

A continuous time version and a generalization of a
Markov-recapture model for trapping experiments

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Institute of Statistics
Mimeograph Series No. 2507
North Carolina State University
Raleigh, North Carolina

June, 1998

Abstract

Wileyto et al. (1994) propose a four state discrete time Markov process, which describes the structure of a marking-capture experiment as a method of population estimation. They propose this method primarily for estimation of closed insect populations. Their method provides a mark-recapture estimate from a single trap observation by allowing subjects to mark themselves. The estimate of the unknown population size is based on the assumption of a closed population and a simple Markov model in which the rates of marking, capture, and recapture are assumed to be equal. Using the one step transition probability matrix of their model, we illustrate how to go from an embedded discrete time Markov process to a continuous time Markov process assuming exponentially distributed holding times. We also compute the transition probabilities after time t for the continuous time case and compare the limiting behavior of the continuous and discrete time processes. Finally, we generalize their model by relaxing the assumption of equal per capita rates for marking, capture, and recapture. Other questions about how their results change when using a continuous time Markov process are examined.

Key words: Capture-recapture experiment; discrete and continuous time Markov process; uniformization; transition probability matrix; multinomial distribution; maximum likelihood estimation; population size estimation; program MAPLE, program SURVIV.

1 Introduction

When studying animal populations, one of the main purposes is to estimate the population size N , and capture-recapture models have been frequently used to achieve this goal. Ecologists and wildlife biologists are usually interested in sampling a population several times. In this situation, it is necessary to keep a complete capture history of those animals that have been captured at least once. Wileyto et al. (1994) point out that in the case of insect populations, mark-recapture models have not been very successfully used because they usually involve intense labor, and they often provide few or no recaptures. Also, the initial stage involves mass rearing of insects for release, or capture with arduous care to maintain subjects in good condition. When trapping is used to monitor insects in agricultural systems, release may be unacceptable to industry. The method requires sequential visits to the traps in order to obtain an estimate.

They propose an alternative method which only involves placement of traps, and provides a single trap observation by allowing subjects to mark themselves. They describe a probability model that relates the events of capture and recapture under the following setting and assumptions:

- (1) half the traps are converted into passive marking stations where subjects may visit and leave marked, while the remaining half continues to capture individuals permanently.

Example: Traps might consist of the usual wing or pitfall traps baited with food or pheromone lures; marking stations would use identical structures and baits, but they will be filled with a fluorescent dye and modified to allow escape (Wileyto et al. 1994).

(2) Assumptions:

- (a) Population is closed (apart from trapping).
- (b) Rates of marking and capture are equals.

2 Assumption violations

Closure assumption

The population is closed to additions (births or immigrants) or deletions (deaths or emigrants). If the population is growing or subject to input and outflow of any sort, the estimator may perform poorly. Wileyto et al. (1994) conduct a simulation study in which they showed that depending upon the rate of population turnover, the positive bias in the estimator can be enormous. Their estimator works well if the population is turning over at 10 percent of the trapping rate, or if the probability of unobserved animals is relatively large.

Although closure is a strong assumption that rarely holds in a biological population, it can be at least approximated if a study is properly conducted over a short period of time relative to migration or reproduction. If the closure assumption is valid, then closed models are very useful because they can allow for relaxation of the assumption of equal catchability (Otis et al. 1978, White et al. 1982, and Pollock et al. 1990.)

Rates of marking, capture, and recapture are equal

This assumption is very difficult to achieve in practice because capture probabilities can be affected by different factors such as inherent differences among individuals in the population (heterogeneity), time variation, and behavioral (or trap) response (Pollock 1991). Some animals are more or less likely to be caught than others due to differences in species, sex, age, size, social dominance, number and placement of traps or other inherent characteristics (heterogeneity). Capture probabilities can change during the period of the study depending on weather conditions (time variation). For example, a cold rainy day during the study might reduce activity of the animals

and reduce the probability of capture (White et al. 1982). The trapping method used can also affect the trap response and consequently the capture probability. Baiting traps, for example, are likely to lead to a trap happy response where marked animals are more likely to be captured than unmarked animals. Inherent heterogeneity among animals in the population causes negative bias on estimates of N while behavior responses may cause positive or negative bias on estimates of N . A trap happy response produces a negative bias, and consequently underestimates the population size N , whereas a trap shy response causes positive bias and overestimates the population size N . Several models that allow for relaxation of this assumption have been proposed. For further details about assumption relaxation, examples, or practical applications of capture-recapture analysis with closed population models see Pollock (1974), Otis et al. (1978), Seber (1982), White et al. (1982), Pollock et al. (1990), and Pollock (1991), Rexstad and Burnham (1991).

Wileyto et al. (1994) use simulations to address violation of the assumptions of equal catchability due to heterogeneity (inherent factors of the individuals), and equal catchability due to time variation. However, by assuming that the rates of marking, capture, and recapture are equal, they assume that there are not differences in capture probabilities due to trap response. This last assumption need not to be made. We will relax this assumption by allowing different rates of marking, capture and recapture. Although, it may seem reasonable to assume that the rates of capture and marking are equal, it may not be reasonable to assume that the rate of recapture is equal.

In this paper, we propose a model in which assumption (b) is no longer needed, and we also no longer need to use the discrete Markov process, instead we can directly use the continuous time version, which might be more reasonable since we are sampling in continuous time.

3 The model by Wileyto et al. (1994)

Wileyto et al. (1994) propose a four-state Markov process where three transitions in state can take place. They assume that these transitions are equal in magnitude, equal per capita rates λ for marking, capture, and recapture. The process involves a closed population that undergoes self-marking, capture, and recapture of self-marked individuals. The state vector (F, M, C, R) represents the population $N = F + M + C + R$ in which

F: number of individuals that are free and unmarked

M: number of individuals that are marked yet free

C: unmarked captured individuals

R: recaptured individuals

$(F, M, C, R) = (N, 0, 0, 0)$ is the state vector when the traps are initially placed.

[Figure 1 near here]

The above diagram is a graphical representation of the transition probabilities for the discrete time Markov chain matrix (A) ¹. However, we want to that describes probabilities of transitions from one state to another assuming that in any small time interval, any free individual becomes captured with probability λ , marked with probability λ , or remains free with probability $(1 - 2\lambda)$, while a marked individual becomes recaptured with probability λ or remains free with probability $(1 - \lambda)$.

The one step transition matrix of the embedded discrete time Markov process of their model is

$$A = \begin{bmatrix} 1 - 2\lambda & \lambda & \lambda & 0 \\ 0 & 1 - \lambda & 0 & \lambda \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (1)$$

After trapping has begun, the probability that a population member may be found in any of the categories F, M, C, or R at time t , is given by the elements in the first row of the t^{th} power of the matrix A , A^t , which represents the transition probabilities after t time units.

¹Notation: In an effort to be consistent with the notation used in Wileyto et al. (1994), we will use A for the discrete time Markov chain one step transition matrix, and later will use P for the infinitesimal matrix of the continuous time Markov chain. Note, however, that the notation for discrete and continuous transition matrices are reversed in Taylor and Karlin (1994) from the notation used in this paper.

$$A^t = \begin{bmatrix} (1-2\lambda)^t & (1-\lambda)^t - (1-2\lambda)^t & 1/2 - \frac{(1-2\lambda)^t}{2} & 1/2 + \frac{(1-2\lambda)^t}{2} - (1-\lambda)^t \\ 0 & (1-\lambda)^t & 0 & 1 - (1-\lambda)^t \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (2)$$

4 A continuous time version of Wileyto et al. (1994)'s model

Justification

In the real world, time is generally accepted as being a continuous quantity and is allowed to assume any value in the continuous set of real numbers. In an insect population the continual survival and growth highly depend on the movement of individuals within that population in search of food and suitable mates. The modeling of these biological processes usually involve continuous time systems (Curry, 1987). However, the mathematical analysis of some phenomena in nature can be simplified by using a discrete time system as an approximation of continuous time systems. The methodology of converting continuous-time Markov chains into equivalent discrete-time Markov chains is known as uniformization. Uniformization relies on the fundamental memoryless property (Cassandras 1993). Discrete time systems have traditionally been used as an approximation of continuous time systems. However, when using this approximation a great deal of information can be missed or the analysis can produce misleading results. The key point for a discrete time system is the sampling interval and its relation to the properties of continuous-time changes. For a good approximation, the sampling interval needs to be chosen with little or no loss of information when the sample is taken. The estimation of population size and the accuracy of our estimates would greatly depend on the stability of the system and how many points in time are being used for estimation. If the system is in equilibrium (or close to equilibrium), using a discrete time model as an approximation of a continuous time system might be appropriate, but if we are far away from equilibrium the discrete approximation will not provide accurate estimates. We will illustrate this point with an example after introducing a continuous time version of this model. For a comparison of the dynamics of continuous and discrete event systems see Cao (1989).

