On the Emergence of Intersexual Selection: Arbitrary Trait Preference Improves Female-Male Coevolution

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Abstract

Sexual selection is a fundamental aspect of evolution for all eukaryotic organisms with mating types. This paper suggests intersexual selection is best viewed as a mechanism which to compensate for the unavoidable dynamics of coevolution between sexes that emerge with isogamy. Using the NKCS model it is shown by varying fitness landscape size, ruggedness, and connectedness how a purely arbitrary trait preference sexual selection mechanism proves beneficial with high dependence between the sexes. This is found to be the case whether one or both sexes exploit such intersexual selection.

Keywords: allosome, diploid, isogamy, meiosis, NKCS model

1. Introduction

Sexual selection is the component of natural selection usually referring to both opposite-sex mate choice and same-sex competition for mating opportunities. It is beyond the scope of this paper to review the (considerable) literature on the many aspects of sexual selection and the reader is referred to [2] for a recent overview. Of specific interest here is that males and females can be seen to be *coevolving* within their species. Notably, that this need not be to their mutual benefit has been used to explain phenomena such as female-damaging genitalia and sperm selection (e.g., [13]). At an abstract level coevolution is typically considered as the coupling together of the fitness landscapes of the interacting species. Hence the adaptive moves made by one species in its fitness landscape causes deformations in the fitness landscapes of its coupled partner(s). In this paper Kauffman and Johnsen's [12] NKCS model is used to explore the coevolutionary behaviour of two sexes and how this is affected by a simple mate choice scheme, i.e., intersexual selection. In particular, it is shown how the emergence of “any gene” preference can prove beneficial, in contrast to the general assumption of a degree of correlation between trait preference and so-called “good gene” selection (e.g., [6])

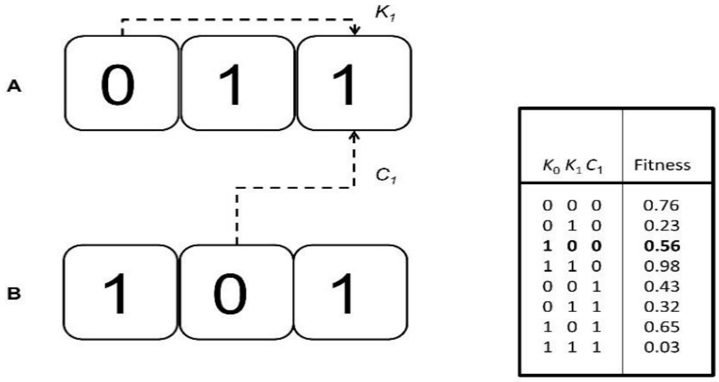
It has been suggested [4] that the emergence of sex – defined as successive rounds of syngamy and meiosis in a haploid-diploid lifecycle - enabled the exploitation of a rudimentary form of the Baldwin effect [3]. Key to this explanation for the evolution of sex in eukaryotes is to view the process from the perspective of the constituent haploids. A diploid organism may been seen to simultaneously represent two points in the underlying haploid fitness landscape. The fitness associated with those two haploids is therefore the fitness achieved in their combined form as a diploid; each haploid genome will have the same fitness value and that will almost certainly differ from that of their corresponding haploid organism due to the interactions between the two genomes. That is, the effects of haploid genome combination into a diploid can be seen as a simple form of phenotypic plasticity for the individual haploids before they revert to a solitary state during reproduction. In this way evolution can be seen to be both assigning a single fitness value to the region of the landscape between the two points represented by a diploid’s constituent haploid genomes, i.e., a simple form of generalization, and altering the shape of the haploid fitness landscape. In particular, the latter enables the landscape to be smoothed under a rudimentary Baldwin effect process (after [9]). This paper extends the new view of eukaryotic sex to consider mating types and their coevolution.

2. The NKCS Model

Kauffman and Levin [11] introduced the NK model to allow the systematic study of various aspects of fitness landscapes. In the standard model, the features of the fitness landscapes are specified by two parameters: N, the length of the genome; and K, the number of genes that has an effect on the fitness contribution of each (binary) gene. Thus increasing K with respect to N increases the epistatic linkage, increasing the ruggedness of the fitness landscape. The increase in epistasis increases the number of optima, increases the steepness of their sides, and decreases their correlation. The model assumes all intragenome interactions are so complex that it is only appropriate to assign random values to their effects on fitness. Therefore for each of the possible K interactions a table of $2^{(K+1)}$ fitnesses is created for each gene with all entries in the range 0.0 to 1.0, such that there is one fitness for each combination of traits. The fitness contribution of each gene is found from its table. These fitnesses are then summed and normalized by N to give the selective fitness of the total genome.

Kauffman and Johnsen [12] subsequently introduced the abstract NKCS model to enable the study of various aspects of *co*evolution. Each gene is said to also depend upon C randomly chosen traits in each of the other S species with which it interacts. Altering C, with respect to N, changes how dramatically adaptive moves by each species deform the landscape(s) of its partner(s), where increasing C typically increases the time to equilibrium. Again, for each of the possible $K+(SxC)$ interactions, a table of $2^{(K+(SxC)+1)}$ fitnesses is created for each gene, with all entries in the range 0.0 to 1.0, such that there is one fitness for each combination of traits. Such tables are created for each species (Figure 1).

Following [10], a mutation-based hill-climbing algorithm, where the single point in the fitness space is said to represent a converged species, is used here to examine the properties and evolutionary dynamics of variations to the NKCS model. That is, the population is of size one and a species evolves by making a random change to one randomly chosen gene per generation. The “population” is said to move to the genetic configuration of the mutated individual if its fitness is greater than the fitness of the current individual; the rate of supply of mutants is seen as slow compared to the actions of selection. Ties are broken at random.



