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Sharp gene pool transition in a population affected by phenotype-based selective hunting

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Abstract. We use a microscopic model of population dynamics, a modified version of the well known Penna model, to study some aspects of microevolution. This research is motivated by recent reports on the effect of selective hunting on the gene pool of bighorn sheep living in the Ram Mountain region, in Canada. Our model finds a sharp transition in the structure of the gene pool as some threshold for the number of animals hunted is reached.

PACS. 87.23.-n Ecology and evolution – 05.10.Ln Monte Carlo methods

1 Introduction

The impact of anthropic activities on ecologic equilibria is a common and urgent problem that challenges the scientific community to find new and sharper solutions for sustainable resource management. In particular, new data and studies have pointed out how the traditional approaches, focused only on demographic and ecological factors, ignoring the possibility of evolutionary changes, are hiding part of the problem [1]. A clear evidence for such phenomena is particularly well demonstrated by the effects of overfishing [3]. Actually, we can look at this activity as a good paradigm, as some sort of large scale experiment on life history evolution, that gives a strong support to the thesis of the speeding up of evolutionary processes as a result of human activities. In fact, fishing causes a highly selective mortality depending on a particular trait (size). The variability of a trait that confers a difference in survival and, as a consequence, in reproductive success, added to the fact that this trait variation is inherited, causes the population to evolve in a direction that opposes the trait bias of harvesting [4]. We can easily find other examples in many different areas of biology. It is well known, for instance, that bacteria are able to rapidly develop resistance to many antibiotics. Evolution of immunity to such a drug, that could occur, albeit with a very low probability, even without human intervention, can be reached within a few years of the commercial usage of a new antibiotic [2]. By the same token, the attempt to control the overpopulation of European domestic rabbits in Australia, that grew up to a plague, through the introduction of myxomatosis was frustrated by the effect of a fast evolutionary response to the disease. Even if there is no clear quantitative measure of the speed with which evolution responds, it is possible to find growing evidence that evolutionary shifts are sometimes very fast, comparable to the lifespan of a human being (microevolution). Support to this consideration is given by recently published data related to a long term study of the effects of trophy hunting on a population of bighorn sheep on the Ram Mountain, Canada [5]. From this study it emerges that, in a timespan of just 30 years, selective hunting based on some phenotype character – horn size in this particular case – can have caused the depletion of the genes that confer rapid body and horn growth. In fact, an observed decline in mean breeding values for weight and horn size indicates a microevolutionary response to hunting selection.

The main aim of this work is to show that a simple computational model of population dynamics, the Penna Model [6], is capable of reproducing such process. To be specific, our interest is to show how can we obtain a stable solution for a population subjected to microevolution and to give a full description of its dynamics. For this purpose, we will describe the dynamics of a diploid sexual population, representing each individual by its diploid genome, simulated by two sets of coupled bit-strings. An allele is encoded by two homologous bits in each of these bit-strings. The collective behaviour of these agents is dictated by a set of simple rules that we sum up in what follows. Introduction of new individuals in the population is obtained through a reproductive cycle that simulates birth. Each individual of a reproductively active couple generates, through a meiotic cycle with crossing-over two haploid gametes that, after the introduction of some mutations, combine to form a new genetic strand. Crossing is obtained cutting at a random position each string of the

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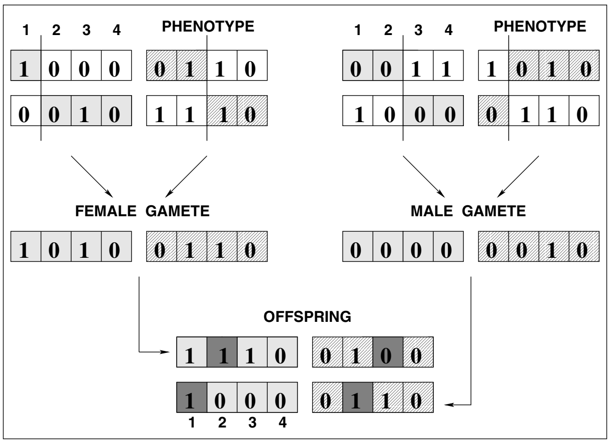

Fig. 1. Representation of the reproductive cycle. The diploid genome is represented with its age-structured part (light-shaded background) and the bit-strings that encode for phenotype (diagonal stripes in the background). As a first step, the genetic strands are crossed and recombined. A random choice determines the haploid gamete, as shown in the second step. Finally, some new mutation are added (dark-shaded squares) and the gametes combine to form a new genetic strand.

parent's genome and combining the left part of one with the right part of the other. In so doing, two new combination of the original genes are generated, and the haploid gamete is chosen randomly to be one of these (see Fig. 1).