A continuous time Markov process differs from a discrete time Markov process because the holding times in each state are not constant but rather are exponentially distributed. It is possible to obtain the infinitesimal matrix P for a continuous time Markov chain from an embedded discrete time Markov process with the one step transition matrix A by assuming that the holding times (sojourn) are exponentially distributed, i.e. $h_j = \mu_j e^{-\mu_j t}$ for $t \geq 0$ and $\mu_j = 1$ for $j = 1, 2, 3, 4$ (Cassandras 1993, Howard, R. 1971). So that

$$P_{ij} = [A - I]_{ij} \mu_j \quad (3)$$

This equation is derived from expanding $A = e^{P\Delta t}$

$A = I + P\Delta t + o(\Delta t)$, therefore,

$P \approx \frac{A - I}{\Delta t}$, where I is the identity matrix, and Δt is assumed to be equal to 1, an arbitrary unit of time.

Since the exponential distribution is memoryless, the time at which state j was entered does not affect the future behavior of the process. Since the future can be affected only by the current state i , the Markov property is satisfied.

The infinitesimal matrix for a the continuous time Markov chain is given by

$$P = \begin{bmatrix} -2\lambda & \lambda & \lambda & 0 \\ 0 & -\lambda & 0 & \lambda \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad (4)$$

Then, the transition probabilities after time t is given by

$$P(t) = e^{Pt} = \begin{bmatrix} e^{-2\lambda t} & -e^{-2\lambda t} + e^{-\lambda t} & 1/2 - \frac{e^{-2\lambda t}}{2} & \frac{e^{-2\lambda t}}{2} - e^{-\lambda t} + 1/2 \\ 0 & e^{-\lambda t} & 0 & -e^{-\lambda t} + 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (5)$$

5 A more general model: on the assumption that transition rates are equal

The proportion of the population that traps will catch (trap efficiency) is often used to estimate the population size. Different factors such as time, behavioral response to the capture, and other inherent factors of the individuals, affects the capture probabilities. A more general model will assume that the transition rates from one state to another are different. A generalization of the continuous time Markov model assuming different transition rates will give us the following results:

The infinitesimal matrix is given by

$$P = \begin{bmatrix} -\lambda_1 - \lambda_2 & \lambda_2 & \lambda_1 & 0 \\ 0 & -\lambda_3 & 0 & \lambda_3 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad (6)$$

and the transition probabilities after time t is given by

$$P(t) = \begin{bmatrix} e^{-(\lambda_1 + \lambda_2)t} & \frac{(-e^{-(\lambda_1 + \lambda_2)t} + e^{-\lambda_3 t})\lambda_2}{-\lambda_3 + \lambda_1 + \lambda_2} & -\frac{\lambda_1(-1 + e^{-(\lambda_1 + \lambda_2)t})}{\lambda_1 + \lambda_2} & -\frac{(-\lambda_3 e^{-(\lambda_1 + \lambda_2)t} + e^{-\lambda_3 t}\lambda_1 + e^{-\lambda_3 t}\lambda_2 + \lambda_3 - \lambda_1 - \lambda_2)\lambda_2}{(-\lambda_3 + \lambda_1 + \lambda_2)(\lambda_1 + \lambda_2)} \\ 0 & e^{-\lambda_3 t} & 0 & -e^{-\lambda_3 t} + 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (7)$$

A diagrammatic representation of this model is shown in Figure 2.

[Figure 2 near here]

6 Limiting behavior

Since this is not an irreducible ergodic chain (instead it is a reducible absorbing chain), the state probabilities do not converge to a unique, stable distribution that does not depend on the initial vector. This is reducible absorbing chain with two transient states (F, M) and two absorbing states (C, R). The limiting matrix corresponds to a degenerate distribution in which the final state depends on the initial state. Therefore, the process has a stationary distribution but its limiting distribution does not exist. In this section we study the limiting behavior of the process.

The limiting behavior of the continuous time model is given by,

$$\lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} e^{Pt} = \begin{bmatrix} 0 & 0 & \frac{1}{2} & \frac{1}{2} \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (8)$$

As it was expected, this limiting behavior also corresponds to the limiting behavior of discrete time model, $\lim_{t \rightarrow \infty} A^t$.

In the more general model given in the previous section,

$$\lim_{t \rightarrow \infty} P(t) = \lim_{t \rightarrow \infty} e^{Pt} = \begin{bmatrix} 0 & 0 & \frac{\lambda_1}{\lambda_1 + \lambda_2} & \frac{\lambda_2}{\lambda_1 + \lambda_2} \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad (9)$$

Figures 3 and 4 show the mean trajectories followed by the population categories over time based on the continuous time model. Note that as $t \rightarrow \infty$, half of the population will be eventually captured and the other half will be recaptured after being marked. Since in figure 2 the transition

rate (λ) is 0.01, it takes longer to the population to be absorbed in the capture (C) and recapture (R) states compared to figure 1 where λ is ten times bigger ($\lambda = 0.10$)

Figures 5 and 6 show the mean trajectories for two cases in which the rates of marking, capture, and recapture are different. Note that the asymptotic behavior of the proportion of captured and recaptured animals is not directly affected the recapture rate (λ_3); however, λ_3 plays a key role in terms of how fast the population is absorbed in the recapture state (R) once the animals have been marked. Another interesting aspect of this model is that after a long period of time, the number of captures and recaptures is proportional to the transition rates of capture and marking respectively. In figure 5, we assume that $\lambda_1 > \lambda_2$ (insects are more likely to be captured than marked), then the number of captured individuals will be $(\lambda_1 - \lambda_2)$ percent higher than the number of recaptured individuals. Conversely, in figure 6 $\lambda_2 > \lambda_1$, and here the number of recaptured animals is $(\lambda_2 - \lambda_1)$ percent higher than the number of captured animals. Finally, if $\lambda_1 = \lambda_2$, we will have the case shown in figure 3 and 4.

[Figures 3 to 6 near here]

7 Estimation of population size, N

Here we follow the same procedure for estimation suggested by Wileyto et al. (1994). The maximum likelihood method was used for parameter estimation because of the desirable properties of maximum likelihood estimators: asymptotically unbiased, normally distributed, and minimum variance (Casella and Berger 1990). Combining the probabilities associated with the states F and M (unobserved individuals), a multinomial model describes the probabilities of finding population members in each of three categories after an event of concurrent marking and trapping (Wileyto et al. 1994). After an arbitrary trapping time, the probabilities associated with the trinomial model are:

$$\pi_1 = p = \text{probability of an individual being unobserved}$$

$$\pi_2 = \frac{1}{2}(1 - p^2) = \text{probability of an individual being captured but unmarked}$$

$$\pi_3 = \frac{1}{2}(1 - p)^2 = \text{probability of an individual being marked and recapture}$$

where p is a parameter related to time (t) and the transition rate λ . From the transition probabilities after time t , $P(t)$, we can deduce that $p = e^{-\lambda t}$.