K_0 K_1 C_1	Fitness
0 0 0	0.76
0 1 0	0.23
1 0 0	**0.56**
1 1 0	0.98
0 0 1	0.43
0 1 1	0.32
1 0 1	0.65
1 1 1	0.03

Figure 1: The NKCS model: Each gene is connected to K randomly chosen local genes and to C randomly chosen genes in each of the S other species. Connections and table shown for one gene in one species for clarity. Here N=3, K=1, C=1, S=1.

Figure 2 shows example behaviour for one of two coevolving species where the parameters of each are the same and hence behaviour is symmetrical. The effects of mutual fitness landscape movement are clearly seen. All results reported in this paper are the average of 10 runs (random start points) on each of 10 randomly created NKCS fitness landscapes, i.e., 100 runs, for 20,000 generations, for each parameter configuration. The (average) final fitness of the converged population is used for comparisons. Here $0 \leq K \leq 10$, $1 \leq C \leq 7$, S=1, for N=20 and N=100. Figure 3 shows how increasing the degree of connectedness (*C)* between the two landscapes causes fitness levels to fall significantly (T-test, $p<0.05$) when $C \geq K$ for N=20. Note this change in behaviour around C=K was suggested as significant in [10], where N=24 was used throughout. However, Figure 3 also shows how with N=100 fitness *always* falls significantly with increasing C (T-test, $p<0.05$), regardless of K.

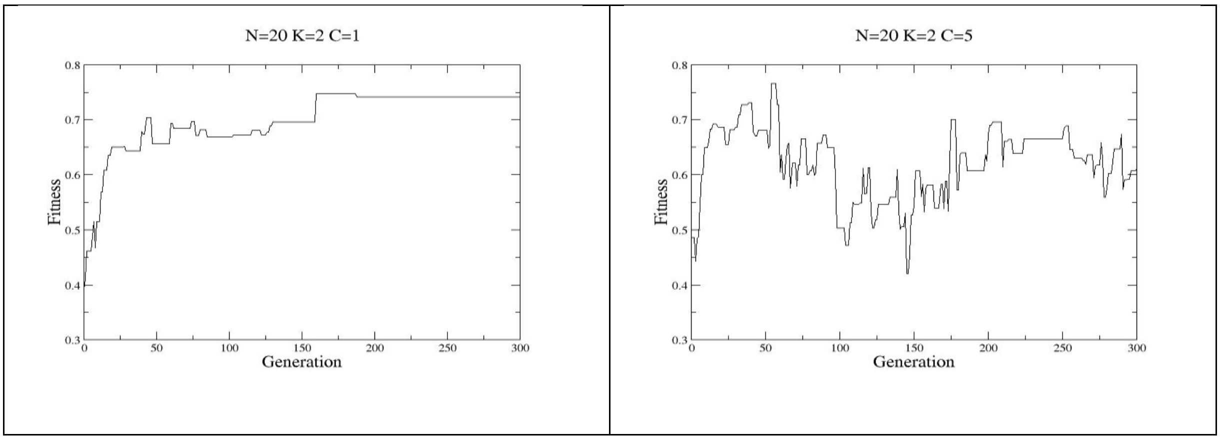


Figure 2: Showing example single runs of the typical behaviour of the standard NKCS model of coevolution with different degrees of landscape coupling (*C*).

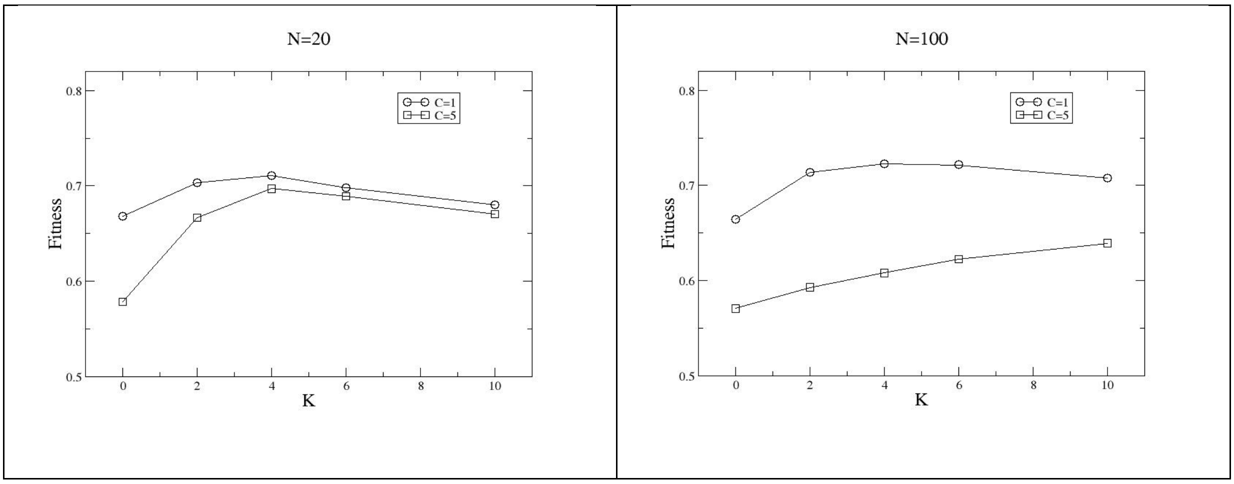


Figure 3: Showing the fitness reached by converged populations of coevolving asexual haploids after 20,000 generations on landscapes of varying ruggedness (*K*), coupling (*C*), and length (*N*).

