

Who runs fastest in an adaptive landscape: Sexual versus asexual reproduction

Kerstin Holmström and Henrik Jeldtoft Jensen*

Department of Mathematics, Imperial College London, South Kensington campus, London SW7 2AZ, U.K.

Abstract

We compare the speed with which a sexual, respectively an asexual, population is able to respond to a biased selective pressure. Our model focuses on the Weismann hypothesis that the extra variation caused by crossing-over and recombination during sexual reproduction allows a sexual population to adapt faster. We find, however, that the extra variation amongst the progeny produced during sexual reproduction for most model parameters is unable to overcome the effect that parents with a high individual fitness in general must mate with individuals of lower individual fitness resulting in a moderate reproductive fitness for the *pair*.

Keywords: mode of reproduction, cost of sex, speed of adaptation.

Short title: Sex and reproductive fitness.

1 Introduction

It is generally assumed that an important contribution to overcoming the evolutionary cost of sexual reproduction is the greater genetic variation among the progeny of sexual parents, caused by crossing-over and recombination, compared to asexually reproduced offspring. The greater variation in the sexual population is assumed to produce more choice for natural selection and might thereby enable swifter adaptation. This is the hypothesis of Weismann [Burt, 2000]. Several recent experimental studies have been interpreted as supporting Weismann's hypothesis [Colegrave, 2002, Colegrave et al., 2002, Kaltz and Bell, 2002]. These experiments observe a larger variation in the reproductive fitness (rate of reproduction) when sexual reproduction is involved and this produces a faster adaptation of the sexual

*Author for correspondence (h.jensen@imperial.ac.uk; URL: <http://www.ma.imperial.ac.uk/~hjens>)

population. Thus it might seem that Weismann's suggestion has been verified and fully understood.

However, we believe that there are still issues to be clarified concerning the details of the mechanisms behind Weismann's hypothesis. The question we discuss here is the following: It is evident that crossing-over and recombination may lead to greater genotypical variation amongst the progeny but what matters for selection is the differential excess fitness (reproduction rate) of sexual reproduction compared with asexual reproduction. How is the greater genotypical variation amongst individuals able to lead to a larger reproduction rate of the *pair of parents*? The essential point is that in a sexual population the individual of highest fitness typically will have to mate with an individual of lower fitness.

We use here a simple schematic mathematical model of evolution in genotype space and study the speed with which the population is able to climb a fitness gradient. Although our model is simple, it is nevertheless representative, as far as testing Weismann's hypothesis, of any approach in which the fitness of the sexually reproducing pair is obtained by combining measures of fitness of the two individuals involved in the reproductive event. We find that the sexual population generically exhibit a greater spread in genotype space compared with the asexual population. However, only in extreme cases does this greater variation in genotype space lead to a larger variation in the reproduction rate and thereby to a superior adaptability for the sexual population.

2 The Model

Genotype space: We consider a population of individuals each characterised by their specific genotype determined by a position vector \mathbf{S} in genotype space \mathcal{S} . For simplicity we model \mathcal{S} by a two dimensional $L_x \times L_y$ grid, i.e. $\mathbf{S} = (S_x, S_y)$, where S_x and S_y are integers: $S_x = 1, 2, \dots, L_x$ and $S_y = 1, 2, \dots, L_y$, with periodic boundary conditions in the y -direction. We have used $L_x = L_y = 100$ for the study reported here. The number of individuals at position \mathbf{S} at time t is given by $n(\mathbf{S}, t)$.

Reproduction rate: The genotype determines directly the reproduction rate, or the

