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ON SEX, MATE SELECTION AND EVOLUTION: AN EXPLORATION

Klaus Jaffe

Instituto Venezolano de Investigaciones Científicas, and
Universidad Simón Bolívar, Apartado 89000, Caracas 1080, Venezuela
e-mail : kjaffe@usb.ve

ABSTRACT: Mate selection strategies may be as important, or even more important to the evolutionary process than natural selection. The practical importance of strategies such as the selection for “good genes” and assortative mating are emerging in both theoretical and experimental biology. Several other mate selection strategies are possible, although little is known about them. Here I explore, the range of diverse mate selection strategies known to us, both from theory and observation of nature, and the analogies between the dynamic properties of mate selection strategies in biological evolution, and those of partner selection strategies in game theory and economic evolutionary theory. The aim of this exploration is not to review the extensive literature on the subject, but to detect research agendas that might help us in our understanding of the dynamic consequences of mate (partner) selection strategies in biology, economics, artificial intelligence and sociology. Insight into the working of diverse mate selection strategies might eventually even increase our understanding of the biological basis for beauty and the adaptive value of love.

INTRODUCTION

Biological evolution is not possible without reproduction, and among sexual organisms; reproduction is not possible without mating or the fusion of two gametes. The guiding principle in the present analysis is that mating is very unlikely to be random in nature and that mechanisms selecting for mates are as important, or even more important, in guiding evolution, than the mechanism of natural selection (see Fig 1). Mate selection strategies have often been referenced to in studies of sexual selection (Maynard-Smith 1978, Eberhard 1985, 1996), but have rarely been studied on their own merit. Despite the fact that mate selection strategies have received little attention in theoretical biology, they have emerged to be fundamental in explaining biological phenomena in recent experimental studies. For example, the type of mate selection strategy modeled has been shown to be fundamental in determining if sex may emerge and be maintained in agent based simulations of biological evolution (Jaffe 1996, 2000). Here I explore the potential that an increased understanding of the working of mate selection strategies might have in the understanding of life and its evolution. I then suggest that analogies with partner selection strategies, in games theoretical analyses of the emergence and maintenance of cooperation, might be based on fundamental principles underlying both, biological evolution and behavioral economy.

The concept "mate selection", differs intuitively from that of "sexual selection" in subtle ways, mainly in matters of emphasis. "Mate selection" refers to the process by which individuals select a partner for reproduction; whereas "sexual selection" (see for example Andersson and Iwasa 1996), refers to the differential abilities of individuals to acquire mates in competition with other individuals of the same sex. Sexual selection implies that individuals compete for the access to the most desirable mate; whereas mate selection allows for the fact that not all individuals of one sex desire the same individual of the opposite sex, reducing the need for competition. These subtle differences may have a tremendous impact on the dynamics of the evolutionary process as slightly different mate selection algorithms produce large differences in the outcome of evolution (Jaffe 1998, 1999). For example, in the case of the emergence and maintenance of sex, the type of mate selection algorithm programmed determines the success of sexual populations vs. asexual ones (Ochoa and Jaffe 1999). This was made clear when it was evidenced that the adaptive advantage of haploid sexual populations subject to parasite pressures, reported by Hamilton et al (1990) was caused by the "hidden" mate selection criteria used in the algorithms of the model, putting in doubt the "red queen" theory for the maintenance of sex (Ochoa and Jaffe 1999). This case exemplifies the

importance of mate selection mechanisms in understanding evolutionary phenomena and the consequences that the neglect of mate selection might have in theoretical biology.