3. Mating Types in the NKCS Model: Coevolving Sexes

The emergence of isogamy, ie, mating types, was not considered in the explanation for the evolution of two-step meiosis with recombination mentioned above [4]. However, the presence of allosomes - XY in animals and ZW in birds, some fish, reptiles, insects, etc. – can also be explained as a mechanism by which a haploid genome may vary the amount of learning it experiences when paired with another to form a diploid organism. Importantly, taking the view of the constituent haploid genomes, the presence of an heterogametic sex creates the situation where, as evolution converges upon optima, a given haploid containing the common (X or Z) allosome will typically experience two significantly different fitness values simultaneously within a population due to genetic differences between the two sexes; two fitness contributions from the common allosome will almost always exist with two mating types. It has recently been shown that the extra (approximate) fitness value information can prove beneficial to the learning/generalisation process described above by adding further landscape smoothing [5, p54+].

The NKCS model can be extended to consider the coevolution of diploids with mating types and sex chromosomes (Figure 4). To introduce autosomes and allosomes to the standard model, the original haploid genomes of length *N* are subdivided into *n*=2 equally sized chromosomes, i.e., there are 2*n* chromosomes per diploid. A (converged) sub-population of a homogametic sex is said to exist along with a (converged) sub-population of a heterogametic sex. Given the widely discussed role of female sexual selection upon males in birds, the ZW chromosome system is used here. A functional differentiation is imposed upon the heterogametic sex fitness function such that the fitness values in the table for the Z chromosome are constructed as usual and those for the W chromosome made by subtracting the corresponding value from 1.0.

Autosomes undergo two-step meiosis with recombination whereas allosomes do not undergo recombination (see [5, p59] for discussion). The sex of the offspring is determined by which allosome is (randomly) selected from the heterogametic sex. Once the resulting overall diploid genome is created, mutation is applied to each haploid as before.

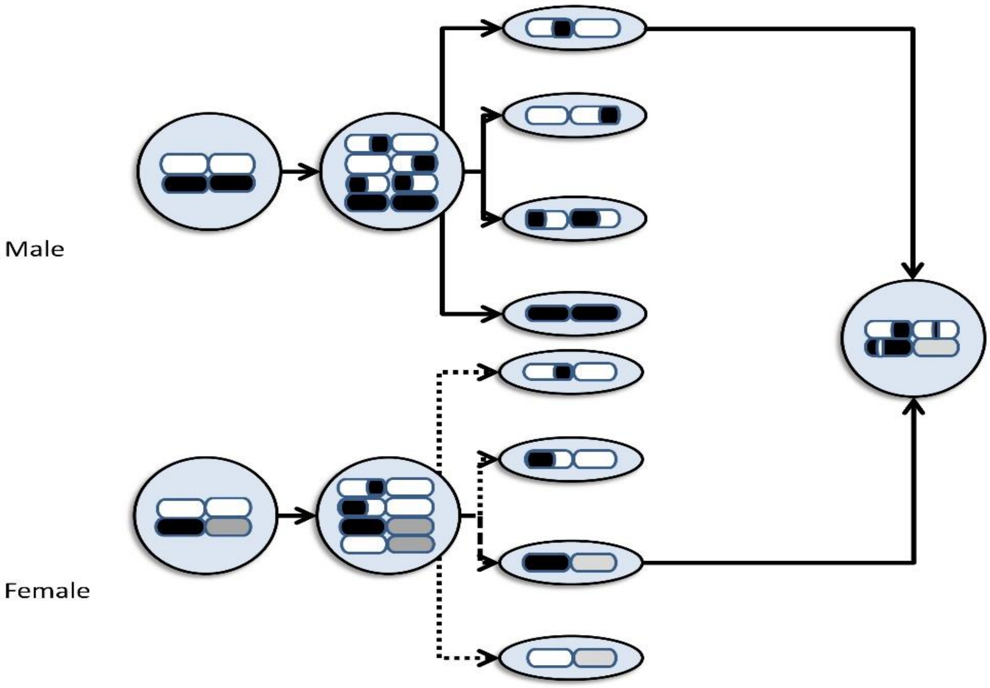


Figure 4: Showing the haploid-diploid cycle with two-step meiosis as implemented with converged sub-populations of females and males (ZW system assumed).

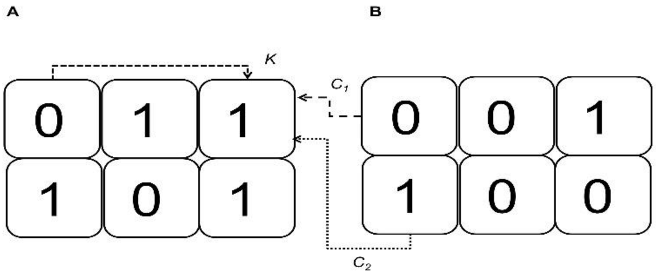


Figure 5: The NKCS model extended to diploids: Each gene is connected to *K* randomly chosen local genes and to *C* randomly chosen genes in *each* of the genomes in the other species/populations. Connections for one gene in one genome of one species/population shown for clarity. The fitness contribution of each *K* and *C* combination is found from the associated fitness table (Figure 1). Total fitnesses are normalised by 4*N*. Here *N*=3, *K*=1, *C*=1, *S*=1.

