

**Sex promotes gamete selection:
A quantitative comparative study of features favoring the evolution of sex**

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Abstract: Explaining the maintenance of sexual reproduction remains one of the greatest challenges in biology. The theoretical oddity of sex is based on at least three advantages that asexual organisms have over sexual ones: 1- Asexuals, by not producing males, have a two fold advantage over sexuals, regarding the number of reproductive individuals; 2- Sexuals have an evolutionary disadvantage over asexuals, in that a rare alleles that increases fitness of one parent, for example, is not necessarily transmitted to the offspring, due to segregation. 3- Asexuals do not have to find a mate in order to reproduce. Here I present the results of evolutionary tournaments performed using the agent based computer simulation Biodynamica. The tournaments explored the relative merits of various features that have been proposed to affect the putative advantages of sexual reproduction, including ploidy, mate selection, large reproductive variance of males, low mutation rates, gamete selection, reduced cost for the production of males, thelytoky vs. parthenogenesis, variable environments and complex genomes. The model allowed for a quantitative comparison of the effect of these features on the adaptive value of sex. The results showed that the production of large number of gametes (for example “masting” in massive flowering of trees or spermatozoa of most animals) inducing gamete selection, together with: non random mate selection, increased variance in male reproductive success and/or low mutation rates, allowed sexual agents to out-breed asexual ones, despite the three disadvantages for sex cited above. The work suggests that gamete cycles and alloigenesis, common to most sexual plants, fungi and animals, should be viewed as a new level for natural selection to work. Mate and gamete selection are more efficient in the use of biomass, energy and time, than natural selection at the level of organisms, helping to make sexual reproduction an evolutionary success.

INTRODUCTION

What selective forces maintain sexual reproduction and genetic recombination in nature? The answer to this question has been an elusive mystery (1-3). Asexual reproduction is theoretically much more likely to occur than sexual one due to at least three inherent advantages: 1- parthenogenic females do not need to find mates; 2- they produce twice as many daughters and four times as many granddaughters compared to the average sexual ones; 3- and natural selection drives adaptation and thus selection of relevant genetic traits much faster in asexual organisms compared to sexual ones, as an allele that increases fitness to one of the parents is not necessarily transmitted to the offspring due to segregation (1). The first two advantages cited are also enjoyed by sexual organisms with no separation of sexes, such as certain types of hermaphrodites. Despite these relative theoretical advantages of asexuality, most of the higher organisms are sexual.

Various hypotheses have been put forward to explain this mystery (4, for example). I will group them into four broad categories:

1- The ecological genetic models, that state that the genetic information needed for successful adaptation, when tracking ever changing environments, is better produced and saved with recombination. For example, the Red Queen Hypothesis postulates that sex is adaptive in variable environments or under variable parasite pressure, because it enables genetic variation, rapidly creating and spreading advantageous traits in the population (5-8). However, simulations of diploid organisms, with algorithms designed to guaranteed random mating, showed that the Red Queen Hypothesis is not sufficient in explaining the maintenance of sex (9)

2- The mutation models, which are of two kinds. The positive mutation models or Fisher-Muller hypothesis (10-13, for example), propose that sex, allowing for recombination, is advantageous because it allows beneficial mutations that arise in different individuals to be placed together on the same genome. The negative mutation models or the mutation-accumulation models (14-20), which suggest that sex is adaptive because it performs, through recombination, the efficient removal of deleterious mutations. However, there are no widely accepted convincing demonstrations, using simulations, nor good experimental evidences, to support these arguments.

3- The selection models, which assume that sex allows the working of new levels of selection. For example, germline competition (21), mate selection (see review in 22) and gamete selection (22), which emerges because of sex, allow for the selection of 'good genes' by orientating the evolutionary process towards the fixation of beneficial traits (23-26). Specifically, assortative mating (mating between genetically similar individuals) has been shown to be very successful in increasing the fitness of sexual species (27-29). Assortative mating accelerates adaptation by dampening the disruptive effect of large genetic variance in populations, allowing for a modulation of sexual reproduction in ways that allows an optimization of variance.

4- Sex, allowing for the existence of males, may intensify natural selection on them. Recent propositions suggest that differential male mating success (higher variance in male than in female fitness), can drastically reduce mutational load in sexual populations with or without any form of epistasis (30-32), adding evidence to the suggestion that in sexual reproduction, male organisms are the preferred vehicles for selection, when males show greater reproductive variance than females. This seems to be the case in haplo-diploid organisms where adaptation is accelerated in relation to pure diploids (33), and where selection of males implies automatically the selection of a single set of alleles.

Simulation experiments have shown that at least three features favor sexual reproduction.

1- Diploidy or haplo-diploidy favors sex if compared to haploid or polyploid organisms (24). This result is congruent with the known fact that in nature there is an abundance of sexual organisms among diploids and a scarcity of sex among haploid organisms.