reproductive fitness, $\phi(\mathbf{S}, t)$ in the following way

$$\phi(\mathbf{S}, t) = \frac{1}{1 + \exp[-W]}. \quad (1)$$

The statistical weight $W(\mathbf{S}, t)$ is given by

$$W(\mathbf{S}, t) = \alpha S_x - \mu N(t). \quad (2)$$

Here the first term represents a linear increase ($\alpha > 0$) in the reproduction rate along the x -direction in genotype space. In the second term $N(t) = \sum_{\mathbf{S}} n(\mathbf{S}, t)$ represents the total number of individuals at time t , and μ determines the carrying capacity of the system. For fixed $N(t)$ the fitness landscape corresponding to $W(\mathbf{S}, t)$ in Eq. (2) is a smooth upwards tilted plane. Assume for a moment that the entire population is placed on one location in genotype space, say \mathbf{S}^0 , and assume further more that adaptation cannot take place (zero mutation rate). A stationary population size is then determined by the balance between the reproduction [$N \rightarrow N + N\phi(\mathbf{S})$] and ensuing annihilation of individuals [$(1 + \phi(\mathbf{S}))N \rightarrow (1 + \phi(\mathbf{S}))N(1 - p_{kill})$], leading to $\phi(\mathbf{S}) = p_{kill}/(1 - p_{kill})$. From this expression we find the population size, for a given carrying capacity μ , by use of Eq. (1) and (2),

$$N = \frac{1}{\mu}[\alpha S_x^0 - \ln\left(\frac{\phi}{1 - \phi}\right)] = \frac{1}{\mu}[\alpha S_x^0 - \ln\left(\frac{p_{kill}}{1 - 2p_{kill}}\right)]. \quad (3)$$

When mutations are allowed the population can adapt (done by increasing the S_x component of the position in genotype space) to the environment and thereby increase the population size for a given value of the carrying capacity parameter μ . We have used the following parameter values: $\alpha = \ln 3/45$ and $\mu = \ln 3/450$ and $p_{kill} = 0.2$ which leads to the linear dependence $\langle N \rangle = 10\langle S_x \rangle + 450$ of the average number of individuals $\langle N \rangle$ on the population averaged x -coordinate $\langle S_x \rangle$ in genotype space.

In order to be able to represent a more rough landscape we choose fraction of genotype positions \mathbf{S}_h at random and denote them fitness holes. These sites are infinitely unfit corresponding to $\phi(\mathbf{S}_h) = 0$, i.e. individuals with a genotypical composition equal to one of the \mathbf{S}_h locations cannot produce offspring. The fitness landscape produced by this procedure resem-

bles Gavrilets' notion of the holey fitness landscape [Garvilets, 1999, Gavrilets et al., 1998, Gavrilets et al., 2000].

Time step : The system is simultaneously updated. First all individuals are allowed to reproduce by the relevant probability to be described below. After reproduction annihilation occurs, during which individuals are removed from the system with probability p_{kill} . This probability is constant in time and equal for all genotypes.

Asexual reproduction: Let us now describe how reproduction is represented in the model. We begin with the asexual case. All $N(t)$ individuals are allowed to produce one offspring with the genotype specific probability $p_{off}(\mathbf{S}) = \phi(\mathbf{S}, t)$. The offspring will be of the same genotype \mathbf{S} except when mutations occur, which happens with a constant probability p_{mut} , to be thought of as the genomic mutation rate per reproduction event. The mutant is placed at random on one of the four nearest neighbour sites.

Sexual reproduction: A procedure is needed to determine the reproduction rate of a *pair* from the genotypes of two individuals. First a mate of genotype \mathbf{S}_{mate} is found for each individual i of genotype \mathbf{S}_i for $i = 1, 2, \dots, N(t)$, This is done by randomly choosing the mate amongst all the individuals present on genotypical positions less than a distance d_{max} away from \mathbf{S}_i . Each of the $N(t)$ pairs will produce offspring with the respective probability

$$p_{off} = \sqrt{\phi(\mathbf{S}_i)\phi(\mathbf{S}_{mate})}. \quad (4)$$

The variation amongst the offspring induced by crossing-over and recombination is represented by placing the offspring on a site \mathbf{S}_{off} selected randomly with uniform probability within an ellipse with eccentricity e and major half axis of length $a = [1/2 + |\mathbf{S}_1 - \mathbf{S}_2| + 1/2]/2e$ placed symmetrically around \mathbf{S}_1 and \mathbf{S}_2 , see Fig. 1. The extend to which the offspring are allowed to end up *outside* the region in genotype space *between* the two parents is characterised by what we call the recombination factor $r = 1/e$. The larger the value of r the more likely it is to find the offspring to the right (or to the left) of both parents, see Fig. 1. In the special case where both parents are of identical genotype, i.e. $\mathbf{S}_i = \mathbf{S}_{mate}$, the offspring is give the same genotype as the parents, i.e. $\mathbf{S}_{off} = \mathbf{S}_i$.

