

Biodiversity through sexual selection

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Abstract

What engenders biodiversity? Natural selection certainly adapts species to their ecological niches, but does it really create all of the new niches and new species to fill them? Consider: the most successful, complex, and numerous species on earth are composed of sexually-reproducing animals and flowering plants. Both groups typically undergo a form of sexual selection through mate choice: animals are selected by conspecifics and flowering plants are selected by heterospecific pollinators. This common feature suggests that the evolution of biodiversity may be driven not simply by natural-selective adaptation to ecological niches, but by subtle interactions between natural selection and sexual selection. This paper presents theoretical arguments and simulation results in support of our view that sexual selection creates new fitness peaks (and thus new niches), helps species escape from old local optima to find new, better peaks, and promotes speciation to increase the number of lineages searching for peaks. Natural selection is a precondition for biodiversity (because it permits ecological adaptation), but sexual selection may often be a more direct cause of species diversity for animals and flowering plants. The paper concludes with implications for evolutionary engineering, human evolution, and conservation priorities.

1 Introduction

Most research on biodiversity asks about biodiversity as product rather than process: how much biodiversity has there been, is there, and should there be? (See e.g. Wilson & Peter, 1988.) This concern for counting species is reasonable given our appalling efficiency as agents of extinction. But our best hope of promoting biodiversity over the long term may be to understand better the evolutionary processes that actually produce biodiversity – ecosystems rich with species, adaptations, and innovations. In this paper we take a step in that direction, discussing one major, often overlooked process capable of engendering biodiversity: sexual selection.

At first glance, it might seem obvious that natural selection does all the work of biodiversification. Darwin's engine of ecological adaptation seems likely to be the engine of ecological diversification as well. But natural selection is mainly a hill-climber in the fitness landscape. It brings species closer to adaptive peaks, but does it really create new peaks, promote shifts from one peak to another, or increase the number of species doing hill-climbing? In fact, Darwin's (1859) *Origin of species* did not offer any plausible mechanism of peak-production, peak-hopping, or speciation (Wilson, 1992, p. 52); it only suggested that natural selection can hill-climb fitness peaks to produce complex adaptations. We propose that Darwin's (1871) other favorite process, sexual selection, can fill these gaps. While natural selection explains most adaptation, sexual selection can explain much of biodiversity. As we will argue and demonstrate through simulations, sexual selection through mate choice can (1) create new dynamic adaptive peaks in the fitness landscape, corresponding to a population's mate preferences, which can shift about rapidly and stochastically and lead the population to explore new regions of phenotype space; (2) allow populations to escape current local optima to find new naturally-selected fitness peaks; and (3) split old species apart into new ones through a form of spontaneous sympatric speciation, increasing the number of lineages exploring phenotype space.

There are good *a priori* reasons to look to sexual selection as a wellspring of biodiversity, even before knowing many details of its operation. Sexual selection has traditionally been considered a minor, peripheral, even pathological process, tangential to the main work of natural selection and largely irrelevant to such central issues in biology as speciation, the origin of evolutionary innovations, and the optimization of complex adaptations (for a historical review see Cronin, 1991). But this traditional view is at odds with the fact that the most complex, diversified, and elaborated taxa on earth are those in which mate choice operates: animals with nervous systems, and flowering plants. The dominance of these life-forms, and the maintenance of sexual reproduction itself, has often been attributed to the advantages of genetic recombination. But recombination alone is not diagnostic of animals and flowering plants: bacteria and non-flowering plants both do sexual recombination. Rather, the interesting

common feature of animals and flowering plants is that both undergo a form of sexual selection through mate choice. Animals are sexually selected by opposite-sex conspecifics (Darwin, 1871; see Cronin, 1991), and flowering plants are sexually selected by heterospecific pollinators such as insects and hummingbirds (Darwin, 1862; see Barth, 1991). Indeed, Darwin's dual fascination with animal courtship (Darwin, 1871) and with the contrivances of flowers to attract pollinators (Darwin, 1862) may reflect his understanding that these two phenomena shared some deep similarities.

Sexual selection arises in any competition to fulfill the mate choice criteria imposed by the brains (and bodies) of the opposite sex. The nervous-system-mediated decisions that implement mate choice play a very important role in evolution, because brains are a special sort of generator of selective forces. The nervous systems of organisms make choices that affect the survival and reproduction of other organisms in ways that are quite different from the effects of inanimate selection forces (as first emphasized by Morgan, 1888). This sort of *psychological selection* (Miller, 1993; Miller & Freyd, 1993) by animate agents – that is, selective forces stemming from the psychology and behavior of individuals – can have much more direct, accurate, focused, and striking results than simple *biological selection* by ecological challenges such as unicellular parasites or *physical selection* by habitat conditions such as temperature or humidity. Sexual selection is only one form of psychological selection that is likely to promote biodiversity. For example, psychological selection by predators can favor the diversification in prey species of mimicry, camouflage, warning coloration, and protean (unpredictable) escape behavior. But because sexual selection typically acts within one species, both the mate choice preferences and preferred traits can evolve more rapidly than psychologically-selected traits between species. (See, e.g., Moynihan, 1975, for a discussion of the diversification of mating displays within cephalopod species and the conservation of predator warning displays between them.) Hence, in this paper we emphasize the evolutionary effects of mate choice, because it is probably the strongest, most common, and best-analyzed form of psychological selection.

Of course, sexual selection does not operate alone – the physical and biological environment is always imposing natural selection as well. So how does sexual selection interact with natural selection? The traditional answer has been that sexual selection either copies natural selection pressures already present (e.g., when animals choose high-viability mates), making it redundant and impotent, or introduces new selection pressures irrelevant to the real work of adapting to the ecological niche (e.g., when animals choose highly ornamented mates), making it distracting and maladaptive (Cronin, 1991). In this paper we take a more positive view of sexual selection. By viewing evolution as a process of search, optimization, and diversification in an adaptive landscape of possible phenotypic designs, we can better appreciate the *complementary roles* played by sexual selection and natural selection. We suggest

that the successful diversity of sexually-reproducing animals and flowering plants is no accident, but is due to the complex interplay between the dynamics of sexually-selective mate choice and the dynamics of naturally-selective ecological factors. Both processes together are capable of generating evolutionary innovations and biodiversity much more efficiently than either process alone.