The main conclusion of a previous theoretical study of mate selection strategies, using the agent based computer simulations Biodynamica (Jaffe 1999), is that mate selection is not likely to be random in nature. Several mate selection strategies confer higher fitness to individuals using them, and have a higher evolutionary stability than random mating. The conclusions reached in that study, which I will contrast against experimental evidence in this exploration, were:

1. Mate selection criteria for “good genes” seems to be the best evolutionary strategy. In order to increase adaptation efficiently, this strategy has to screen a large number of genes. Thus, phenotypes, affected by a large number of genes are predicted to be very efficient as mate selection signals.
2. Assortative mating (non-random mating resulting from a preference for similar partners), should be common in diploid organism, but excessive genetic similarity between mates is also to be avoided. That is, strategies that maximize outbreeding should be rare and should occur mainly in populations where individuals are genetically related. For each species and population, an optimal degree of genetic similarity between successful mates should be expected.
3. Adaptive value of several mate selection strategies is additive. Thus, mate selection mechanisms are expected to be quite sophisticated in that individuals should select mates based on several criteria which reflect not only good genes, but also similar genetic composition and other features.
4. Gamete selection (i.e. sperm competition and sperm selection, etc) may complement or even substitute mate selection mechanisms

Here I postulate that mate selection might have a role in biological evolution that has been neglected in theoretical studies. The effect of mate (or partner) selection algorithms on the evolutionary process is not a trivial artifice but a fundamental characteristic of dynamic processes underlying evolutionary phenomena in both, biological and cultural evolution. Its importance has been obscured, partially, due to at least two oversimplifications in theoretical models:

- 1- The effect of mate selection algorithms on the evolution of sexually reproducing organisms will depend on the type of ploidy modeled. That is, sexual

reproduction seems to be adaptive for diploids but not necessarily for haploids (Jaffe 2000). Yet many theoretical studies assume that results from models on haploids can be extended without further consequences to diploids. This is clearly not the case. Despite the fact that ploidy is rarely explicitly accounted for in simulation models, comparisons between different models should improve our understanding of the underlying evolutionary dynamics.

2- Mate selection can be exercised by males, females or both sexes. It is very likely that in most species, both sexes exercise selectivity in choosing their mates, but, depending on the sex that performs the largest investment in reproduction, it should also be the most selective. Focusing the study of mate selection behavior on a single sex might obscure the mate selection strategy at work in the species under study.

The aim of this exploration, thus, is to open new roads, and widen some old ones, in the search of generally applicable evolutionary mechanisms.

SEXUAL SELECTION MECHANISMS

Selecting mates for 'good genes'

The most obvious mate selection strategy, conferring large advantages to populations using them, is the strategy selecting for 'good genes' in the opposite sex. This strategy was shown to be the most successful in evolutionary terms among all the possibilities tested (Jaffe 1999). Thus, it is reasonable to expect it to be very common in nature.

If choice for mates with 'good genes' presupposes that some mates have better genes than others, the resulting selection against inferior mates causes such genetic variability to disappear. This paradox may be resolved when substantial variability is maintained at a balance between selection and mutation. Alternatively, populations may exhibit genetic polymorphisms maintained by frequency-dependent selection or hybrid vigor. Examples are: Experimental evidence on female choice, provided by Lesna and Sabelis (1999) in a local population of soil predatory mites that exhibit genetic variation in preference for two prey species, showed that hybrids between selected preference lines are superior or inferior in population growth rate, depending on the composition of the diet. They showed that females in this population mate disassortatively when hybrids are superior, but switch to assortative mating otherwise. Thus, mate choice in this example varies with diet and is tuned to

incorporate 'good genes' in the offspring, that is, genes that promote the population growth rate of the offspring on the same diet as that experienced by the parents. In this way, hybrid success and mate choice act together in maintaining or eliminating genetic polymorphism in local populations.

In Jaffe (1999) I showed that the more "good genes" are selected through mate selection, the greater the average fitness of the population and the more probable that the alleles coding for these mate selection strategies are maintained in a population. Thus, individuals using several signals for assessing "good genes" in their mates should be favored by evolution. Yet, some signals are very good in assessing the goodness of several genes simultaneously. One such signal seems to be facial and body symmetry (Pennisi 1995, Moeller and Thornhill 1998). Body odors have also been implied in this category of mate selection signals among humans (Rikowski and Grammer, 1997).

