

Mate choice theory and the mode of selection in sexual populations

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Indirect new data imply that mate and/or gamete choice are major selective forces driving genetic change in sexual populations. The system dictates nonrandom mating, an evolutionary process requiring both revised genetic theory and new data on heritability of characters underlying Darwinian fitness. Successfully reproducing individuals represent rare selections from among vigorous, competing survivors of preadult natural selection. Nonrandom mating has correlated demographic effects: reduced effective population size, inbreeding, low gene flow, and emphasis on deme structure. Characters involved in choice behavior at reproduction appear based on quantitative trait loci. This variability serves selection for fitness within the population, having only an incidental relationship to the origin of genetically based reproductive isolation between populations. The claim that extensive hybridization experiments with *Drosophila* indicate that selection favors a gradual progression of "isolating mechanisms" is flawed, because intra-group random mating is assumed. Over deep time, local sexual populations are strong, independent genetic systems that use rich fields of variable polygenic components of fitness. The sexual reproduction system thus particularizes, in small subspecific populations, the genetic basis of the grand adaptive sweep of selective evolutionary change, much as Darwin proposed.

evolution | genetic variability | natural selection | population genetics

Choice-Dependent Selection

Beginning with Darwin and intensifying in the last 20 years, choice of mate, particularly by the female, has been widely documented in many animals (fish, reptiles, birds, mammals, and insects), and has included gamete choice in plants (1–5). Occasional reversals of the role of the sexes in choice mechanisms are well known. Random mating has been a useful basic assumption in theoretical population genetics (6), but it ignores the possibility of nonrandom mating systems resulting from variable mating propensities of the participants. Female choice, for example, appears to single out for mating a small minority of males having very high Darwinian fitness. Little attention, however, has been given to characterizing the members of the mating group genetically and to discern to what degree there is genetic variance within this special group. Many populations in which choice occurs manifest conspicuous inherited secondary sexual characters, particularly in males.

In laboratory or field-plot experiments involving artificial selection for quantitative characters, mate choice is necessarily in the hands of the investigator, who imposes artificial mate selection that accumulates genetic changes in a particular character. In the present context, it is significant that advance caused by artificial selection is usually accompanied by declines of fertility within the selected lines (7, 8). Although rarely emphasized, this result is seen in most laboratory and field-plot manipulations in genetics because these were carried out without regard to the retention of any natural mate choice system. The observed progression of infertility, even as selective advances continue, appears to be largely caused by investigator disruption of the natural choice system. This rich field is open for new investigation.

Genetic Variability in the Choice System

Crucial evidence for genetic control of many sexual characters now exists. For example, data on RNA transcript levels have been used to reveal the existence of a wealth of genes expressing themselves during the life cycle of *Drosophila melanogaster* (9). The technique enables recognition of 4,028 active genes. Only $\approx 22\%$ of these are previously named *Drosophila* genes with a known phenotype. Characters and organs relating to reproduction in adult flies showed 215 active genes in males and 144 in females. Evidence from the study of protein variability in *Drosophila* also suggests that the proteins associated with the reproductive system, are, on average, twice as diverse as those from tissues not related to reproduction (10, 11). Thus, extensive fields of genes, though largely lacking specific genetic analysis, exist and are available to provide a potentially very high genetic variance among mature adult individuals at the reproductive stage of the life cycle.

Genetic analyses of choice systems in natural populations are few. This is due largely to the inadequacy of standard methods of laboratory genetic analysis to deal with complex behavioral and morphological characters, especially if they are sex-limited. Males, for example, commonly inherit and manifest syndromes of striking morphological and physiological sex-related characters that are specifically deployed in the mating process. Nevertheless, their genetic architecture and natural variability is largely unknown.

Natural mate choice systems, however, appear to remain reasonably intact in wild-type laboratory stocks of *Drosophila* that have been established as separate cultures descended from a single, naturally inseminated wild female (12). Such "isofemale lines" constitute a valuable type of basic population sample because they initially reflect the natural choice of mate by the female. In some cases, the operation of natural mate choice appears to be well preserved in progeny over a number of generations and can be studied in the laboratory. Even as some declines of mating procedures are observed, stock culture appears to allow many of the genetic elements of natural mate choice to be retained and studied (13).

