From regeneration to escape the extinction in population experiments

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Stochastic modelling in population dynamics
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1. Motivation

to explain some phenomena arising in the behavior and development of the biological populations

- How long does take the final establishment of a biological population in a certain environment?

  As there is always a positive probability of extinction, it is possible to have several unsuccessful trials before the biological populations start to grow irreversibly or explode;

- What conclusions one can draw from an early extinction of a biological population? Does it imply that the offspring mean in these environments is low?

- What kind of inferences one can make on the fertility rate of the process from the data of total progeny?

- Similarly, our study might help decision-makers to take a well-grounded choice.

- P. Haccou, P. Jagers and V. A. Vatutin (2005): **Branching Processes: Variation, Growth, and Extinction of Populations, Cambridge University Press, Cambridge**;

- "One of the very points of branching processes theory is the establishment of the paradoxical possibility of frequent extinction in spite of general growth. Thus the extinct species population could well have been supercritical, but just suffered from bad luck."

- Are there practical situations where the populations instantly restored from extinction?

- distributional and inferential properties of the **time to extinction** and total progeny conditioned on extinction of branching processes

2. Background

In the **discrete-time case**, the problem concerning the total progeny was investigated in:

- P. Jagers (1975): **Branching Processes with Biological Applications.** London: John Wiley and Sons.

- T. Harris (1989): **The Theory of Branching Processes.** Dover Publications Inc., New York.

- S. Karlin, S. Tavaré (1982): Detecting particular genotypes in populations under non random mating. Math. Biosci., v. 59, 57-75. – the asymptotic behavior of the probabilities of hitting the absorbing states, the times needed to hit these states, and the conditional distributions of the number of particles (for the models allowing catastrophes).

- F. T. Bruss, M. Slavtchova-Bojkova (1999): On waiting times to populate an environment and a question of statistical inference. J. Appl. Probab., v. 36, 261-267. – the problem of inference from expected waiting times and expected progeny on fertility rates was treated for the first time.

- M. Slavtchova-Bojkova (2000): Computation of waiting time to successful experiment using age-dependent branching model. Ecological Modeling , v. 133, 125-130. – the above results were generalized in **continuous time**, i.e. when the newly introduced populations are supposed to be Bellman-Harris branching processes.

- A. G. Pakes (1993): Absorbing Markov and branching processes with instantaneous resurection. Stochastic Processes and Appl., v.48, 85-106.

- A. Y. Chen, E. Renshaw (1990): Markov branching processes with instantaneous immigration. Probab. Theory Rel. Fields, v. 87, 209-240. – populations are quickly restored from extinction, by reintroductions, or rapid migration, as in island biogeography.

3. Model in continuous time

Consider a population branching process $(Z(t) : t \geq 0)$ having a state-space the non-negative integers with zero as an absorbing state.

$$Z_0 = 1, \quad T_0 = 0, \quad T = \inf\{t : Z(t) = 0\} \leq \infty$$

In addition, let us suppose that $(Z_t : t \geq 0)$ is **Sevast'yanov's age-dependent branching process (Bellman-Harris branching process)**

