Simulated emergence of cyclic sexual-asexual reproduction

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Motivated by the cyclic pattern of reproductive regimes observed in some species of green flies ("aphids"), we simulate the evolution of a population enduring harsh seasonal conditions for survival. The reproductive regime of each female is also seasonal in principle and genetically acquired, and can mutate for each newborn with some small probability. The results show a sharp transition at a critical value of the survival probability in the winter, between a reproductive regime in the fall that is predominantly sexual, for low values of this probability, or asexual, for high values.

PACS numbers: 87.23.Cc, 07.05.Tp, 64.60.Cn

1. INTRODUCTION

The question of why sexual reproduction prevails in the immense majority of metazoan species still defies a complete and satisfactory answer - for a recent review we direct the reader to Reference [1]. A number of different theories have been put forth to try to explain this puzzle, but all have so far fallen short of becoming a paradigm in the field. One of the major difficulties one finds in this research is the lack of convincing observational data with which to compare one's theoretical effort. This is especially critical when addressing the onset of sexual reproduction itself, and in this case we can only speculate about this origin, but cannot test these speculations. A more promising line of research lies in analyzing the maintenance of sexual reproduction against the establishment of an apparently more efficient asexual variety. This efficiency stems from the absence of the necessity to generate males, which by itself alone should give the asexual variety the upper hand against a competing sexual alternative [2,3]. Explaining the evolutionary choice favoring sexual reproduction in spite of its shortcomings has been the long-term goal for a number of researchers in this area.

It is not surprising that computer simulations have become a major tool in this field over the last few years. With the introduction of a number of simple simulational models, theoretical ideas began to be put to a "live" test on virtual populations. These models encompass dynamic rules that mimic the action of natural evolution in a variety of ways, and create a manageable representation of the conflict between selection and mutation, believed to be the driving evolutionary force. Among the models that have been used, we make special mention of the bit-string class, using Monte Carlo techniques [4–7]. They seem particularly well suited to represent the microscopic dynamics of genetic evolution and allow for a very efficient coding on personal workstations; recent and comprehensive reviews of a popular model of this class, the Penna model, are available in the literature [8–10].

Penna's model has in fact been recently used to address the foregoing problem. The greater genetic diversity generated by sexual reproduction and its consequences, such as survival after catastrophes [11] and winning when in competition against an asexual variety in the presence of genetically coupled parasitism [12], were already considered in its context. A recent simulation including the action of pleiotropic genes, i.e. those that have multiple effects, showed that in a region of its parameter space sexual reproduction generates larger equilibrium populations than its asexual counterparts when evolving independently [13]. We report here on the use of a modified Penna model in a different, though closely related, problem.

The problem in question here is that of the holocyclic behaviour of some species. By this is meant the capability shown by these species of seasonally alternating their reproductive regimes. Of particular interest in this class of species are the aphids, or green flies.

Aphids are a group of about 4,400 species of small insects that feed on the phloem fluid of plants [14,15]. Many species of aphids attack important agricultural crops, and are therefore of major economic importance, and display complex life cycles. They are one of the few groups of animals that undergo cyclical parthenogenesis, that is, the alternation of a varying number of asexual generations (parthenogenesis) with a single generation of sexual reproduction. All asexual generations are entirely female. Species that produce both sexual and asexual morphs are called holocyclic, as opposed to those anholocyclic ones that undergo obligate parthenogenesis. In a holocyclic life cycle both asexual and sexual morphs are produced at different times of the year. Males are present only in one part of the life cycle. They are usually produced only in the autumn by parthenogenetic females. Females reproducing sexually produce just one egg, that in temperate regions overwinters and hatches only in the spring.
The purpose of the present work is to study the emergence of an holocyclic life cycle through a simple evolutionary model, with dynamics designed to mimic the main features of the relation between the aphids and their environment. To summarize, we show that this simple model has a first order holocyclic transition dependent on one parameter. On one side of the transition there is no alternation of reproductive regime and the species is asexual; on the other, the holocyclic order is chosen by evolution as a means of insuring the survival of the species.

This paper is organized as follows: in the next section we present the model that was used to simulate an aphid-like species; our results are discussed in Section III, and we conclude in Section IV.