Mutations can occur with the same probability p_{mut} as in the asexual case. When a mutation occur the offspring is moved to one of the nearest neighbour sites of the position \mathbf{S}_{off} .

We emphasise that the specific function in Eq. (4) is inessential. We obtain qualitative identical results when we instead of Eq. (4) use other functional forms for p_{off} which satisfies the seemingly reasonable requirement that p_{off} is a number between the individual fitnesses $\phi(\mathbf{S}_i)$ and $\phi(\mathbf{S}_{mate})$: for example one can replace Eq. (4) by $p_{off} = [\phi(\mathbf{S}_i) + \phi(\mathbf{S}_{mate})]/2$.

It is also important to point out that although the population grows monotonically in size as it moves to the right in genotype space, the average reproduction probability $\langle p_{off}(\mathbf{S}) \rangle$ remains constant. The reason for this is that the increase in fitness caused by the increase in αS_x in Eq. (2) is compensated by the carrying capacity term $-\mu N(t)$ in this equation.

3 Results

In order to compare the efficiency with which the two different types of reproduction respond to a selective pressure, we compare the evolution under the same conditions (i.e. same α and μ in Eq. (2)) of a solely sexually reproducing population with a solely asexually reproducing population. In both the asexual and sexual case five different genotypes are initiated with 100 individuals each. They are chosen so that the average S_x -coordinate $\langle S_x \rangle = 5$. The five positions are $\mathbf{S} = (4, L_y/2), (5, L_y/2), (6, L_y/2), (5, L_y/2 + 1), (5, L_y/2 - 1)$. This gives an initial reproduction probability for all the 500 individuals of about $p_{off} = 0.252$. The exact number of starting genotypes does not effect the nature of the movement through genotype space.

We monitor the time it takes the population's centre of mass $\langle \mathbf{S} \rangle$ to move in genotype space from $\langle \mathbf{S} \rangle = 5$ to $\langle \mathbf{S} \rangle = 85$. During this motion we find that $\langle \mathbf{S} \rangle$ to very a good approximation increases linearly with time.

Under the evolutionary dynamics the population moves to the right. Although the dynamics is diffusive in nature the population remains confined to a rather narrow region

along the S_x and S_y axes while the population gradually moves to larger S_x values. This is shown as the peaks in $n(\mathbf{S}, t)$ in Fig. 2. The dispersive action of the diffusion in genotype space produced by the mutations, and the crossing-over effect in the sexual case, is counteracted by the effect of $-\mu N(t)$ in Eq. (2). The reproduction probability $p_{off}(\mathbf{S})$ of individuals left behind, at genotype positions with small S_x values, will decrease with time because the term $-\mu N(t)$ increases as a result the reproductive activity of individuals with higher S_x values. As soon as the reproductive probability of a site \mathbf{S} becomes permanently smaller than the killing probability, $p_{off}(\mathbf{S}, t) < p_{kill}$, the population on that site is bound to go extinct.

We now summarise the behaviour of the model. First we consider the case without any fitness holes in genotype space. The sexually reproducing population is found only to adapt more rapidly than the asexually reproducing population for substantial variation amongst the prodigy or low mutation rate. This is illustrated in Fig. 3. For a given mutation rate, the data points indicate the threshold value, r_{thr} , of the recombination factor where, for increasing r , sexual reproduction becomes more effective than asexual reproduction. It is remarkable that a sexually reproducing population is only able to adapt faster than an asexually reproducing population if the recombination factor r is significantly larger than 1. Further more we note that the threshold value of r_{thr} is slowly increasing with increasing mutation rate. This is, of course, to be expected since the asexual population is able to adapt faster with increasing mutation rate.

It is clearly difficult to relate in a detailed way the mutation rate p_{mut} in this model to real biological mutation rates. Fig. 3 shows that this is not an essential problem for the interpretation of our results since the same qualitative behaviour is found for all values of the mutation rate p_{mut} . Namely, recombination factors r significantly in excess of 1 is needed for all values of the mutation rate to make the sexual population the most adaptive.