Another such signal is body size. For example, Mueller and Mazur (2001) showed recently that human females use male body size as a criterion for sexual selection, causing an open ended selection process for stature. Another sophisticated mate selection mechanism for good genes described for humans is selection for mates with exceptional cognitive abilities, explored by Miller and Todd (1998). Another indirect measure of "good genes" is boldness. Godin and Dugatkin (1996) for example, showed that female guppies prefer bold males (that showed more willingness to risk approaching predators) which happen to be also more brightly colored.

Trade offs

Detecting the mate with the best combination of genes might not be a simple task. Therefore, we might expect that the trade off between the cost of searching for the optimal mate and the benefits of mating with the second best will influence mate selection behavior (Todd 1997). Todd suggested that a practical and simple solution to this trade off is mate selection for "the best" or "the closest you can get". Another proposed solution is based on the fact that the intensity of mate selection also affects the success of the mate selection strategy in such a way that extensive screening does not improve the evolutionary dynamics and that optimal searching efforts can be achieved by screening a relatively low number of mates (Jaffe 1999). Excessive screening for mates did not seem to improve the efficiency of mate selection, but rather tended to diminish it, although slower so in large populations.

Another solution to the problem of choosing "the best mate" in finite time is to let the

environment do the selection. Some species use the outcome of natural selection to assess the genetic quality of males, using mate selection to intensify natural selection (as is common for genetic algorithms in artificial intelligence). This has been shown to be the case at least with the house sparrow (Griffith et al. 1999) where sons resemble their fathers with respect to sexual ornaments, but where the resemblance is mainly due to post-hatching environmental effects rather than shared genes.

Avoiding “bad genes”

Another advantage of sex is that it might provide a mechanisms for eliminating deleterious genes (Kondrashov 1984, 1988). This is the complementary strategy to the one selecting for ‘good genes’. For example, Siller (2001) showed that differential male mating success (or, more generally, higher variance in male than in female fitness), can drastically reduce mutational load in sexual populations with or without any form of epistasis. This type of mechanism, however also requires strong mate preference of “good genes” or genes with a low deleterious mutation load. Thus, Siller’s model can be viewed as a “good gene” selection strategy.

Repellent phenotypes in mate searching behaviors might be expected to exist although little experimental evidence for it has been provided. One such mechanism is referred to as mate choice strategies searching for genetic compatibility, although only few experimental evidence has piled up until now (Tregenza and Wedell 2000), probably more due to a lack of searching than due to a lack of such mate selection strategies in nature.

Assortative mating

The importance of assortative mating in biological evolution was postulated by Davis (1995) and Jaffe (1998). Here I do not discriminate between active and passive assortative mating. That is, individuals may chose genetically similar reproductive mates actively or external constraints may force low dispersal rates, imposing mating among similar mates (high inbreeding). In both cases the result is that mating occurs among genetically similar individuals. Assortative mate selection strategies have a strong penetrating power, displacing other alleles in simulations of gene selection (Jaffe 1999). The advantage of assortative mating in simulations of gene selection is based on the fact that females select males which have their alleles for assortative mating, increasing the frequency of these alleles relative to other alleles, making it a strategy with high evolutionary stability. Assortative mating also reduces excessive

allelic variability caused by sexual reproduction, especially among genetically complex organisms. It allows fit females to maintain (not diluting) their advantageous genetic composition during reproduction, providing their offspring with a similar advantageous genetic outfit. It accelerates the extinction of sub-optimal genetic combinations, as contrary to strategies selecting for good genes, assortative mating induces suboptimal females (or individuals with a high load of deleterious genes) to mate with suboptimal males, thus accelerating the extinction of suboptimal alleles.

Some controversial evidence for assortative mating among humans exist (Thiessen and Gregg 1980, Buss 1989, Rushton 1989, Grammer 1989, Voland and Engel 1990, Jaffe and Chacon 1995, but see the open peer commentaries in Rushton 1989 for example), but most experimental studies have been performed while studying speciation. For example, assortative mating related to communication of the relevant signals and assessment of the quality of mates, induces at the population level a pattern of diverse characteristics. For example, Werner and Todd (1997) point out that the evolution of high levels of song diversity is possible when sexual rather than natural selection is the mechanism responsible for evolution, a finding that could be related to the high level of diversity among human.