The likelihood function will be,

$$L(N, p) = \frac{N!}{(N - C - R)! C! R!} \left(\frac{1}{2}\right)^{C+R} p^{N-C-R} (1 - p^2)^C (1 - p)^{2R}, \quad (10)$$

and the log-likelihood

$$\log(L(N, p)) = \ln \left[\frac{\Gamma(N + 1)}{\Gamma(N - C - R + 1)\Gamma(C + 1)\Gamma(R + 1)} \left(\frac{1}{2}\right)^{C+R} p^{N-C-R} (1 - p^2)^C (1 - p)^{2R} \right], \quad (11)$$

solving for the system of equations given by

$$\frac{\partial \log(L)}{\partial N} = 0 \quad \text{and} \quad \frac{\partial \log(L)}{\partial p} = 0$$

we obtain the MLE of N and p .

The simultaneous solution to this system of equations is cumbersome (see MAPLE output in the appendix), in particular when finding the partial with respect to N . One alternative approach consists in conditioning the likelihood respect to the observed data, $C+R$ or sample size. A product of conditional multinomials will lead us to the very well known binomial distribution. Using this part of the conditional multinomial (the binomial) we can estimate N as a function of our sample size ($C+R$) and \hat{p} . This will lead us to the following estimator of population size (N), and probability of unobserved individuals (p):

$$\hat{N} = \frac{C + R}{1 - \hat{p}}, \quad (12)$$

$$\hat{p} = 1 - \frac{C + R}{\hat{N}} \quad (13)$$

Also, solving the equation $\frac{\partial}{\partial p} \log(L) = 0$ leads us to the following estimators,

$$\hat{N} = \frac{-C\hat{p}^2 - R\hat{p}^2 - 2R\hat{p} - C - R}{-1 + \hat{p}^2}, \quad (14)$$

$$\hat{p} = \frac{-R + \sqrt{\hat{N}^2 - C^2 - 2CR}}{\hat{N} + C + R}, \quad (15)$$

and solving for the system of equations (12) and (14), or, the system (13) and (15), we find the maximum likelihood estimators for N and p in terms of C and R,

$$\hat{N} = \frac{(C + R)^2}{2R}, \quad (16)$$

$$\hat{p} = \frac{C - R}{C + R} \quad (17)$$

which correspond to the estimates derived by Wileyto et al. (1994). A local maximum of the log-likelihood is also given by $\hat{N} = C + R$, and $\hat{p} = 0$. If $C < R$, $\hat{p} < 0$ which makes nonsense. The corresponding theoretical approximation of variances of the estimators for equations (16) and (17) are also given by Wileyto et al. (1994),

$$Var(\hat{N}) = \frac{N(1 + 2p - p^2)}{(1 - p)^2}, \quad (18)$$

$$Var(\hat{p}) = \frac{1 + p}{Np}, \quad (19)$$

and

$$Cov(\hat{N}, \hat{p}) = \frac{1 + p}{1 - p} \quad (20)$$

they used the inverse of the information matrix to derive (18), (19) and (20).

Because R might be zero and \hat{N} given by (16) is positively biased, they propose a modified version for the estimator of N, namely, adding 1 to R in the denominator. They argue that this is a reasonable thing to do since $E\left(\frac{1}{R+1}\right) \approx \frac{1}{E(R)}$ when $R > 4$. The new estimator proves to be less biased than equation (16) and is given by

$$\hat{N} = \frac{(C + R)^2}{2(R + 1)} \quad (21)$$

However, Wileyto et al. 1994 point out that if $E(R) < 5$, the modified version (21) provides large negative bias.

In our general case, π_i will have a more complicated formula involving λ_1 , λ_2 , and λ_3 ; however, estimation will follow the same principles as above, and the estimators remain unchanged. Estimation of the λ_i is possible with the use of program SURVIV (White 1983). For a detailed and comprehensive description of how to use program SURVIV for parameter estimation see Alpizar-Jara (1994). Formulae for π_i in the general case are given by the following equations,

$$\begin{aligned}\pi_1 &= e^{-t(\lambda_1+\lambda_2)} + \frac{(e^{-\lambda_3 t} - e^{-t(\lambda_1+\lambda_2)})\lambda_2}{\lambda_1+\lambda_2-\lambda_3} \\ \pi_2 &= \frac{\lambda_1(1-e^{-t(\lambda_1+\lambda_2)})}{\lambda_1+\lambda_2} \\ \pi_3 &= \frac{(\lambda_3 e^{-t(\lambda_1+\lambda_2)} - (\lambda_1+\lambda_2)e^{-\lambda_3 t} + \lambda_1+\lambda_2-\lambda_3)\lambda_2}{(\lambda_1+\lambda_2-\lambda_3)(\lambda_1+\lambda_2)}\end{aligned}\tag{22}$$

Notice that when $\lambda_1 = \lambda_2 = \lambda_3 = \lambda$ we obtain the values of π_i used in the likelihood above.

A problem with this approach is that we need to estimate more parameters. We will be overparameterizing the model, and therefore the model will be unidentifiable. To be able to estimate three parameters we will need to sample at least three occasions (three sampling times). In addition, sometimes the quality of the data is not good enough to estimate that many parameters. However, a two parameter model seems reasonable to me. For example, if λ_1 and λ_2 are equal, but λ_3 is different, in these case we need to sample on at least two occasions.

Sampling at least twice also allows a check of the steady state assumption implicit in Wileyto et al. (1994). For example, in figure 3, a sample at time 5 would not meet the steady state assumption and would underestimate the probability of capture. Hence, the estimate of N , (21), will be an overestimate. For the same scenario, a sample at time 20 would only produce a small effect in the estimate of N . This example illustrates part of our point in the justification for section 4.

8 Simulation results

Although figure 7 does not represent the results of simulations, we will comment on it in this section for convenience, and for future interpretation of the simulation results. This figure is basically the same plot presented by Wileyto et al (1994) as figure 2b. Figure 7 shows how the ratio $\frac{\hat{N}}{N}$ changes for different values of p and for $N=100, 250, 1000, 10000$. I use equation (21) for explicit calculations in this plot. It is clear that the larger p gets, the larger the bias is. Also, the higher the population size is, the less biased the estimator is.

[Figure 7 near here]

To evaluate the performance of the modified version of \hat{N} (21) under violation of the assumption of equal catchability due to inherent characteristics of the individuals, we run 500 simulation trials for populations of $N = 100, 1000$, and 10000 individuals assuming that each member of the population has its own probability of being captured, marked and recapture $\lambda_j, j = 1, \dots, N$. As one of the simulation methods in Wileyto et al. (1994), we assume that λ_j comes from a half normal distribution with mean 1 and standard deviation 0.2, and that multinomial probabilities are generated for each individual based on the cell probabilities given by the formulae use in the likelihood function (10). We fixed $t=1$ as the arbitrary unit of time. This choice of $t=1$, provides values of p ranging from 0.20 to 0.67 approximately, which corresponds to values of p for which the ratio $\frac{\hat{N}}{N}$ remains almost unchangeable and close to 1 (see figure 7), at least when $N = 1000$ or 10000 .

In figure 8, we show boxplots representing distributions of the ratio $\frac{\hat{N}}{N}$ for the 500 trials under each scenario ($N = 100, 1000, 10000$). Deviations from 1 represent biases. As it was expected, results of these simulation runs show that the estimator is negatively biased. Bias is more severe when the real population size is small. For instance, when $N = 100$ the mean value of the ratio $\frac{\hat{N}}{N}$ is around 0.94 which indicates that on average the true population size is underestimated by six percent of the total number of individuals. Note that as the population increases, the estimator is less biased. In a population of 1000 individuals, on average we only underestimate the population size by approximately two percent of the total number of individuals. No much gain in bias or precision is obtained when increasing the population size from $N = 1000$ to $N = 10000$. In terms

of precision, the estimator is more precise as N increases.