2- Sex provides advantage in changing heterogeneous environments. Thus, realistic simulations have to include complex and changing environments (see review in 34).

3- Sex introduces a possibility for a harmonious evolution of complex genomes, where optimal levels of genetic variation are required. That is, sex allows the creation of different sets of alleles and reshuffles them on different genomes until optimum combinations are achieved through natural selection of the organisms expressing the genome. This advantage is visible only if a sufficient large number of evolving loci is simulated (13, 29).

Thus, any realistic simulations have to contemplate agents that adapt to changing environments by mutating and recombining a diploid multiloci genome. The simulations presented here incorporate these features.

The adaptive value of sex may be found in an additive or in a synergistic combination of several factors (34, for example), which can not be evidenced using analytical methods nor simple linear analysis. In addition, each author has used its own analytical framework and thus, quantitative comparisons between the various different propositions for the adaptive value of sex and recombination have been lacking. Here I use an agent based computer model that allows the simulation of several of the proposed mechanism discussed above, allowing to compare the proposed putative adaptive features, simulating the various forms of sex known to exist in nature. The model *Biodynamica* used here has been “validated” by showing to have heuristic properties in explaining or predicting experimental data. The model was successful in explaining many aspects of the emergence of genetic resistance to antibiotics and pesticides (35); it predicted divergent behavior in the production of males in facultative sexual nematodes (36); and it predicted the importance of economic aspects in the evolution of social behavior (37).

In the present study, the model *Biodynamica* was used to explore quantitatively the relative advantages of various features that have been proposed to affect sexual reproduction. These features include: ploidy, mate selection (assortative mating and selection for "good genes"), large reproductive variance of males, low mutation rates, gamete selection, reduced cost for the production of males, thelytoky vs. parthenogenesis, variable environments and complex genomes. The exploration was made in the form of evolutionary tournaments between the various features listed

METHODS

The simulation model *Biodynamica* (see 24-25, 28-29, 33, 35, software available at 45) was used. This multi-agent adaptive model simulates each individual as an autonomous agent (organism) that interacts with the environment and with other individuals, according to five evolutionary steps (see below) and to the alleles each agent carries in its various loci, as given in Table 1. Simulations consisted of competitions between agents expressing alleles coding for different reproductive strategies. That is, a population was created in which alleles were initially distributed randomly among the corresponding loci of all agents. Only two alleles coding for different reproductive strategies (in general, monosexual diploid vs. the strategy to be tested), were monitored in each simulation, and the other genes were left to evolve freely. The frequency of occurrence of each of these two alleles, coding for different reproductive strategies, in the surviving agents, was monitored during the evolutionary process. The sexual types simulated were: asexual or monosexual haploids (parthenogenetic), monosexual diploids (thelytoky), bisexual, haplo-diploid and hermaphrodites. Other types of reproduction, such as clonal reproduction of diploids were explored elsewhere (24, 29). The population of agents, after being created, suffered a 5 step evolutionary process, which was repeated each time step. The detailed code can be read on the help feature of *Biodynamica*. In summary, the algorithms of the computer simulation model achieved the following:

Mate selection: Females of bisexual species choose a male of the same species, whereas hermaphrodites mated with any conspecific individual. When random mating was simulated, females and hermaphrodites mated with a randomly chosen mate, whereas in assortative mating females and hermaphrodites mated with the genetically most similar mate among 20 randomly chosen individuals (an exhaustive exploration of this parameter can be found in 25). Genetic similarity was estimated by comparing the phenotypes of both individuals. When no sexually mature mate was found by a females or hermaphrodites, the individual did not reproduce during that time step if bisexual, or reproduced monosexually if hermaphrodite.

Reproduction: The reproductive strategy applied for haploid or diploid organisms. Bisexual organisms could mate randomly or assortatively. Monosexual organisms did not mate and simulated parthenogenesis or thelytoky: In monosexual haploids (asexuals), the individual transmitted all its genes to the offspring (cloning) with no variance except that allowed by mutations, simulating asexuality. Monosexual diploids did not mate and produced offspring by uniform random crossovers of the alleles in each loci of the parent. Bisexuals produced equal numbers of males and females randomly. Males could mate several times each time step but only females or hermaphrodites could bear offspring. Non mated bisexual females did not reproduce. Hermaphrodites tested here produced only females and reproduced similar to bisexuals if finding another hermaphroditic female, or else reproduced as the corresponding monosexuals. Hermaphrodites thus, mated assortatively with females having the same disposition for sex, even when mating randomly regarding all other loci. In haplo-diploid reproduction, males were haploid and females diploid and males developed from unfertilized females. Females produced offspring according to an algorithm based on genetically and phenotypically determined clutch size (see Table 1), transmitting their genes following Mendelian rules of independent assortment (free recombination). If sexual, each parent provided half of its alleles to the newborn, so that for each locus, one allele came from each parent if diploid, or each parent had a probability of 0.5 to transmit its allele to each locus if the organism was haploid or the offspring a haplo-diploid male. Bisexual organisms paid the two fold cost of sex, if compared to monosexual organisms, due to the explicit simulation of males, except for sexual hermaphrodites, where all individuals could produce offspring.