Some species of Hawaiian *Drosophila* are especially useful because complicated syndromes of mating behavior exist, including displays of males on lek sites, and long courtships involving female choice are found and are amenable to laboratory analysis (13).

Remarkably, when marked and tested, about a third of surviving, mature, healthy, courting wild-type males of the Hawaiian species *Drosophila silvestris* within an isofemale line are never accepted by females. Conversely, a small number of male individuals are accepted repeatedly (12).

Study of single pairs of this species show that courtship may be broken off by the female at any one of many different stages. On reaching a near-final stage, some females may permit tactile stimulation of the abdomen by a cluster of male-limited foreleg bristles by a male that has reached a position standing directly behind her. These bristles appear to be pivotal in inducing a final

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acceptance or rejection move by the female. This partially sex-linked, male-limited polygenic character has high heritability (14) and shows extensive polymorphism both within and between certain local natural populations of this species (12). The bristle character, however, appears to be only one of a hierarchical cascade of other male and female courtship-related characters that may also be under the same type of quantitative genetic control that is manifested by other similar morphological characters (13).

Population Size and Inbreeding

The choice systems discussed here have one overriding effect: they confine natural reproduction to a small, often very small, number of individuals relative to census numbers in the population. Choice thus imposes a small effective population size and some correlated inbreeding. Conventionally, inbreeding has been considered inimical to long-term evolutionary change because of a theoretical effect on loss of genetic variability (6). For quantitative characters, however, the story may be different. At least five generations of sibling pair matings are required before significant deleterious effects of inbreeding occur (15). Experiments with maize reveal that small inbred populations retain very extensive quantitative genetic variability (16).

Small populations in which choice systems remain intact appear to be protected from harmful loss of genetic variability by the presence of strong balanced polymorphisms (17) that may encompass key quantitative trait loci (18, 19). This kind of heterosis should be distinguished from the F_1 luxuriance observed when two inbred populations are crossed. Although useful in certain artificial breeding programs, it is nonetheless clear that this luxuriance effect is ephemeral and is largely destroyed by breakdown due to genetic recombination in later generations (20). Selection at the level of reproductive function preserves and transmits the positive survival results of natural selection that have preceded the reproductive phase of the life cycle. For example, a particular female may be able to use cues to choose a male with a relatively small handicap (21) that may have survived tests under a prereproductive regime of natural selection similar to that of the choosing female. This “processing effect” by the female increases the probability that survivorship is maximized. In these cases, the results of selection at mating (usually called “sexual selection”) might be reasonably included under the broader term of natural selection.

This concept suggests that mate choice may be viewed as a natural coadaptation of male and female functioning to preserve the basis of augmented power of natural selection. Selection for high fitness is genetically expensive, because the cost of mating includes the elaboration of syndromes of genetic variability that will generate relatively few individuals having high Darwinian fitness. The rest are lost in the natural course of reproduction. This principle can be important in determining fitness in both sexes of both animal and plant individuals.

Behavior that has been variously described as “sexual conflict” or “sexual antagonism” between male and female (22) may be confined to expendable individuals of relatively low Darwinian fitness, and thus are interesting laboratory constructions that have no evolutionary importance in nature.

Selection involving mate choice appears to have been the major force in the evolution of many characters seen in sexually reproducing forms. The most striking of these in animals tend to be male-limited; they are at least partly sex-linked and consist of syndromes associated with a single recombinant X chromosome, which the male receives from the female parent. In the female, the paired X chromosomes are free to undergo extensive recombination at meiosis, especially if polymorphic intraspecific inversions are few or absent. In the presence of balanced polygenic polymorphism, each male will receive a single, unique recombinant X chromosome haplotype. The tendency toward X

chromosomal structural homozygosity in females of the sexually dimorphic Hawaiian *Drosophila* is very pronounced (23). This results in an extensive field of individually different, genetically variable males confronting the choosing female.

