

## Sex, Flies, and the Genetic Consequence of Small Population Size

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### Abstract

Based on results of mate preference studies conducted on Hawaiian *Drosophila* it is suggested that the dynamics of sexual selection play a critical role in genetic differentiation during founder events. The demographic nature of founder populations results in a shift in the distribution of mating types within the population. That is, females that are too choosy in mate selection, under conditions of small population size, may not encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, strong selection for less choosy females will result in a shift in gene frequencies toward the genotypes of less choosy females. Under these circumstances, the population is now provided with a genetic milieu where previously co-adapted gene complexes become available for recombination. Novel recombinants may be generated which provide the genetic variability required for the founder population to adapt to the new habitat or environment. Thus, the dynamics of sexual selection can be a synergist for species formation.

### Introduction

As recently as two decades ago, Mayr (1982) remarked: "Speciation ...now appears as the key problem of evolution. It is remarkable how many problems of evolution cannot be fully understood until speciation is understood..." During the ensuing 20 years, there has been renewed interest in understanding the process of speciation. At least two books that address questions of speciation and the evolutionary processes of species formation have been published. Otte & Endler (1989) edited the volume *Speciation and its Consequences* and Lambert & Spencer (1995) published the edited volume *Speciation and the Recognition Concept*. However, it is not the intent of this paper to discuss the various models of speciation and the reader is referred to these two references for a comprehensive review of the topic.

There is little doubt that *adaptation* is the central theme of the evolutionary process and that natural selection results from the interaction between heritable phenotypic variation within populations and the extrinsic environment in which such populations live. In the formulation of his theory of natural selection, Darwin (1859) made the following statement:

"It may metaphorically be said that natural selection is daily and hourly scrutinizing, throughout the world, the slightest variation; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life."

Darwin (1859) also proposed the theory of sexual selection to explain the sexually dimorphic characters he observed among a wide diversity of organisms, but suggested that sexual selection was less important than natural selection in bringing about evolutionary change. He stated:

"Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; while natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. Sexual selection is a struggle between individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring..."

Until recently, most biologists accepted the notion that natural selection is the most dominant force in evolutionary processes. Even Darwin acknowledged that "sexual selection will also be dom-

inated by natural selection tending towards the general welfare of the species.” He also recognized that the major issue with his sexual selection model is “...in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of offspring to inherit their superiority than their beaten and less attractive rivals. Unless this result does follow, the characters which give to certain males an advantage over others could not be perfected and augmented through sexual selection.”

Darwin’s theory of sexual selection challenged theoreticians to formulate hypotheses for the evolution of female preference for, and the evolution of, secondary sexual traits in males. It may be useful to briefly discuss one of the most notable of these models. The runaway selection model (Fisher, 1930) inferred that the evolution of a sexually dimorphic character in males could result in a correlated response in the female’s preference for that character. The model predicted that sexual selection within an interbreeding population would influence female choice and male characteristics to coevolve very rapidly (O’Donald, 1977, 1980; Lande, 1981, 1982; Kirkpatrick, 1982). Furthermore, female preference for a certain male character tends to select for extreme forms of that character until natural selection steps in to maintain the optimum phenotype for that particular environment. The paradox of the runaway selection model is that the opposing forces of sexual selection and natural selection result in reduced genetic variability for such secondary sexual characters in the males. However, without genetic variation, selection can no longer occur; and unless secondary sexual characters either are linked to or are pleiotropic effects of other components of fitness, such conspicuous characters would be energetically and developmentally costly to produce, and individuals possessing such traits would be in greater danger of predation.

In recent years, there has been significant interest in the role of sexual selection and its influence on “the mutual adjustment of the sexes to what may be called the intraspecific sexual environments” (Carson, 1978). The key word in the previous statement is “intraspecific”; sexual selection is indeed an “intraspecific” phenomenon and that while sexual selection can play a very important role in species formation, it is not a “mechanism” by which genetic isolation between daughter populations is selected. Carson (2003) stated that while the Biological Species Concept continues to underlie much of the research in evolutionary biology, he suggested that “...an important consequence of strong mate choice systems is to cast serious doubt on the validity of this theory.” He argued that the intraspecific sexual selection system within an interbreeding population “...develops its own complex fitness-associated characters”, which are not adversely affected by the occasional hybridization with sympatric or parapatric populations. Over time, the “fitness-associated characters” that arise within a population due to natural as well as sexual selection may confer reproductive barriers that prevent interbreeding with populations within its geographic range. In Carson’s view, any genetically-based inter-group isolation that might result from mate choice systems would be wholly incidental side effects and would not represent “selection of genes for isolation”.

