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Hard harvesting of a stochastically changing population

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HIGHLIGHTS

- We have investigated hard harvesting (removal of a fixed number of individuals, each generation) of a stochastically changing population.
- A new phenomenon occurs, where the dynamics may be driven to an impossible regime, where it cannot continue (termination).
- Termination occurs even in populations with the tendency to grow.
- We determine a statistical description of hard harvesting and termination.

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ABSTRACT

We consider a population whose size changes stochastically under a branching process, with the added modification that each generation a fixed number of individuals are removed, irrespective of the size of the population. We call removal that is independent of population size 'hard harvesting'. A key feature of hard harvesting occurs if the size of the population is smaller than the fixed number that are harvested. In such a case, the dynamics cannot continue and must terminate. We find that even for populations with a tendency to grow, there is a finite probability of termination. We determine the probability of termination, and given that termination occurs, we characterise the statistical properties of the random time to termination. We determine the impact of hard harvesting on the size of the population, in populations where termination has not occurred.

1. Introduction

In this work we consider a population that evolves in discrete generations. The adults reproduce in a given generation and then die, leaving offspring that are harvested at the end of the generation. The remaining individuals constitute the adults of the next generation. We assume the size of population varies due to two components, one of which is stochastic, the other deterministic, as follows.

1. In each generation, every adult contributes a random number of offspring from a specified distribution, under a branching process, and then dies, with the offspring remaining.
2. At the end of each generation, a number of offspring are removed from the population (harvested), at a level that is independent of the population size. The remaining offspring constitute the adults of the next generation.

The net outcome is that the population size varies stochastically.

Because the number of offspring removed is independent of the population size, we describe their removal as *hard harvesting*. Hard harvesting may have different applications and implications in a variety of different subjects where branching processes play a role, such as ecology and genetics (Ewens, 1979; Feller, 1951a; Karlin and Tavare, 1983), as well as physics (Pázsit and Pál, 2007; Christensen and Moloney, 2005), seismology (Helmstetter and Sornette, 2002) and finance (Cox et al., 1985). Here we focus on the implications of hard harvesting for biological populations whose size changes stochastically. While we are not aware of investigations on the implications of hard harvesting for such populations, there is mathematically motivated work which has investigated some of the equations that appear under a continuous approximation (Feller, 1951a,b).

We can list some possible applications of hard harvesting (the list is not exhaustive). The most direct application is to the blind harvesting of a population that, uninterrupted, would be expected to exhibit the stochastic growth associated with a branching process. Each generation (i.e., each year, in an annual organism) a fixed number of individuals are simply removed from the population. This could happen, for example, in a scientific survey

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of the population that is regularly carried out over time (Hutchinson, 1978). More generally, any problem with the same character, i.e., the removal of members of a *stochastically changing population* (i.e., not necessarily with the tendency to increase), at a fixed rate, independent of the population size, falls under the description of hard harvesting. Analogously, a population with a fixed outflow each year, e.g., a country with a net number of emigrants, independent of the population size, or a stochastically growing ant colony, with a fixed rate of attrition, could fall under the scenario described by the model. In epidemiology, a branching process represents a simple model of a disease that is spread by individuals who are infectious for a limited period of time (Pénisson, 2014), with the number of new cases generated by an infectious individual corresponding to their 'offspring'. It follows that if, as a health policy, a number of individuals are removed from the population of infectious individuals (i.e., quarantined/hospitalised) while they are infectious, and if the number removed is independent of the actual number of infectious individuals, then this would also fall under the model considered here. While we do not explicitly consider it in the present work, if the level of harvesting were a *random function of time*, but again independent of the population size, then the harvesting could represent the consumption of a prey population of either a single apex predator (Hallam and Levin, 1986), or a conserved population of predators (Myerscough et al., 1992).

In this work we shall restrict analysis to the simplest model involving the hard harvesting of a stochastically changing population, where a *fixed number* of individuals are removed from a population each generation. This model is fundamental in character, applicable in its own right, and provides a rich starting point for more complex problems.

An essential and new aspect of hard harvesting is that it cannot always be carried out. If the total number of offspring produced in one generation is, by chance, smaller than the fixed number that is removed in a generation, then the harvesting cannot occur. In such a case, the dynamics cannot continue and must terminate, as discussed below.