This paper extends our earlier work on genetic algorithm simulations of sexual selection (Miller, 1994; Miller & Todd; Todd, 1996; 1993; Todd & Miller, 1991, 1993) to the domain of biodiversity. We begin with a discussion of how sexual selection can create new peaks – that is, new niches to be filled – in the adaptive landscape, and simulation results showing the power of mate preferences to influence the course of evolution as it chases after those peaks. But natural selection too creates fitness peaks, and in section 3 we show how sexual selection can help a population escape from one naturally selected peak to find another. Such peak creation and exploration is necessary for biodiversity, but it does not explain the existence of multiple species across multiple peaks – we turn to this issue, speciation, in section 4. We conclude with a consideration of the implications of this work for both the biological sciences and various engineering domains.

2 Generating new adaptive peaks in the fitness landscape

The selective forces of both natural and sexual selection create “peaks” in the adaptive landscape – sets of traits that are more favored than other traits – that can drive a population's evolution. Natural selection typically results in convergent evolution onto a few (locally) optimal ecological niches established by the combined selective forces of other species and physical environmental characteristics. Because these niches are constrained by relatively stable physical factors or tightly-interwoven ecosystems, the niches and the ecological roles they provide will often be rather stable themselves. Thus, the adaptive landscape peaks constructed by natural selection will tend to arise and shift only slowly over time (except in relatively rare cases of tight co-evolution – see Futuyma & Slatkin, 1983), an effect hinted at in the long-term equilibria of the number of species and families in any given geographic region across millions of years (Wilson, 1988).

In contrast, sexual selection allows a species to create its own peaks in the fitness landscape – those phenotypes that are currently most desired as potential mates. This self-defining aspect of sexual selection via mate choice can result in rapidly shifting adaptive peaks that lead the population on a fast course through unexplored regions of phenotype space, as we will see. To visualize this process, imagine a population of individuals situated in some abstract phenotype space (say, a two-dimensional space, with dimensions corresponding to phenotypic size and color). Each individual has a particular mate preference function

that specifies how likely it is to mate with others of a given phenotype in their species. Imagine that this probability-of-mating (POM) function is cone-shaped, centered over some point in phenotype space¹. In this case, the individual's desire to mate with another individual will be highest at the center point, and will fall off linearly with distance in the phenotype space until it hits zero – total disinterest in mating – for all phenotypes beyond some radial distance away from the central 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.

We can then sum a whole population's set of individual conical mate preferences over the phenotype space to create a final total mountain range of mating probabilities. Those individuals who are lucky enough to have phenotypes perched at a high elevation in this mountain range (corresponding to “sexual ideals”) will be sought after by many other individuals wishing to mate with them. It is these pinnacles in the range of mate choice consequences that represent the adaptive peaks that sexual selection creates, via the desires of the individuals in a given population. And these psychologically-created peaks literally compose the environment to which individuals adapt through sexual selection. (These peaks, of course, are combined with those stemming from natural selection to create the complete adaptive landscape on which a given species evolves, but we can talk about the contributions of each force separately to emphasize their differences. See Heisler, 1994, for a related discussion.)

But because mate preferences (and thus probability-of-mating functions) are determined by genes that can evolve, this apparently stable mountain range of sexual preferences is actually, over a longer time scale, more like a storm-tossed ocean with wave-peaks rising and falling as generations go by. Sexual selection can fluidly create new adaptive peaks as preferences change, or shift the locations of existing ones in phenotype space. Because the mate choice mechanisms that constitute the sexually selective environment can themselves evolve under various forces, the environment and the adaptations – the traits and preferences – can co-evolve under sexual selection, as Fisher (1930) realized. This creates a causal flow of sexual selection forces that is bi-directional, and thus, as a coupled feedback system, often rapid, complex, and chaotic.

What factors influence the positions and movements of sexual-selective peaks in phenotype space? One important contributor is the current distribution of available phenotypes, which will of course be affected by natural selection. In this case, mate preferences will change over time to reflect population structure because individuals with preferences centered in densely

populated regions of phenotype space will find a plethora of acceptable mates, and will likely have more offspring. So under this pressure the peaks of POM functions will generally evolve towards the peaks in the current phenotypic frequency distribution of individuals.

In particular, if a population is perched atop a naturally selected adaptive peak due to stabilizing selection (as most populations are most of the time) then mate preferences will often evolve to favor potential mates near the current peak. In this way, sexual selection will tend to reinforce the stabilizing natural selection that is currently in force. But if a population has been evolving and moving through phenotype space, then mate preferences can evolve to “point” in the direction of movement, conferring more evolutionary “momentum” on the population that it would have under natural selection alone. These sorts of directional mate preferences (Kirkpatrick, 1987; Miller & Todd, 1993) can be visualized as a population-level vector that continually pushes an adaptive peak in some direction in phenotype space. The selective pressures represented by that peak in turn can keep the population evolving along a certain trajectory, in some cases even after natural selection forces have shifted. In sum, (directional) mate preferences will often evolve to be congruent with whatever (directional) natural selection is operating on a population. Sexual selection may thereby smooth out and reinforce the effects of natural selection.

But sexual selection vectors (and their associated adaptive peaks) can often point in directions different from natural selection vectors, resulting in a complex evolutionary interplay between these forces. For example, stochastic genetic drift can act on mate preferences as it can on any phenotypic trait; this effect is important in facilitating spontaneous speciation and in the capriciousness of runaway sexual selection. Intrinsic sensory biases in favor of certain kinds of courtship displays, such as louder calls or brighter colors, may affect the direction of sexual selection (Guilford & Dawkins, 1991; Ryan, 1990; Ryan & Keddy-Hector, 1992). Learned preferences can become more exaggerated through the phenomenon of “peak shift,” well-known from behaviorist psychology (Guilford & Dawkins, 1991). An intrinsic psychological preference for novelty, as noted by Darwin (1871) and studied in the “Coolidge effect” (Dewsbury, 1981), may favor low-frequency traits and exert “apostatic selection” (Clarke, 1962), a kind of centrifugal selection that can maintain stable polymorphisms, facilitate speciation, and hasten the evolution of biodiversity. Thus, a number of effects may lead mate choice mechanisms to diverge from preferring the objectively highest-viability mate as the sexiest mate. These effects will in turn make sexually selected peaks differ from naturally selected peaks in the adaptive landscape, allowing sexual selection to lead an evolving population into new regions of phenotype space.

