the initial population's preference vectors SW, towards the natural-selective peak, so that natural and sexual selection pull in the same direction at first. The results over 500 generations are shown in Figure 5. This time, as we would expect, the population moves very rapidly toward the fitness peak, first heading SW, then straight S, and then straight W. The population converges on the peak within 50 generations here, compared to the 200 generations it took in the previous case of opposition. As before, the population remains at the peak, with preferences continuing to point SW, for many generations. But once again, the directional preferences begin to drift after a while, sexual selection soon rears its seductive head, and the population begins to

move N in phenotype space, leaving the fitness peak behind. Thus, even though the directional mate preferences were initialized to complement natural selection, there is nothing to keep them in line. The preferences can ultimately evolve their own agenda, to which the population is (at least partially) subject.

Overall, these simulations show some of the capricious power of directional mate preferences to affect the course of evolution under sexual selection, with or without natural selection. Without natural selection, directional sexual selection can make a population wander through phenotype space at a fairly steady rate, along a trajectory that shows high directional consistency and momentum over the short term, but that changes directions unpredictably over the long term. When natural selection is applied as well, directional sexual selection can result in more rapid evolution toward an adaptive fitness peak, slower evolution toward such a peak, or even divergence away from a peak, depending on the directions the preference vectors evolve. Clearly, sexual selection forces in general and directional mate preferences in particular can play powerful roles in evolution, sometimes even dominating strong and consistent natural selection pressures. We will now turn to ways that simulating sexual selection may prove useful, both in assisting the evolution of human technology and in understanding evolution in nature.

# 5 Applications of Simulating Sexual Selection

## 5.1 Practical/Applied Uses

The relationship between natural selection and design optimization has been explored at great length and used to great effect in many practical contexts. But because sexual selection has often been considered a pathological, minor, non-adaptive force, it has often been overlooked as a design tool. We present three possible ways that methods for design optimization through simulated natural selection might be aided by including some simulated sexual selection.

First, to the extent that mate preferences evolve to be ‘utilitarian’ preferences for viability rather than ‘pathological’ preferences for arbitrary displays, sexual selection can reinforce ongoing natural selection, making it faster, more robust, and more consistent. In this paper, we have focused more on arbitrary preferences, but there is strong evidence from biology that many mate preferences do pick out viability indicators (e.g. Hamilton & Zuk, 1982). The ability of mate preferences to respond to viability indicators may be particularly useful and important when the mapping from phenotype to natural-selective fitness is noisy. In essence, selective mate preferences can allow a population to internalize natural-selective pressures, conferring some sexual-selective momentum on a population while it climbs an adaptive peak under the influence of natural selection.

Second, sexual selection can be thought of as imposing an automatic, emergent form of ‘fitness scaling’, so that ad-hoc methods such as pre-defined scaling algorithms and rank-based selection do not have to be used. Selective mate preferences based on the observed viability of potential mates will tend to increase the effective fitness variance in a population. Among many bird species for example, most male adults are healthy enough to survive, so there is little variance in their natural-selective fitness. But only a few are healthy enough to produce brilliant, sexually-preferred plumage (Hamilton & Zuk, 1982), so there is large variance in their sexual-selective fitness. Since sexual-selective fitness is highly correlated with natural-selective fitness in such cases, the former can be thought of as magnifying the latter. In general, sexual selection’s ability to magnify natural-selective fitness differences may increase the power and consistency of natural selection in a way analogous to fitness scaling. So sexual selection could keep a population evolving along even when the objective variance in natural-selective fitness is rather small.

Finally, sexual selection can allow spontaneous sympatric speciation (see Todd & Miller, 1991). This sort of speciation may allow more efficient niche exploration and exploitation in complex adaptive landscapes with multiple peaks. If a population does not have the ability to spontaneously speciate, then it must remain fairly coherent and climb only one adaptive peak at a time. To explore a complex adaptive landscape then, one would have to go through many simulation runs to be sure that different adaptive peaks have been explored. But with spontaneous speciation, a population can split up to climb different adaptive peaks as they are encountered, without the experimenter knowing ahead of time how many peaks there are or where they can be found. With a large enough initial population, a single evolutionary run might be sufficient to explore most of the peaks in the fitness space, because the run will generate a branching phylogeny with separate species exploring separate peaks.

In essence, searching without spontaneous speciation through sexual selection is like sampling with replacement over many computationally expensive runs (i.e. it can be highly inefficient). Searching *with* spontaneous speciation on the other hand is like sampling with replacement during one big integrated run. For example, there may be many different ways of designing an efficient jet engine, but a normal one-species genetic algorithm will only be able to explore one adaptive peak in the space of possible designs at a time, and may keep climbing that same peak in run after run. But a large simulation with sexual selection and spontaneous speciation may be able to produce a range of species corresponding to a range of distinct, highly optimized engine designs.