The results in Fig. 3 can be understood in terms of how the velocity of the centre of mass of the population depends on the recombination factor for the two types of reproduction. This is illustrated in Fig. 4. Per construction the velocity of the asexually reproducing

population is independent of the recombination factor. The velocity of a sexually reproducing population increases rapidly with increasing recombination factor, but decreases with increasing maximum distance d_{max} between two reproducing parents. This finding may be understood in the following terms. Consider a reproduction event involving a *most fit* individual, i.e. an individual on one of the positions, say \mathbf{S}^* , in genotype space with the highest value of the S_x -coordinate among the genotypical positions occupied at the present instant in time. I.e., the positions in genotype space with $S_x > S_x^*$ are all unoccupied. An increase in the recombination factor leads to an increase in the range of possible S_x -values of the offspring's genotype and thereby assists the displacement of the population to large values of S_x . Consider again this *most fit* individual \mathbf{S}^* . The average reproduction rate of \mathbf{S}^* is obtained from Eq. (4) by averaging over all potential individuals present within the distance d_{max} . The larger the value of d_{max} the smaller the S_x values of the possible mates. Small values of S_x lead to small reproduction values according to Eqs. (1), (2) and (4).

The results discussed in this section are all for the case where no fitness holes are present. In this case the simulations can readily be compared with the iterative master equation for the population density in genotype space $n(\mathbf{S}, t)$. These are cumbersome to write down but can easily be solve by numerical methods. In this way we have confirmed the ensemble averaged results described above.

4 The effects of holes

To represent the anticipation that many totally unviable genotypes exist, we introduce a random selection of genotype positions which are unable to reproduce. Individuals can arrive at one of these positions as a result of mutation from a nearby site. Individuals on such a site, say \mathbf{S}_h , may be selected for reproduction attempts. In both the sexual and asexual case this reproduction attempt can, however, not lead to offspring since $\phi(\mathbf{S}_h) = 0$. The individuals on the trap sites leads to an overall fall in the reproduction rate on other sites through their contribute to the $-\mu N(t)$ term in W , see Eq. 2. This is only natural as all individuals existing at a given moment in time represent a demand on the carrying capacity

of the system. One might expect that the sexually reproducing population would be more likely to find a path through this rugged fitness landscape than an asexually reproducing population. After all, the sexually reproducing population may jump over holes in the fitness landscape when $d_{max} \geq 2$. In fact, as soon as $d_{max} \geq \sqrt{2}$ the sexual population can pass to next nearest neighbour sites of already occupied positions in genotype space, whereas the asexual offspring can at most move to a nearest neighbour site when a mutation occurs. This enables the sexual population to follow paths through the rugged fitness landscape which are inaccessible to the asexual population.

In Fig. 5 we show as a function of the density of holes the probability that a population is able to find an adaptive path through the rough fitness landscape in the course of a fixed number of time steps $T = 10^6$ for mutation rate $p_{mut} = 0.01$. We present results for two cases: A) $d_{max} = \sqrt{2}$ with $r = 1.270$ and B) $d_{max} = \sqrt{5}$ with $r = 1.408$. In both cases r is calibrated such that, in the absence of holes, the sexual population moves with the same velocity through genotype space, as the asexual population with $p_{mut} = 0.01$ does.

The simulations clearly show that, once holes are present, the asexual reproduction in general is better suited to move through the rough fitness landscape, and that large values of d_{max} , rather than allowing the sexual population to more easily find a way around the traps, has the opposite effect. This behaviour is explained by the fact that the sexually reproducing population more often places offspring in the holes than the asexual population does.

5 Discussion

It is interesting to relate our results to the width of the population along the x-axis in genotype space and to the width of the distribution of the reproduction probabilities. We find that the population that is able to adapt most rapidly always has the *broadest* distribution of reproduction probabilities p_{off} . This is entirely consistent with Weismann's idea that greater variation enables adaptation to occur faster because natural selection has more choice to act upon [Burt, 2000]. What is not consistent with Weismann's hypothesis is

that sexual reproduction does not always lead to the larger variation. In Fig. 6 we show the average velocity of adaptation of the sexual and asexual population as function of the standard variation $\sigma_{p_{off}}$ of the reproduction rate of the respective population for many different combinations of control parameters.