[Figure 8 near here]

We also evaluate the effect of changing the distribution of λ_j from a normal(1,0.2) to a uniform distribution with the same mean and variance ² for the case in which the true population size is 100 individuals. The results of these simulation runs are shown in figure 9.

[Figure 9 near here]

Note that when λ_j are assumed to be normally distributed, the distribution of \hat{N} shows more extreme values and slightly higher variability than when λ_j are assumed to be uniformly distributed. This result was expected since the range of \hat{p} is reduced when changing the distribution to uniform. The range of \hat{p} in the case of the uniform distribution will be between 0.26 and 0.52 approximately. This reduction in the range of \hat{p} will cause a reduction in the variability of the estimator of N . In term of bias, there are no differences, in both cases the estimator is negatively biased and underestimates the true population size in about six percent of the total population. In general, these simulation results indicate that violation of the assumption of equal catchability due to inherent characteristic of the individuals causes negative bias on the estimates of N . In their simulations results, Wileyto et al. (1994) additionally analyze confidence intervals and the percentage of coverage of the estimators.

9 Conclusion and future research directions

In this paper, we have showed that it is simple to analyze the continuous time version of the model proposed by Wileyto et al. (1994). The continuous time version might be more reasonable to use since we are sampling in continuous time. Furthermore, a more general model which relaxes the assumption of equal rates of marking, capture, and recapture is suggested. We have also analyzed the limiting behavior of the process, and we have found that the limiting behavior analysis provides the same results for the discrete and continuous time processes.

²To do this transformation, solve the system of equations $\frac{a+b}{2} = \mu$ and $\frac{(b-a)^2}{12} = \sigma^2$ for a and b , and obtain $a = \mu - \sqrt{3}\sigma$ and $b = \mu + \sqrt{3}\sigma$ which define the desired uniform distribution

More work needs to be done to evaluate the performance of the estimator under violation of the closure assumption. Possibilities for relaxation of this assumption need to be explored; perhaps the use of removal methods and other open population models (eg. Jolly-Seber) can be alternative options.

Possible modifications of the model based on reasonable biological assumptions can also be explored. For example, if captured individuals that were not marked are allowed to be recaptured, how will the process change? How will the result change?

Field work applications to test this method are also needed. Wileyto et al. (1994) use data of a known population size of the Indianmeal moth (*Plodia interpunctella*) to illustrate how their method works. They show that the method produces estimates of N that are very reasonable to what they expected. They point out that self-marking methods that allow tests of fit are currently under development. They also stress the need of more data to determine whether there are any systematic biases that occur in the field.

Another area that needs exploration is the section on parameter estimation. Estimation of the transition rates can be achieved using the program SURVIVE (White 1983). Alpízar-Jara (1994) uses program SURVIVE to obtain parameter estimates from a multinomial model in which the cell probabilities are functions of the parameter from an exponential power series, similar ideas can be use to obtain estimates for the marking, capture and recapture rates. Also, if real data are available, the same procedure can be used to estimate these rates.

We can also make use of the available tools and properties of the Markov chain to answer questions such as, what is the mean time until absorption, or what is the probability of absorption in the capture (C) or recapture (R) states given that the process start in state free (F). To answer these questions, a first step analysis will prove to be useful. A sensitivity analysis of the parameters can also be performed.

Finally, more simulation runs to tests for other assumption violations need to be performed. For example, to test for violation of the assumption of different rates and heterogeneity of the individuals simultaneously we could generate three different random variables $\lambda_{1j}, \lambda_{2j}, \lambda_{3j}$ drawn from a normal population with different means, μ_1, μ_2, μ_3 respectively and common variance σ^2 . Then we can examine the performance of \hat{N} in terms of bias and precision.

Note: At the time that this paper was written P.E. Wileyto has already generalized his model to relax the assumption of equal rates of marking and capture (Wileyto 1994), but we were not aware of it. Wileyto (1995) has also used simulation studies to examine violation of the assumptions: closure and open populations, individuals are not uniformly catchable, marking and trapping rates vary over time, unequal response to marking stations and traps, and behavior changes after marking. However, his model is still based on a discrete time Markov process rather than a continuous time Markov process.

Acknowledgments

We are grateful to Dr. Kenneth H. Pollock for his useful insights and for suggesting the paper by Wileyto et al. (1994) as a paper to work on a project for BMA610 Stochastic Modeling, class of Spring '95.

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11 APPENDIX

[> with(linalg):

[A. DISCRETE AND CONTINUOUS TIME MODELS

[> A:=matrix(4,4,[1-2*lambda,lambda,lambda,0,0,1-lambda,0,lambda,0,0,1,0,0,0,0,1]);

$$A := \begin{bmatrix} 1-2\lambda & \lambda & \lambda & 0 \\ 0 & 1-\lambda & 0 & \lambda \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

[> evalA:=eigenvals(A); evecA:=eigenvecs(A);

$$\text{evalA} := 1-2\lambda, 1-\lambda, 1, 1$$

$$\text{evecA} := [1, 2, \{[0, 1, -1, 1], [1, 0, 2, 0]\}, [1-2\lambda, 1, \{[1, 0, 0, 0]\}], [1-\lambda, 1, \{[1, 1, 0, 0]\}]$$

[>

[> P:=matrix(4,4,[-2*lambda,lambda,lambda,0,0,-lambda,0,lambda,0,0,0,0,0,0,0,0]); latex(P,Ptex);

$$P := \begin{bmatrix} -2\lambda & \lambda & \lambda & 0 \\ 0 & -\lambda & 0 & \lambda \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

[Solving as a linear system compartmental model

[> Ap:=transpose(P); b:=array([0,0,0,0]);

$$Ap := \begin{bmatrix} -2\lambda & 0 & 0 & 0 \\ \lambda & -\lambda & 0 & 0 \\ \lambda & 0 & 0 & 0 \\ 0 & \lambda & 0 & 0 \end{bmatrix}$$

$$b := [0, 0, 0, 0]$$

[> linsolve(Ap,b); eigenvals(Ap);

$$[0, 0, -\lambda, -\lambda]$$

$$-2\lambda, -\lambda, 0, 0$$

[>

[> ONEM:=toeplitz([1,1,1,1]); ONEV:=array([1,1,1,1]); IPPO:=evalm(inverse(P+ONEM));

$$ONEM := \begin{bmatrix} 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{bmatrix}$$

$$ONEV := [1, 1, 1, 1]$$

[> PE:=evalm(exponential(P,t)); evalPE:=eigenvals(PE);

$$\text{evalPE} := e^{(-2\lambda t)}, e^{(-\lambda t)}, 1, 1$$

[>

[> At:=matrix(4,4,[(1-2*lambda)^t,(1-lambda)^t-(1-2*lambda)^t,(1-(1-2*lambda)^t)/2,(1+(1-2*lambda)^t)/2-(1-lambda)^t,0,(1-lambda)^t,0,(1-(1-lambda)^t),0,0,1,0,0,0,0,1]);

$$At := \begin{bmatrix} (1-2\lambda)^t & (1-\lambda)^t - (1-2\lambda)^t & \frac{1}{2} - \frac{1}{2}(1-2\lambda)^t & \frac{1}{2} + \frac{1}{2}(1-2\lambda)^t - (1-\lambda)^t \\ 0 & (1-\lambda)^t & 0 & 1 - (1-\lambda)^t \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

[> evalAt:=eigenvals(At);

$$\text{evalAt} := (1-2\lambda)^t, (1-\lambda)^t, 1, 1$$

[> AE:=evalm(exp(-t)*exponential(A,t));

[> evalAE:=eigenvals(AE);

$$\text{evalAE} := e^{(-t)} e^{((1-2\lambda)t)}, e^{(-t)} e^{((1-\lambda)t)}, e^{(-t)} e^t, e^{(-t)} e^t$$

```
[ > with(linalg):
```