In further research, we hope to substantiate these applications. We suspect that some combination of mate preference types may prove very useful in optimization. Directional preferences for viability indicators could be used to facilitate the exploitation of adaptive peaks and speed hill-climbing. Directional preferences for arbitrary traits may facilitate the exploration of complex phenotype spaces. And non-directional assortative mate preferences may facilitate spontaneous sympatric speciation and therefore efficient and automatic niche specialization.

## 5.2 Scientific/Theoretical Uses

Sexual selection has been such a neglected part of evolutionary biology and evolutionary psychology, and involves such mathematically intractable dynamics, that computer simulations of sexual selection will probably play a critical role in our scientific understanding of evolution in general. In the following three areas computer simulation may prove particularly fruitful; we intend to explore these in future research.

(1) Simulations can very probably help theoretical evolutionary biologists and mathematical population geneticists understand the complex dynamics of sexual selection, especially formally intractable interactions between evolving mate preferences and evolving phenotypes. Sexual selection dynamics may underlie both the microevolutionary processes that generate capriciously elaborated traits, and certain macroevolutionary processes such as speciation. If so, sexual selection may be primarily responsible for the vast biodiversity of sexually reproducing animals and flowering plants (which themselves undergo a kind of cross-species sexual selection by pollinators). We suspect that much of the evolution assumed driven by natural selection could turn out to be better explained as a product of sexual selection, and that computer simulation will be valuable in demonstrating this.

(2) Simulations may help comparative biologists and paleontologists better understand the ubiquity, structure, function, and origin of adaptations resulting from sexual selection. Likewise, they may help comparative and evolutionary psychologists understand the origins, mechanisms, and functions of mate preferences, and their effects on the emergence of certain kinds of behaviors, especially those associated with courtship. This use may prove critical in human psychology because it seems to us likely that the human brain itself has been enlarged and elaborated through runaway sexual selection, and functions conspicuously as a long-term courtship device (Miller, 1993).

(3) Simulations of sexual selection may help establish the general importance of ‘psychological selection’ (Miller, 1993), i.e. the causal effect of evolved mental mechanisms (such as selective mate preferences) on the further course of evolution. As such, simulations of sexual selection may illuminate other evolutionary processes (e.g. the evolution of camouflage, warning coloration, mimicry, and protean behavior) wherein the nervous systems of other animals constitute the primary selective environment. Because nervous systems are very different from other kinds of selective environments, we might expect that they can lead to distinctive kinds of evolutionary processes and outcomes.

# 6 Conclusions

Natural selection typically results in convergent evolution onto a few (locally) optimal solutions given pre-established problems posed by the econiche. Sexual selection in contrast often results in an unpredictable, divergent pattern of evolution, with lineages speciating spontaneously and exploring the space of phenotypic possibilities according to their capriciously evolved mate preferences. Some evolutionary biologists view sexual selection as a maladaptive process because it results in highly elaborated, physiologically expensive traits that sometimes impair an organism’s ability to cope with other organisms (e.g. conspecifics, pathogens, parasites, prey, and predators) or with the physical environment. But this is an overly restricted view of what adaptive behavior means. In runaway sexual selection, members of a population adapt to the mate preferences of their conspecifics. These mate preferences are perceptual, motivational, emotional, and behavioral mechanisms that are just as real and important as the perceptual mechanisms that predators use to locate prey: if camouflage and warning coloration are legitimate adaptations, then so must be sexually-selected traits. And the adaptations produced through sexual selection, such as the peacock’s tail, the mandrill’s face, and the human’s brain (Darwin, 1871; Miller, 1993), fulfill all the usual criteria for being legitimate complex adaptations (Williams, 1966): clarity of function, complexity of design, and efficiency and reliability of operation.

Traditionally, empirical evolutionary biology has had trouble with sexual selection because the mechanisms that drive it (that is, mate choice mechanisms) are hidden away in the heads of animals rather than displayed out in the open like more obvious aspects of the econiche. Also, the adaptations that sexual selection produces (e.g. courtship displays) can only be evaluated if one understands the mate choice mechanisms that they are designed to excite. Indeed, empirical studies of mate choice in animals did not really begin in earnest until theoretical population geneticists (e.g. O’Donald, 1980; Lande, 1981; Kirkpatrick, 1982) confirmed the possibility of runaway sexual selection. The history of sexual selection research is a clear example of good theory preceding and priming the acquisition of empirical data. However, there are frustrating limits on how much theory one can build with mathematically tractable formal models of evolution. Computer simulation can circumvent these limits. Furthermore, the mate choice mechanisms that cause evolution by sexual selection are themselves subject to evolution, leading apparently to problems of circular causality. But it is in such situations of apparent circular causation that explicit simulation modelling of complex interactions can be most useful. The complex interactions we investigated among evolving mate choice mechanisms, assortative mating, sexual selection, and speciation would have been difficult if not impossible to derive by traditional mathematical analysis. Thus, the study of sexual selection offers unique prospects for computer simulation to guide biological theory and empirical research.