Mechanisms and signals for assortative mating

Several behavioral and physiological mechanisms providing for possibilities of assortative mating can be imagined. The most simple mechanism is dispersal inertia among individuals in populations, so that related individuals will have larger probabilities to meet each other for mating. A more elaborate mechanism, for which abundant experimental evidence is available, is imprinting (learning at a critical early age) the visual images of parents and then using these images for mate choice, as first discovered in birds (Lorenz 1935). Yet assortative mating does not mean preference for mates that are identical to parents. For example female songbirds are known to imprint songs early in life and then prefer males with songs slightly “unfamiliar” to the one of their father (McGregor and Krebs 1982).

This kind of mate preference design based on imprinting may also be at work among humans because they also imprint the faces of their parents (Le Grand et al. 2001). This visual memory may then be used to establish criteria for beauty, which in turn are used to select a mate, producing as a consequence assortative mating. A test for this mechanism would be experiments comparing inter-sexually the facial similarity between parents and mates, were a

greater similarity between faces of parents and mates than between mates is expected. That is, high facial resemblance should be evidenced between spouses and same sex parents. (This kind of mechanism could also explain why dogs and their owners seem to resemble each other).

MATE SELECTION AND SPECIATION

An interesting and widely explored effect of mate selection algorithm on the evolutionary dynamics is speciation (Todd and Miller 1991, Miller and Todd 1994, Price 1998). New species may arise when previously conspecific populations no longer interbreed successfully, even when they are living in the same place. This reproductive isolation can often be explained as an incidental by-product of other evolutionary changes. But whether natural selection ever acts directly to increase isolation has been a controversial question ever since Dobzhansky championed the idea in 1937. The proposal is straightforward - when populations have diverged genetically to the extent that the offspring of within-population mating are more fit than hybrid offspring, selection favors an increase in assortative mating.

Dieckmann and Doebeli (1999) developed a model that integrates a combination of different features and show that sympatric speciation is a likely outcome of competition for resources. The model used multilocus genetics to describe sexual reproduction in an individual-based model, and considered the evolution of assortative mating (where individuals mate preferentially with like individuals) depending either on an ecological character affecting resource use or on a selectively neutral marker trait. In both cases, evolution of assortative mating often leads to reproductive isolation between ecologically diverging subpopulations. When assortative mating depended on a marker trait, and was therefore not directly linked to resource competition, speciation occurred when genetic drift broke the linkage equilibrium between the marker and the ecological trait.

Assortative mating increases reproductive isolation, reducing the exchange of genes between the populations (Butlin and Tregenza 1997). Higashi et al (1999) showed that sympatric speciation may be caused by sexual selection even without disruptive natural selection. Specifically, they showed that variation in a male secondary sexual character with two conspicuous extremes and the corresponding variance in female mating preference around no preference, may jointly evolve into bimodal distributions with increasing modal divergence of the male and female traits, pulling a population apart into two pre-zygotically isolated populations. This mode of speciation, driven by two runaway processes in different

directions, is promoted by an increase in the efficiency of females in discriminating among males or a decrease in the cost of male conspicuousness.

Greene et al (2000) showed the existence of disruptive selection on a sexual ornament, plumage coloration, in yearling male lazuli buntings (*Passerina amoena*). In habitats with limited good-quality nesting cover, the dullest and the brightest yearlings were more successful in obtaining high-quality territories, pairing with females and siring offspring, than yearlings with intermediate plumage. This pattern reflects the way that territorial adult males vary levels of aggression to influence the structure of their social neighborhood. Adult males showed less aggression towards dull yearlings than intermediate and bright ones, permitting the dull yearlings to settle on good territories nearby. Fitness comparisons based on paternity analyses showed that both the adults and dull yearlings benefited genetically from this arrangement, revealing a sexually selected male-male cooperation.