In the absence of environmental change, many generations of inbreeding in small populations without out-crossing should lead, not to monomorphism, as is so often assumed, but to balanced selective polygenic equilibria on which selection can continue to operate. In some cases, mate choice may encounter a relatively stable environment as happens when a species has achieved a mature state of balance with the environment. As a result, choice may become stabilized and generate very little evolutionary change. If the environment undergoes change, however, retention of the capacity to generate genetic variance by recombination is promoted by the presence of balanced polymorphic states. Introduction of new genetic variability from outside the population at this stage may contribute to the building by recombination of newly enhanced selective response. Thus, the system remains open to the generation of new variability because an occasional rare hybridization can result in an enrichment of these balanced polymorphisms.

Selection Favoring Reproductive Isolating Barriers Is Questionable

The widely followed “Biological Species Concept” is based on a theory that was advanced and widely championed early in the last century by Dobzhansky (24) and Mayr (25). This proposes that a major function of selection in variable, genetically differentiating natural populations is to favor accumulation of genes that function as “isolating mechanisms” between populations that are in contact with one another. Although it continues to motivate much research in evolutionary biology (22), this theory has been criticized as an improper guide to the understanding of the process of genetic differentiation between populations (12, 26, 27). I continue the argument here that an important consequence of strong mate choice systems is to cast serious doubt on the validity of this theory. Stated simply, the sexual reproduction system in each surviving population develops its own complex fitness-associated characters both internally and geographically. These function independently and are not negatively affected by occasional hybridization with adjacent populations evolving under similar or slightly dissimilar environmental influences. Given space and time, of course, internal fitness-selection may indeed incidentally confer a state of reproductive incompatibility with other populations.

I therefore challenge the long-held conventional wisdom that the numerous experiments with *Drosophila* populations support the “isolation” hypothesis. Since about 1940, laboratory techniques have been used to observe mating incompatibilities between stocks of strains or species obtained from nature (28). The methods of testing are biologically simplistic, especially in view of the great genetic complexity of sexual behavior. In a commonly used experiment, equal numbers of mature virgin adults of both sexes from the two cultures to be compared are combined in a single mating chamber. Homogamic and heterogamic pairings are then recorded. The assumption is made that, in this biologically confusing mix, there is random mating within each group. This leads to the further assumption that many of the observed reproductive characters relate only to the presence or absence of genes that support genetic isolation. This ignores the crucial point that the characters within each group have evolved as major supports for intra-group choice systems related to selection for fitness. The results of mixing males and females of two populations that come from independently evolved systems of mate choice are thus basically flawed, because the experimental results are necessarily based on disturbed and unnatural mating conditions, obfuscated by the inability of the investigator

to distinguish between selection for fitness and assumed selection for sexual isolation or its reinforcement.

Mate choice theory, furthermore, can offer a simple solution for certain puzzling results encountered over the years in experimental studies in population genetics. An example is the “founder effect.” Most natural populations display size fluctuations. When a large sexual population is naturally or experimentally forced through a few founder individuals, size reduction appears to sometimes cause a shift in genetic conditions underlying certain reproductive mechanisms in the descendent population. The nature of such changes have not been well understood. In an insightful review (29), bottlenecked populations, in experiments with various *Drosophila* species, do not clearly demonstrate the presence of any reproductive isolation. As argued in the present article, however, such data are flawed as a measure of reproductive isolation. On the other hand, a few data sets do occur that can be explained as due simply to chance shifts by random drift in the complex genetics of the mate choice system between the newly bottlenecked population and its ancestral form (30).

Genetic shifts of the above sort, unrelated to genetic isolation, appear to also occur after natural population bottlenecks of *Drosophila* species as they colonize newly formed volcanoes or islands. During the last 5 million years in Hawaii, new islands, volcanoes, and surface lava flows have been continually and successively added at the southeast end of the archipelago. By using inversion markers, ancestral and derived populations at both the species and infraspecies level can be recognized with great precision (31).

When mating behavior has been compared between a species from an older island with that of a closely related species from a newer island, a strikingly consistent result is obtained. The females from the older islands discriminate against males from the younger island. Conversely, females from the younger island show much less discriminatory behavior (32). Over time, the older population in a relatively stable environment appears to have built up an increasingly complex mate choice system. Some elements of this discriminatory fitness system, however, appear to be lost after the constriction of population size at the time of the establishment of a newer population.