In their combined form as a diploid, each haploid genome will have the same fitness value and it will almost certainly differ from that of their corresponding haploid organism due to the interactions between the two genomes. After [4], the fitness of a diploid genome is here the average of its constituent haploids. For example, when X-inactivation occurs in mammals the choice is typically random per cell lineage in the placenta and hence the fitness contribution of the allosomes remains a composite of the two chromosomes. Although not included here for simplicity, the use of dominance in general is predicted to decrease with increasing K from the above explanation for the emergence of sex, as was subsequently demonstrated in [5, p57]. Figure 5 shows how epistatic connections are considered in a diploid where each gene depends on K local genes and C genes in each of the genomes of its partner. Here each gene can have two different fitness values depending upon the degree of homogeneity with its partner. Hence the overall fitness total of a diploid is in the range $[0,4N]$ and so the total is normalised by $4N$ to determine its fitness for selection, applied as above.

Figure 6 shows the typical behaviour seen for various combinations of genome size (N) and within (K) and between (C) sex dependence. As anticipated by the traditional model (Figure 3), increasing the dependence between the sexes increases the effects of their adaptations upon each other, with the average of the male and female fitnesses dropping as a consequence.

Whilst direct comparison to the traditional model above is not valid, comparison can be made to two asexual diploid populations coevolved on the same set of fitness landscapes. That is, following [4], the performance of sex in a coevolutionary context can be explored here. Recall that it was previously shown in a non-coevolutionary scenario that sex proves beneficial with increasing fitness landscape ruggedness (K) due an inherent smoothing effect. Figure 7 shows examples of how the same general benefit is seen with $N=20$, regardless of C, with sex resulting in higher fitness (T-test, $p<0.05$) when $K>2$. The same is seen when $N=100$, although only for $K>6$ when $C=1$. Hence sex appears to remain beneficial in the face of fitness landscape movement caused by coevolution.

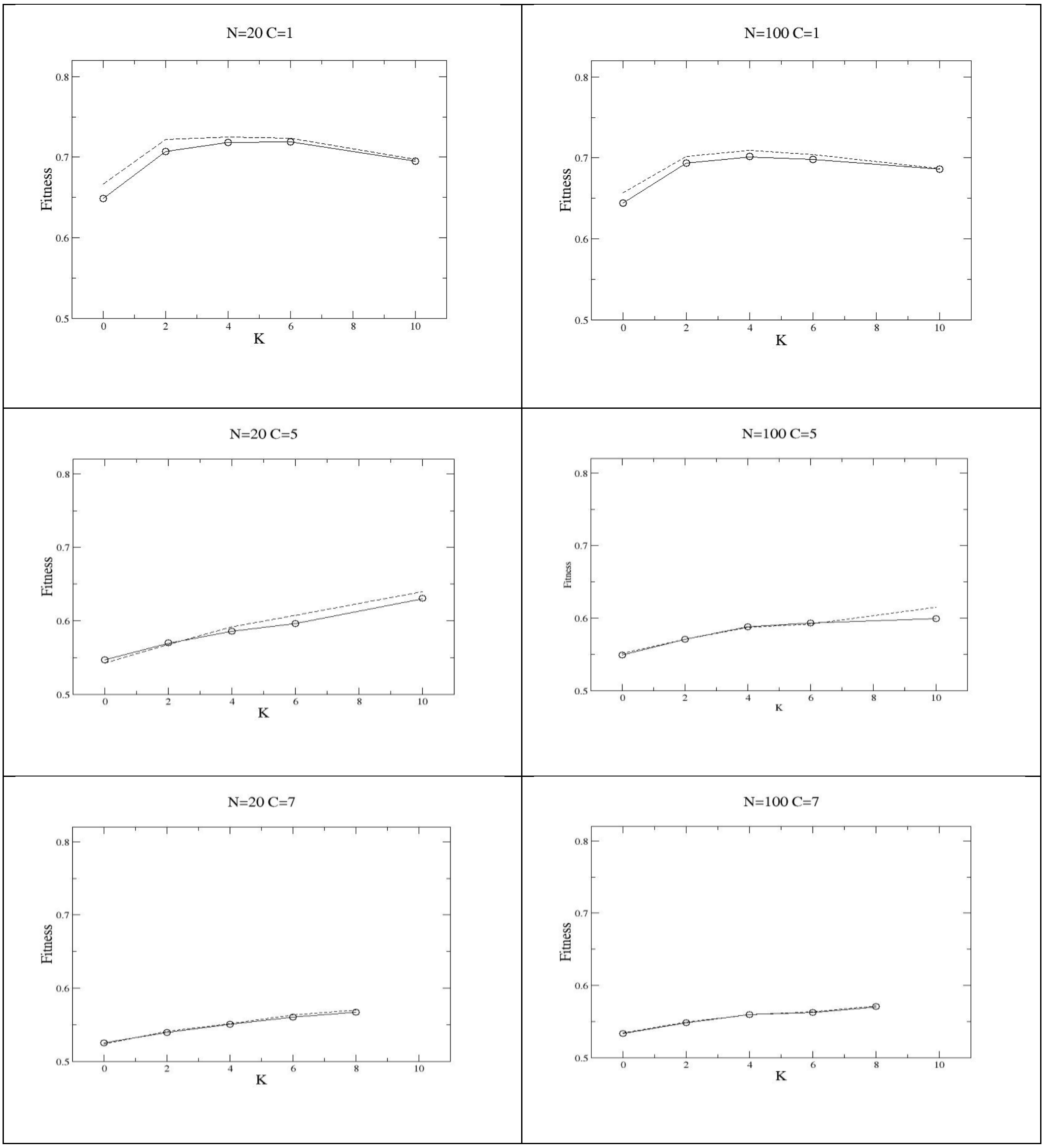


Figure 6: Showing the fitness reached after 20,000 generations for a sexual diploid species treated as a coevolutionary scenario on landscapes of varying ruggedness (*K*), coupling (*C*), and length (*N*). The fitness shown is the average of the males and females. The dashed line shows female fitness.