Jiggins et al (2001) focused on speciation when facilitated by ecological adaptations that directly causes assortative mating. They showed that a shift in colour pattern mimicry was crucial in the origin of two butterfly species. The sister species *Heliconius melpomene* and *Heliconius cydno* recently diverged to mimic different model taxa, and the experiments showed that their mimetic coloration is also important in choosing mates. Assortative mating between the sister species means that hybridization is rare in nature, and the few hybrids that are produced are non-mimetic, poorly adapted intermediates. Thus, the mimetic shift has caused both pre-mating and post-mating isolation. In addition, individuals from a population of *H. melpomene* allopatric to *H. cydno* court and mate with *H. cydno* more readily than those from a sympatric population. This suggests that assortative mating has been enhanced in sympatry.

Sexual selection may facilitate speciation because it can cause rapid evolutionary diversification of male mating signals and female preferences. Divergence in these traits can then contribute to reproductive isolation. The sensory drive hypothesis predicts that three mechanisms underlie divergence in sexually selected traits: (1) habitat-specific transmission of male signals; (2) adaptation of female perceptual sensitivity to local ecological conditions; and (3) matching of male signals to female perceptual sensitivity. Boughman (2001) tested for these mechanisms, in three spine sticklebacks (*Gasterosteus* spp.) that live in different light environments. He showed that female perceptual sensitivity to red light varies with the extent of redshift in the light environment, and contributes to divergent preferences. Male nuptial color varies with environment and is tuned to female perceptual sensitivity. The extent of divergence among populations in both male signal color and female preference for red is correlated with

the extent of reproductive isolation in these recently diverged species. These results demonstrate that divergent sexual selection generated by sensory drive contributes to speciation.

Another example is provided by Lande et al (2001). They investigated the mechanisms of speciation in cichlid fish by analyzing population genetic models of sexual selection on sex-determining genes associated with color polymorphisms. The models were based on a combination of laboratory experiments and field observations on the ecology, male and female mating behavior, and inheritance of sex-determination and color polymorphisms. The models explained why sex-reversal genes that change males into females tend to be X-linked and associated with novel colors, using the hypothesis of restricted recombination on the sex chromosomes, as suggested by previous theory on the evolution of recombination. The models revealed multiple pathways for rapid sympatric speciation through the origin of novel color morphs with strong assortative mating that incorporate both sex-reversal and suppressor genes. Despite the lack of geographic isolation or ecological differentiation, the new species coexisted with the ancestral species either temporarily or indefinitely.

The theoretical work by Kondrashov and Kondrashov (1999) suggests that even under a scenario of disruptive selection, sympatric speciation is possible. They found that the increase in the number of variable loci affecting fitness facilitates sympatric speciation, whereas the increase in the number of variable loci affecting mate choice has the opposite effect. Clearly, mate selection might be as important or even more important than geographical isolation in speciation.

Dissortative mating and immune systems

Outbreeding and specifically dissortative mating, i.e. mating with genetically different mates in respect to one or more characters, has been proposed as an efficient mechanism for the maintenance of genetic variance in genes responsible for the working of the immune system. For example, Brown (1995) proposes the existence of a link between the genes coding for immune response, the Major Histocompatibility Complex (MHC), body odors and mate preferences, whereby odors help mates to assess the presences of MHC genes different from their own in their potential mates. Among humans Weedekind et al. (1995) proposed that individuals select their mates so as to increase the variability of the immune systems, by preferring mates with a different MHC, as detected through body odors.

The variance in genes responsible for the immune response might also be achieved by a choice of reproductive strategies. Polyandry for example also increase genetic variance. For example, in bumble bees, Baer and Schmid-Hempel (1999) showed that the variation in polyandry affects parasite loads and fitness of the offspring. Such mechanisms seem to be common, at least among insects (Arnqvist and Nilsson 2000).