In this paper, I review a model that describes a possible mechanism by which sexual selection plays an important role in not only maintaining levels of genetic variability especially during small population size, but also in generating new genetic recombinants that provide the basis for selection following population bottlenecks. Based on mate preference studies on Hawaiian *Drosophila* species, it is suggested that sexual selection plays a dominant role, especially during the initial stages of species formation and serve as a possible mechanism for the “genetic reorganization” that accompanies founder event speciation (Carson, 1971; Carson & Templeton, 1984). Also, some previously unpublished data from natural populations of two species of Hawaiian *Drosophila*, *D. silvestris*, and *D. heteroneura*, provide further evidence of recent and ancient natural hybridization between sympatric populations of these two species, which suggests that two separate founder colonizations led to the evolution of the present day species.

#### **Asymmetrical Mating Preference and Speciation via the Founder Principle**

Often, when mate choice experiments between two species or even two populations of the same species are conducted, the outcome is asymmetrical preference. That is, the males of species A may

be readily accepted by the females of species B. However, in the reciprocal direction, males of species B are strongly discriminated against by females of species A. While early *Drosophila* researchers observed mating asymmetries in mate preference experiments (e.g., Dobzhansky & Streisinger, 1944; Bastock, 1956; Reed & Reed, 1950; Rendel, 1951), the significance of such asymmetries was not clearly understood. It was often explained by the presence of differential mating propensity or perhaps differences in sexual maturation between the populations. It was not until more recent studies by Kaneshiro (1976, 1980, 1983) that inference was made that the dynamics of sexual selection during small population size provided the mechanism for shifts in the “sexual environment” of the population. It was suggested that during conditions of small population size, there is strong selection for less choosy females in the population since highly discriminating females may never encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, there would be a shift in the mating distribution of the population towards an increased frequency of less choosy females. Thus, in mate preference experiments between newly derived populations and older more ancient populations, asymmetrical mating preferences were frequently observed. Females from the derived, more recently bottlenecked population mated with males from the ancestral population equally well as males from its own population and often even more so. However, females from the ancestral population, strongly rejected males from the derived population. These observations led to early conclusions that the results of mate preference experiments could be valuable for determining the direction of evolution between pairs of species based on the asymmetrical mating preference (Kaneshiro 1976, 1980, 1983; Kaneshiro & Kurihara, 1981; Arita & Kaneshiro, 1979; Ahearn, 1980; Powell, 1978; Ohta, 1978; Giddings & Templeton, 1983; Dodd & Powell, 1986). Following the initial paper by Kaneshiro (1976) in which it was suggested that mate preference experiments could be useful in predicting the “direction of evolution”, a number of other studies (Watanabe & Kawanishi, 1979; Wasserman & Koepfer, 1980; Markow, 1981) that also showed asymmetrical mating preference among *Drosophila* populations concluded that the direction of evolution could well be in the opposite direction as predicted by Kaneshiro’s hypothesis.

Three articles published in Volume 21 of the *Evolutionary Biology* series (1987, M. Hecht, B. Wallace & G. Prance, eds.) presented arguments either for or against the Kaneshiro hypothesis. In Ehrman & Wasserman’s chapter (Chapter 1) entitled, “The significance of asymmetrical sexual isolation,” the authors concluded “The direction of asymmetrical isolation, taken by itself, is an unreliable indicator of direction of evolution.” In Chapter 2, DeSalle & Templeton concluded “One of the primary strengths of the Kaneshiro model is that it makes predictions that can be tested both in the laboratory and in the field.” The authors also stated “...recent molecular studies confirm the validity of the Kaneshiro model when its assumptions are satisfied and confirm the validity of Ehrman and Wasserman’s central thesis that the Kaneshiro predictions are not universally valid.” In Chapter 3, Kaneshiro & Giddings concluded “...the generality of the models discussed in the chapters in this volume can only be determined by the rigorous studies of groups other than the endemic Hawaiian drosophilids. The challenge is not just to determine whether mating asymmetries exist within the groups of organisms being studied and whether the direction of evolution predicted by the various asymmetry models points to the correct direction based on other evidence. Rather, we hope that investigators will ask the question of why such asymmetries exist and how they arose.”