¹ In general, this function will be maximal for some phenotype, and will fall off more or less gradually for increasingly dissimilar phenotypes, according to the species' generalization curves, so a cone is a reasonable approximation. The exact shape of this function for any particular species, though, is not generally known; but the behavior of our model is robust across different function assumptions.

2.1 Macroevolutionary effects of sexually selected adaptive peaks

To demonstrate the powerful, often unpredictable way in which mate preferences can create new adaptive peaks and drive the long-term course of evolution, we developed a simulation of a population evolving under directional sexual selection. We eliminated natural selection – that is, differences in survival rates – from this simulation, so that the effects of sexual selection would be clearer (but we will reintroduce it in the next section). We present here a bare-bones description of the simulation and the phenomena we have observed relevant to the creation of biodiversity; more details can be found elsewhere (e.g. Miller & Todd, 1993).

To simulate the evolution of a population of individuals choosing whom to mate with based on their own preferences, we modified a genetic algorithm in the following way: to get into the next generation, an individual does not have to score well on some natural selection fitness function, but rather must choose a suitable mate and be chosen by that individual in return. An individual’s mate preferences are defined in terms of some particular phenotype (that is, a fixed position in phenotype space), which we call its sexual reference position (SRP). For the simulations presented here, we use an SRP situated at the phenotype-space location of one of an individual’s two parents². Given a particular SRP, the peak of the cone-shaped mate preference probability-of-mating (POM) function described earlier is offset some distance away from the SRP in a particular direction, with both distance and direction variables genetically specified. This yields a directional mating preference of the kind we discussed in the previous section.

The (binary) 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 individual’s preference function (POM) is offset from its sexual reference (SRP), and one gene determines the distance of this offset. Together, these three genes determine the individual’s mate preference vector. Finally, one more gene determines the individual’s “pickiness” in choosing other mates – that is, the generalization radius of its POM function.

As with most genetic algorithms, the population size is fixed in these simulations, at 100 individuals³. To create the next generation of individuals, we use the following sexual selection method: First, two individuals are selected randomly from the population (a “mom” and a “dad” – though there are no actual sexes in

this model). Random selection here means there are no natural selective forces at work. Next, the 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 mate preference function on his parent-imprinted reference position). This corresponds to the usual situation of choosier mate choice on the part of members of just one sex (typically females).

At this point, the mom’s probability of mating with the potential dad is determined, by seeing how well his phenotype matches her POM function, and the dad’s probability of mating with the mom is determined in a complementary fashion. These two probabilities are multiplied (representing mutual consent) to yield an overall probability of mating, a die is thrown, and if the parents get 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 (50 successful matings).

It is important to remember just what is evolving in this population. The phenotypic locations of individuals, controlled by their two phenotype trait genes, will change from generation to generation, evolving in response to sexual selection pressures exerted by the mate preferences of the population as a whole. The preferences themselves, coded in the two phenotype preference genes, also evolve from generation to generation, tracking the locations of the individuals (i.e. potential mates) in the population. For the simulations in this section, we specified a small minimum length (.02 units out of the full 1.0 range) for the directional preference vectors to ensure that they wouldn’t devolve to be effectively non-directional, and we used a (small) fixed width (also .02 units – but these values are not critical) for the POM functions to keep overly indiscriminate individuals, who would mate with anyone, from evolving. But the phenotypes and the direction of the preference vectors are always free to evolve, and these are the genes of most interest here, as we will now see.

We begin with the initial population of 100 individuals clustered in the center of a square phenotype space, each with a randomly-set directional mate preference. After this we turn the population loose, letting both phenotypes and preferences evolve freely, and record where the process of continually creating and chasing new sexually selected adaptive peaks takes the population over successive generations. In Figure 1, we show data from five separate runs of the average phenotypic location of the population as it evolves over 1000 generations under directional sexual selection. (The runs are superimposed on the same plot, but had no influence on each other.) These runs clearly show

²This is not the only way an SRP can be determined, but it corresponds to the natural situation of sexually imprinting on a parent, which occurs in many bird species and some other vertebrates as well – see Todd & Miller, 1993. Similar results are obtained with SRPs that correspond to the individual’s own phenotype or an evolved phenotypic preference; we have explored imprinting largely because of our interest in the interactions between learning and evolution.

³In our next generation of models we are eliminating the fixed population size, because it puts too strong a limit on the number of species we can evolve and thus limits the potential biodiversity.

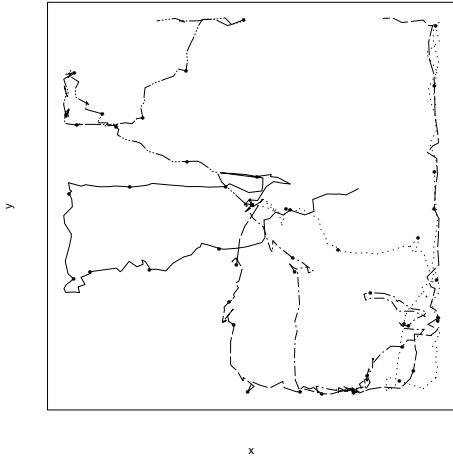


Figure 1: Sexual selection using directional mate preferences. Five runs, each plotted with different line-styles, showing the rapid movement of the population average phenotype across 1000 generations per run (dots mark each 100th generation).

two main effects: sexually selected adaptive peaks tend to shift in an inertia-laden way, generating the longish straight portions of the paths, and they are subject to random perturbations that can add up over the long term to unpredictable shifts in direction. In contrast, when we evolve a population using sexual selection with non-directional mate preferences (centered on each individual’s SRP, rather than offset from it), the population average phenotype merely drifts and jiggles slowly from its starting-point in the center. (There are also edge effects in these runs due to the non-toroidal phenotype space we used; but these could be interpreted as physical limits on the variation of certain phenotypic traits, for instance the maximum reflectivity an individual’s display surfaces can attain.)

This simulation shows the capricious nature of directional sexual selection, and the way in which it can create shifting adaptive peaks that pull a population along a rapid but winding trajectory through phenotype space. The short-term evolution is adaptive: phenotypic traits adapt to the current mate preferences, climbing up the current sexually selected fitness peak. 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 – adaptive peaks nor species – can ever win, but which keeps them running quixotically across phenotype space.