particle's life length τ has distribution

$$G(t) = P(\tau \leq t), \quad G(0^+) = 0$$

particle's reproduction at age t

$$h_t(k) = P(\xi = k | \tau = t), \quad t > 0, \quad k \geq 0$$

$$h(t; s) = \sum_{k=0}^{\infty} h_t(k) s^k, \quad |s| \leq 1.$$

$\{(Z_t(n)) : n = 1, 2, \ldots\}$ be i.i.d. copies of $Z(t)$

$$H_n = \sum_{0 \le j \le n} T_j, \quad (n \ge 1).$$

$$\{T_n\} \text{ are } \text{ i.i.d.r.v.}$$

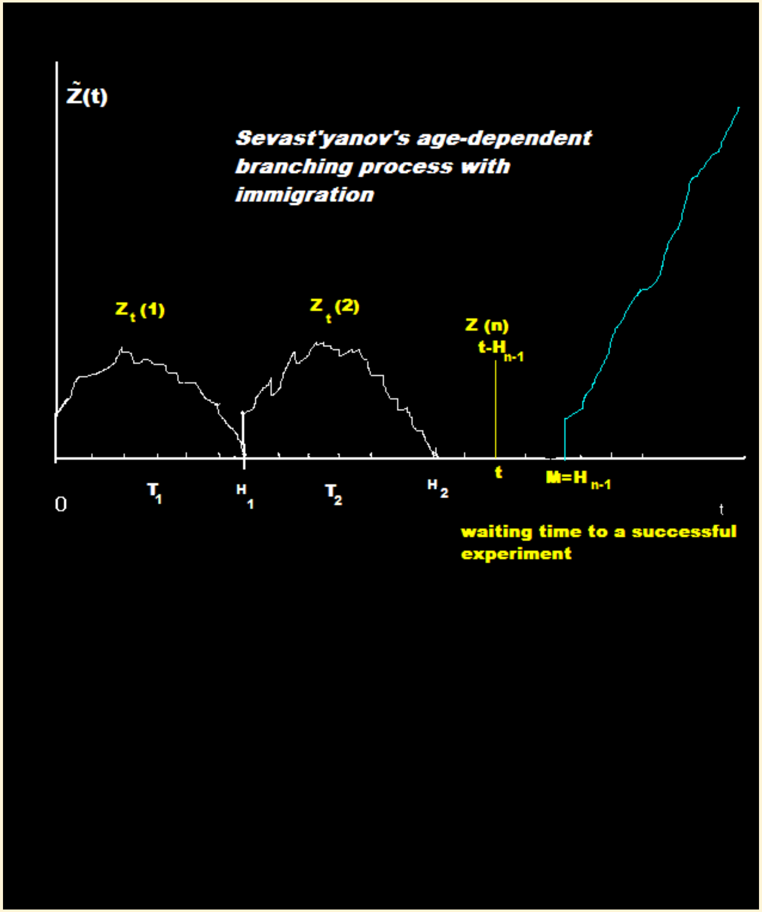
Thus H_n is the time of the n-th extinction event ($H_0 = 0$ means that the entire process begins with an extinction at $t = 0^-$).

Hence $N = \sup\{n : T_n = \infty\}$ is the number of extinction events (including the event at $t = 0^-$).

Then, the process we are interested in is

$$\widetilde{\mathbf{Z}}_{\mathbf{t}} = \mathbf{Z}_{\mathbf{t}-\mathbf{H}_{\mathbf{n}-\mathbf{1}}}(\mathbf{n})$$

if $\quad H_{n-1} \le t < H_n \quad (n = 1, \ldots, N).$



Z̃(t)
Sevast'yanov's age-dependent branching process with immigration
Z_t(1)
Z_t(2)
Z(n) t-H n-1
0
T1
H1
T2
H2
t
M=H n-1
t
waiting time to a successful experiment

Life cycles

For the branching process $(\widetilde{Z}_t)_{t\geq 0}$ we shall call life cycles the intervals

(H_{n-1}, H_n), $n = 1, 2, \ldots, N-1$ on which

$$\inf_{H_{n-1}<t<H_n} \widetilde{Z}_t > 0.$$

Thus $(\widetilde{Z}_t)$ may have several life cycles, the last one always being infinite, provided the process is super-critical. If the process is sub-critical it will have a.s. infinitely many life cycles.

Lifetime of the process $(\widetilde{Z}_t)_{t\geq 0}$ before escaping from extinction

$M =: H_{n-1}$ of immigration, i.e. the "birth time" of that process $Z_n(t)$, which finally survives or the last exit time from the state zero.

We shall also study the distribution and expectation of the lifetime M. Finally, we shall analyze the total progeny during the lifetime of the process $(\widetilde{Z}_t)_{t\geq 0}$ and shall obtain its expectation and variance.

4. Theoretical Results

Suppose $q = P(T < \infty) < 1$.

$$\tau(\theta) := E(e^{-\theta T}), \quad \tau(0) = q.$$

Let

$$F(t) = P(T \le t) = \int_0^t h(u; F(t-u))dG(u).$$

Theorem 1.

The Laplace-Stieltjes transform $\lambda(\theta) := E(e^{-\theta M})$ (of the total waiting time until the initiation of that cycle whose path goes to infinity), is

$$\lambda(\theta) := \frac{1-q}{1-\tau(\theta)}.$$

The total progeny of a life cycle

We are interested in the total progeny V of a life cycle and its expectation, in order to make some inferences on the fertility rates of the particles. Let $g(s;t) = E(s^V; T \leq t)$.

Theorem 2.

The expected total progeny V of a life cycle satisfies the following equation:

$$\nu(t) := E(V; T \leq t) = F(t) + \int_0^t \nu(t-y) h'_s(y; F(t-y)) dG(y),$$

where

$$F(t) = P(T \leq t) = \int_0^t h(u; F(t-u)) dG(u).$$

In the case $\tilde{m} \neq 1$ (i.e. non-critical cases) the expected total progeny of a life cycle is:

$$E(V; T < \infty) = \frac{1}{1 - h'(q)}.$$

5. Numerical Method for Bellman-Harris branching processes

- M. E. Jacobson(1985): Computation of Extinction Probabilities for the Bellman-Harris Branching Processes. Math. Biosci., v. 77, 173 - 177. – a numerical investigation of the rate of convergence of the extinction probability for a discrete-time age-dependent branching process was carried out.