Variation: In each offspring, randomly selected genes mutated, changing their allelic value randomly. The probability of a mutation occurring in a given offspring was determined by the value of the allele in gene 2 (Table 1). A more detailed exploration of the effect of various mutation rates on the outcome of simulations with Biodynamica is given in (29)

Phenotypic expression: As commonly done with genetic algorithms (and as it is known to occur frequently in real organisms), total allelic dominance was simulated. That is, in diploid organisms, only one allele per loci was expressed phenotypically during the lifetime of each organism. The allele to be expressed phenotypically was selected randomly at birth. Of course, many other ways to model phenotypic expression exist, such as additivity of alleles, dominance, etc. Some of them have been explored previously with Biodynamica. For example, in (29) simulations of dominance or recessiveness, improved or diminished the odds of a given allele to spread in a population. The system simulated here gives results that are intermediate to dominance and recessiveness. Additivity was not simulated as most phenotypic features modeled had non-linear properties (see Table 1)

Selection: The model did not use simplified fitness functions, but reproduction and individual survival were decomposed into different aspects for selection to act. Individuals were excluded from the population at the end of each time step when their age exceeded their genetically prefixed life span. The survival of individuals was in addition dependent on population density, where survival probability was 0 if $r_1 * N_t \geq ops * r_2$ and 1 if $r_1 * N_t < ops * r_2$; where ops is the optimal population size or carrying capacity, N_t the population size at time-step t and r_1 and r_2 are random real numbers uniformly distributed between 0 and 1. Individuals not possessing the resistant phenotype of genes 6 to 8 in Table 1 were killed randomly, with probabilities that varied randomly each time step from 0 to 0.9, simulating an environment in which three different biocides or parasites trimmed the population by killing non resistant individuals. (For simulations using capricious parasites subjected to fluctuating epistasis see 9).

Optimal size of populations was 800 and the initial size of the populations was 400 but reached 800 individuals after 4 to 8 time steps. Other values were also explored but the results are omitted, as they did not change the findings presented here. The present parameters were chosen as they produced the most clear-cut outcome. Any combination of parameters can be run using the model Biodynamica available from the web.

All reproductive systems were modeled as indicated elsewhere (29), except for sperm selection (Sp) which was modeled for the first time here, in two different formats: Sp(10,3) male produced 10 haploid spermatozoa, each containing one allele per loci taken from the father's diploid genome at random. The spermatozoon possessing the alleles with the lowest value in loci 6, 7 and 8 (see Table 1), i.e. showing resistance towards biocides, was used to fertilize a randomly chosen haploid gamete from the female, following the rules of meiosis. Sp(30,5) males produced 30 spermatozoa that were selected based on alleles with the largest values in loci 3 and 4, i.e. expressing a proxy for increased survival probability and fertility, and the lowest value in loci 6, 7 and 8 (see Table 1). Other combinations than Sp(10,3) and Sp (30,5) were tested and produced intermediate results, congruent with what is reported here, and thus, are not further presented here. The features chosen for sperm selection were those that had previously shown a positive effect on adaptation when studying mate selection (25). Different male variance in reproduction was achieved by modeling different life histories for female and male fertility. Retarding male reproductive maturity relative to females decreased the reproductive variance of males.

During the tournaments, agents coding for sexual reproduction did not reproduce with agents coding for monosexuality. The tournaments presented simulated variable environments, diploidy, and the presence of more than four loci suffering adaptation, as previous studies showed the relevance of these features to the evolutionary maintenance of sex (24, 29).

Table 1: Genes or loci and their possible alleles defining the agents-organisms. Simulations allowed mutant alleles to appear in the range given below. Initial populations had individuals possessing alleles indicated in that range.

Gene	Range for values of alleles	Effect on phenotype or meaning of the value of the allele
1	0-4	Reproductive strategy: monosexual haploid (0), monosexual diploid (allele 1), bisexual diploid (2), haplo-diploid (3), hermaphrodite diploid (4).
2	0-10	Mutation rate: from 0.2 (allele 0) to 10^{-7} (allele 10) mutations per gene in logarithmic decrements
3	0-10	Maximum life span coding for life spans from 0 to 10 time steps.
4	0-10	Clutch size from 0 to 10 offspring.
5	0-5	Minimum age for initiating reproduction of females in number of time steps.
6	0-10	Resistance to biocide 1: Only allele 0 was resistant to that biocide.
7	0-10	Resistance to biocide 2: Idem as gene 6 but for biocide 2.
8	0-10	Resistance to biocide 3: Idem as gene 6 but for biocide 3.
9	1-30	Number of spermatozoa produced by males
10	1-5	Number of genes expressed in the spermatozoa
11	0-1	Mating strategy (0= random mating, 1 = assortative mating)

When the behavior of a given parameters was explored through simulations, it did not suffer mutations. An allelic value was then assigned to the parameter and that value was kept constant during that specific simulation.