3 Escaping local fitness optima through sexual selection

Species do not spend all of their time evolving rapidly through phenotype space. Populations will often be perched on some adaptive peak in the fitness landscape for a time, held there through the optimizing effect of sexual and natural selection acting together. But many such peaks are only local evolutionary optima, and better (or at least other) peaks may exist elsewhere. Once a population has converged on such a locally optimal peak then, how can it move off that peak, incurring a temporary ecological fitness cost, to explore the surrounding adaptive landscape and perhaps find a higher-fitness peak elsewhere?

Wright’s (1932, 1982) “shifting balance” theory in part addresses this problem of escaping from local evolutionary optima (see Futuyma, 1986, p. 174). He suggested that genetic drift operating in quasi-isolated populations can sometimes allow one population to move far enough away from its current fitness peak that it enters a new adaptive zone at the base of a new and (and possibly higher) fitness peak. Once that population starts to climb the new fitness peak, its genes can spread to other populations, so that the evolutionary innovations developed in climbing this peak can eventually reach fixation throughout the species. Thus, the species as a whole can climb from a lower peak to a higher one. (The “Baldwin effect,” in which learning can speed up and guide evolution by allowing adaptive individuals to search the fitness landscape within their lifetimes, is another potential peak-shifting mechanism – see Baldwin, 1896, and Hinton & Nowlan, 1987.)

Wright’s shifting balance model suggests that genetic drift might provide enough random jiggling around the local optimum to sometimes knock the population over into another adaptive zone, but the analysis of adaptive walks in rugged fitness landscapes (Kaufmann, 1993) indicates that this is unlikely to be a common occurrence. Our model of population movement in phenotype space via mate choice is similar to Wright’s shifting balance theory, but it provides a mechanism for exploring the local adaptive landscape that can be much more powerful and directional than random genetic drift: sexual selection. Here, we are relying on a kind of “sexual-selective drift” resulting from the stochastic dynamics of mate choice and runaway sexual selection to displace populations from local optima.

We hypothesize that with mate choice, the effects of sexual-selective drift will almost always be stronger and more directional than simple genetic drift for a given population size, and will be more likely to take a population down from a local optimum and over into a new adaptive zone. Genetic drift relies on passive sampling error to move populations off of economic adaptive peaks, whereas sexual selection relies on active mate choice, which can overwhelm even quite strong ecological selection pressures. As Figure 1 and our earlier simulation analyses (Miller & Todd, 1993) make clear, directional mate preferences drive populations to move through phenotype space much more quickly than

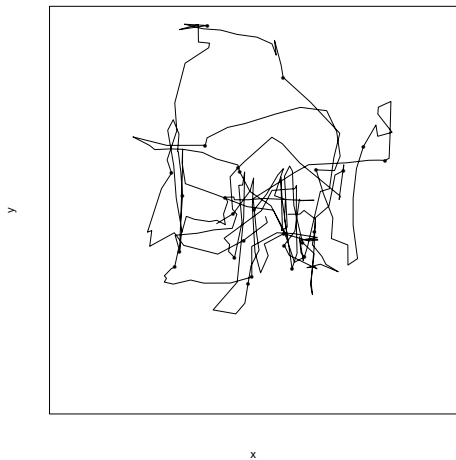


Figure 2: Directional sexual selection allowing a population to escape from a central natural selection fitness peak. One run across 3000 generations (dots mark each 100th generation).

they would under genetic drift alone.

But the runs in Figure 1 included no natural selection. Can we be sure that sexual selection would still allow peak-shifting and peak-jumping if natural-selective peaks were also present? In particular, would sexual selection allow a population to escape from a naturally selected fitness peak, to explore other regions of phenotype space? In Figure 2, we see that the answer to both questions, at least for certain conditions, is yes – sexual selection can operate in our model even when opposed by natural selection.

Here we have introduced a natural selection fitness peak into the center of the phenotype space (with increasing distance from the center yielding linearly lower fitness), so that, when we run the simulation without sexual selection and with only natural selection, the population evolves to cluster around the middle point of the space, no matter where it starts from. In this simulation, though, we see that the evolutionary path of one population over 3000 generations under the simultaneous combined forces of *both* natural selection (center peak) and directional sexual selection (shifting self-defined peak). Clearly, the addition of sexual selection allows the population to escape the naturally selected peak for long periods of time, to explore the surrounding phenotype space. With another stronger naturally selected peak elsewhere in the space, the sexually wandering population will stumble upon it and rise up that peak (before again usually leaving that peak in turn). Thus, sexual selection can be seen as a way of making Wright’s shifting balance model more powerful, by allowing active mate choice dynamics to replace passive genetic drift as the main source of evolutionary innovation.

We can summarize our view of sexual selection’s role in peak-creation and peak-jumping as follows:

Species perched on adaptive peaks will generally have mate choice mechanisms complementary to the natural-selective pressures keeping them there (so that healthy, fit individuals are considered sexy, attractive mates), resulting in long periods of evolutionary stasis for most species, most of the time. But occasionally, directional preferences, or intrinsic perceptual biases in preferences, or genetic drift acting on preferences, can lead to runaway dynamics that take a population (or at least the males) away from the ecological fitness peak towards a new, sexually selected peak. Thus, the effects of mate choice can be visualized as vectors that pull populations away from naturally selected adaptive peaks out on long forays into the phenotypic unknown, where they may or may not encounter new ecological opportunities and evolve economically useful traits.

Sexual dimorphism can promote this peak-jumping (Miller & Todd, 1995): males will often be driven away from ecological fitness peaks faster than females, because of the prevalence of female choice exerting pressure on male trait evolution (Cronin, 1991; for a compelling individual-based simulation, see Collins & Jefferson, 1992). This sexual division of labor could make the exploration of phenotype space even more powerful and efficient. If the males do not encounter a new fitness peak in their phenotypic wanderings, little is lost: the males will have evolved sexually dimorphic courtship innovations, and the females will have evolved mate choice mechanisms to assess those innovations, both of which have some economic (naturally selected fitness) costs but substantial reproductive (sexually selected) benefits.