It has been suggested that selection by females of genetically different males increases allelic variability too much, making this strategy evolutionary unstable compared to random mating (Ochoa and Jaffe 1999). Yet dissortative mating might become evolutionary successful in specific circumstances. For example, dissortative mating might avoid inbreeding depression (Dudash and Carr 1998). Recent publications though give a more sophisticated explanation for the maintenance of genetic variance of the MHC, odors and mate selection (Grosberg and Hart 2000). They showed that contrary to earlier reports, mate selection cannot be a strong force maintaining allorecognition polymorphism in two colonial marine invertebrates. Instead, the regulation of intraspecific competitive interactions appeared to promote the evolution of polymorphisms in these species. Also research among humans suggests that body odors might work rather as general signal for good genes (Rikowski and Grammer 1997)

In simulations of the “Red Queen” hypothesis, in which co-evolution between parasites and host is simulated, dissortative mating based on genes conferring resistance to parasites showed to be more successful than assortative mating (Ochoa and Jaffe 1999). Experimental studies indicate that the system seems to be tuned to avoid inbreeding with close kin (Penn and Potts 1998, Isles et al. 2001). Other experimental evidence suggest that stickleback females selects mates not so much for “different genes” but that they favor males with many MHC genes, to confer greater parasite resistance to the offspring (Reusch et al 2001), making this strategy to look more to like selection for “good genes”. Thus, the view that mate selection strategies optimize defenses against parasites and strengthen immune defenses (mainly the MHC) in offspring needs a thorough revision.

Mixed strategies and others

The literature on courting and mating behavior is too extensive to be reviewed here, but certainly, many other strategies may also produce benefits to population and should appear in

nature. The most likely outcome in nature is probably the use of a mix of mate selection strategies by parents, such as reported for the pied flycatcher (Jarvi et. al. 1987), that optimize rather than maximize genetic variance in their offspring. Other behaviors, such as lekking (Taylor and Williams 1982), might provide the conditions for an efficient working of various mate selection strategies in synchrony. The specific blend of mate selection strategies that achieves the optimum mix of genes certainly depends on a variety of factors, such as the dynamics of the environment and the reproductive strategy used by the species.

Several examples of successful mate selection strategies are based on signals that have no relation to the fitness of the individual emitting it. I refer to these kind of signal as “sex appeal” as they only promote mating without any other concomitant selection. These signals though promote an increase in fitness at the population level. The eventual increase in the fitness of populations formed by individuals which have neutral markers for sexual selection has been explained due to genetic drift (Soler et al. 1996, Jaffe 1999), as the signal for sex appeal may frequently be associated to the presence of good genes (at least in these simulations), eventually becoming a good predictor of fitness. The simulation will then select organisms with both, good genes and the appropriate signal for sex appeal, even if the algorithm used in the simulation does not explicitly relate sex appeal with any additional trait conferring higher fitness. An indirect confirmation of these results is that recent evidence suggest that sexual signals which somehow increase mating success induce divergence of the trait mainly due to sexual selection (Arnqvist 1998), showing that sexual selection may fix genetic traits faster than natural selection.

SOCIAL SELECTION MECHANISMS

The type of mate selection at work in a given species will affect the evolution of social behavior. For example, assortative mating will favor the emergence of alleles coding for cooperative behavior, if compared to random mating (Jaffe 2001). Yet, the working of mate selection strategies in evolutionary processes may be based on more fundamental dynamic principles. That is, dynamic mechanisms that organize biological evolution might also be at work in cultural evolution. Mate selection mechanisms are analogous to partner selection mechanisms that work in social systems that require cooperation between individuals. Thus the selection mechanism studied here might be relevant to the study of economic and social phenomena as they constitute mechanisms regulating optimum levels of variance in evolutionary processes in general.

Although not explicitly stated as a mate selection strategy, the algorithms used for choosing a partner in game theory are analogous to mate selection algorithms. For example, in simulations with sexual diploids I found (Jaffe 1999) that any arbitrary signal guiding mate selection was better than random mating. Similarly Heisler (1985) showed how arbitrary characters could become strong signals for sexual selection. An analogous result in game theory was obtained by Riolo et al. (2001), who, using computer simulations, showed that cooperation can arise when agents donate to others who are sufficiently similar to themselves in some arbitrary characteristic. They called the phenomenon tag-based donation and showed that it can lead to the emergence of cooperation among agents who have only rudimentary ability to detect environmental signals and, unlike models of direct or indirect reciprocity, no memory of past encounters is required.