  The most significant result illustrated by his simulations was the long tail of the distribution of life cycle for the case where the mean number of offspring was 1, as opposed to the quick convergence for the other cases.

- E. D. Powell(1955): Some features of the generation times of individual bacteria. Biometrika, v. 42, 16-44. – found that the life-period of bacteria follows a gamma distribution, and reproduction at death is characteristic of bacteria-like organisms. That is why a discretized gamma density was used for all computations and simulations.

6. Preliminaries and assumptions

- the probability q of eventual extinction of a Bellman-Harris process $(Z(t))$ is the smallest non-negative root q of the equation

$$h(s) = s, \quad h(s) = \sum_{k=0}^{\infty} p_k s^k.$$

$$q = 1 \iff m = h'(1) \leq 1.$$

- m is called the reproduction mean, and the super-critical, critical and sub-critical cases correspond to the relations $m > 1$, $m = 1$ and $m < 1$, respectively.
- l be the maximum number of offspring an individual can have,
- r be the greatest age an individual can live to,
- $g(t) = G'(t)$ be the life cycle density.

$F(t)$ denotes the probability of extinction by time t, $M = H_{n-1}$ is the last instant of immigration in the process $Z(t)$;

$$\text{If } t < r,\ F(t) = p_0 G(t) + \sum_{s=1}^{t-1} \sum_{k=1}^{l} p_k F^k(t-s) g(s),$$

$$\text{If } t > r,\ F(t) = p_0 + \sum_{s=1}^{r} \sum_{k=1}^{l} p_k F^k(t-s) g(s),$$

$$F(t) = P(T \leq t),$$

$$P(T \leq t | T < \infty) = \frac{F(t)}{q},$$

$$E(T|T < \infty) = \frac{1}{q} \int_0^\infty (q - F(t)) dt,$$

$$E(M) = \frac{q}{(1-q)} E(T|T < \infty).$$

7. Numerical results

To study the implications of the above equations for the extinction probabilities we use Mapple 8. Computations were then made with extinction probabilities up to 150 generations.

- we compute the conditional density function of the life cycle T, given extinction for an age-dependent branching process with immigration
- the distribution of the total waiting time M when adopting as a probability density function for cell generation times the $\Gamma(\alpha, \beta)$ form for this distribution with density,

$$g(x) = \frac{e^{-x\beta}\beta^{\alpha}x^{\alpha-1}}{\Gamma(\alpha)}, \quad x > 0$$

  with $\alpha = 6$, and $\beta = 1$.

- We consider two cases for the offspring distribution.

  First we suppose that the offspring distribution belongs to the family of p.g.f. $h_p(s) = p + 0.4s + (0.6 - p)s^2$, parameterized by

$$p = P\{\text{the initial progenitor dies without any offspring}\}.$$

The computational results for $p = 0.05$ (which corresponds to a supercritical case with $m = 1.5$ and $q = 0.09$) are presented in the Figure 1, where we show the conditional density function of the life-period T given that $T < \infty$, $q(t)$ is on the Figure 2 and the conditional density function of the total waiting time M given that $M > 0$ is on the Figure 3.

In addition, we obtained for the conditional expected value of T on the event of certain extinction, i.e. $E(T|T < \infty) = 11.92$ and for the unconditional $E(M) = 1.17$ in this case.

- Secondly, we implemented the computation when the offspring distribution is geometric one with $p = 2/5$ (which corresponds to a supercritical case with $m = 1.5$ and $q = 0.66$). The results about the conditional density function of the life-period T conditioned on extinction $T < \infty$ are on the Figure 4, $q(t)$ is on the Figure 5 and the conditional density function of the total waiting time M given that $M > 0$ is on the Figure 6. We obtain in this case, that $E(T|T < \infty) = 12.46$ and $E(M) = 24.2$.