But if the males do encounter a new adaptive peak to be exploited, much could be gained. If a male courtship innovation, evolved under the force of female choice (or the female mate choice mechanism that judges that male trait), happens to be modifiable into a useful economic innovation, then it will be elaborated through natural selection – and the species will evolve up the new fitness peak as this useful innovation is honed. Having entered a new adaptive zone, the lucky population can rapidly climb the new peak, the innovation can spread to both sexes (i.e. sexual dimorphism can decrease if both sexes benefit from the innovation), and a new species may emerge as it becomes reproductively isolated from other populations. The result could look like a period of rapid evolution concentrated around a speciation event, just as described by punctuated equilibrium theory (Eldredge & Gould, 1972). Moreover, and more speculatively, it could be that if the new adaptive zone happens to be particularly large and fruitful, and the economic innovation proves particularly advantageous, then the event will appear as the establishment of a key evolutionary innovation, and may lead to the formation of new higher taxa. Thus, a lineage that starts out as a sexually-selected fluke may, if successful (i.e. if it subsequently keeps speciating), become retroactively labeled a new genus, family, or even order.

4 Sympatric speciation through sexual selection

4.1 Traditional views of speciation

So far we have seen how sexual selection through mate choice can help a population to explore phenotype space in a rapid, unpredictable manner, with the result that old fitness peaks can be left, and new ones created and conquered. But the world would be a lonely place if only one species at a time participated in this quixotic foray. Clearly there are many species simultaneously finding and filling new environmental niches all the time, so we need a way of explaining the path from one species to many. Speciation, of course, does exactly that. When a biological lineage splits apart into reproductively isolated subpopulations, one “search party” scouring the adaptive landscape for new peaks is replaced by two independent parties – one species becomes two. Here again, we can ask whether mate choice and sexual selection can help promote this aspect of biodiversity, this time by facilitating speciation.

Though vitally interested in both speciation and mate choice, Darwin did not seem to perceive this connection, and the *Origin of species* (1859) in fact offered no clear mechanism of any sort whereby speciation could happen. The biologists of the Modern Synthesis (e.g. Dobzhansky, 1937; Huxley, 1942; Mayr, 1942) saw species as self-defined reproductive communities, and yet often argued *against* the idea that sexual selection, the obvious agent of reproductive self-definition, could induce speciation, because their attitude towards Darwin’s theory of selective mate choice was so hostile (see Cronin, 1991).

Instead, two major theories of speciation developed during the Modern Synthesis, and both suggested that speciating populations are split apart by some divisive force or “cleaver” external to the population itself. The cleaver splits the population in two, physically or 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. For example, a river may shift course to isolate one population from another. Some combination of genetic drift and natural selection then causes the two newly isolated groups to diverge phenotypically and genotypically. Once enough divergence accumulates, the populations can no longer interbreed even when the physical barrier disappears, and so are recognized as separate species. Speciation for Mayr was a side-effect of geographical separation.

In Dobzhansky’s (1937) model of *sympatric* speciation, the cleaver is more abstract: it is a low-fitness valley in an adaptive landscape, rather than a barrier in geographic space. For example, an adaptive landscape might develop two high-fitness peaks (niches) separated by a low-fitness valley. This valley could enforce disruptive selection against interbreeding between the peaks, thereby driving an original population to split and diverge towards the separate peaks in two polymorphic

subpopulations. Dobzhansky 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.

4.2 A model of speciation via sexual selection

But can speciation occur, not through the action of a natural selection cleaver, but as the result of a sexual selection carrot? To test the logical possibility of speciation without either type of cleaver, we first used a form of our sexual selection simulation described in section 2 that allowed for the possibility of spontaneous sympatric speciation. We did this by simply leaving out the directional component of the mate preferences, so that they are determined solely by the individual’s sexual reference position (either based on their parent’s or their own phenotype) and mate pickiness. With this setup, instead of the population running around phenotype space in a mad capricious dash, it oozes about much more slowly, but is also much more likely to split apart – speciate – into two independent species. New species break free from old ones, and they slowly evolve apart under the constant action of genetic drift in this small population size. Often in this low-dimensionality phenotype space the newly formed species will drift back together into a coherent whole, but in nature this is extremely unlikely to happen – speciation is a one-way street (see Todd & Miller, 1991, 1993 for detailed results).

Of course, the most convincing demonstration of the power of sexual selection to create new species that can independently find different niches is to see speciation happen in our model with directional mate preferences in place. In this case, when two new species are formed and their average directional preference vectors point in different directions, the two subpopulations will head off on two rapidly diverging trajectories through phenotype space. This is essential for the creation of true biodiversity – both the formation of new species, and the impetus for them to move away at a good clip from their current fitness peak to other regions of phenotype space, ensuring that they will grow more unique over time.

This feature of continuing rapid species divergence was missing from our early non-directional speciation results, where only the slow process of drift operated to push species apart. But similarly, speciation rarely occurred in the directional selection-inspired wanderings in Figures 1 and 2, primarily because the powerful directional preferences acting there overwhelmed most divisive jostling random effects necessary for the population to split into new species – the individuals, in essence, were swept away by the relentless urge for mates in a certain direction, and never had time to stop

and ponder the random fluctuations that might have allowed them to begin to differ in desires from their fellow species-mates. Therefore, to allow speciation to begin to happen in a directional selection context, we had to break down some of the strength of the directional preferences. We did this by simply doubling the length (number of bits) of the genes that code the phenotypic traits and preferences of individuals, so that mutation will move these values around more slowly. We also kept the directional preference vectors small and the POM pickiness high, to help retard the sexually selected peak shifts.

As a result, when we made these parametric changes to our model, we observed just what we had hoped to see: both the speciation and fairly rapid directional divergence between new species that can be seen in Figure 3. Here we've plotted one run across 1000 generations, showing the location and relative size of each species cluster every 10 generations; when there is more than one species present at a given generation, a line is drawn connecting the centers of each to indicate which ones appeared simultaneously. The species here still tend to stay fairly close together in phenotype space, and to rejoin each other frequently, but these peculiarities may largely stem from the fixed population size. Our next simulations, with larger population sizes and with natural selection in place, are beginning to show that new species can escape from the peaks they are born on to new peaks elsewhere in phenotype space.