[B. GENERAL MODEL

```
[ > A:=matrix(4,4,[1-lambda[1]-lambda[2],lambda[2],lambda[1],0,0,1-lambda[3],0,lambda[3],0,0,1,0,0,0,0,1
]);
```

```
[ > Att:=evalm(A^t);
```

```
[ > At2:=matrix(4,4,[(1-lambda[1]-lambda[2])^t,(1-lambda[3])^t-(1-lambda[1]-lambda[2])^t,(lambda[1]/(lam
bda[1]+lambda[2]))*(1-(1-lambda[1]-lambda[2])^t),(lambda[2]/(lambda[1]+lambda[2]))*(1+(1-lambda[1]-l
ambda[2])^t)-(1-lambda[3])^t,0,(1-lambda[3])^t,0,1-(1-lambda[3])^t,0,0,1,0,0,0,0,1]);
```

```
[ > evalA:=eigenvals(A); evecA:=eigenvects(A);
```

```
[ > P:=matrix(4,4,[-lambda[1]-lambda[2],lambda[2],lambda[1],0,0,-lambda[3],0,lambda[3],0,0,0,0,0,0,0,0,0]);
```

```
[ > PE:=evalm(exponential(P,t)); evalPE:=eigenvals(PE);
```

```
[ >
```

```
[ > At:=matrix(4,4,[(1-2*lambda)^t,(1-lambda)^t-(1-2*lambda)^t,(1-(1-2*lambda)^t)/2,(1+(1-2*lambda)^t)/2
-(1-lambda)^t,0,(1-lambda)^t,0,(1-(1-lambda)^t),0,0,1,0,0,0,0,1]);
```

$$At := \begin{bmatrix} (1-2\lambda)^t & (1-\lambda)^t - (1-2\lambda)^t & \frac{1}{2} - \frac{1}{2}(1-2\lambda)^t & \frac{1}{2} + \frac{1}{2}(1-2\lambda)^t - (1-\lambda)^t \\ 0 & (1-\lambda)^t & 0 & 1 - (1-\lambda)^t \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

```
[ > evalAt:=eigenvals(At);
```

```
evalAt := (1-2λ)t, (1-λ)t, 1, 1
```

```
[ >
```

```
[ > evalAE:=eigenvals(AE);
```

$$evalAE := e^{(-t)} e^{((1-\lambda_1-\lambda_2)t)}, -\frac{e^{(-t)} e^{((1-\lambda_3)t)} \lambda_1^2 + 2 e^{(-t)} e^{((1-\lambda_3)t)} \lambda_1 \lambda_2 + e^{(-t)} e^{((1-\lambda_3)t)} \lambda_2^2}{-\lambda_1^2 - 2\lambda_1 \lambda_2 - \lambda_2^2}, e^{(-t)} e^t, e^{(-t)} e^t$$

```
[ >
```

Next corresponds to the first row of the transition matrices after time t

```
[ > for j from 1 to 4 do
> Att[j]:=simplify(At2[1,j]);
> PE1[j]:=simplify(PE[1,j]);
> AE1[j]:=simplify(expand(AE[1,j]));
> od;
```

```
[ > for j from 1 to 4 do
> Pt1[j]:=matrix(1,1,[simplify(PE[1,j])]);
> od;
[ > latex(stack(Pt1[1],Pt1[2],Pt1[3],Pt1[4]),Ptex);
```

```
[ > for j from 1 to 4 do
> PE1[j]:=simplify(PE[1,j]);
> od;
[ > factor(simplify(Att[1]+Att[2]+Att[3]+Att[4])); simplify(PE1[1]+PE1[2]+PE1[3]+PE1[4]);
simplify(AE1[1]+AE1[2]+AE1[3]+AE1[4]);
```

```
[ > pi1:=combine(PE1[1]+PE1[2],[exp]); pi2:=simplify(PE1[3]); pi3:=combine(simplify(PE1[4]),[exp]);
simplify(pi1+pi2+pi3);
[ > PI:=evalm(matrix(3,1,[pi1,pi2,pi3])); latex(PI,PI);
```

$$\Pi := \begin{bmatrix} e^{(-t\%1)} + \frac{(-e^{(-t\%1)} + e^{(-\lambda_3 t)}) \lambda_2}{\lambda_1 + \lambda_2 - \lambda_3} \\ \frac{\lambda_1 (e^{(-t\%1)} - 1)}{\%1} \\ (\lambda_3 e^{(-t\%1)} - e^{(-\lambda_3 t)}) \lambda_1 - e^{(-\lambda_3 t)} \lambda_2 + \lambda_1 + \lambda_2 - \lambda_3 \lambda_2 \\ (\lambda_1 + \lambda_2 - \lambda_3) \%1 \\ \%1 := \lambda_1 + \lambda_2 \end{bmatrix}$$

C. ESTIMATION OF N AND P

> L:=factorial(N)/(factorial(N-C-R)*factorial(C)*factorial(R))*(1/2)^(C+R)*p^(N-C-R)*(1-p^2)^C*(1-p)^(2R);

$$L := \frac{N! \left(\frac{1}{2}\right)^{C+R} p^{(N-C-R)} (1-p^2)^C (1-p)^{(2R)}}{(N-C-R)! C! R!}$$

> LL:=evalf(log(L));

$$LL := \ln \left(\frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)}}{\Gamma(N-1, C-1, R+1) \Gamma(C+1) \Gamma(R+1)} \right)$$

> DN:=diff(LL,N); Dp:=diff(LL,p);

$$DN := \left(\frac{\Psi(N+1) \Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)}}{\%1 \Gamma(C+1) \Gamma(R+1)} - \frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)} \Psi(N-1, C-1, R+1)}{\%1 \Gamma(C+1) \Gamma(R+1)} + \frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} \ln(p) (1-p)^C (1-p)^{(2R)}}{\%1 \Gamma(C+1) \Gamma(R+1)} \right) / \left(\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)} \right)$$

$$Dp := \left(\frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (N-1, C-1, R) (1-p)^C (1-p)^{(2R)}}{\%1 \Gamma(C+1) \Gamma(R+1)} - 2 \frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C C p (1-p)^{(2R)}}{\%1 \Gamma(C+1) \Gamma(R+1) (1-p)^2} - 2 \frac{\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)} R}{\%1 \Gamma(C+1) \Gamma(R+1) (1-p)} \right) / \left(\Gamma(N+1) \cdot 5000000000^{(C+R)} p^{(N-1, C-1, R)} (1-p)^C (1-p)^{(2R)} \right)$$

> ps:=solve(Dp=0,p); ps1:=simplify(ps[1]); latex(ps1,Ltex);

$$ps := .5000000000 \frac{-2.R + 2.\sqrt{N^2 - 1.C^2 - 2.CR}}{N + C + R}, .5000000000 \frac{-2.R - 2.\sqrt{N^2 - 1.C^2 - 2.CR}}{N + C + R}$$

$$ps1 := -1. \frac{R - 1.\sqrt{N^2 - 1.C^2 - 2.CR}}{N + C + R}$$

> N1:=simplify(solve(Dp=0,N)); latex(N1,Ltex);

$$N1 := -1. \frac{Cp^2 + Rp^2 + 2.Rp + C + R}{-1. + p^2}$$

> N2:=(C+R)/(1-p);

$$N2 := \frac{C + R}{1 - p}$$

> Ps:=N1-N2; Pes:=solve(Ps=0,p); ps1:=simplify(Pes[1]);

$$Ps := -1. \frac{Cp^2 + Rp^2 + 2.Rp + C + R}{-1. + p^2} - \frac{C + R}{1 - p}$$

$$Pes := -1. \frac{-1. C + R}{C + R}, 0$$

$$ps1 := \frac{C - 1.R}{C + R}$$

> PNs:=solve(DN=0,p);