The model allowed for more sophisticated trade offs associated with reproduction, such as penalizing individual born into a large clutch by assigning it a higher mortality, and others (see 24, 25, 29, 33, 35). These trade offs, however, did not affect the relative advantages of the features studied here, and thus, in order to keep the model as simple as possible, these features were dropped.

RESULTS

Figure 1 shows the results of tournament between monosexual diploid agents (organisms reproducing by thelytoky), and organisms with the reproductive system indicated in the vertical axis. Initially, each of the alleles coding for these two reproductive strategies, was carried by 50% of the population. The figure presents the percentage of agents expressing the reproductive system indicated, after simulating 20 time steps (shorter simulations produced results closer to the 50% line and longer simulations produced results more distanced from that line, until populations under the 50% line disappeared as the were completely overtaken by thelytoky).

The results show that bisexual diploid agents suffering high mutation rates (Bi+Hm) performed worst. That is, agents with alleles coding for this strategy were rapidly displaced by

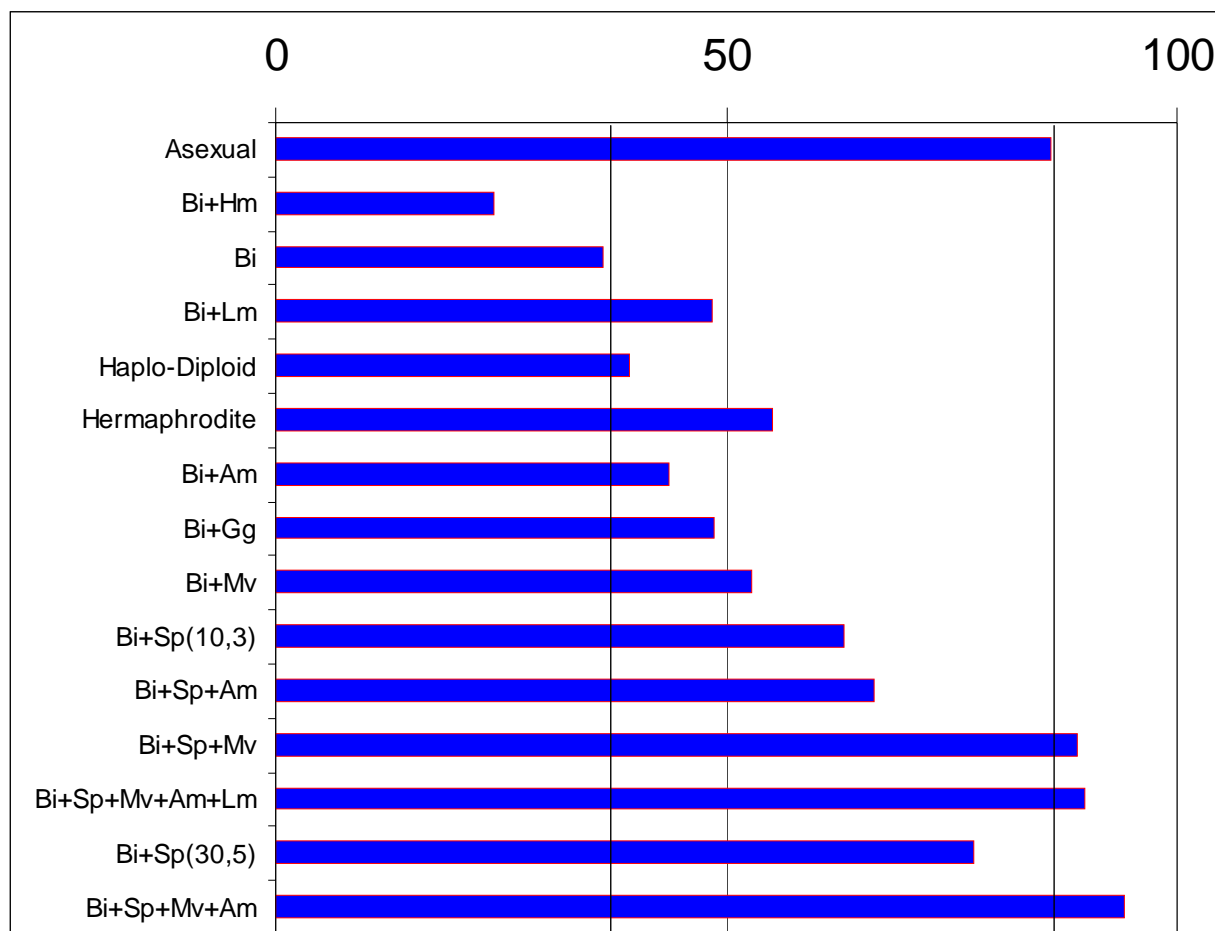
monosexual diploid agents in the simulated evolutionary process. Bisexual diploids with males suffering twice as much reproductive variance as their females (Bi+Mv) outbreed monosexual diploids in these tournaments (i.e. more than 50 % of the alleles in the population became Bi+Mv in 20 time steps), despite suffering from the two fold disadvantage of sex as 50 % of the individuals they breed were males. Hermaphrodites, which in the present simulation do not pay the two fold cost of sexuality, also outbreed monosexual diploids. Low mutation rates (Bi+Lm), agents choosing mates based on assortative mating (Bi+Am) and agents selecting males with “good genes” (Bi+Gg) improved the competitiveness of bisexual diploids (Bi) only slightly. These results roughly confirm previous work mentioned above, showing that low mutations, greater variance in male reproductive success, assortative mating, mating with males possessing ‘good genes’, and hermaphrodites increase the adaptive value of bisexuals.