The passage of time and the death of agents follow rules inspired by biological ageing as described by Medawar's hypothesis of accumulation of bad mutations. A position (locus) of the chronological (age-structured) piece of the genome is read at each time step. If an active mutation is found at this locus, it is added to the current number of harmful mutations; the individual dies when this amount reaches some pre-determined threshold value. In order to be active, a harmful mutation must occur at a homozygote locus, or at a heterozygote one for which the harmful allele is dominant. The number of loci where the allele represented by a bit set to 1 is dominant is fixed, and their position in the genome string is chosen randomly at the beginning of the simulation.

The biological and computational necessity of studying finite populations imposes the introduction of another death factor. It is usually represented by a density-dependent mean-field death probability, called Verhulst factor, proportional to the current size of the population.

The full simulated genome can include, other than the age-structured bit-strings used to introduce the biological clock of the individuals, other pairs of bit-strings that encode for phenotype traits that are responsible for intraspecific and/or environmental interactions. With this technique it is possible to establish a computational representation of competition and/or sexual selection [8–10]. In our present study, we will use just one extra bit-string to represent a single biological trait. A phenotype value is attributed to it by summing over all the active mutations present in the bit-string that encodes this trait – again, we consider as active a mutation at a homozygous locus, or at a heterozygous one where the mutated allele is dominant.

According to this procedure, the phenotype value is an integer between 0 and 32, and is different from the simple sum of all the ones present in the bit-string that determines the genetic distribution. We will refer to this latter number as the trait bit-string value. The essential difference lies in that the phenotype value takes into account the dyploid nature of the genome, through the effects of dominance and homozygose. On the opposite, the trait bit-string value is simply related to the frequency of the 1 allele in the genome.

Bits of the trait bit-strings can mutate from 0 to 1 or from 1 to 0, as opposed to ageing bit-string, that can undergo only bad mutations.

2 Model and methods

In a previous publication [7], the simplest implementation of the Penna model was able to make predictions relative to changes caused by overfishing on a population with a strong relation between age and size. This fact allowed the usage of the age-structured bit-strings of the genome alone for a full description of the relevant interactions.

The idea of the present work is to build up a simple toy model, inspired by the gene pool dynamics of the Ram Mountain population, capable of representing just the fundamental features of a real population.

For this reason, we have chosen to represent each individual by a genome with just two pieces: the first is the age-structured bit-string, while the second bit-string determines the individual phenotype. The classical rules of the Penna model, with a standard logistic Verhulst factor [8], are applied to this population. Under these conditions, the population dynamics obtained is simple and well known: the age-structured part of the genome causes the population to age in accordance with Gompertz law. On the other hand, the trait bit-string value, that does not feel the effect of any interaction, reaches a Gaussian shaped distribution with 16 as the mean value.

We now add to this simple basic model the two main forces that drive the dynamics of the phenotype distribution: sexual selection correlated with the phenotypic aspect and a phenotype-based selective hunting.

Our simulations are inspired by the observational data related to the population of the Ram Mountain [11], where sexual selection in bighorn rams operates in such a way that mating success increases with age, horn length and body size, tending to concentrate the paternities in those more favored rams. In our simulations we represent all the phenotypical dependence of mating success by one single trait. For simplicity, mating success has no age dependence in our implementation.

The first ingredient that is essential to affect the general distribution of the phenotype is to allow for paternity concentration. For this reason it is important to allow a male to mate more than once in each reproductive cycle. At each time step, each female that is reproductively active makes a non-random choice of her mating partner.

The selection is made by choosing among 20 males the one that has the highest phenotype value (extreme dynamics). This sexual selection causes a drift of the trait bit-string distribution towards higher values. In Figure 2 we can see that the distribution, after 100000 time steps, is centered around 26.

The hunting pressure we simulate was inspired by the conditions and laws prescribed in the Ram mountain region [5]. These state that it is allowed to hunt only rams older than four years and "full-curl" trophy rams, up to a maximum number of animals. In our simulations, we hunt male individuals older than 4 and with a phenotype value bigger than 16. The harvesting is implemented in the following way: we do a number of random attempts (approximately equal to the population dimension) of finding individuals that satisfy such characteristics and we stop the hunting when the established threshold number of animals killed is reached.