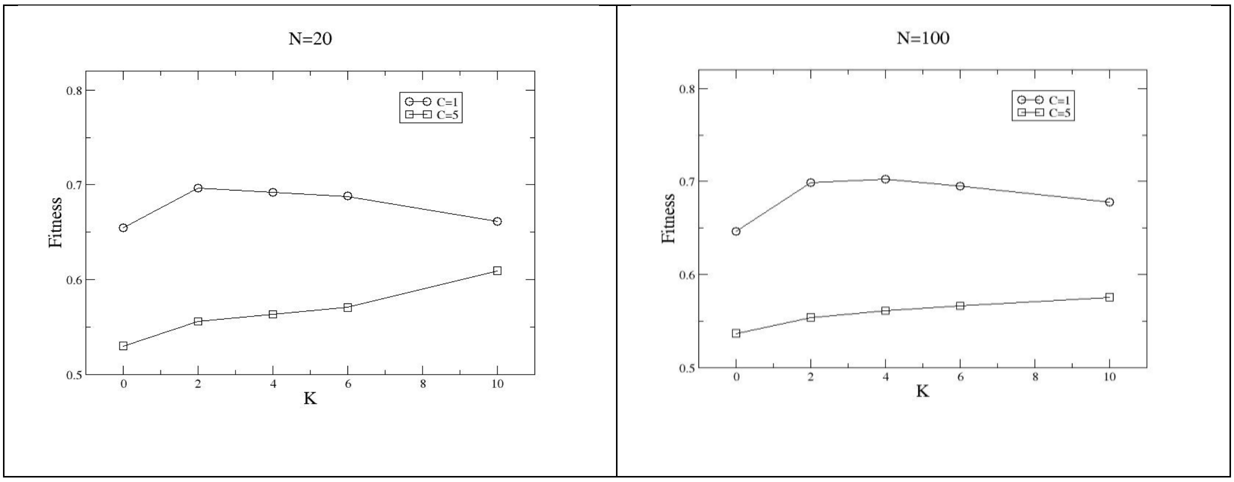


Figure 7: Showing the fitness reached by two populations of coevolving asexual diploids after 20,000 generations on landscapes of varying ruggedness (*K*), coupling (*C*), and length (*N*).

4. Sexual Selection in the NKCS Model

Mate choice sexual selection – whether pre and/or post mating – can be viewed as the imposition of one or more preferred traits by one sex upon the other. This selective pressure is a component of the overall selective pressure an organism experiences. Hence a male peacock’s train is no more an extravagance or handicap than a giraffe’s neck: both are the result of coevolution. It can also be noted that, as with any trait, any correlation between the imposed trait(s) and any other element of an organism’s selective pressure will typically be coincidental. And correlations, or a lack therefore, are likely to change with adaptations made by other organisms within the given organism’s coevolutionary environment over time. That is, “good gene” selection can be expected (eg, [6]) but not ubiquitously (e.g., [1]).

Under this view, the above NKCS model can be altered to include mate choice by the addition of an extra binary string said to represent a preferred set of *N* traits, created at random with the rest of the fitness function, by the choosing sex. Fitness for selection then becomes the fitness used in the previous section and the fraction of genes which match the imposed traits in both genomes of the other sex. Since females are typically the limiting factor in reproduction due to the frequency of opportunity, their investment in offspring rearing, etc., the females are assigned the random binary string of traits here. That is, overall fitness for selection in the male population is now in the range [0.0, 2.0] before normalisation.

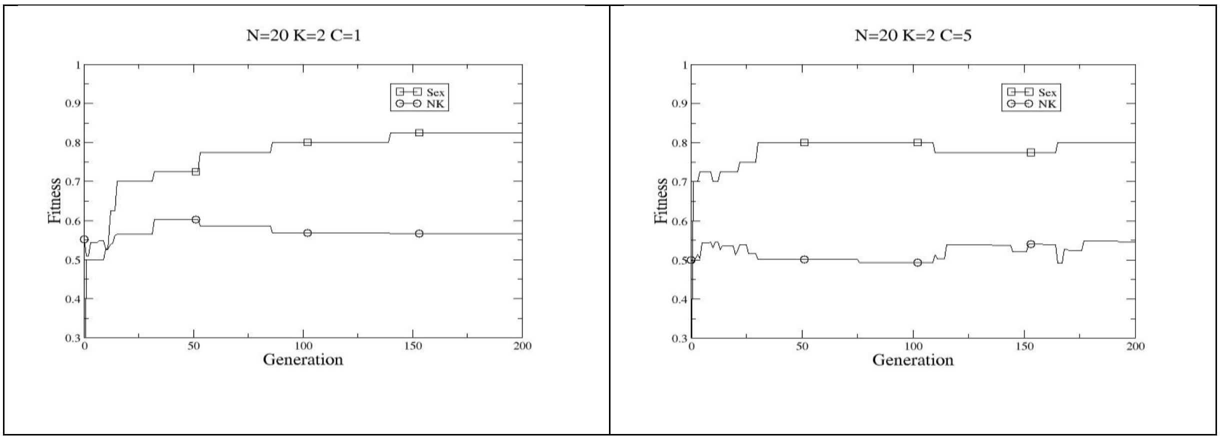


Figure 8: Showing example single runs of the typical behaviour of the NKCS model of coevolution between two sexes with sexual selection and different degrees of landscape coupling (*C*). Contrast with Figure 2.