### **The Differential Selection Model of Sexual Selection**

Based on mate preference experiments on Hawaiian *Drosophila* species and on results of experiments selecting on high and low discrimination among females, Kaneshiro (1989) suggested an explanation for the observed mating asymmetries among related pairs of species in the native drosophilid fauna. The mating experiments indicated that there is a range of mating types segregating among both sexes. That is, among males there are those that are extremely successful at satisfying the courtship requirements of most of the females in the population and indeed these males accomplish most of the matings in the population. There are other males which do very poorly and in fact may not mate at all even if given the opportunity to do so with several receptive females.

Similarly, among females, there are those that exhibit higher threshold levels in mating receptivity and strongly discriminate against most of the males in the population. Within the same populations, there are females that have lower receptivity thresholds and will mate with most of the males in the population.

Kaneshiro (1989) suggested that within an interbreeding population, the most likely mating is between the males that are most successful in satisfying the courtship requirements of females and females that are not so choosy in selecting mating partners. The genetic correlation between these two behavioral phenotypes (i.e., highly successful males and less choosy females) is what maintains the range of mating types in the two sexes generation after generation. In this model then, there is differential selection for opposite ends of the mating distribution in the two sexes and therefore, sexual selection itself serves as the stabilizing force in maintaining a balanced polymorphism in the mating system of the population. Such a model would thus avoid the need for natural selection to play a role in maintaining a normal distribution of mating types segregating in the population. The model also avoids the problem of reduced genetic variability that results from the rapid coevolution of female preference for male traits as is described by the runaway selection model.

The results of the selection experiments (described in Kaneshiro, 1989) support the notion that there is a strong genetic correlation between the two behavioral phenotypes in the two sexes. By selecting for choosy females and males with high mating success simultaneously, it was possible to obtain a line whose mating distribution was significantly different from the parent population. Similarly, it was possible to select for the opposite extreme, i.e., less choosy females. By selection for less choosy females and males that are less successful in mating simultaneously, it was possible to obtain progeny whose mating distribution was significantly different from the parent population but in the opposite direction. The data from the selection experiments clearly indicate that there is indeed a range of mating types segregating in both sexes and that there is a strong correlation between female choosiness and male mating ability. By selecting for both of these behavioral phenotypes simultaneously, it was possible to obtain selected lines at both ends of the distribution in as few as two generations of selection.

### **The Role of Sexual Selection in Founder Event Speciation**

Another feature of the differential selection model described by Kaneshiro (1989) is that the sexual selection system is characterized as a frequency dependent system. That is, when the size of the population is significantly reduced, there can be even stronger selection for less choosy females. Under small population size, females that are very choosy may never encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, there can be a shift in the distribution of mating types in the population until a significant increase in frequency of less choosy females in the population has occurred. Correspondingly, such a shift in mating distribution may be accompanied by a shift in the gene frequencies of the population resulting in the destabilization of the coadapted genetic system that had evolved in the population while adapting to a particular habitat. Such a destabilized genetic environment presents the opportunity for genetic changes conducive to speciation. It is suggested that the breakup of coadapted sets of genes now allows novel genetic recombinants to be generated, some of which may be better adapted to the environmental conditions that led to the reduced population size. Thus, the dynamics of sexual selection in response to significant reduction in population size can play an extremely important role in maintaining levels of genetic variability upon which natural selection can operate in the survival of the population during stress environmental conditions.