> p:=ps1; N:=simplify(N2); PNss:=evalf(simplify(PNs));

$$p := \frac{C - 1.R}{C + R}$$

$$N := .5000000000 \frac{(C + R)^2}{R}$$

$$PNss := e \left(-1. \Psi \left(\frac{C^2 + 2.CR + R^2 + 2.R}{R} \right) + \Psi \left(\frac{C^2 - 1.R^2 + 2.R}{R} \right) \right)$$

D. SIMULATIONS: SPLUS PROGRAMS

```
lambda<-runif(100,0,0.4); lambda<-seq(0,0.4,0.1)
```

Using different p for each individual

```
trials<- 500; Ns<-rep(0,length(trials)); ps<-rep(0,length(trials)); N<-100;
for(k in 1:trials){
  #lambda<-abs(rnorm(N,1,0.2))
  lambda<-runif(N,0.65359,1.34641)
  #t<-seq(0,length(lambda)-1,1)
  t<-1
  p<-exp(-lambda*t)
  p1<-p
  p2<-(1/2)*(1-p^2)
  p3<-(1/2)*(1-p)^2
  U<-sum(p1)
  C<-sum(p2)
  R<-sum(p3)
  Ne <- ((C+R)^2)/(2*(R+1))
  pe <- (C-R)/(C+R)
  Ns[k] <- Ne
  ps[k] <- pe
}
N100<-Ns; p100<-ps; N1000<-Ns; p1000<-ps; N10000<-Ns; p10000<-ps;
N100<-N100/100; N1000<-N1000/1000; N10000<-N10000/10000;
par(omi=c(0.3,0.3,0.8,0.3)); par(mfrow=c(1,3));
boxplot(N100,ylim=c(0.92,1.0))
title("N=100"); abline(h=mean(N100));
boxplot(N1000,ylim=c(0.92,1.0))
title("N=1000"); abline(h=mean(N1000));
boxplot(N10000,ylim=c(0.92,1.0))
title("N=10000"); abline(h=mean(N10000));
mtext(outer=T,"Figure 1:Simulations (500 trials) each individual has its own probability of
being captured or marked, pi=exp(-lambda*t), lambda~N(1,0.2)",side=3,line=1,cex=0.8)
```

Uniform vs normal

```
par(mfrow=c(1,2))
boxplot(N100,ylim=c(0.92,1.0))
abline(h=mean(N100)); title("lambda~normal(1,0.2)");
boxplot(Ns,ylim=c(0.92,1.0))
abline(h=mean(Ns))
title("lambda~uniform(0.65359,1.34641)")
mtext(outer=T,"Figure 1:Simulations (500 trials) each individual has its own probability of
being captured or marked, pi=exp(-lambda*t)",side=3,line=1,cex=0.8)
```



```

par(omi=c(0.3,0.3,0.8,0.3))
p<-seq(0.1,1,0.1)
p1<-p
p2<-(1/2)*(1-p^2)
p3<-(1/2)*(1-p)^2

N<-10000; C<-rep(0,length(p)); R<-rep(0,length(p)); Ne<-rep(0,length(p));

for(i in 1:length(p)){
C[i] <- N*p2[i]
R[i] <- N*p3[i]
Ne[i] <- ((C[i]+R[i])^2)/(2*(R[i]+1))
}
Bias <- Ne/N

lines(p,Bias,lty=4)

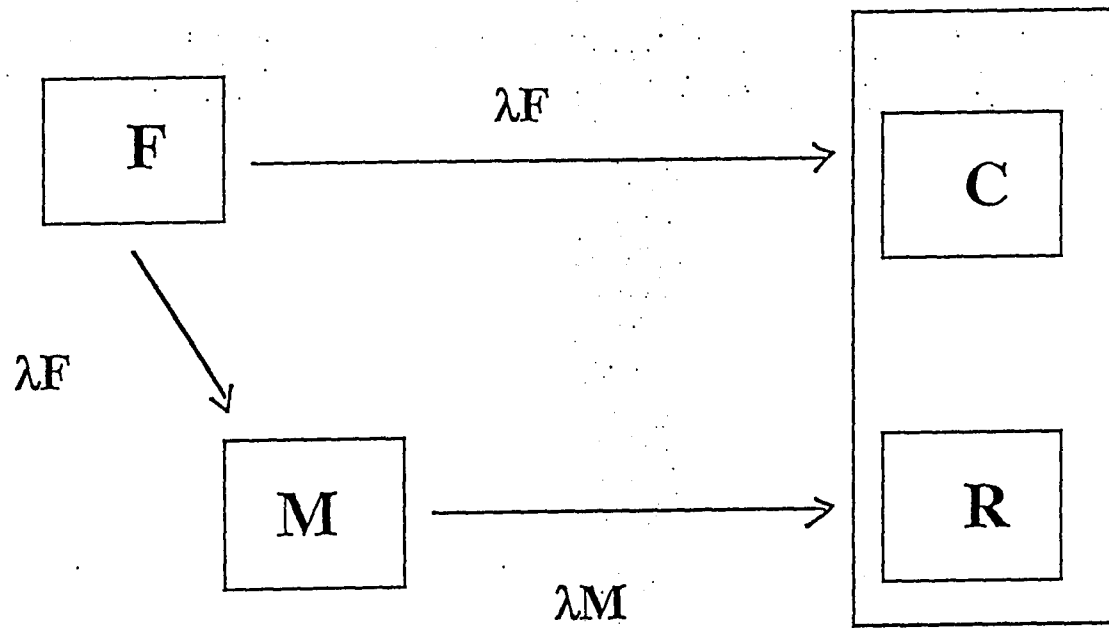
plot(p,Bias,type="l",ylab="Nhat/N",lty=1)
abline(h=0.5)
title("Estimate of N relative to true value")

abline(v=c(0.26,0.52),lty=2)
abline(v=c(0.2,0.67))
legend(locator(1),c("N=100","N=250","N=1000","N=10000"), lty=c(1:4),cex=0.8)

#####
for(i in 1:length(p)){
C[i] <- N*p2[i]
R[i] <- N*p3[i]
Ne[i] <- ((C[i]+R[i])^2)/(2*(R[i]))
}
Bias <- Ne/N
lines(p,Bias,lty=4)
plot(p,Bias,type="l",ylab="Nhat/N",lty=1)
abline(h=0.5)
title("Estimate of N relative to true value")
legend(locator(1),c("N=100,div(R+1)","N=100,div(R)","N=10000,div(R+1)","N=10000,div(R)"
), lty=c(1:4),cex=0.8)

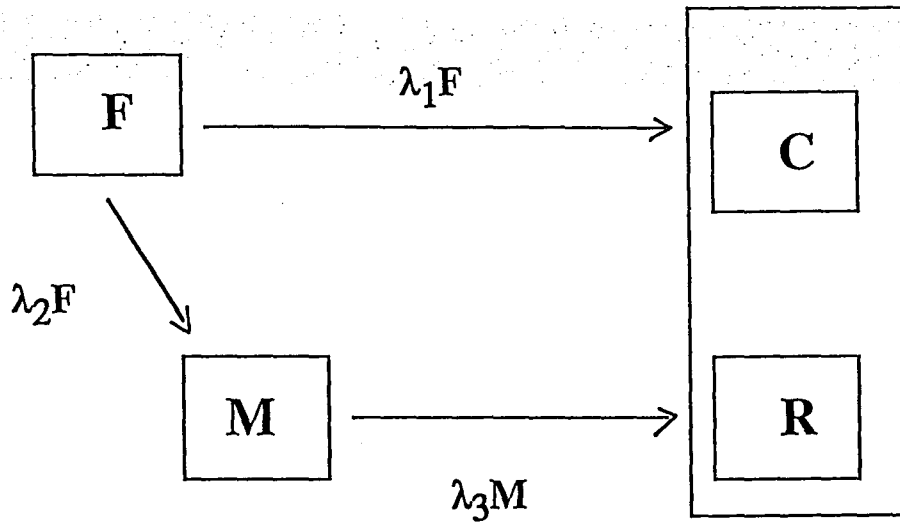
```