With this simulation setting, we leave the population evolving, with no harvesting selection, for 50000 time steps. After this first equilibrium is reached, we switch on the hunting selection. We estimate that after 50000 time steps further a final equilibrium is obtained.

In the simulations, particular attention must be payed to the population size. The real biological population of the Ram Mountain, during the years of observation, was approximately 140 animals, with rather large fluctuations over the years. The simulation of such a small population is really problematic. Not only is it difficult to do a confident statistical analysis of the results, but also the size of the fluctuations destroys the key elements of the model. The general dynamic, in fact, is no longer driven by the bit-string dynamics, but by the Verhulst factor instead, and it is also difficult to find a phenotype equilibrium distribution. For all these reasons we decided to describe the behaviour of a population of about 10000 individuals, considering this the smallest population that it is still suitable for a study with this model and that can allow for a consistent statistical approach. We have performed simulations with about 250000 individuals but it was not possible to point out differences or possibles finite scale effects.

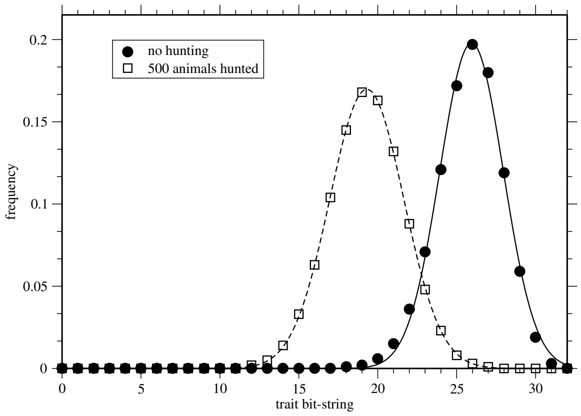

Fig. 2. Trait bit-string distribution for the two equilibrium states (no hunting and hunting pressure equal to 500). The data are well fitted by Gaussians with mean values 25.9 and 19.3, and standard deviations 2 and 2.4 respectively. The parameters used in the simulation are: the Verhulst parameter (130000), the initial population (2000), the minimum reproduction age (8), the maximum reproduction age (32), the number of offsprings (1), the threshold value (3), the same number of mutations (1) and dominant loci (6) for the two bit-strings. We have averaged over 10 different realizations in each case.

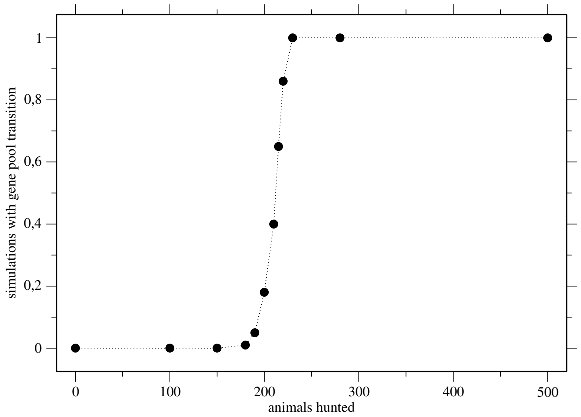

Fig. 3. Fraction of simulations that undergo a transition as a function of the number of animals hunted.

3 Results

We say that the population has undergone a significant variation in its gene pool when the corresponding mean value of the trait bit-string distribution has changed by more than the value of its standard deviation. By this token, the mean value of the trait bit-string distribution is used to define the state of the system.

We have decided to use this parameter instead of the phenotype value to keep our focus on evolutionary changes and variation at the genome level. The choice is, as a matter of fact, immaterial, and the results are qualitatively identical because, in our model, the relation between phenotype and genome is over-simplified and direct, and does not take into account environmental factors.

As we can see in Figure 2 the fundamental state of the system is a distribution centered in 26 with standard deviation of 2. If the hunting selection is switched on, a drift towards lower values is caused. In particular, if we select a hunting threshold of 230 animals for each time step, the distribution has its lowest mean value (19). From this point on, increasing the number of animals hunted will not cause any changes in the distribution. The distribution with mean 19 is thus some sort of equilibrium, or statistically stationary state, and limitations imposed on the hunting process will not affect any further the gene pool of the population.