4.3 Sexual selection, speciation, and the origins of biodiversity

Simulations of this sort, of course, are only one piece of evidence in support of the idea that sympatric speciation through mate choice is important in the creation of biodiversity. There is also biological evidence that speciation rates are indeed higher when selective mate choice plays a more important role. Ryan (1986) found a correlation between cladal diversity in frogs and complexity of their inner ear organs (amphibian papilla), which are responsible for the operation of female choice on male calls. He reasoned that "since mating call divergence is an important component in the speciation process, differences in the number of species in each lineage should be influenced by structural variation of the inner ear [and hence the operation of mate choice]" (p. 1379). Immelmann (1972, p. 167) has argued that mate preferences derived from imprinting on the phenotypes of one's parents may speed speciation in ducks, geese, and the like: "imprinting may be of special advantage in any rapidly evolving group, as well as wherever several closely related and similar species occur in the same region [i.e. sympatric situations]."

Vertebrates are one thing – certainly birds do it. But bees? The enormous diversity of insects (at least 750,000 documented species, maybe as many as 10 million in the wild) might seem at first sight to contradict the notion that mate choice facilitates speciation, since few (except Darwin; see also Partridge, 1994) seem willing to attribute much mate choice to

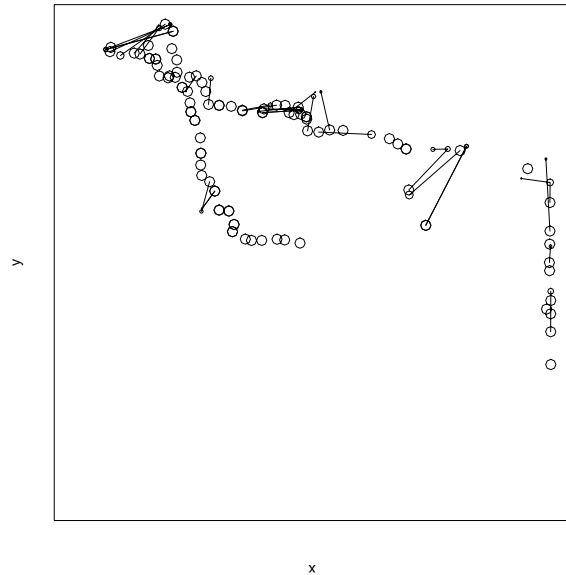


Figure 3: Directional sexual selection and speciation operating simultaneously. One run across 1000 generations, with the locations and relative sizes of each species plotted as a circle every 10 generations; lines connect multiple species present in the same generation, indicating an instance of speciation).

insects. But Eberhard (1985, 1991, 1992) has shown that male insect genitalia evolve largely through the effects of cryptic female choice, in such a way that speciation could be promoted.

Further evidence for speciation through mate choice comes from a consideration of biodiversity and the numbers of species across different kingdoms and phyla. There seems to be a striking correlation between a taxon's species diversity and the taxon's evolutionary potential for sexual selection through mate choice, resulting in highly skewed richness of species across the five kingdoms. Recent estimates of biodiversity suggest there may be somewhere between 10 and 80 million species on earth (May, 1990, 1992). But of the 1.5 million or so species that have actually been identified and documented so far by taxonomists, the animal kingdom contains about 1,110,000, the plant kingdom contains about 290,000, the fungi contain about 90,000, the protists contain about 40,000, and the monera contain only about 5000 (Cook, 1991; Wilson, 1988)⁴. Although the majority of species in each kingdom can undergo some form of genetic recombination through sexual reproduction, only in the animals and the flowering plants is selective mate choice of central importance. Of

⁴It should be noted that sampling biases probably accounts for some of the skewness here: many animals and plants are larger and easier to notice and to classify than fungi, protists, or monera. But it is expected that a large proportion of the species still to be identified are insects and other small, but sexually discriminating, animals (Wilson, 1988).

the 290,000 documented species of plants, about 250,000 are angiosperms (flowering plants) frequently fertilized by animal pollinators. And of the 1,110,000 documented species of animals, those with sufficient neural complexity to allow for some degree of mate choice (particularly the arthropods, molluscs, and chordates) are much more numerous than those without. Thus, species diversity is vastly greater among taxa wherein a more or less complex nervous system mediates mate choice, either a conspecific's nervous system in the case of animals or in a heterospecific pollinator's nervous system in the case of flowering plants.

This pattern is the opposite of what we might expect if allopatric speciation were the primary cause of biodiversity. The effects of geographic separation (allopatry) should obviously be weaker for species whose reproduction is mediated by a mobile animal. Animals can search over wide areas for mates and pollinators can fly long distances. So allopatric speciation would predict lower species diversity among taxa whose reproduction is mediated by mobile animals with reasonably complex nervous systems – just the opposite of what we observe. To further explore the role of selective mate choice in creating species biodiversity, we need to analyze the degree of mate choice in the various taxa more accurately, adjust the speciation rates between taxa for number of generations of evolution (and thus organism size), and if possible take into account the amount of geographic spread and migratory range of the species involved. In this way, we hope to gain more evidence to show that sympatric speciation through mate choice, particularly through assortative mating, is a compelling explanation for the extreme biodiversity of animals and flowering plants, and is thus one of the most powerful mechanisms for dividing up and spreading out evolution's exploratory search of the adaptive landscape.

5 Implications

Species come pretty cheap, on the sexual selection analysis we have described here. New species can arise quickly, spontaneously, and capriciously, through the reproductive isolation caused by divergence of mate preferences and the genitals, secondary sexual traits, and courtship behaviors that they favor (Eberhard, 1985; Andersson, 1994). And “new species are usually cheap species. They may be very different in outward traits, but they are still genetically similar to the ancestral forms and to the sister species that surround them” (Wilson, 1992, pp. 73-74). The resulting differences between sibling species are usually reproductive rather than ecological; the innovations that distinguish species usually serve sexual rather than economic functions. Of course, competitive exclusion will force sibling species occupying close habitats to diverge ecologically to some degree – but these slight ecological specializations will often follow speciation rather than cause it.

This conception may have implications for our conservation priorities and rationales. If we view species simply as repositories of possibly useful biochemicals (selected for some ecological use in the wild and there-

fore possessed of some possible medical use in humans), or of possibly inspirational adaptations to be imitated in artificial systems, our sexual selection model makes it difficult to justify a concern for biodiversity at the species level. This is because sibling species are likely to contain very similar biochemical and ecological adaptations. In an anthropocentric, utilitarian framework, the preservation of genera would be more important than preservation of individual species, because genera represent the taxonomic level corresponding to interesting ecological innovations.