In the evolution of island biota such as has been observed in the endemic Drosophilidae of the Hawaiian Islands, it has been suggested that the most likely mode of speciation is what has been referred to as founder event speciation. In most cases, the most probable scenario is that a single fertilized female is blown from one island to an adjacent island where a new colony may be established if suitable habitat and oviposition sites are readily available. During the initial stages of colonization

when the population size is small, there would be strong selection for females that are less choosy in mate selection because females that are highly discriminating may never encounter males that are able to satisfy their mating requirements. As suggested in the differential selection model then, within a few generations, there would be a shift in the distribution of mating types in the population toward an increased frequency of less choosy females. There would be a corresponding shift in the gene frequencies of the population followed by a destabilization of the coadapted genetic system. In subsequent generations, novel genetic recombinants may be generated some of which are better adapted to the new habitat. These genotypes are strongly selected, especially if they are linked or correlated with the genotypes of the less choosy females. Clearly, at least during the initial stages of colonization immediately following the founder event, the dynamics of sexual selection may play an important role in producing a genetic environment that is conducive to the formation of new species.

### Sexual Selection and Natural Hybridization

In an article on natural hybridization, Arnold (1992) stated:

“Natural hybridization and introgression...may lead to...the merging of the hybridizing forms...the reinforcement of reproductive barriers through selection for assortative (conspecific) mating...the production of more or less fit introgressed genotypes...[or] to the formation of hybrid species.”

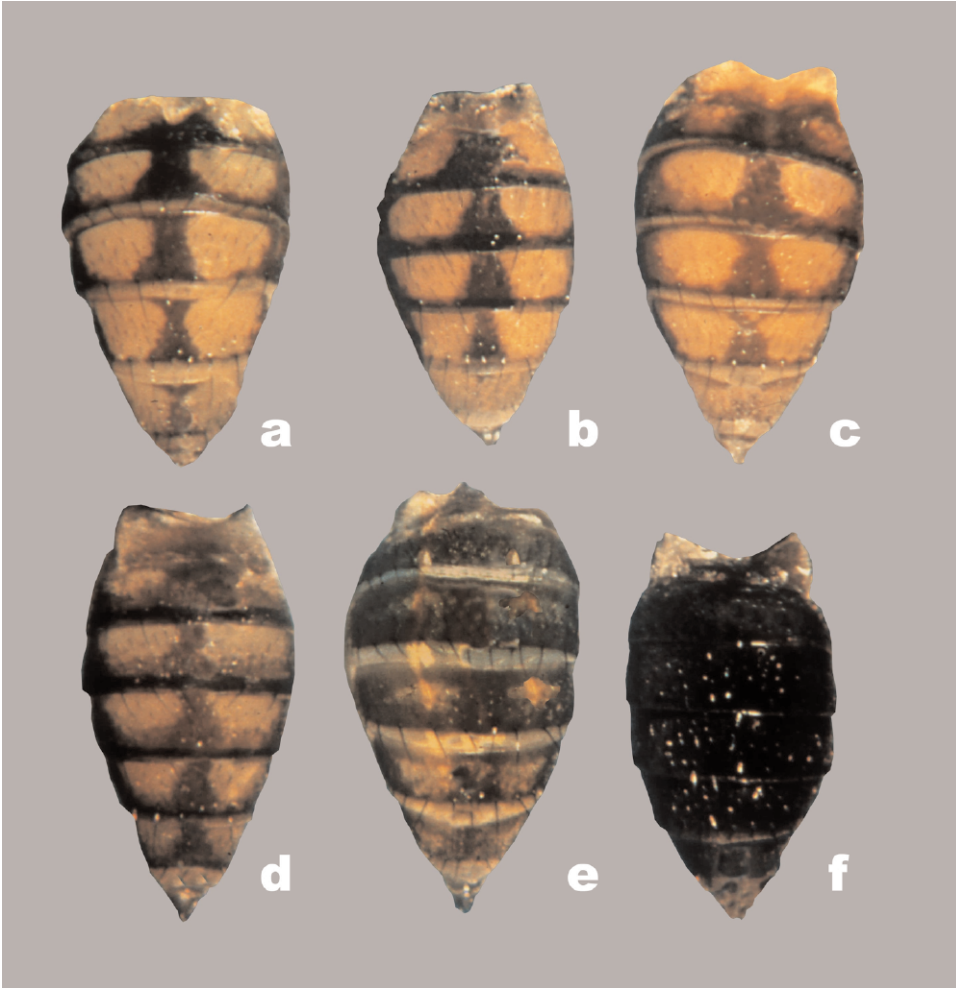
Then in his book entitled “Natural Hybridization and Evolution” published in 1997, Arnold stated:

“...the hypothesis addressed in this book is that natural hybridization affects the evolutionary history of the groups in which it occurs primarily through the production of novel genotypes that in turn lead to adaptive evolution and/or production of new lineages. This hypothesis is not new...most recent studies of natural hybridization have, at best, viewed this process as a tool for defining barriers to gene exchange to infer how speciation...might occur. In contrast, I will examine these barriers to facilitate predictions concerning what hybrid genotypes may be produced, because an array of hybrid genotypes represents material for evolution.”

In a paper published by Kaneshiro (1989), it was suggested that under certain conditions, sexual selection as described by the differential selection model actually “permits” natural hybridization between closely related species. Again, a strong frequency-dependent component in the dynamics of the sexual selection system results in an increased frequency of less choosy females over a few generations of small population size. Under these conditions then, the probability that females of the affected population may accept the courtship overtures of males from a related species is greatly increased. Interestingly, many (but certainly not all) of the documented cases of natural hybridization are unidirectional. That is, more often than not, there is evidence of “leakage” of genetic material from one population into another but not vice versa.

Among the Hawaiian *Drosophila*, there are two well-documented cases of natural hybridization: between *D. setosimentum* and *D. ochrobasis* and between *D. silvestris* and *D. heteroneura*. In the case of *D. setosimentum* and *D. ochrobasis* from a particular locality on the Island of Hawai‘i, approximately 2% (4 out of 180) of the individuals were determined to be either F<sub>1</sub> or backcross offspring. Using easily distinguishable markers in the banding sequence of the polytene chromosomes in both species as well as a very distinctive “null” allele in *D. ochrobasis* at the esterase (est-1) locus, Carson *et al.* (1975) were able to determine the parental origin of the hybrids. The data indicated that one of the *D. setosimentum* females collected from the wild population had mated with a *D. ochrobasis* male. However, the other three individuals were determined to be backcross individuals and the direction of the original interspecific matings could not be definitively determined.

Kaneshiro & Val (1977) first reported on the natural hybridization between *D. heteroneura* and *D. silvestris* which are found sympatrically over most of the island of Hawai‘i. From the Kahuku Ranch area near the south end of the island, they found that 1.1% (6 out of 534) of the individuals were of hybrid origin. Here, there are no chromosomal or electrophoretic markers that distinguish the two species. However, there are morphological features that clearly distinguish the two species and a quantitative genetic analysis of these morphological differences (Val, 1977) permitted inferences about the parents of diagnosable hybrid individuals. In Kaneshiro & Val’s (1977) study, only



**Figure 1.** Dorsal view of abdominal patterns of **a.** *Drosophila heteroneura*; **b–e.** *Drosophila silvestris* from various localities on the Island of Hawai‘i where *D. heteroneura* is present; **f.** *D. silvestris* from the Kohala Mts. where *D. heteroneura* is absent.

F<sub>1</sub> hybrid individuals were reported, since determination of F<sub>2</sub> or backcross individuals required metrical analyses. In a subsequent study, Carson *et al.* (1989) conducted the necessary metrical analyses on all wild-caught individuals of both species collected from the Kahuku Ranch area and determined that approximately 1.7% (18 out of 1064) of the individuals were of hybrid origin. Based on the metrical analyses, it was determined that the hybrids were the result of matings between *D. silvestris* females and *D. heteroneura* males, and the backcross individuals appear to be the result of F<sub>1</sub> hybrid (*D. silvestris* females × *D. heteroneura* males) females × *D. silvestris* males. One other hybrid individual between these two species has been collected from a second locality on the island (Carson *et al.* 1989). This individual was also determined to be a backcross offspring resulting from an F<sub>1</sub> hybrid (*D. silvestris* female × *D. heteroneura* male) female × *D. silvestris* male.