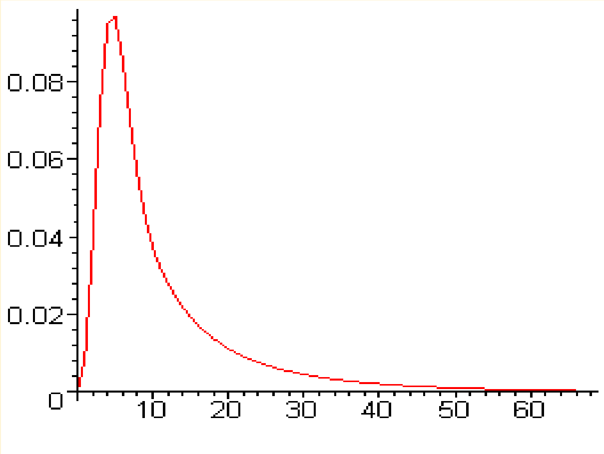


Fig.1.Conditional density function of life-period T, parametric reproduction

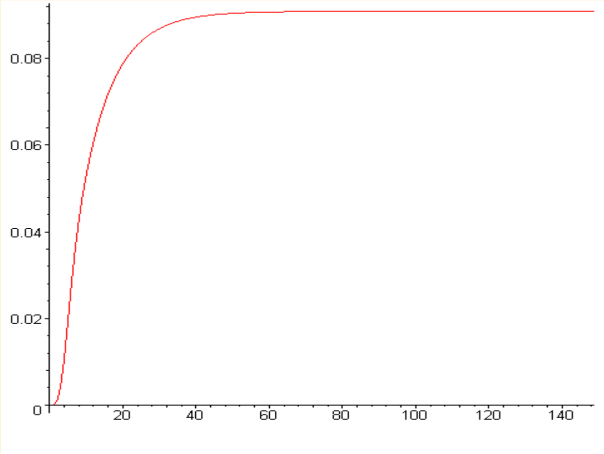


Fig.2.Probability of extinction by time t, parametric reproduction

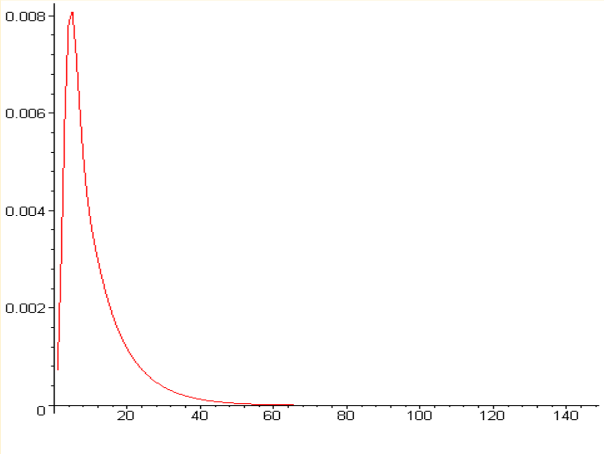


Fig.3.Density function of the total waiting time M, parametric reproduction