Figure 8 shows example (co)evolutionary dynamics for the average species where the males' fitness includes the degree of match to the females' trait preferences. As can be seen, in contrast to the typical dynamics seen in such coevolutionary models above (Figure 2), the effects of mutual fitness landscape movement can be reduced as *C* increases. Comparing Figure 6 to Figure 9 shows how for *N*=20, with *C*<5 fitnesses – whether the females' or the species' average - are worse than without the intersexual selection, regardless of *K* (T-test, *p*<0.05). When *C*=5 the simple mechanism proves beneficial when *K*<4 and when *C*=7 for *K*<8 (T-test, *p*<0.05). In contrast, no benefit is seen when *N*=100 for all *K* (T-test, *p*≥0.05). Figure 9 also shows how the sexual selection fitness component of the males' fitnesses generally decreases with increasing *K* and is almost always lower when *N*=100 compared to when *N*=20*.*

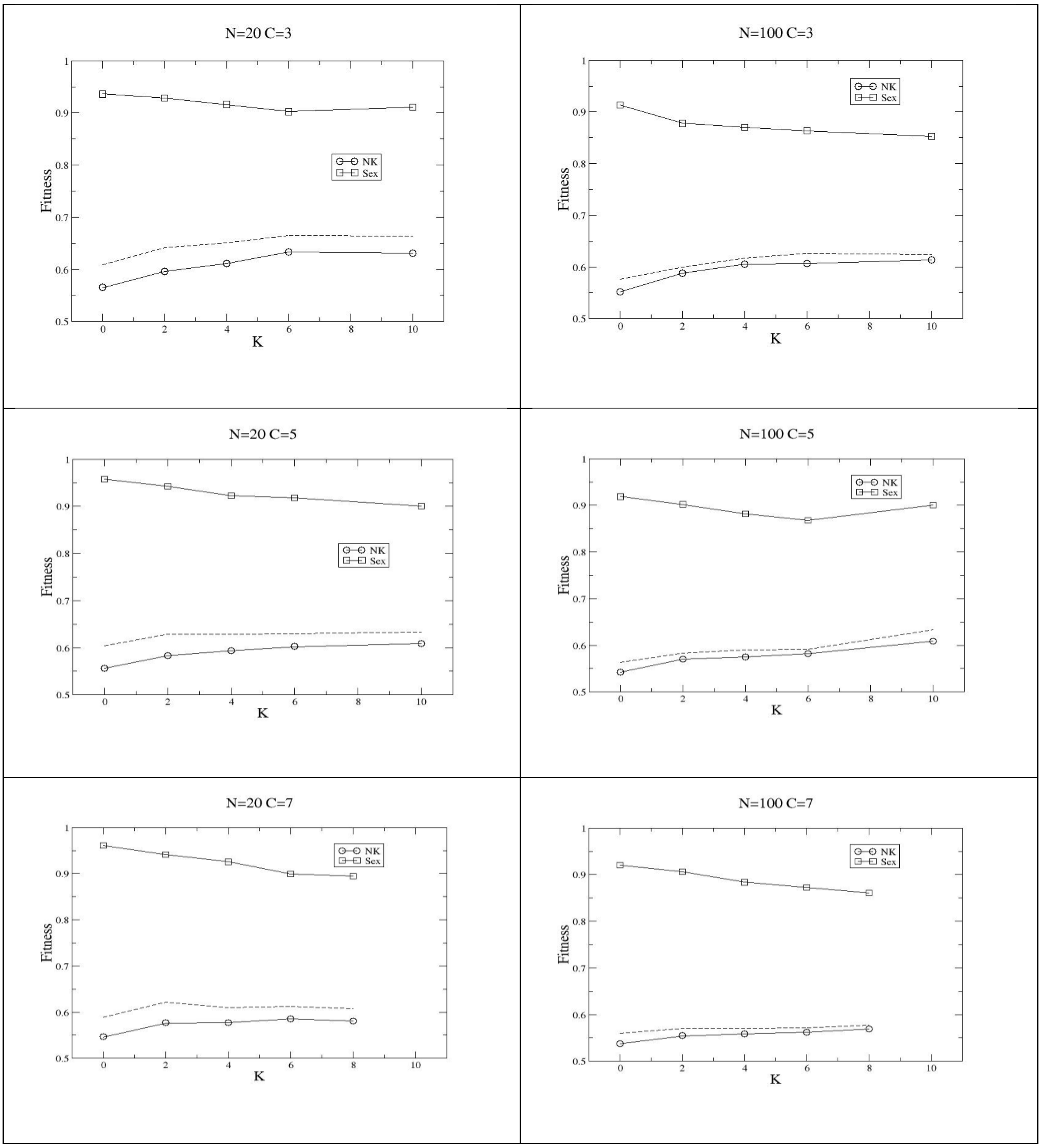


Figure 9: Showing the fitness (original and sexual) reached after 20,000 generations for a diploid species treated as a coevolutionary scenario exploiting simple sexual selection by females on landscapes of varying ruggedness (*K*), coupling (*C*), and length (*N*). The fitnesses shown are the average of the males and females. Dashed lines show female fitness.

The same general results are seen if the sexual selection component of male fitness is calculated using the fraction of trait match on the first genome only rather than both, and is significantly worse if the matching genome is chosen at random per generation (not shown). Similarly, if the template is reduced in size, i.e., the number of traits is reduced, from *N* to *N*/2 such that matching only occurs on the two sex chromosomes, results remain the same as in Figure 9 (not shown).