Thus, in all of the documented cases of hybrid individuals between *D. silvestris* and *D. het-*

*eroneura*, the direction of original interspecific cross is unidirectional, i.e., *D. silvestris* female  $\times$  *D. heteroneura* male. One other bit of evidence indicates that the leakage of genetic material occurs in the same direction. In the Kohala Mountains in the northern part of the island, where only *D. silvestris* has been found (i.e., *D. heteroneura* is absent there), the abdomen of *D. silvestris* is black in all individuals (Fig. 1f). In all other localities where both species occur sympatrically, the yellow and black abdomen pattern characteristic of *D. heteroneura* (Fig. 1a) appears to be segregating in the *D. silvestris* populations (see Figs. 1a–f). These observations indicate that natural hybridization has occurred between these two species at all localities where they are sympatric (i.e., except in the Kohala Mts where *D. heteroneura* is absent). This evidence indicates that introgression has occurred unidirectionally, again from *D. heteroneura* into *D. silvestris*.

### Concluding Remarks

It is suggested that sexual selection is a truly dynamic process that is influenced by density-dependent factors. The differential sexual selection model discussed here may provide an explanation of how genetic variability may be generated even under conditions of small population size over a few generations. Shifts in the distribution of mating types during population bottlenecks result in a genetic environment that is conducive to the generation of novel recombinants. The generation of novel genetic recombinants and the selection for genotypes that are better adapted to changing environmental conditions are enhanced by the sexual selection system especially when the population is subjected to drastic reduction in size. The notion of increased genetic variability during small population size is certainly contrary to classical population genetic models. For example, Mayr (1963), in formulating his founder principle model, emphasized the loss of genetic variability due to genetic drift during the period of reduced population size following the founding of a new colony. Nei *et al.* (1975) concluded that the genetic variability of populations faced with small population size "...is expected to decline rapidly but, as soon as population size becomes large, it starts to increase owing to new mutations." However, there is much evidence that genetic variability may be maintained even when populations are subjected to drastic reduction in size. Fitch & Atchley (1985) reported that old inbred laboratory strains of mice carry large amounts of genetic variability. Carson (1987) reported that a highly inbred stock of *D. silvestris*, which was originally established from a single fertilized female collected from nature, was polymorphic for three inversions in chromosome 4, even after nearly 10 years in the laboratory.

The differential sexual selection model also provides a mechanism by which hybridization between co-existing species is permitted under certain demographic conditions. It is not suggested that introgression is extensive tending toward the destruction of the genetic integrity of the hybridizing species. Rather, it is suggested that there may be "leakage" of genetic material across species barriers that further enhances the population's ability to maintain and even increase levels of genetic variability during reduction in population size.

Clearly, sexual selection models such as the differential selection model provide important insights into mechanisms of species formation, but could also be applied to the development of more effective conservation management programs involving rare and endangered species. Based on the work on the Hawaiian Drosophilidae, it is clear that in most cases, populations that have been subjected to reduction in size due to environmental stress still have the genetic capacity to generate novel genetic recombinants via the differential sexual selection model. Sexual selection should certainly be taken into consideration in captive breeding programs if the goal is to ensure the maintenance of genetic variability. It may also apply to understanding of issues of insecticide resistance which appear to evolve rapidly following treatment. Thus, the demographics of small populations and the genetic consequences of reduced population size as well as the dynamics of the sexual selection system are extremely important aspects of the evolutionary process.

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This paper is dedicated to the memory of Professor D. Elmo Hardy who served as my mentor during much of my undergraduate and graduate career at the University of Hawaii. October 2003 marks the 40th anniversary since Elmo hired me as a dishwasher on the Hawaiian *Drosophila* Project when I was a second year student at the University of Hawaii. I was a pre-med student at the time but by the time I completed my undergraduate degree I was “hooked” and decided on a graduate program researching the evolutionary biology of the Hawaiian Drosophilidae under Elmo’s mentorship. To this day, I continue to investigate the evolutionary processes involved in the explosive speciation of this group and owe much of the success in my career to Elmo’s influence and unselfish mentorship during my undergraduate and graduate years at the University of Hawaii.

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