The above finding has been followed up by making comparisons of mating behavior between intraspecific populations of different ages on a single island. *D. silvestris* is endemic to the new island of Hawaii. The island has large numbers of successively younger, dated lava flows that are often adjacent but spatially separate. Most of the lava flows with populations of *silvestris* are newly vegetated and are thus free to receive colonists from older flows.

The oldest of the lava flows on the island of Hawaii are ≈ 0.5 million years old. Populations show significantly decreased female choice in a stepwise fashion when those from newer flows are compared with their apparent ancestral forms on nearby or adjacent older lava flows (33). Thus, colonization of new flows appears to be accompanied by mild founder effects that reduce the complexity of the female choice system that had previously been built up in the older population living in a different, more stable environment. Such events should be viewed simply as shifts in small newly colonized populations occurring before a renewed intensity of choice-guided evolutionary change in the new environment. For some years during this work, this phenomenon was interpreted, I think incorrectly, as an “asymmetrical isolating mechanism.”

Accordingly, random drift associated with a founder event appears to induce a chance “resetting” of the female choice mating system back to a somewhat simpler one. Over time, normal intrapopulation selection tends to build up a new, more complex choice system. This can explain much of the curious data on the genetic effects of bottlenecks in sexual populations.

Conclusion

Although the detailed genetic basis of mate and/or gamete choice is not well understood, evidence exists that this process is nevertheless a powerful component of natural selection within sexual populations. At each generation, the genotypes of an evolutionary unit (34) are forced through the DNA of a very small number of gametes. Generation times in sexual forms are exceedingly short in geological terms, a fact that reflects the ubiquitous power of natural selection to continually alter genotypes. Pan-selectionism is indeed the major principle that underlies adaptive evolution. I argue that mate choice theory requires that the genetic change induced by selection be concentrated in demographically quite small subspecific populations (34–36).

Choice mechanisms have resulted in the selection of elaborate morphological and behavioral characters that appear to screen the genotypes resulting from prereproductive natural selection. Although traditionally referred to as “sexual selection,” these processes are better viewed as ones that evaluate and discriminate between the fitness properties of each individual organism so screened (21). A corollary of this is that these physiological and morphological premating characteristics have evolved in direct response to this fitness-screening process.

The primary cause of these character sets is the determination of Darwinian fitness within the sexual population. Nevertheless, a large section of evolutionary biology, where mating has been assumed to be at random, proposes the further assumption that these characters are the result of selection for isolating mechanisms and their reinforcement.

Certain population models (37, 38) suggest that genetic divergence due to sexual selection, even though arising as enhancers of Darwinian fitness, may secondarily serve to produce what is thought to be sexual isolation between groups. These models, however, use an assumption that I believe is unwarranted: that selection in populations is leading toward a full closure of reproductive isolation as a characteristic of a certain level of divergence, namely, the species level.

The field of “isolation assumption” needs to be reexamined and reevaluated in animals, flowering plants, or fungi with complex sexual systems. Indeed there appears to be very little, if any, evidence that reproductive systems and incipient adaptations in local populations are seriously perturbed by hybridization, even between locally adjacent populations. The characters would therefore not be likely to be favored for contributing to any sort of isolating function, either directly or indirectly.

This fitness-evaluating system, which is repeated from generation to generation under slightly changing environments, is always blind to any perceived goal (39). The common continued use of the term “speciation” in the literature is counterproductive because it implies that a totally genetically isolated species level is somehow a crucial major point toward which the evolutionary process is leading. Use of speciation views any observed reproductive isolation at the species level as if nature were conforming to some sort of transcendental human-conceived “goal” favoring genetic isolation.

The concept of choice-guided natural selective forces entertained in this article renders moot the discussions that have long raged in the past century over allopatric versus sympatric “modes” of genetic divergence. Such dichotomy of ideas is irrelevant in view of the overriding power of intrapopulation evolutionary forces, such as choice-related selection, that function only at the level of the local population or evolutionary unit. These selective forces respond strictly to the contingent situation, with the outcome depending on conditions in the current existing environment. The result is viewed as being independent of events that are occurring in adjacent populations where, by definition, the environment is different. This view is close to that originally proposed by Darwin (1) before the genetic clarifications of the 20th century.

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