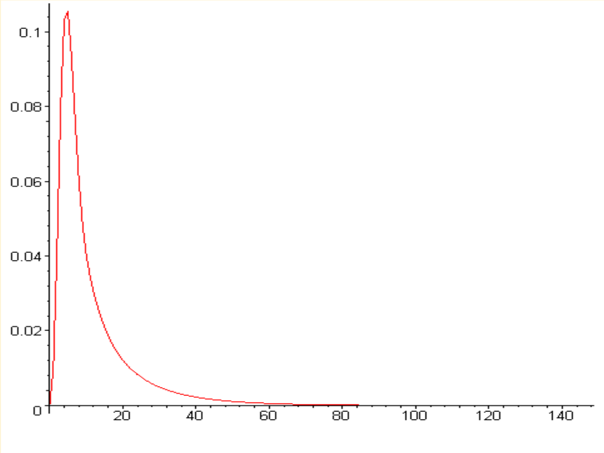


Fig.4.Conditional density function of life-period T, geometric reproduction

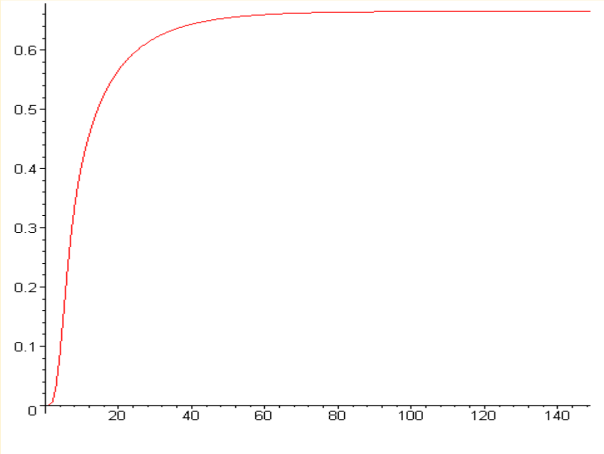


Fig.5.Probability of extinction by time t, geometric reproduction

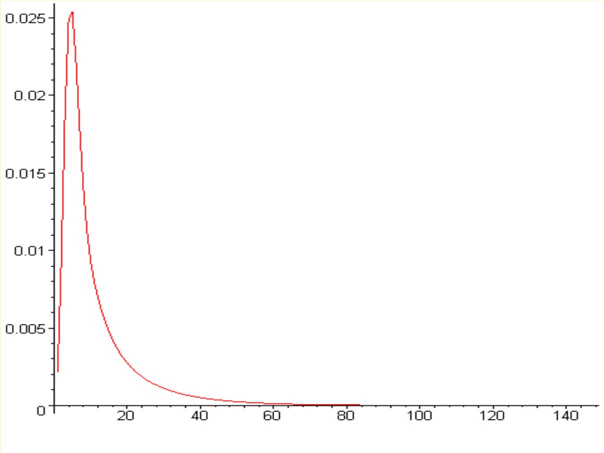


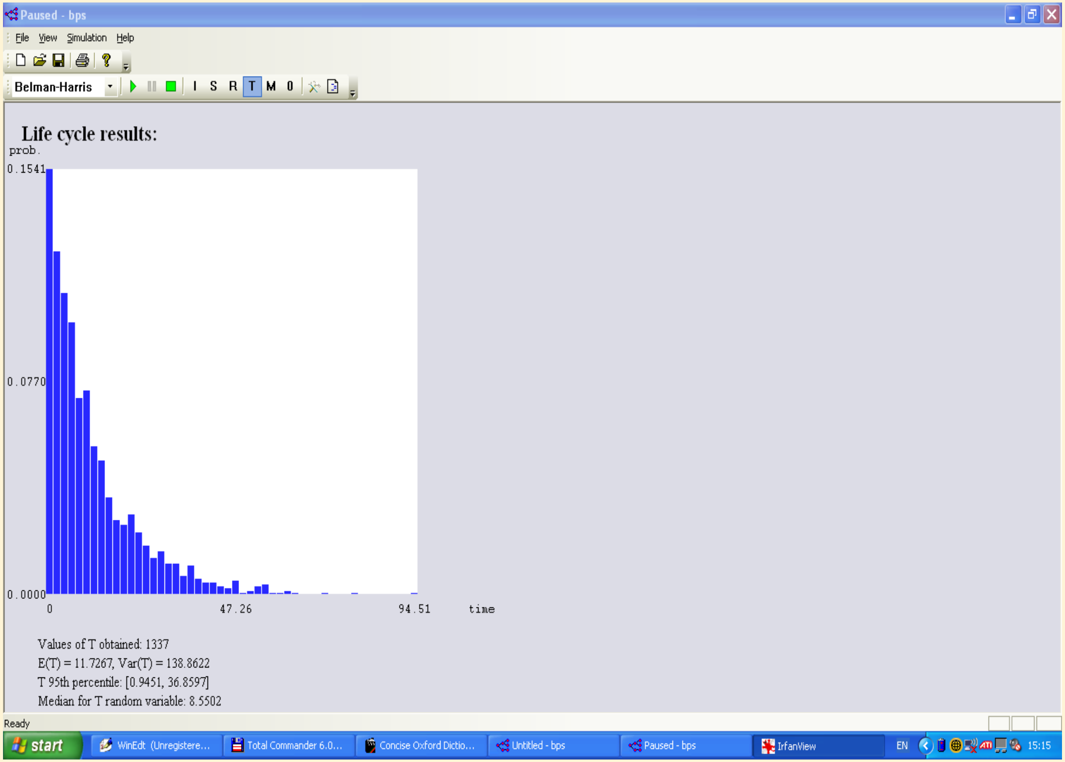
Fig.6.Density function of the total waiting time M, geometric reproduction