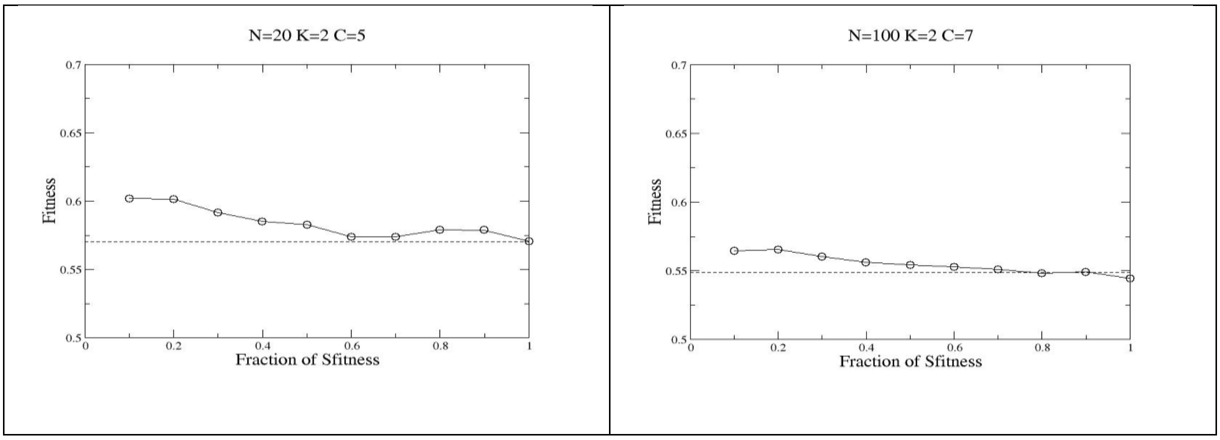


Figure 10: Showing examples of how varying the weighting/strength of sexual selection affects species' fitness after 20,000 generations. The dashed line shows fitness without sexual selection (Figure 6).

In the above, intersexual selection fitness was equally weighted (0.5) with the underlying NKCS fitness function – male selection fitness was the sum of the two values. Figure 10 shows examples of how varying the weighting can vary the benefits of sexual selection, particularly for lower values (<0.5). These results suggest that tuning the strength of sexual selection to match the underlying coevolutionary dynamics represents an important adaptive mechanism for a species (e.g., see [8] for discussion in dynamic environments).

Thus far the preferred traits of the choosing sex were incorporated as a separate component of the overall fitness landscape of the other sex – and they were unchanged throughout evolution. Of course, this unlikely to be the case generally. Figure 11 shows examples of how varying the frequency of changing one randomly chosen preferred trait can vary the benefits of intersexual selection. As can be seen, the benefit of the simple mechanism is lost as the frequency of change increases and so they can be expected to evolve relatively slowly. It can be noted that, in birds, whilst sexual selection is known to accelerate the evolution of mating traits compared to other traits in males, no similar effect is seen in females [14].

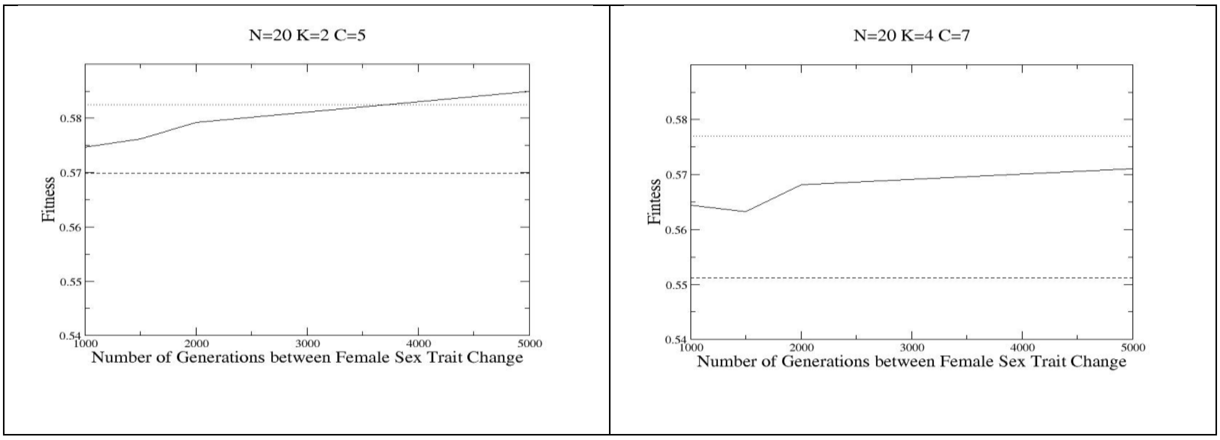


Figure 11: Showing examples of how the rate of varying the preferred traits of the female affects species' fitness after 20,000 generations. The dotted line shows fitness with unchanging traits (Figure 9) and the dashed line shows fitness without sexual selection (Figure 6).

Finally, Figure 12 shows results from when both males and females are exploiting the simple sexual selection mechanism. When $N=20$ and $C<5$, fitnesses are worse than without sexual selection (Figure 6) for all K (T-test, $p<0.05$), the same when $C=5$ for all K (T-test, $p \geq 0.05$), and when $C=7$ fitnesses are improved for $K>2$ (T-test, $p<0.05$). When $N=100$ and $C<5$ fitnesses are worse for all K (T-test, $p<0.05$), when $C=5$ they are worse when $K<2$ and better when $K>4$, and when $C=7$ fitnesses are improved when $K>2$ (T-test, $p<0.05$). Recall that no benefit was seen from one mate exploiting sexual selection in the more complex case of $N=100$ above. Further, in comparison to one mate using the mechanism (Figure 9), there is no significant change when $N=20$. When $N=100$, for $C<7$ and $K<4$ fitnesses are worse but improved when $K>4$ (T-test, $p<0.05$). Similarly, when $C=7$ fitness are worse when $K<2$ and improved when $K>2$. Hence a benefit is again typically seen with increasing C.