But there is another, more aesthetic view possible, that would value the unique secondary sexual traits and courtship behaviors of sibling species for their own sake, regardless of their human utility. Indeed, though books on biodiversity usually contain verbal arguments stressing the economic benefits of biodiversity, their cover art usually evokes the wondrously diverse colors and sounds of animal courtship. Perhaps we can learn to combine our romantic empathy with our appreciation of sexual selection to value biodiversity at the species level for its true evolutionary significance: as a literal expression of millions of different modes of sexual love.

What role could simulated sexual selection play in evolutionary engineering, evolutionary robotics, and artificial life? If mate choice has been critical to the innovation, optimization, and diversification of life on our planet, we might expect that mate choice will also prove important in the design of complex artificial systems using genetic algorithms and other evolutionary optimization techniques. Evolutionary engineering methods are often defended by claiming that we have a “sufficiency proof” that natural selection alone is capable of generating complex animals with complex behaviors. But this is not strictly true: all we really know is that natural and sexual selection *in concert* can do this. Indeed, the traditional assumption in genetic algorithms research that sexual recombination *per se* is the major advantage of sexual reproduction (Goldberg, 1989) may be misleading. If instead the process of selective mate choice is what gives evolutionary power and subtlety to sexual reproduction, then current genetic algorithms work may be missing out on a major benefit of simulating sex.

In previous papers (Miller, 1994; Miller & Todd, 1995) we argued in more detail that sexual selection has five potential benefits in such simulations: it can (1) speed optimization by increasing the accuracy of the mapping from phenotype to fitness, by decreasing the sampling error characteristic of most natural selection; (2) speed optimization by increasing the effective reproductive variance in populations even when survival-relevant differences are minimal, by imposing an automatic, emergent form of fitness scaling; (3) promote escape from local optima, by augmenting genetic drift with more powerful, directional forms of sexual-selective drift; (4) promote the emergence of complex innovations, insofar as sexually-selected courtship traits or mate preferences can become modified to ecological functions; and (5) promote spontaneous speciation, automatically increasing the number of lineages doing

evolutionary search when multiple fitness peaks are present. In general, if we view sexual selection as a process of search for new peaks in the adaptive landscape and escape from old ones, and natural selection as a process of hill-climbing and optimization of those peaks, we can see how each handles a share of the classic explore/exploit tradeoff that must be faced by any adaptive system (Holland, 1975/1992). We hope other researchers will join us in investigating these hypotheses.

Finally, we turn to sexual selection and human mental evolution (see also Miller, 1993; Ridley, 1993). The evolution of the human brain can be seen as a problem of escaping a local optimum: the ecologically efficient, ape-sized, 500 cc. brain of the early *Australopithecenes*, who were pretty good at bipedal walking, gathering, scavenging, and complex social life. During the rapid encephalization of our species in the last two million years, through the *Homo habilis* and *Homo erectus* stages up through archaic *Homo sapiens*, our ancestors showed very little ecological progress – tool making was at a virtual stand-still, the hunting of even small animals was still quite inefficient, and we persisted alongside unencephalized *Australopithecene* species for well over a million years.

These facts suggest that large brains did not give our lineage any significant ecological advantages until the last 100,000 years, when big-game hunting and complex tool-making started to develop quite rapidly – long after we had attained roughly our present brain size. Instead, we propose that the human brain probably evolved through runaway sexual selection operating on both males and females to elaborate various forms of cultural courtship behaviors such as language, humor, music, dance, art, and intellectual creativity (Miller, 1993; in press). Sexual selection for creativity really means mate choice for behavioral, linguistic, and conceptual diversity, with co-evolution of the cognitive capacities for appreciating these more distinctly human forms of biodiversity. Thus, we reach a happy concordance: the same sexual selection process that has engendered such biodiversity in our world could have also engendered in us the perceptual, cognitive, moral, and aesthetic capacities to appreciate that diversity at many levels, from the spectrum-spanning colors of beetles through the endless improvisations of bird song to the cognitive combinatorial explosion that we call human imagination.

References

Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist*, 30, 441-451.

Barth, F. G. (1991). *Insects and flowers: The biology of a partnership*. Princeton: Princeton Univ. Press.

Clarke, B. C. (1962). The evidence for apostatic selection. *Heredity (London)*, 24, 347-352.

Collins, R. J., & Jefferson, D. R. (1992). The evolution of sexual selection and female choice. In F. J. Varela and P. Bourguine (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.

Cook, L. M. (1991). *Genetic and ecological diversity: The sport of nature*. London: Chapman & Hall.

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

Darwin, C. (1859). *On the origin of species*, 1st ed. London: John Murray.

Darwin, C. (1862). *On the various contrivances by which orchids are fertilized by insects*. London: John Murray.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.

Dewsbury, D. A. (1981). Effects of novelty on copulatory behavior: The Coolidge Effect and related phenomena. *Psychological Review*, 89(3), 464-482.

Dobzhansky, T. (1937). *Genetics and the origin of species*. (Reprint edition 1982). New York: Columbia U. Press.

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

Eberhard, W. G. (1991). Copulatory courtship and cryptic female choice in insects. *Biological Review*, 66, 1-31.

Eberhard, W. G. (1992). Species isolation, genital mechanics, and the evolution of species-specific genitalia in three species of *Macroductylus* beetles. *Evolution*, 46(6), 1774-1783.

Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology*, pp. 82-115. San Francisco: Freeman, Cooper.

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

Futuyma, D. J. (1986). *Evolutionary biology*, 2nd ed. Sunderland, MA: Sinauer.

Futuyma, D. J., & Slatkin, M. (Eds.). (1983). *Coevolution*. Sunderland, MA: Sinauer.

Goldberg, D. E. (1989). *Genetic algorithms in search, optimization, and machine learning*. Reading, MA: Addison-Wesley.

Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behavior*, 42, 1-14.

Harvey, I., Husbands, P., & Cliff, D. (1992). Issues in evolutionary robotics. In J.-A. Meyer, H. L. Roitblat, & S. W. Wilson (Eds.), *From Animals to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior*, pp. 364-373. Cambridge, MA: MIT Press.

Heisler, I. L. (1994). Quantitative genetic models of the evolution of mating behavior. In C. R. B. Boake (Ed.), *Quantitative genetic studies of behavioral evolution*, pp. 101-125. Chicago: University of Chicago Press.