8. Simulation experiments

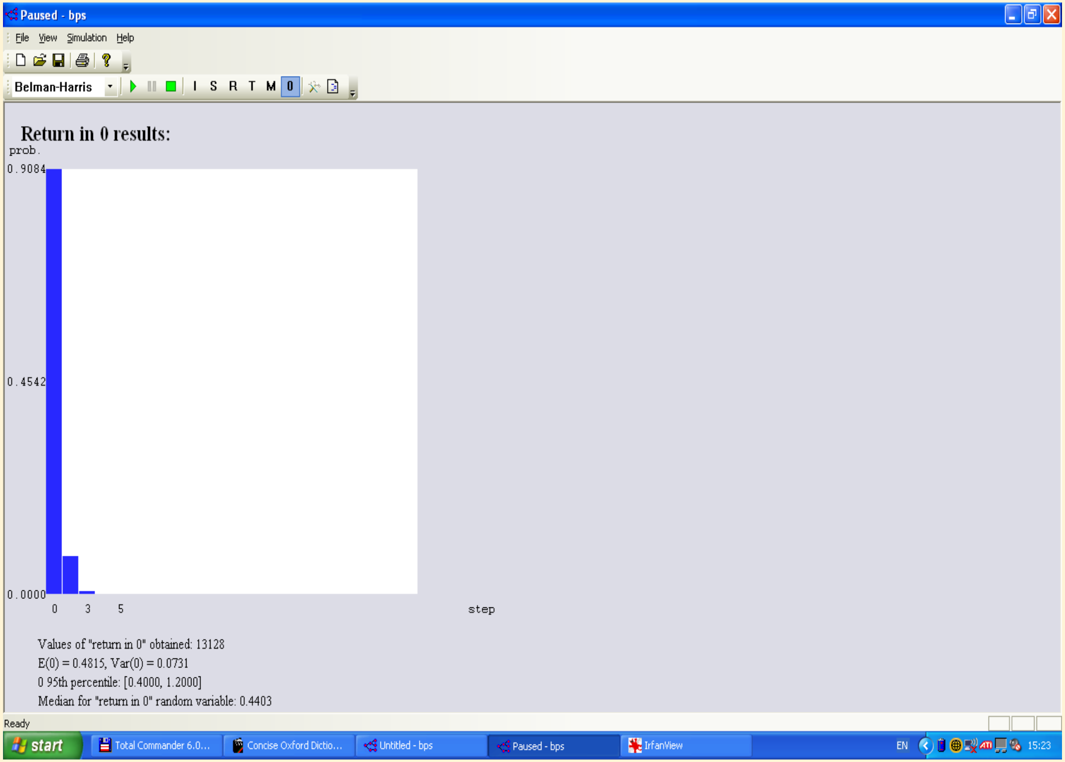
A code for simulation system for branching processes is developed. No programming is necessary and all input data can be entered in user-friendly dialog boxes and graphics and (numerical) results can be easily and quickly obtained.

The results can be stored in the Database table and may be analyzed easily. The code can be used for actual design, prediction and estimation of the parameters of different classes of branching processes, both in discrete and continuous time.

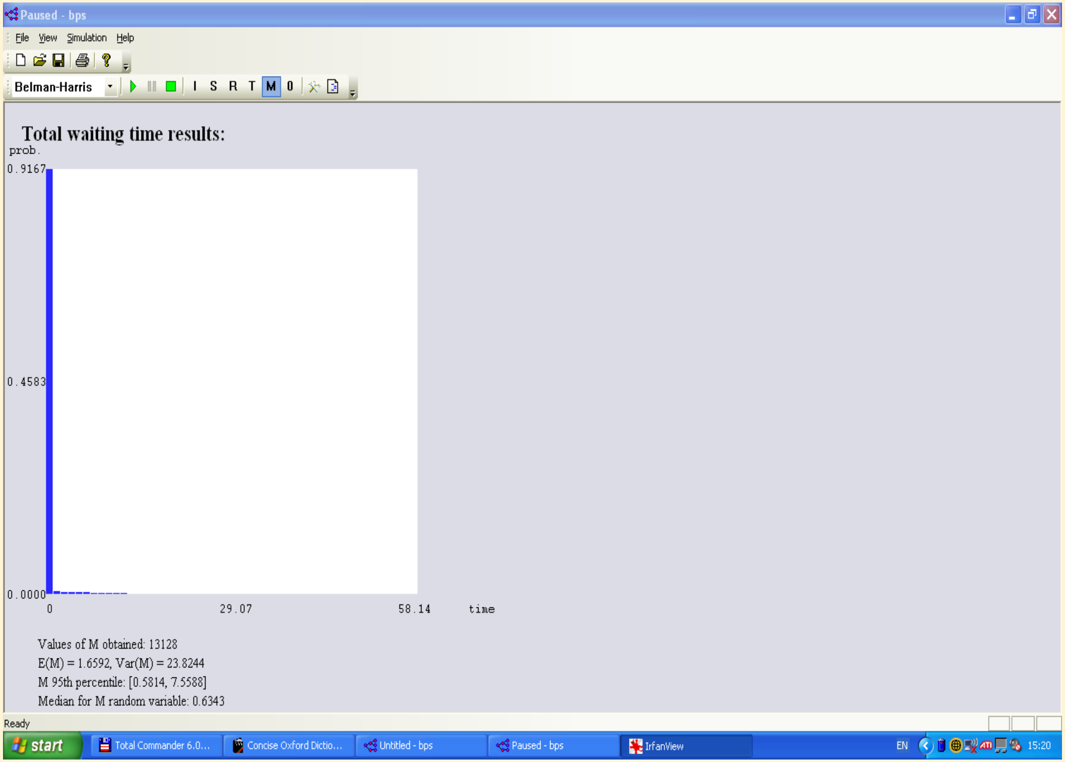
The SIMULATION SYSTEM is a simple professional tool that might be used by biologists, engineers and decision-makers for simulation of the processes which could appear to be suitable for modeling of some real world problems related to population and repopulation experiments.