We note that even for populations that, on average, grow over time, there is still a non-zero probability of termination of the dynamics. Termination takes a random time to occur and if termination is probable, then the mean value of this time is a measure of how long hard harvesting of such a population can typically be carried out. In the example of the scientific survey, described above, this time is a measure of how long the survey can be carried out before either a change of practice or abandonment of the survey is required. In the case of a disease, this time is a measure of how long before the number of new cases is below the number of infectious individuals that are quarantined. If termination is improbable, then population growth that is subject to hard harvesting has an appreciable chance to continue indefinitely.

In this paper we proceed by first establishing the appropriate statistical distribution of the population. We then employ a continuous approximation, which leads to a diffusion equation. This allows us to determine the key aspects of the effects of hard harvesting on a stochastically changing population, namely: (i) the probability of termination, (ii) statistical properties of the termination time, and (iii) the impact of hard harvesting on the size of populations whose dynamics has not terminated.

2. Model

Let M_t denote the number of adult individuals in a population at generation (time) t, where t takes the discrete values 0, 1, 2, … . The stochastic change of the population, in going from generation t to generation $t+1$, follows from all adults in generation t reproducing, via a branching process, and then dying. The adults leave offspring, which are subject to hard harvesting (removal, independent of the population size) at the end of the generation t, and the survivors become the adults of generation $t+1$. The behaviour of the population is described by the stochastic difference equation

$$M_{t+1} = \sum_{j=1}^{M_t} \xi_j - h \tag{1}$$

where ξ_j is the random number of offspring that are produced by the j'th individual in a given generation, and h is the number of offspring that are removed (harvested) each generation. The value of the sum in Eq. (1) has the value zero if M_t is zero.

We model the ξ_j in all generations as independent and identically distributed random variables whose possible values are 0, 1, 2, …, and whose expected values and variances are

$$E[\xi_j] = 1+s, \quad \mathrm{Var}(\xi_j) = \sigma^2. \tag{2}$$

The value of the growth-rate-parameter, s, must exceed -1, but is otherwise arbitrary. We shall primarily consider small values of $|s|$. We take the value of the harvesting level, h, that appears in Eq. (1), to be a positive integer that is independent of time.

In Eq. (1), the fixed quantity h is subtracted from the sum. However, the value of the sum varies over time and there is the possibility that, at some time, h exceeds the value of the sum and the right hand side of Eq. (1) becomes negative. If this occurs then Eq. (1) leads to a negative value of the population size in the next generation, which is not a meaningful value. To deal with the possibility that M_t can become negative we have two alternatives. (i) *Modify* Eq. (1), by preventing M_t becoming negative in some way, so that no problems are encountered in the dynamics and they can meaningfully continue. (ii) *Terminate* the dynamics if M_t becomes negative, recognising that M_t has been driven to an unfeasible regime. We take the view that the dynamics of Eq. (1) are simple and fundamental and rather than modifying Eq. (1) in an arbitrary way, we shall fully pursue the logic of the model, and adopt the second alternative, namely of terminating the dynamics at the time that M_t becomes negative, if such a time occurs. We thus assume that hard harvesting of a population is carried out, unchanged in manner, possibly indefinitely or until such time that it becomes impossible to implement.

We note that in probability theory, some consideration is given to stochastic processes that are artificially killed (stopped). For example, a particle undergoing Brownian motion can be defined to be killed when it hits the boundary of a domain (Chung and Zhao, 1995). This is distinct from the termination that occurs as a result of hard harvesting, where the intrinsic dynamics, alone, has the possibility of driving the system to a point where it cannot continue.

3. Time of termination and the joint distribution

In what follows, we shall start Eq. (1) at an initial time of $t=0$ with an initial population size (number of adults) of n, i.e., $M_0=n$. We shall assume $n>0$, since $n=0$ is of no interest (if $n=0$ then M_1 is always $-h$ and termination always occurs in the first generation[1]). To simplify the notation, we shall generally adopt the convention of not explicitly indicating that both probabilities and averages (expected values) are conditional on there being n adults in the population at time $t=0$; this conditioning will be left implicit.

[1] We take the view that termination is necessary when the dynamics of a population causes it to enter an impossible region. A population which has gone extinct (i.e., achieved size 0) is not at an impossible value. Thus while we could define termination to occur at $M_t=0$ we do not do so. In more general models, where there are additional features of the dynamics (e.g., including hard harvesting that is not independent of time), we can envisage a population staying at 0 for some time, possibly even going positive afterwards. Thus generally, extinction (achieving 0) and termination are distinct concepts.