Figure 1



Markov Model of Marking Recapture
(Wileyto et al. 1994)

Figure 2



Markov Model of Marking Recapture
(generalization)

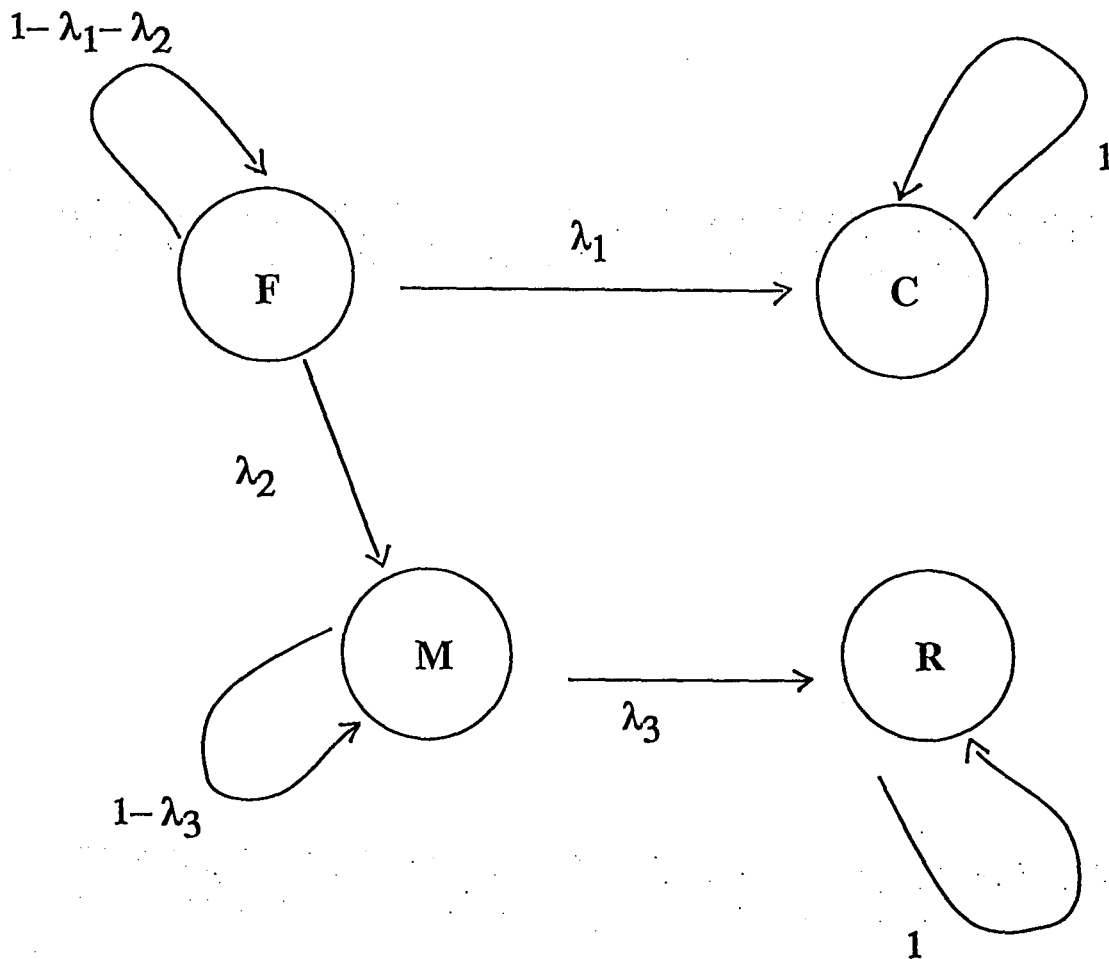


Figure 3. Deterministic time course

$$(\lambda = 0.10)$$

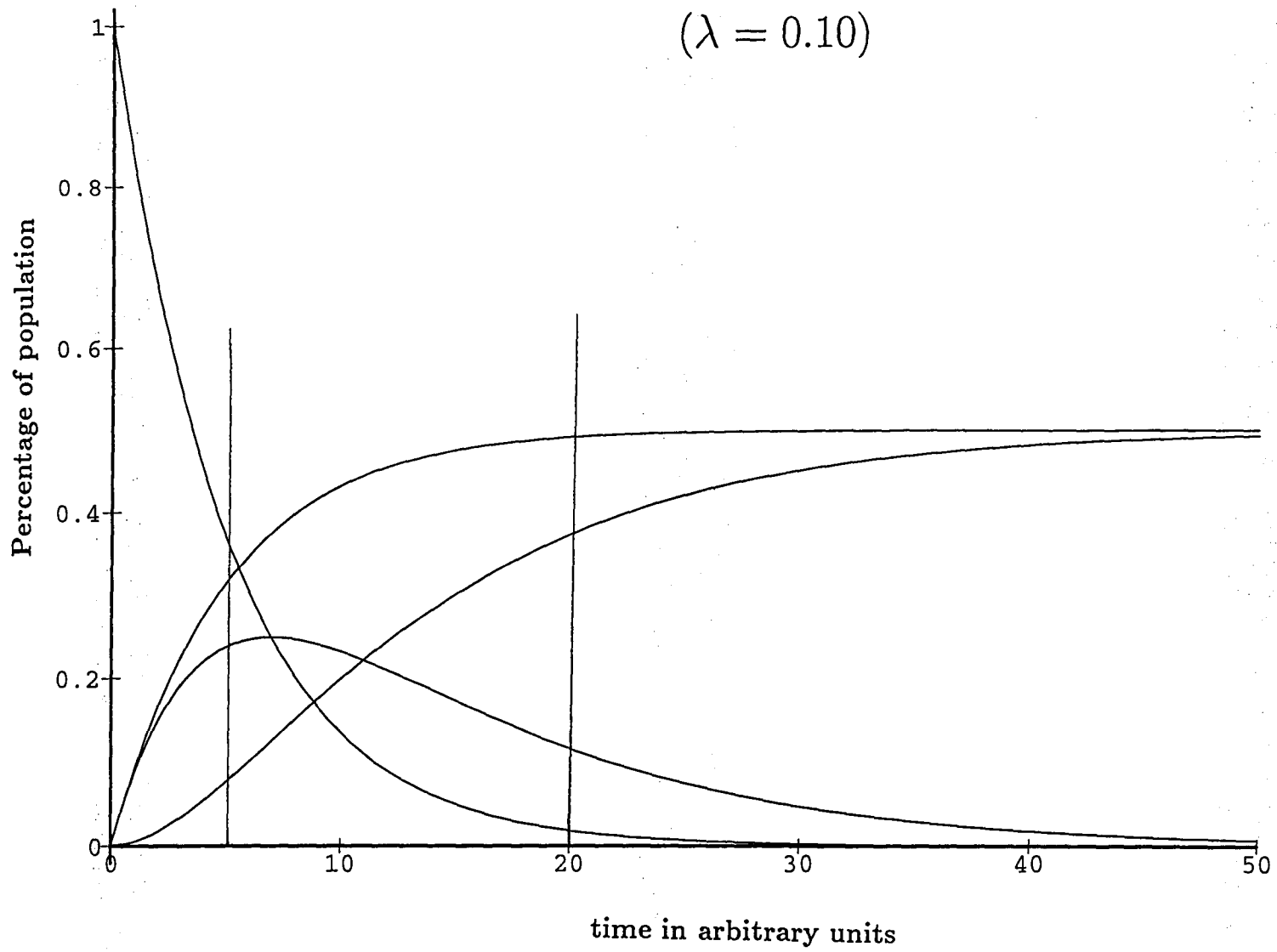


Figure 4. Deterministic time course