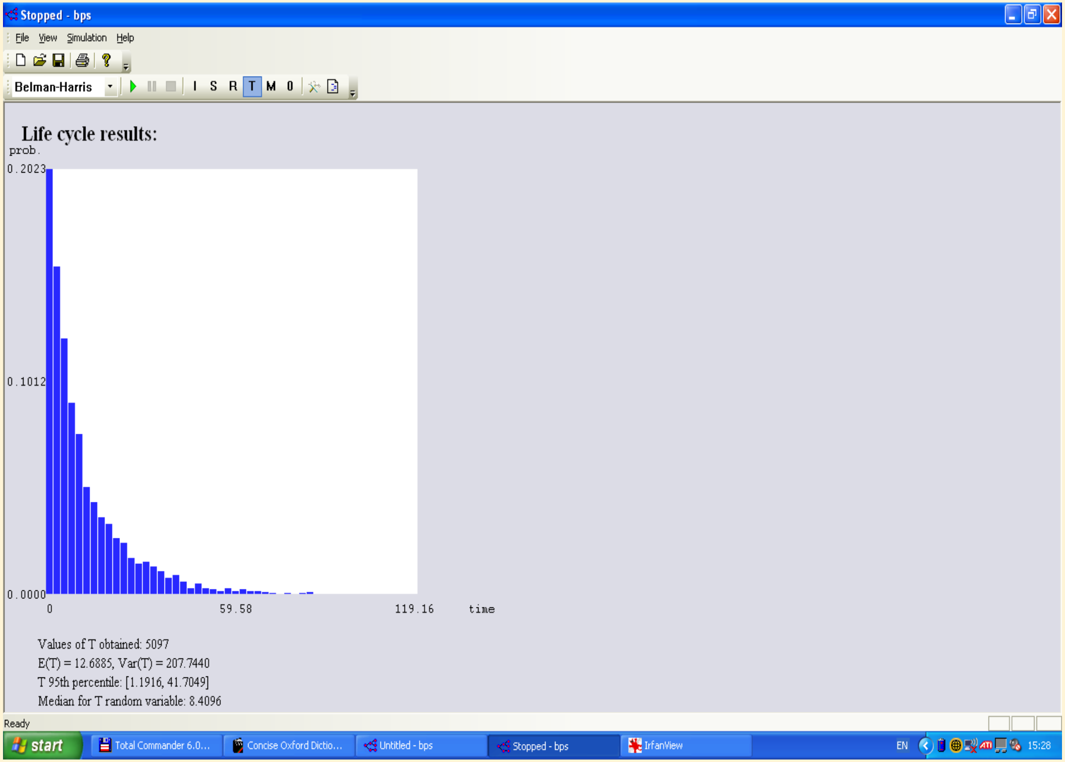
Conditional density function of life-period T, parametric reproduction



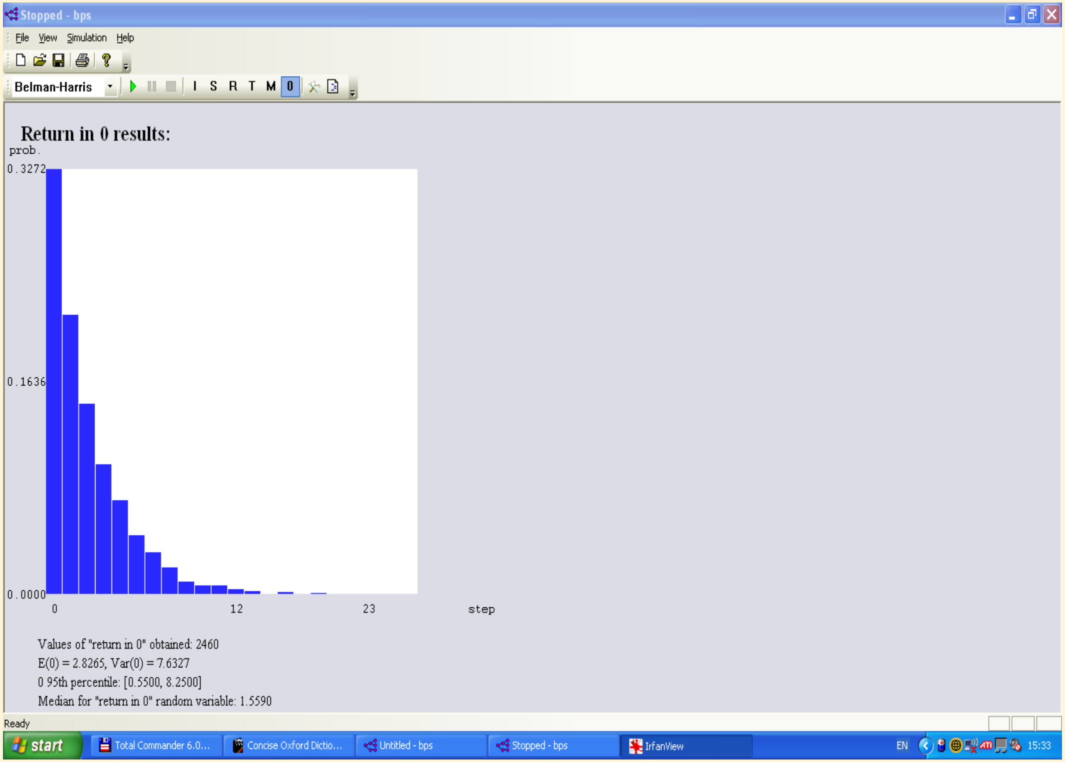
Conditional density function of the returns in zero by t, parametric reproduction