Hinton, G. E., & Nowlan, S. J. (1987). How learning guides evolution. *Complex Systems*, 1, 495-502. (Also reprinted in R. Belew and M. Mitchell (Eds.), *Adaptive individuals in evolving populations: Models and algorithms*. Reading, MA: Addison-Wesley, 1996.)

Holland, J. H. (1975). *Adaptation in natural and artificial systems*. Ann Arbor: University of Michigan Press. (2nd ed. 1992, Cambridge, MA: MIT Press.)

- Huxley, J. S. (1942). *Evolution: The modern synthesis*. New York: Harper.
- Immelmann, K. (1972). Sexual and other long-term aspects of imprinting in birds and other species. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), *Advances in the study of behavior*, vol. 4. New York: Academic Press.
- Kauffman, S. A. (1993). *Origins of order: Self-organization and selection in evolution*. New York: Oxford University Press.
- 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 & M. B. Andersson (Eds.), *Sexual selection: Testing the alternatives*, pp. 67-82. New York: Wiley.
- Koza, J. (1993). *Genetic programming*. Cambridge, MA: MIT Press/Bradford Books.
- Lande, R. (1980). Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution*, *34*, 292-305.
- Lande, R. (1987). Genetic correlation between the sexes in the evolution of sexual dimorphism and mating preferences. In Bradbury, J. W., & Andersson, M. B. (Eds.), *Sexual selection: Testing the alternatives*, pp. 83-95. New York: John Wiley.
- Langton, C. L., Farmer, J. D., Rasmussen, S., & Taylor, C. (Eds.). (1992). *Artificial Life II*. Addison-Wesley.
- May, R. M. (1990). How many species? *Phil. Trans. Royal Soc. London B, Biological Sciences*, *330*(1257), 293-304.
- May, R. M. (1992). How many species inhabit the earth? *Scientific American*, *267*(4), 42-48.
- Mayr, E. (1942). *Systematics and the origin of species*. (Reprint edition 1982). New York: Columbia U. Press.
- Miller, G. F. (1993). Evolution of the human brain through runaway sexual selection. Unpublished Ph.D. thesis, Psychology Department, Stanford University.
- Miller, G. F. (1994). Artificial life through sexual selection. In Cliff, D. (Ed.), *Artificial Intelligence and Simulation of Behavior Quarterly*, Special issue on Artificial Life in the U. K.
- Miller, G. F. (in press). A review of sexual selection and human evolution: How mate choice shaped human nature. In C. Crawford and D. Krebs (eds.), *Evolution and human behavior: Ideas, issues, and applications*. Lawrence Erlbaum.
- Miller, G. F. & Freyd, J. J. (1993). Dynamic mental representations of animate motion: The interplay among evolutionary, cognitive, and behavioral dynamics. Cognitive Science Research Paper 290, University of Sussex. Submitted as a target article for *Behavioral and Brain Sciences*.
- Miller, G. F., & Todd, P. M. (1993). Evolutionary wanderlust: Sexual selection with directional mate preferences. In J.-A. Meyer, H. L. Roitblat, & S. W. Wilson (Eds.), *From Animals to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior*, pp. 21-30. Cambridge, MA: MIT Press.
- Miller, G. F., & Todd, P. M. (1995). The role of mate choice in biocomputation: Sexual selection as a process of search, optimization, and diversification. In W. Banzhaf & F.H. Eeckman (Eds.), *Evolution and biocomputation: Computational models of evolution*, pp. 169-204. Berlin: Springer-Verlag.
- Morgan, C. L. (1888). Natural selection and elimination. *Nature*, Aug. 16, 370.
- Moynihan, M. (1975). Conservatism of displays and comparable stereotyped patterns among cephalopods. In G. P. Baerends, C. Beer, & A. Manning (Eds.), *Function and evolution in behavior: Essays in honour of Professor Niko Tinbergen, FRS*. Oxford: Clarendon Press.
- Partridge, L. (1994). Genetic and nongenetic approaches to questions about sexual selection. In C. R. B. Boake (Ed.), *Quantitative genetic studies of behavioral evolution*, pp. 126-141. Chicago: University of Chicago Press.
- Ridley, M. (1993). *The red queen: Sex and the evolution of human nature*. London: Viking.
- Ryan, M. J. (1986). Neuroanatomy influences speciation rates among anurans. *Proc. Nat. Acad. Sci. USA*, *83*, 1379-1382.
- Ryan, M. J. (1990). Sexual selection, sensory systems, and sensory exploitation. *Oxford Surveys of Evol. Biology*, *7*, 156-195.
- Ryan, M. J., & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, *139*, S4-S35.
- Simpson, G. (1944). *Tempo and mode in evolution*. New York: Columbia U. Press.
- Szalay, F. S., & Costello, R. K. (1991). Evolution of permanent estrus displays in hominids. *J. Human Evolution*, *20*, 439-464.
- Todd, P. M. (1996). Sexual selection and the evolution of learning. In R. Belew and M. Mitchell (Eds.), *Adaptive individuals in evolving populations: Models and algorithms*. Reading, MA: Addison-Wesley.
- Todd, P. M., & Miller, G. F. (1991). On the sympatric origin of species: Mercurial mating in the Quicksilver Model. In R. K. Belew & L. B. Booker (Eds.), *Proceedings of the Fourth International Conference on Genetic Algorithms*, pp. 547-554. San Mateo, CA: Morgan Kaufmann.
- Todd, P. M., & Miller, G. F. (1993). Parental guidance suggested: How parental imprinting evolves through sexual selection as an adaptive learning mechanism. *Adaptive Behavior*, *2*(1), 5-47.
- Wilson, E. O. (1988). The current state of biological diversity. In E. O. Wilson & F. M. Peter (Eds.), *Biodiversity*. Washington, DC: National Academy Press.
- Wilson, E. O. (1992). *The diversity of life*. Cambridge, MA: Harvard University Press/Belknap.
- Wilson, E. O., & Peter, F. M. (1988). *Biodiversity*. Washington, DC: National Academy Press.
- Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proc. Sixth Int. Congr. Genetics*, *1*, 356-366.
- Wright, S. (1982). Character change, speciation, and the higher taxa. *Evolution*, *36*, 427-443.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology*, *53*, 205-214.