2. THE MODEL

One of the main features of the environmental impact on the aphids is their great susceptibility to winter conditions. The majority of the population cannot survive in very cold conditions. On the other hand, aphid eggs generated by sexual reproduction resist harsh weather conditions. They overwinter and hatch only when spring comes. These are the elements to be introduced into a model that intends to test the hypothesis that the onset of holocyclic order is a direct consequence of evolution dynamics acting on cold-susceptible species.

The model we worked with is an adaptation of the Penna model for age-structured populations, to which we added the features described above. Since the phenomenon in question does not depend on the age structure, this model is not the only possible choice. Nevertheless, it has a very simple representation of the conflict between mutations and selection, which is central to any evolutionary problem, together with a built-in mechanism that decreases the survival probability with age, that other models have to introduce in an ad hoc way. We will briefly describe the Penna model in its mixed sexual-meiotic parthenogenesis version. A similar version of this model - but without the specific aphid-type dynamics - was used in Ref. 12.

The genome of each (diploid) organism is represented by two computer words. In each word, a bit set to one at a position ("locus") corresponds to a deleterious mutation - a "perfect" strand would be composed solely of zeros. The reader should note that we don’t allow in this context for a beneficial mutation in the wildtype genome, that would eventually lead us to the problem of speciation. The effect of a harmful mutation may be felt by the individual at all ages equal to or above the numerical order of that locus in the word. As an example, a bit set to one at the second position of one of the bit-strings means that a harmful effect may become present in the life history of the organism to which it corresponds after it has lived for two time periods. The diploid character of the genome is related to the effectiveness of the mutations. A mutation in a position of one of the strands is felt as harmful either because of homozygose or because of dominance. For the former, a mutation must be present in both strings at the same position to be effective. The concept of dominance on the other hand relates to loci in the genome in which a mutation in just one strand is enough to make it affect the life of the organism. The life span of an individual is controlled by the amount of effective mutations active at any instant in time. This number must be smaller than a specified threshold to keep the individual alive; it dies as soon as this limit is reached.

Reproduction is modeled by the introduction of new genomes in the population. Each female becomes reproductive after having reached a minimum age, after which she generates a fixed number of offspring at the completion of each period of life. The meiotic cycle is represented by the generation of a single-stranded cell out of the diploid genome. To do so, each string of the parent genome is cut at a randomly selected position, the same for both strings, and the left part of one is combined with the right part of the other, thus generating two new combinations of the original genes. The selection of one of these completes the formation of the haploid gamete coming from the mother.

The difference between sexual and parthenogenetic reproduction appears at this stage. For the first, a male is selected in the population and undergoes the same meiotic cycle, generating a second haploid gamete out of his genome. The two gametes, one from each parent, are now combined to form the genome of the offspring. Each of its strands was formed out of a different set of genes.

For meiotic parthenogenesis, all genetic information of the offspring comes from a single parent. Its gamete is generated through the meiotic cycle described above and then cloned to compose an homozygous genome for the offspring. For both regimes, the next stage of the reproduction process is the introduction of M independent mutations in the newly generated genetic strands. In this kind of model it is normal to consider only the possibility of harmful mutations, because of their overwhelming majority in nature. If male offspring can be born, the gender of the newborn is then randomly selected, with equal probability for each sex.

A last ingredient of the model is a logistic factor, called the Verhulst factor, which accounts for the finite carrying capacity of the environment for this particular species. It introduces a mean-field probability of death for an individual, coming from causes with dynamics not included in the model, and for computer simulations has the benefit of limiting the size of populations to be dealt with. This factor is essentially the ratio between the actual population in any time step and a parameter of the model, traditionally and perhaps improperly called the carrying capacity of the
environment. Because it is not connected to the quality of the individual’s genome, the usage of this factor in a model of evolutionary dynamics has its shortcomings [16], and one has to make sure that the outcome of the simulations is not biased by the particular choice of strategy for its implementation.