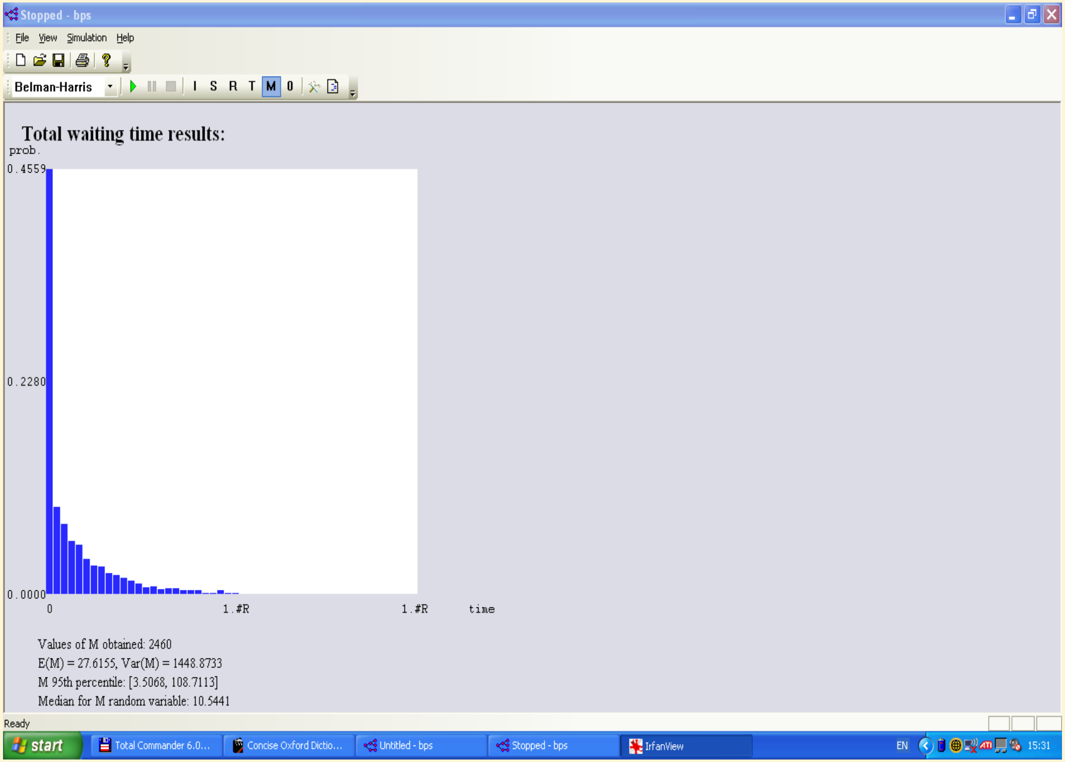
Conditional density function of the total progeny V, parametric reproduction



Conditional density function of life-period T, geometric reproduction



Conditional density function of the returns in zero by t, geometric reproduction



Conditional density function of the total progeny V, geometric reproduction

9. Discussion

In population experiments it is usually easier to see if a new introduction has been successful than to know whether, and when, extinction has occurred. In many cases statistical data are only provided by interest groups, hunters, photographers, etc. Independent control studies to assess the prior probability of extinction are likely to be environment-biased. On the other hand, it is not always possible to reduce the prior probability of extinction by releasing a large numbers of animals. The point is that extinction involves a very strong bias.

THANK YOU VERY MUCH

FOR YOUR ATTENTION!