We performed a hundred different simulations, for each set of parameters, to investigate the behaviour of the gene pool as a function of the number of animals hunted. The results are shown in Figure 3. It emerges that, for values smaller than 200, the fraction of simulations with a mean value of the trait bit-string distribution smaller than 23 is negligible. For 200 kills, in 20% of the simulations the

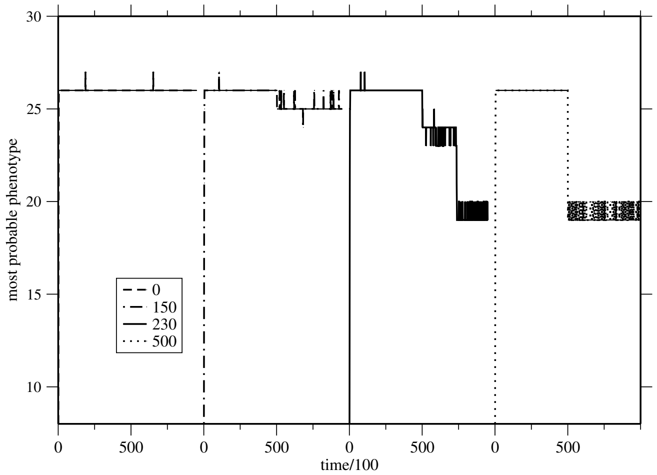

Fig. 4. The most probable value (mode) assumed by the trait bit-string distribution as a function of time. When there is no hunting it reaches the value 26 and does not change any more. For 150 animals hunted, from time step 50.000 on, this value moves to 25. For 230, it changes to 24 before stabilizing at the state of equilibrium at 19. In the last simulation, for 500 animals hunted, the mode undergoes a sharp transition towards 19. The time coordinate is shifted to a different origin for each simulation for clarity.

model suffers a transition of the trait bit-string distribution to reach a mean value close to 19. By increasing the number of animals killed, the number of simulations that undergo the transition also increases, and, for values larger than 230, all the simulations end up with a distribution with a mean value close to 19. An interesting and not so intuitive result is that not all the possible states are visited by the phenotype distribution as the number of animals hunted is varied. There is a forbidden region between 21 and 23, never visited by the mean value of the trait bit-string distribution. As a result, the model has only two different stationary states.

If we look at the dynamical behaviour of the model (see Fig. 4), it is possible to notice that the evolution of the system is really abrupt, and only 100 time steps are sufficient to drive the trait bit-string values from one state to the other (for 500 animals hunted, all the simulations reached the transition in less than 100 time steps). This fact is particularly interesting because it shows how fast the sharp transition that we are describing occurs. For this reason, we claim that our model can well represent the phenomenon of microevolution that has motivated our work. A fast transition is not the only possible outcome though, in fact, in some simulations where the number of animals hunted is between 210 and 230, the trait bit-string value becomes metastable before reaching the stationary state, and the time-scale of the transition becomes large.

4 Conclusion

In this paper, we provide an example of how studies of microevolutionary processes may be undertaken with the usage of microscopic models of population dynamics. By a careful selection of the key ingredients, we show that a toy model that mimics the main features of some particular gene pool dynamical behaviour can single out the dominant structures of its trajectories in phase space. In our particular case, these features relate to a biological trait that identifies preferred mating partners and also hunting trophies. The competition that results from this situation generates a transition in the gene pool repertoire of the population as some threshold number of animals are killed, both in the results of our simulations and in the observational data.

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References

1. M.V. Ashley, M.F. Willson, O.R.W. Pergams, D.J. O'Dowd, S.M. Gende, J.S. Brown, Biol. Conserv. **111**, 115 (2003)
2. S.R. Palumbi, Science **293**, 1786 (2001)
3. R. Law, ICES J. Mar. Sci. **57**, 659 (2000)
4. D.O. Conover, S.B. Munch, Science **297**, 94 (2002)
5. D.W. Coltman, P. O'Donoghue, J.T. Jorgenson, J.T. Hogg, C. Strobeck, M. Festa-Bianchet, Nature **426**, 655 (2003)
6. T.J.P. Penna, J. Stat. Phys. **78**, 1629 (1995)
7. T.J.P. Penna, A. Racco, A.O. Sousa, Physica A **295**, 31 (2001)
8. J.S. Sá Martins, S. Moss de Oliveira, G.A. de Medeiros, Phys. Rev. E **64**, 021906 (2001)
9. A. Ticona, T.J.P. Penna, Braz. J. Phys. **33**, 619 (2003)
10. K. Luz-Burgoa, S. Moss de Oliveira, J.S. Sá Martins, D. Stauffer, A.O. Sousa, Braz. J. Phys. **33**, 623 (2003)
11. D.W. Coltman, M. Festa-Bianchet, J.T. Jorgenson, C. Strobeck, Proc. R. Soc. Lond. B **269**, 165 (2002)