A surprising result was the strong positive effect of simulating spermatozoa, on the competitiveness of bisexual diploids. This strategy was more successful the more spermatozoa were simulated and the more genes were expressed in the spermatozoa (compare Bi+Sp(10,3) and Bi+Sp(30,5)). Other features had an additive effect on the competitiveness gained by the presence of spermatozoa, as the increased success of “combo” strategies showed (compare Bi+Sp(10,3) with Bi+Sp+Am and Bi+Sp+Mv). Adding a multitude of strategies does not seem to have dramatic effects on the competitiveness of bisexual agents (Bi+Sp+Mv+Am+Lm). A very successful combo strategy was simulating large number of spermatozoa and of genes expressed in these spermatozoa together with assortative mating and larger male reproductive variance (Bi+Sp+Mv+Am). These combo strategies were the only ones to out-compete the asexual strategy (monosexual haploids).

As the competitiveness of a given strategy may vary when the partners in the tournament vary, I made tournaments between asexual organism (monosexual haploids reproducing by cloning) and bisexual “combo” organism of the type Bi+Sp(30,5)+Mv+Am. These organisms outbreed asexual organisms in 66 % of the tournaments in less than 20 time steps, in the presence of the two-fold cost of sex (2000 simulations).

Tournaments between a mix of agents, each using one of the sexual strategies mentioned, showed that agents expressing spermatozoa out-breed all others most of the time. That is, the odds of out-breeding all other agent types after 20 time steps, calculated from 2000 simulations was: 40% for bisexuals producing spermatozoa, 26% for asexuals, 11% for haplo-diploids, 10% for hermaphrodites, 9% for bisexuals and 4% for monosexual diploids. In male producing species, agents used assortative mating and males had larger reproductive variance than females. Similar results can be obtained by downloading the program Biodynamica (<http://atta.labb.usb.vc/Klaus/Programas.htm>) and running Demo24.

Figure 1: Percent of alleles of the given reproductive strategy present in a population of 800 agents in relation to alleles coding for monosexual diploids (thelytoky), when alleles coding for both strategies are competing between them in a single population. Bars smaller than 50% indicate strategies less efficient than monosexual diploids; bars larger than 50% indicate strategies that are more successful than the monosexual diploids. Each bar is the average of 2000 simulations using the agent based computer simulation Biodynamica (Jaffe, 1995). Tournaments were run, starting with populations having a 50/50 proportion of alleles for monosexuality and for the ones indicated in the y axis. Abbreviations indicate; Bi: bisexual, Haplo-Diploid: females are diploid and males haploid, Am: assortative mating, Gg: females select males for good genes, Mv: reproductive variance in males was twice the variance for females, Lm: low mutation rate was 0.008 mutations per loci, Hm: high mutation rate was 0.2 mutations per loci. Else 0.04 random mutations per loci were simulated. Sp(x,y) indicate simulation of x spermatozoa per male expressing y genes.



I simulated a population of agents possessing alleles coding for number of spermatozoa produced by the male, and the number of genes expressed in each spermatozoa (alleles 9 and 10 in Table 1). The alleles were distributed initially randomly and uniformly and they were allowed to mutate and evolve. When monitored over a 100 time-step period, we observe that the frequency distribution of alleles shifts towards alleles coding for larger number of spermatozoa (Figure 2) and for larger number of genes expressed by spermatozoa (Figure 3). Thus, clearly, large number

of spermatozoa and large number of genes expressed by spermatozoa are adaptive features in the present virtual scenario.

Figure 2: Average of results from 200 simulations of populations of 1000 agents evolving in changing environment.