We notice that adaptive velocity and $\sigma_{p_{off}}$ are linearly related and that only for very substantial recombination factors is the sexually reproducing population able to adapt faster than the asexual. When this happens the sexual population does have the greatest variation in p_{off} . Recombination factors r much larger than one seems of little biological relevance since $r > 1$ frequently leads to offspring which may be reproductively isolated from one of its parents in the sense that the distance to one of the parents may exceed d_{max} . Thus, in the model considered here a sexual population is unable to adapt faster than an equivalent asexual population except for, what seems to be, biologically extreme choices of parameters.

The reason we find that Weismann's hypothesis is unable to explain the superiority of sexual reproduction is not that the idea that greater variation leads to faster adaptation is wrong. The problem is that sexual reproduction events involving the most fit individuals will typically involve less fit mates. This hinders the individuals with the best adapted genotype to spearhead the adaptation of the sexual population.

Of course the Weismann hypothesis is not the only reason why sexual reproduction might be evolutionary superior to asexual reproduction. Kondrashov discuss a large number of different hypotheses and emphasis in particular the ability of recombination to eliminate deleterious mutations from the genome [Kondrashov, 1993]. Perhaps no single general mechanism can be identified as the most important for the evolution and maintenance of sex (see e.g. [Hurst and Peck, 1996]) in which case the explanation may have to rely on case specific mechanisms (see e.g. [Peck and Waxman, 2000, Doncaster et al., 2000]).

We have studied Weismann's hypothesis in it simplest form and have been forced to conclude that within the framework of individual genotypical fitnesses combined, in the sexual case, to give the fitness of the reproducing pair, the extra variation in genotype space of the sexual population is in realistic cases not able to produce the needed excess

in reproductive fitness to make the sexual population able to out compete the asexual population. The sexual population's greater variation of genotypes tends to be neutralized by the necessity of the most fit individual to mate with individuals of lower fitness.

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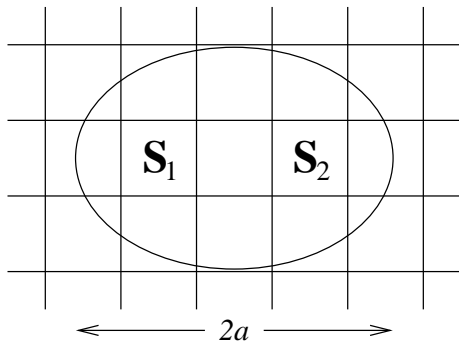


Figure 1: Ellipse with $r = 1.4$. S_1 and S_2 denote the sites of the two parents. The distance a is the major axis defined in the text.

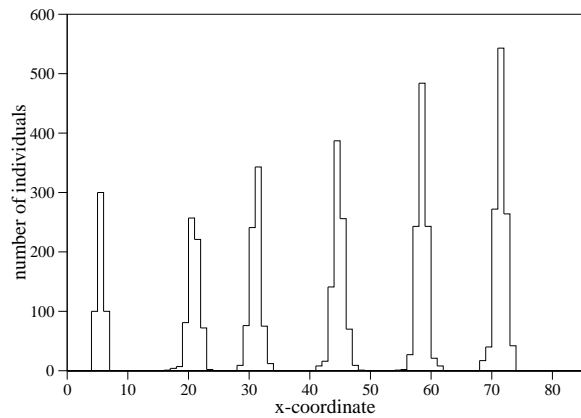


Figure 2: The peak in the population density moving to the right along the S_x axis in genotype space. The data is for a sexually reproducing population with $p_{mut} = 0.01$, $d_{max} = \sqrt{2}$ and $r = 1.27$. The time between each small peak is equal to 6000 time steps.