The passage of time is represented by the reading of a new locus in the genome of each individual in the population, and the increase of its age by one. After having accounted for the selection pressure of a limiting number of effective (harmful) mutations and the random action of the Verhulst dagger, females that have reached the minimum age for reproduction generate a number of offspring. The simulation runs for a pre-specified number of time steps, at the end of which averages are taken over the population(s).

In the mixed sexual-parthenogenesis version, each female in the population has a season-dependent reproductive mode, which is also genetically inherited. Four bits in the genome represent the reproductive mode for each season. A bit set to 0 (1) in a position indicates that at the season associated to that particular position this female will generate offspring through sex (meiotic parthenogenesis). This reproductive pattern is passed on to the female offspring. Mutations can also occur on this pattern, with some probability. One out of the four seasons is randomly selected and the reproduction mode for that season is switched.

The duration of the seasons is set to some number of time periods. At each time step, the season to which it corresponds is calculated. In the fall, females that reproduce by parthenogenesis can generate both male and female offspring. In the winter, the carrying capacity of the environment is reduced by some factor, called here the compression, or burdening, factor. Individuals with age zero that were generated by sexual reproduction - and are protected by the eggshell - suffer only from the normal Verhulst factor, representing the action of predators, and do not age; they only hatch in the spring. All the others, irrespective of gender, age or reproductive pattern, suffer the action of the enhanced Verhulst factor. The fertility of females also depends on the reproductive regime, and we fixed it to 1 offspring per time period for sexual reproduction.

Averages are taken of the total population, number of females with each reproductive pattern - both total and only the ones mature for reproduction - for each season. These numbers are normalized to the normal carrying capacity.

The runs from which our data was collected had as common parameters 12 aphid time periods for season duration, thus fixing our time scale as roughly a week per time step, a probability for reproductive pattern switching of 0.01, and an equal selection of each gender for asexually-generated offspring in the fall. In all cases, the initial population had a season-independent sexual reproductive pattern, and was composed of the same number of individuals in each gender.

For the values of the standard parameters of the Penna model we used:
1) Carrying capacity: $C = 800 000$;
2) Threshold of harmful mutations: $T = 3$;
3) Minimum reproduction age: $R = 10$;
4) Mutation rate: $M = 2$;
5) Birth rate: $b = 10$ per female per time step for asexual reproduction;
6) Initial population: 10 000 males and 10 000 females.

3. SIMULATION RESULTS

We begin by showing the total population for each season in Figure 1. The figure for the population is normalized to the normal carrying capacity of the environment, one of the parameters of the model. Data is collected as an average over the last 960 steps of a run of 50 000 Monte Carlo steps, for winter compression factors of 10 and 100. In both cases, the population increases from spring to fall, and decreases, as expected, in the winter season. For a compression factor large enough, the harsh conditions in this last season cause the population to vanish almost completely. The species does not disappear thanks to the remaining offspring of females that reproduced sexually during the last time step in the fall.

Figure 2 shows the fraction of mature females - those that have an age greater that the minimum reproduction age - that reproduce sexually in each season. If the winter has a mild effect on the effective carrying capacity, the evolution pressure favors reproduction through asexual meiotic parthenogenesis. Sexually-reproducing females are still present in the population, as a result of a small probability of back mutations from the prevailing asexual mode. The situation changes dramatically when the effects of the winter get stronger. If the corresponding compression factor is capable of bringing down the population in winter time to a small enough fraction of the normal carrying capacity, the reproductive regime in the fall switches to a largely predominant sexual variety. The data shown in this histogram correspond to situations that are way out of the transition region, and must be compared with Figure 1. In particular, the data shown there for the winter season determine what we see in the present histogram for the fall season.
The data for the winter season in Figure 2 deserve a short comment. Since the mature female population in winter time has all but vanished for a compression factor of 100, evolution exerts no pressure whatsoever over the reproductive regime in this season. As a consequence, the distribution of females among the two regimes is random, and the resulting fraction of sexually reproducing ones fluctuates around 0.5.