Normal sexual selection is a process of a species equilibrating to its own sexual preferences; runaway sexual selection is a process of a species catalyzing its own directional evolution driven by its own sexual preferences. Computer simulations of both processes can take on a simpler, more elegant, more self-referential form than simulations of natural selection that require the researcher to construct an arbitrary, pre-defined, external fitness function or environment. For this reason, we suspect that simulation results concerning sexual selection may sometimes prove more robust, generalizable, and biologically relevant than results concerning natural selection that require very precise modelling of preexisting environmental conditions and selection forces. We invite other researchers interested in the simulation of adaptive behavior to come in from the dry, glaring parking lot of natural selection, where species adapt to their niches like Buicks scraping their way into parking spaces, and enter the enticing fantasy-land of sexual selection, which overflows with dark tunnels of love, roller-coaster rides of exponential ascent and decline, mirrored funhouses in which species get caught in infinite cycles of self-reflection and self-distortion, and vast, seductive mazes of bizarre phenotypic extravagance, from which no species emerge untransformed.

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## References

Andersson, M.B. (1982). Female choice selects for extreme tail length in a widowbird. *Nature, 299,* 818-820.

Catchpole, C.K. (1980). Sexual selection and the evolution of complex song among European warblers of the genus *Acrocephalus*. *Behavior, 74,* 149-166.

Collins, R.J., and Jefferson, D.R. (1992). The evolution of sexual selection and female choice. In F.J. Varela and P. Bourgine (Eds.), *Toward a practice of autonomous systems: Proceedings of the First European Conference on Artificial Life* (pp. 327-336). Cambridge, MA: MIT Press/Bradford Books.

Cronin, H. (1991). *The ant and the peacock: Altruism and sexual selection from Darwin to today.* New York, NY: Cambridge University Press.

Eberhard, W.G. (1985). *Sexual selection and animal genitalia*. Cambridge, MA: Harvard University Press.

Fisher, R.A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon Press.

Hamilton, W.D., and Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218,* 384-387.

Hillis, W.D. (1992). Co-evolving parasites improve simulated evolution as an optimization procedure. In C.G. Langton, C. Taylor, J.D. Farmer, and S. Rasmussen (Eds.), *Artificial Life II* (pp. 313-324). Redwood City, CA: Addison-Wesley.

Huxley, J.S. (1938). The present standing of the theory of sexual selection. In G.R. de Beer (Ed.) *Evolution: Essays on aspects of evolutionary biology* (pp. 11-42). Oxford: Clarendon Press.

Kauffman, S.A. and Johnson, S. (1992) Co-evolution to the edge of chaos: Coupled fitness landscapes, poised states, and co-evolutionary avalanches. In C.G. Langton, C. Taylor, J.D. Farmer, and S. Rasmussen (Eds.), *Artificial Life II* (pp. 325-370). Redwood City, CA: Addison-Wesley.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution, 36,* 1-12.

Kirkpatrick, M. (1987). The evolutionary forces acting on female preferences in polygynous animals. In J.W. Bradbury and M.B. Andersson (Eds.), *Sexual selection: Testing the alternatives* (pp. 67-82). New York: Wiley.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci., 78,* 3721-3725.

Miller, G.F. (1993). *The evolution of protean behavior through psychological selection: Adaptive unpredictability, sexual selection, and human encephalization.* Unpublished doctoral thesis. Stanford, CA: Psychology Department, Stanford University.

O'Donald, P. (1980). *Genetic models of sexual selection*. Cambridge, UK: Cambridge University Press.

Ryan, M.J. (1985). *The Tungara frog*. Chicago: University of Chicago Press.

Todd, P.M., and Miller, G.F. (1991). On the sympatric origin of species: Mercurial mating in the Quicksilver model. In R.K. Belew and L.B. Booker (Eds.), *Proceedings of the Fourth International Conference on Genetic Algorithms* (pp. 547-554). San Mateo, CA: Morgan Kaufmann.

Todd, P.M., and Miller, G.F. (submitted). *Evolution "without" natural selection: Sexual selection for speciation and learning.* Submitted to the Proceedings of the Third Artificial Life Conference.

Williams, G.C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.