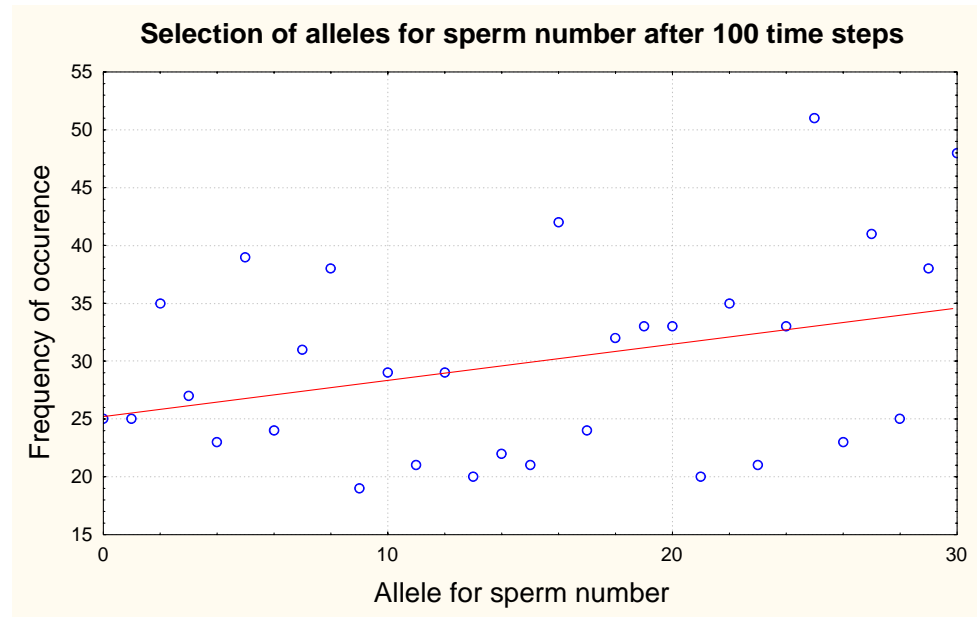


Figure 3: Average of results from 200 simulations of populations of 1000 agents evolving in changing environment.



DISCUSSION

The results of the tournaments show that the various proposed adaptive advantages of sex tested, improve the performance of sex, *vis a vis* non sexual alternatives. However, none of these features on their own give a definite advantage over asexuality. Only when a gamete selection mechanism is modeled, such as spermatozoa selection, together with a selection mechanism of males, sex becomes indisputable superior to no-sex. That is, the more “non-limiting” selection the genome suffers (through gamete selection and/or mate selection) prior to fertilization, the more efficient the evolutionary process becomes. “Non-limiting” refers here to selection that does not necessarily reduce the reproductive output of the individual.

The simulation results clearly show that not all the features proposed to favor the emergence and/or maintenance of sex have the same weight in terms of their effect on the evolutionary dynamics. Although all the features that had been reported to favor the maintenance of sex, when tested with Biodynamica, actually favored the emergence of sexual strategies in the virtual organisms simulated, they did it in widely different degrees. The single most successful feature tested, favoring sex, was gamete selection.

An evolutionary advantage gamete selection may provide is the opportunity for selection to act on haploid gametes, where single strings of alleles may be expressed without a shielding effect of the twin alleles. This provides an opportunity for efficiently weeding out incompatible combination of alleles, deleterious mutations and other non adaptive genetic features, prior to the production of costly organisms that are then subjected to natural selection. This potentially enormous advantage may explain why all sexual organisms have a gamete cycles (generational alternance, alloigenesis or metagenesis). Males of most diploid species produce huge numbers of spermatozoa. This feature may be adaptive because it provides the opportunity for spermatozoa selection to occur. Strong spermatozoa selection augments the likelihood that genomes lack incompatible combinations of alleles from different loci and that they possess high genetic quality, increasing the speed and flexibility of adaptation (38). In real organisms, each spermatozoon is practically unique in its particular combination of alleles due to spermiogenesis, and only few of these unique genetic combinations can actually be submitted to natural selection by producing a viable offspring. A proposed mechanism favoring the evolutionary emergence of gamete selection is genetic compatibility (39). This would imply that spermatozoa are strongly selected for genetic compatibility by proteins and immuno-active chemicals in the vaginal secretions. Sterility achieved due to immuno-incompatibility between couples, expressed at the level of spermatozoa in the Fallopian tubes, is very well known in humans and other mammal species.

Another complementary process may well be spermatozoa selection. Seminal plasma (and vaginal fluids) provide an environment where spermatozoa with a low deleterious mutation load and with a good working biochemical-metabolic engine that depends on critical proteins (40), are more likely to survive. The odds of producing a haploid genome for a spermatozoa by mitosis, that contains the “best” alleles from all the loci in the precursor diploid genome, is proportional to g^2 , where g is the number of loci that may affect the outcome of sperm selection. Thus, an efficient sperm selection system, acting on a few hundred house keeping proteins expressed in a healthy spermatozoa, will require hundred of thousands spermatozoa, in order to select the “best” combination of alleles available in the fathers genome.