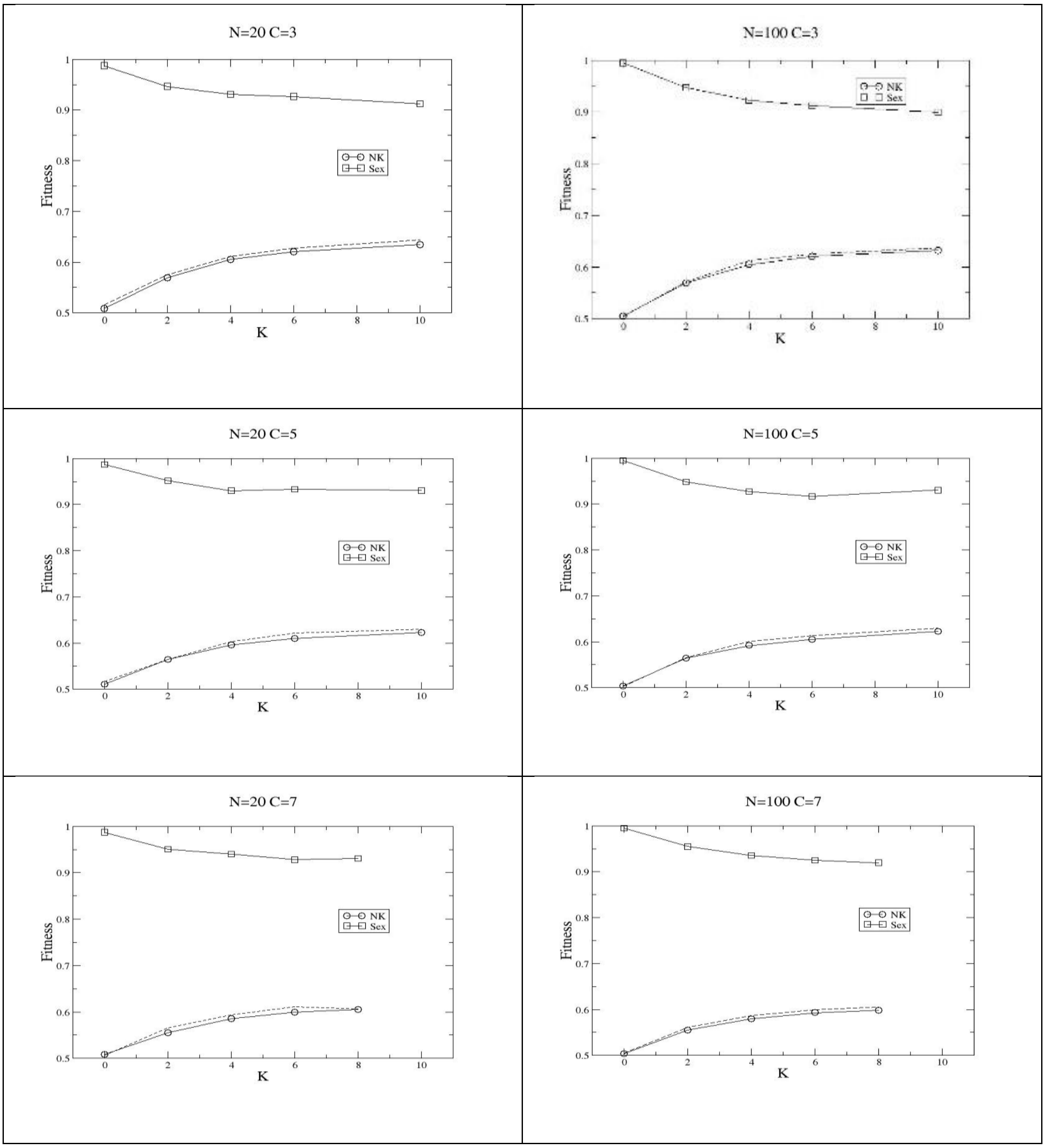


Figure 12: Showing the fitness (original and sexual) reached after 20,000 generations for a sexual diploid species treated as a coevolutionary scenario exploiting simple sexual selection by *both* females and males on landscapes of varying ruggedness (*K*), coupling (*C*), and length (*N*). The fitnesses shown are the averages of the males and females. Dashed lines show female original fitness.

Conclusion

This paper has considered intersexual selection as within species coevolution caused by the emergence of sex chromosomes. Using the NKCS model, the typical behaviour seen for various combinations of genome size (N) and within (K) and between (C) sex dependence have been explored with and without the extra selection component. As anticipated by the traditional model, increasing the dependence between the sexes increases the effects of their adaptations upon each other, with fitnesses dropping as a consequence. Possible sources of high dependence between the sexes include the obligate nature of their reproduction, offspring rearing, social structures, etc.

It has been suggested that in its simplest form, mate choice can be viewed as the imposition of one or more preferred traits by one sex upon the other. Significantly, this result removes the need for any degree of correlation between the fitness pressures of either sex for intersexual selection to evolve. Thereafter, selection may fine-tune the preferred traits, to the benefit or detriment of the other sex. Selecting for more pronounced, and therefore less ambiguous, traits may follow, for example. It has been shown that under the coevolutionary view, even if that trait choice is arbitrary (random), this represents a mechanism by which the degrees of evolutionary freedom of one sex are reduced by the other, i.e., it reduces the amount of fitness landscape movement *if* the preferred traits represent a relatively steady (target) component of the overall selection pressure experienced. This might emerge since females consistently preferring a certain trait(s) in their male partner during their lifetime would potentially reduce the variance they experience in nesting, offspring rearing, etc. in comparison to selecting a mate at random each time. Reducing variance over evolutionary time typically increases fitness. Moreover, this is seen to be true for both female fitness and the overall species/population fitness (see [7] for related discussions).

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