Another example is provided by Gintis et al (2001) who propose an explanation of cooperation among unrelated members of a social group in which cooperation evolves because it constitutes an honest signal of the member's quality as a mate, coalition partner or competitor, and therefore results in advantageous alliances for those signaling in this manner. The model was framed as a multi-player public goods game that involves no repeated or assortative interactions, so that non-cooperation would be a dominant strategy if there were no signaling benefits. They showed that honest signaling of underlying quality, by providing a public good to group members, can be evolutionarily stable, and can proliferate in a population in which it is initially rare, provided that certain plausible conditions hold, including a link between group-beneficial signaling and underlying qualities of the signaler that would be of benefit to a potential mate or alliance partner. This scenario is analogous to the mate selection strategy based on 'good genes' as described in Jaffe (1999).

Evolution of indirect reciprocity might have arisen by image scoring. For example, Nowak and Sigmund (1998) showed that cooperation might pay because it confers the image of a valuable community member to the cooperating individual. An analogous mechanism might be conceived for mate selection. Individuals with large reproductive success (i.e. many mates) might be more attractive to future mates, not because of any intrinsic signal they possess but because of the "image" of having many mates. Indications of such a mate selection systems have been described for guppies and called mate choice copying (Briggs et.

al. 1996, for example) although its existence has been questioned (Lafleur et. al. 1997).

CONCLUSIONS

Despite the sensitivity of evolution to the type of mate selection strategy in use, few theoretical studies focus on the mate selection algorithms. Most examples presented here dealt only with one of two types of mate selection strategies: Preference for “good genes’ and assortative mating; but other strategies may certainly also produce benefits to population.

In a similar vein, most studies presented here were based on animals, yet mating strategies among flowering plants should equally profit from mate or gamet selection strategies evolved to optimize genetic variance. Little is known about them in plants, other that they certainly exist (Barrett 1998). Thus, fruitful research in mate selection strategies might be expected to come from studying in much more detail mating strategies in flowering plants.

Sex, ploidy and mate selection are all devices that have evolved to improve evolvability (Jaffe 2000). The emergence of such mechanisms are difficult to explain in terms of the survival of the fittest. But the particular “run away” evolutionary process that is intrinsic to sexual selection (Andersson and Iwasa 1996, Holland and Rice 1998) and to assortative mating (Jaffe 1999), might explain their prevalence in biological organisms. Pure sexual selection in which females chose males with strong sexual signals or sex appeal not directly related to fitness, induced rapid fixation of the allele producing the highest “sex appeal”. Populations with this mate selection strategy also have a higher survival probability compared to random mating.

The evolutionary dynamics of these mate selection strategies produce a slight but continuous increase over time in the frequency of alleles coding for them. Sexual selection increases the mating success of the emitter, and thus increase its fitness, producing a run-away sexual selection (Houde and Endler 1990, Bakker 1993, Houde 1994, Holland and Rice 1998). Stronger sexual signals (i.e. sex appeal) are fixed very fast by the evolutionary dynamics. This dynamic mechanism is that of an “auto-reinforcing strategy” or “self-enhancing strategy” with very high probabilities to be fixed genetically in a population once it emerged. The evolutionary dynamics and the prevalence in nature of these “self-enhancing” evolutionary strategies are certainly worthwhile research topics in the future, as their working is based on fundamental dynamic devices and thus, should be present in all evolutionary processes, from the biological to the cultural.

Finally, I propose the use of the concept of mate selection instead of that of sexual

selection, as mate selection seems to be a more general term than sexual selection, allowing to explore a vast and unknown territory of fundamental dynamic phenomena. Understanding the underlying evolutionary logic of mate selection strategies might eventually help in understanding biological basis for beauty and the adaptive value of love.

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Figure 1: Graphical illustration of the dynamic processes occurring in the simulation model

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