Sperm selection may also eliminate deleterious mutations, if the mutations affect the spermatozoa's phenotype. Experimental evidence for lower motility and lower fertility in mutated spermatozoa is available (see 41 for example).

It is often believed that spermatozoa express the genotype of the diploid parent so that all spermatozoa from a single individual or phenotypically identical. This assumes that the haploid genotype lies dormant and is not expressed. This mechanism has been proposed as a way to prevent selfish alleles competing within the ejaculate (See 3 for a revision). Although the working of such a mechanism can not be excluded in all cases, it clearly does not apply in many cases. Spermiogenesis allows the expression of the haploid genome before chromatin condensation and the formation of the final spermatozoon (42). Another evident case is found in haplodiploid organisms, which have haploid males and thus this mechanism can not work. In many instances, including diploid vertebrates, direct or indirect evidence for unique spermatozoa phenotypes have been found (43-44). Thus, even if only a few genes are expressed phenotypically, and these genes are central to basic protein networks (40), spermatozoa selection would be an important driving force of evolution in sexual organisms. Other physiological and developmental mechanisms, such as germline competition (21) would also achieve a similar result.

The simulations presented here simulated selection of male gametes. Selection of female gametes is also possible and would increase the adaptive value of male selection of females (26). Its working, though, should be different, as female gametes are in much shorter supply. Exploring this topic will probably reveal many interesting features.

The present study did not explore the effect of the complexity of the genome in stabilizing sex in evolutionary terms, as this aspect was studied in great detail elsewhere (29). Nor does the study discover any new form of evolutionary mechanism favoring sex that had not been proposed before. The contribution of this study is to attempt to value for the first time in quantitative terms, the relative importance of a number of features in favoring the evolutionary dynamics of sex. In this context, our study strongly suggests that an important adaptive advantage of sexual reproduction is the opening of new levels of selection. Two falsifiable predictions can be made: 1- Sophisticated spermatozoa selection mechanisms, or other gamete selection mechanisms, should be common in nature, even among monosexual organisms. 2- The ratio: number of spermatozoa in an ejaculate / maximum female gametes naturally accessible with a single ejaculate, should be orders of magnitude smaller for haploid than for diploid males, as haploid males do produce spermatozoa by thelytoky.

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References

- 1 Maynard-Smith, J.M. The Evolution of Sex. Cambridge University Press, U.K. (1978)
- 2 Judson, O.P. & Normak, B.B. Ancient asexual scandals. *Trend. Ecol. Evol.* **11**: 41-46 (1996)
- 3 Hurst, L.D. & Peck, J.R. Recent advances in the understanding of the evolution and maintenance of sex. *Trend. Ecol. Evol.* **11**: 46-52 (1996)
- 4 Kondrashov, A.S. Classification of hypothesis on the advantage of amphimix. *J. Hered.* **84**: 372-387 (1993)
- 5 Bell, G. & Maynard Smith, J. Short-term selection for recombination among mutually antagonistic species. *Nature*, **328** : 66-68 (1987)
- 6 Hamilton, W.D., Axelrod, R. & Tanese, R. Sexual reproduction as an adaptation to resist parasites (A review). *Proc. Nat. Acad. Sci. (USA)*, **87**: 3566-3573 (1990)
- 7 Ebert, D. & Hamilton, W.D. Sex against virulence: The coevolution of parasitic diseases. *Trend. Ecol. Evol.*, **11** : 79-82 (1996)
- 8 Howard, R.S. & Lively, C.M. Parasitism, mutation accumulation and the maintenance of sex. *Nature*, **367** : 554-556 (1994)
- 9 Ochoa, G. & Jaffe, K. On sex, mate selection and the Red Queen. *J. Theor. Biol* **199**: 1-9 (1999)
- 10 Fisher, R. A. Genetic Theory of Natural Selection. Oxford University Press. 1930.
- 11 Muller, H. J. Some genetic aspects of sex. *Am. Nat.* **66**: 118–138 (1932).
- 12 Crow, J. F. & Kimura, M. Evolution in sexual and asexual populations. *Am Nat* **99**: 439-450 (1965)
- 13 Otto, S.P. & Barton, N.H. The evolution of recombination: removing the limits to natural selection. *Genetics* **147**: 879-906 (1997)
- 14 Muller, H.J. The relation of recombination to mutational change. *Mut. Res.*, **1**: 2-9 (1964)
- 15 Hill, W.G. & Robertson, A. The effect of linkage on limits to artificial selection. *Genet. Res.* **8**: 269-294 (1966)
- 16 Kondrashov, A.S. Deleterious mutations as an evolutionary factor. I. The advantage of recombinations. *Genet. Res.* **44**: 199 (1984)
- 17 Kondrashov, A.S. Deleterious mutations as an evolutionary factor. III. Mating preferences and some general remarks. *J. Theor. Biol.* **131**: 487-496 (1988)
- 18 Kondrashov, A.S. The asexual ploidy cycle and the origin of sex. *Nature*, **370** : 213-216 (1994)
- 19 Taylor, P.D. & Williams, G.C. The lek paradox is not resolved. *Theor. Pop. Biol.* **22**: 392 (1982)
- 20 Heisler, I.L. A quantitative genetic model for the origin of mating preferences. *Evolution* **36**: 1283 (1984)
- 21 Hastings, I.M. Potential germline competition in animals and its evolutionary implications. *Genetics*, **123**: 191-197 (1989).
- 22 Jaffe, K. Sex, mate selection and evolution. Comments on Theoretical Biology (2002)
- 23 Kodric-Brown, A. & Brown, J.H. Anisogamy, sexual selection, and the evolution and maintenance of sex. *Evolut. Ecol.* **1** : 95-105 (1987)
- 24 Jaffe, K. The dynamics of the evolution of sex: Why the sexes are, in fact, always two? *Interciencia* **21**: 259-267 and errata in **22**: 48 (1996)
- 25 Jaffe, K. On the adaptive value of some mate selection strategies. *Acta Biotheor.* **47**: 29-40 (1999)