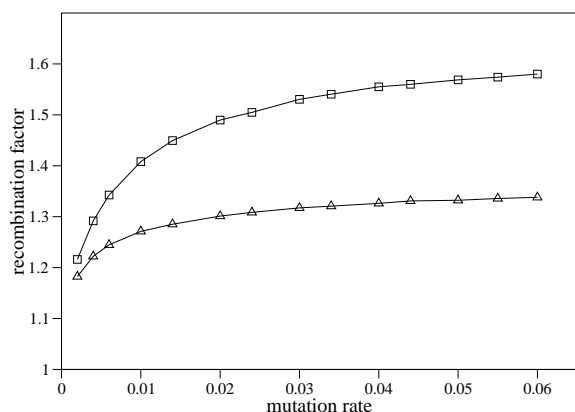


Figure 3: The competition between sexual and asexual reproduction for two different values of d_{max} . The signatures are: \triangle corresponds to $d_{max} = \sqrt{2}$ and \square to $d_{max} = \sqrt{5}$. For a given d_{max} , sexual reproduction most efficiently response to the selective pressure above the relevant curve, below the curve asexual reproduction is superior.

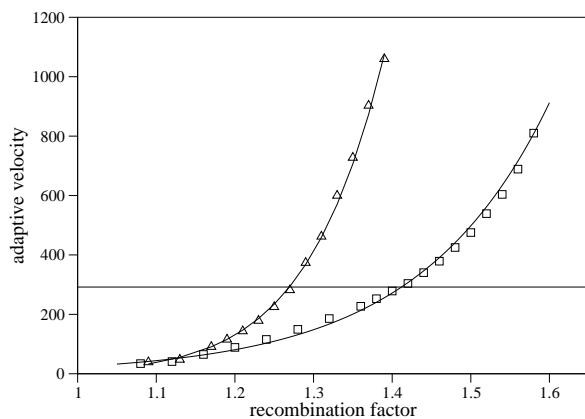


Figure 4: The adaptive velocity of a sexually reproducing population for different values of the recombination factor and different values of $d_{max} = \sqrt{2}$, \triangle , and $\sqrt{5}$, \square , respectively. The straight line represent the velocity (229×10^{-5} square/time step) of an asexually reproducing population for the same value of the mutation rate $p_{mut} = 0.01$. The two intersection points mark the minimum recombination factors at which sexual reproduction is superior to asexual ditto.

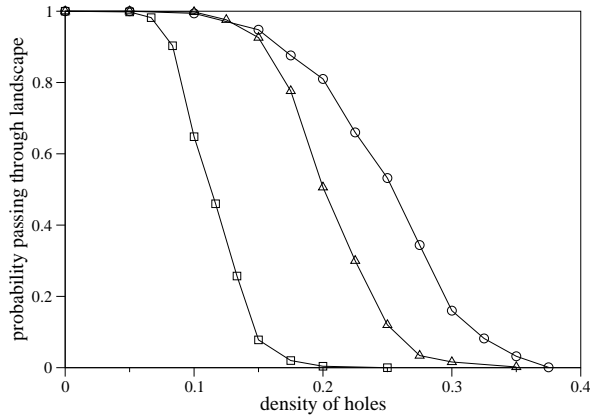


Figure 5: The fraction of the population that on average is able to pass through a rough fitness landscape with traps. The signatures are as follows: \circ asexual population, Δ sexual population with $d_{max} = \sqrt{2}$ and $r = 1, 27$, \square sexual population with $d_{max} = \sqrt{5}$ and $r = 1.41$. In all cases $p_{mut} = 0.01$ and each data is averaged over 500 realisations.

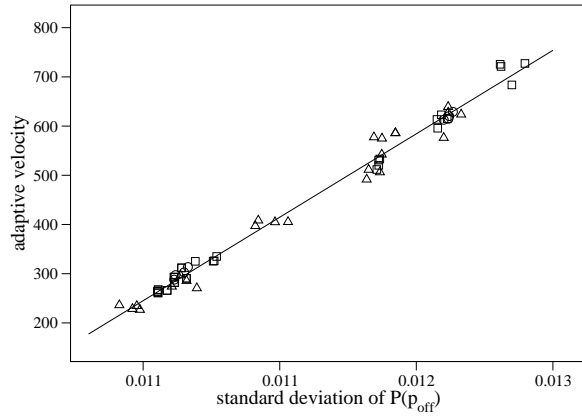


Figure 6: Average adaptation velocity as function of the standard deviation of the distribution of reproduction rates. The data are for $p_{mut} = 0.01$ and 0.03 , $d_{max} = \sqrt{2}$ and $\sqrt{5}$ for a range of different recombination factors r .