We proceed to characterize the transition between the anholocyclic and holocyclic regimes. The order parameter of this transition is clearly the fraction of sexually reproducing females in the fall season, which is 0 in one regime and 1 in the other. Figure 3 shows the behaviour of this parameter as a function of the surviving population in winter. A very sharp switch in regimes can be seen when this parameter is 0.0049. Some of the runs near the transition region also had an unusually long relaxation time. These two characteristics point to the identification of a first order transition, and the long relaxation times can be associated to long-lived meta-stable states equivalent to super-cooled states in fluid transitions. A sharp transition of this kind has also been found in the study of the evolution of reproductive regimes in rapidly mutating ecologies [12], and may well be an universal feature of living systems.

The natural candidate in the model to act as a measure of the distance to the transition point appears at first to be the compression factor. But the simulation results show very strong fluctuations in the order parameter when this compression parameter is in the range 10.5 - 12.5. A closer examination of the outcome of these simulations clarifies this situation. In Figure 4 the final temperature of the population is shown as a function of this compression factor. Results are shown for 10 different runs for each value of this parameter, lasting 200 000 Monte Carlo steps each. The dispersion of the final population for a compression factor in the above range causes an end result that can be in either side of the transition. Although not directly accessible as an input parameter to the simulations, the real control variable in this case is the surviving population in the winter, and Figure 3 is an eloquent support for this claim. Also shown in Figure 4 are the average values for the population in winter as a function of the compression factor, with error bars representing the standard deviation. The horizontal dotted line stands for the value of the population at the transition point, 0.0049.

4. CONCLUSIONS

As was already shown in Ref. [12], in a stable environment and when no pleiotropic genes are present, the advantage of not having to carry males gives asexual reproduction the upper hand in a direct competition against sex. This is seen by the small fraction of females that carry a sexual reproductive pattern in spring and summer shown in Figure 1. And even when their offspring are given the advantage of the eggshell protection in winter time, the switching of the dominant mode of reproduction in the fall only occurs for a very small surviving population in the winter. For large values of this surviving population, the pattern of reproduction is asexual and season-independent, switching to a cyclic asexual-sexual season-dependent one when the surviving population is smaller than some threshold. The establishment of a holocyclic order in the population derives thus from the advantages of overwintering under eggshell protection, and has no direct relation to the genetic diversity generated by sex. We could identify it as a first-order process driven by the surviving population; this claim is supported by the sharp transition observed when the fraction of sexually reproducing females in the fall is considered as an order parameter for this transition.

ACKNOWLEDGMENTS

We are greatly indebted to F. Delmotte, who introduced us to specialized literature on the biology of aphids, and to our referee for a number of suggestions that improved the clarity of our presentation and updated our references. J.S.S.M.’s work is supported as a Visiting Fellow by CIRES, University of Colorado at Boulder, and A.R. acknowledges financial support by the Brazilian agency CNPq.

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FIG. 1. The histogram shows the surviving population with age > 0 in each season, as a dimensionless fraction of the carrying capacity parameter $C$. The shaded bars represent data for a small winter compression factor of 10 and the light bars data for a large factor of 100. In this last case the population completely vanishes in winter time, except for the offspring of females that reproduced sexually in the fall - not represented in this graph.
FIG. 2. The dimensionless fraction of mature females - those that have already reached the minimum age for reproduction - that reproduce sexually in each season is shown in this histogram. Again, shaded bars correspond to a compression factor of 10, whereas light bars represent data for a factor of 100. For the former case, females that reproduce sexually are present very marginally in the population. As for the latter, almost all females reproduce sexually in the fall. For the winter, the value of 0.5 simply reflects a non-biased random choice, since there are no females alive to reproduce.
FIG. 3. The dimensionless fraction of sexually-reproducing females in the fall as a function of the surviving population in winter, expressed as a dimensionless fraction of the carrying capacity parameter $C$. It is clear that this surviving population is in fact the parameter that controls the onset of the transition from a predominantly parthenogenetic regime to a sexual one, as its value decreases.
FIG. 4. The surviving population in winter time - expressed as a dimensionless fraction of the carrying capacity $C$ - as a function of the dimensionless compression factor. The transition region, standing for values of this last factor between 10.5 and 12.5, show a large dispersion for the final population. The dotted horizontal line represents the value of this population at the transition, 0.0049. Also shown - as diamonds in the plot - are the averages for each compression factor, together with the standard deviations.