- 26 Cunningham, E.J.A. & Birkhead, T.R. Sex roles and sexual selection. *Anim. Behav.*, **56**: 1311-1321 (1998)
- 27 Davis, C.H. The effect of assortative mating and environmental variation on selection for sexual reproduction. *Evolutionary Theory* **11** : 51-53 (1995).
- 28 Jaffe, K. Sex, mate selection and evolution. In : Lecture Notes in Computer Science 1447 : Evolutionary Programming VII, Springer Verlag, V.W. Porto, N. Saravanan, D. Waagen and A.E. Eiben (Eds.), pp. 483-492 (1998)
- 29 Jaffe, K. Emergence and maintenance of sex among diploid organisms aided by assortative mating. *Acta Biotheor.* **48**: 137-147 (2000)
- 30 Trivers, R. L. Sexual selection and resource-accurring abilities in *Anolis garmani*. *Evolution* **30**: 253 –269 (1976)
- 31 Agrawal, A. F. Sexual selection and the maintenance of sexual reproduction. *Nature* **411**: 692-695 (2001)
- 32 Siller, S. Sexual selection and the maintenance of sex. *Nature* **411**, 689 – 692 (2001)
- 33 Jaffe, K. On the relative importance of Haplo-Diploidy, Assortative Mating and Social Synergy on the Evolutionary Emergence of Social Behavior. *Acta Biotheor.* **49**: 29-42 (2001)
- 34 West, S.A., Lively, C.M. & Read, A.F. A pluralist approach to sex and recombination. *J. Evol. Biol.* **12**: 1003-1012 (1999)
- 35 Jaffe, K., Issa, S., Daniels, E. & Haile, D. Dynamics of the emergence of genetic resistance to pesticides among asexual and sexual organisms. *J. Theor. Biol.* **188**: 289-299 (1997)
- 36 Rincones, J., Mauleon, H. & Jaffe, K. Bacteria modulate the degree of ampimix of their symbiotic entomopathogenic nematodes in response to nutritional stress. *Naturwissenschaften* **88**: 310-312 (2001)
- 37 Silva, E.R. & Jaffe, K. Expanded food choice as a possible factor in the evolution of eusociality in Vespidae *Sociobiol.* **39**:25-36 (2002)
- 38 Cohen, J. Sperms galore: why mammals produce large numbers of spermatozoa. *Science Spectra* **16**: 14-20 (1999)
- 39 Tregenza, T. & Wedell, N. Genetic compatibility, mate choice and patterns of parentage: invited review. *Mol Ecol.* **9**: 1013-27 (2000)
- 40 Jeong, H., Mason, S.P., Barabási, A.L. & Oltvai, Z.N. Lethality and centrality in protein networks. *Nature* **411**: 41-42 (2001)
- 41 Skalhegg B.S., Huang Y., Su T., Idzerda R.L., McKnight G.S. & Burton K.A. Mutation of the Calpha subunit of PKA leads to growth retardation and sperm dysfunction. *Mol. Endocrinol.* **16**:630-639 (2002)
- 42 Hecht, N.B. The making of a spermatozoon: a molecular perspective. *Dev. Genetics* **16**: 95-103 (1995)
- 43 Ren D, Navarro B, Perez G, Jackson AC, Hsu S, Shi Q, Tilly JL, Clapham DE. 2001. A sperm ion channel required for sperm motility and male fertility. *Nature* **413**: 603-609.
- 44 Evans JP, Zane L, Francescato S, Pilastro A. Directional postcopulatory sexual selection revealed by artificial insemination. *Nature* **421**:360-363 (2003).
- 45 Biodynamica, a simulation model of biological evolution (for a windows environment)
<http://atta.labb.usb.ve/Klaus/Programas.htm>