$$(\lambda = 0.01)$$

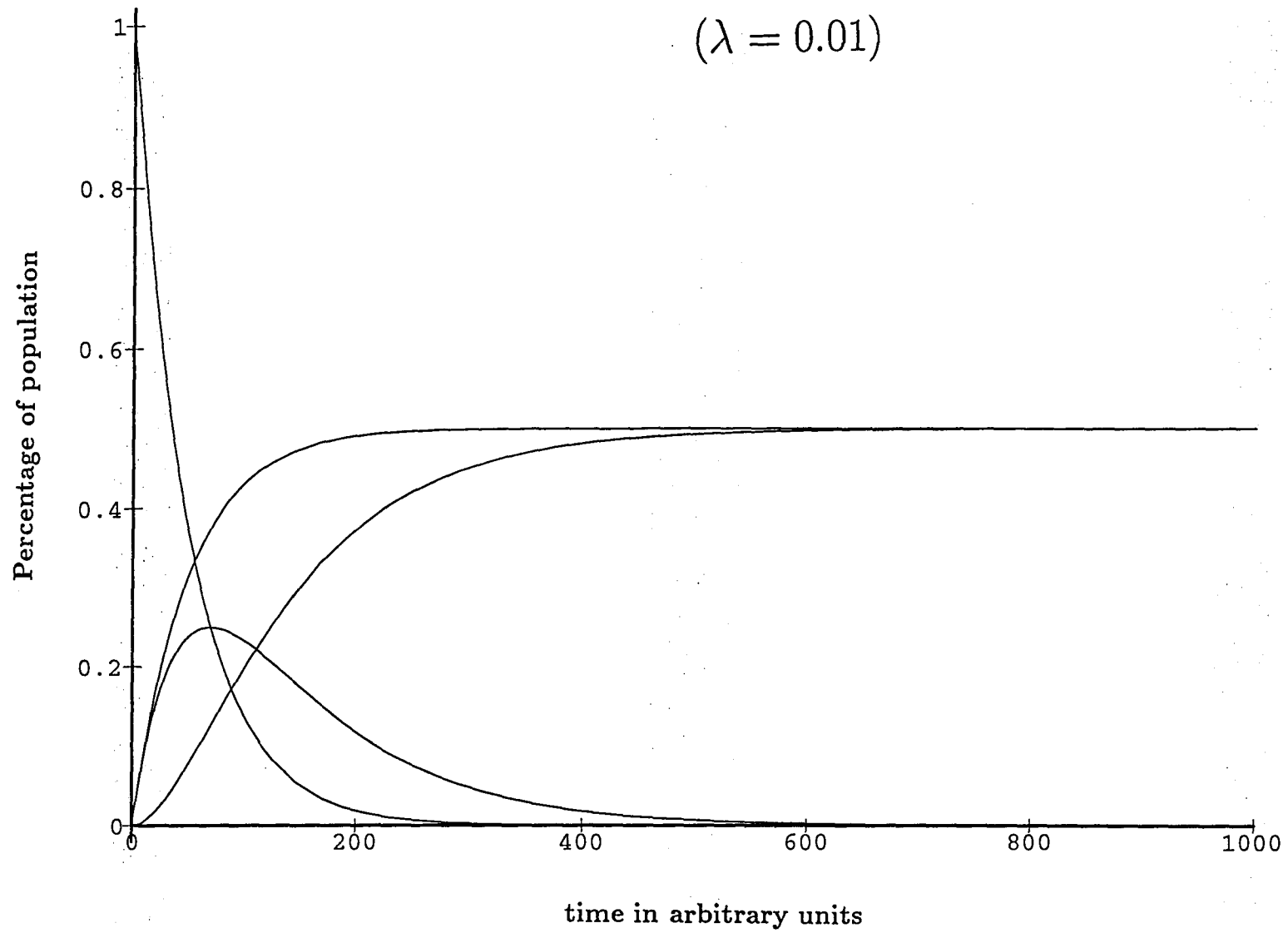


Figure 5. Deterministic time course

$$(\lambda_1 = 0.03, \lambda_2 = 0.02, \lambda_3 = 0.04)$$

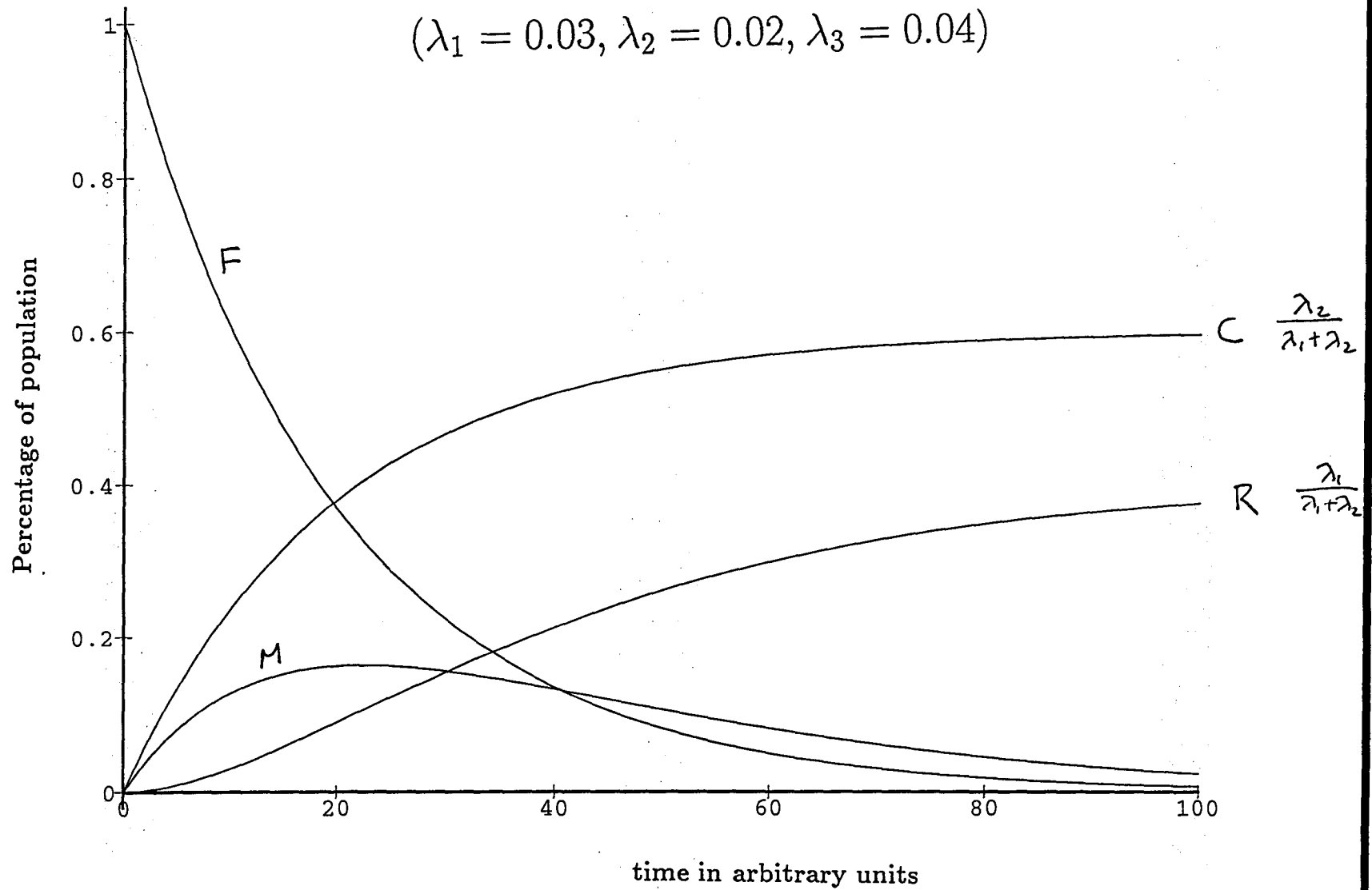


Figure 6. Deterministic time course

$$(\lambda_1 = 0.01, \lambda_2 = 0.02, \lambda_3 = 0.01)$$

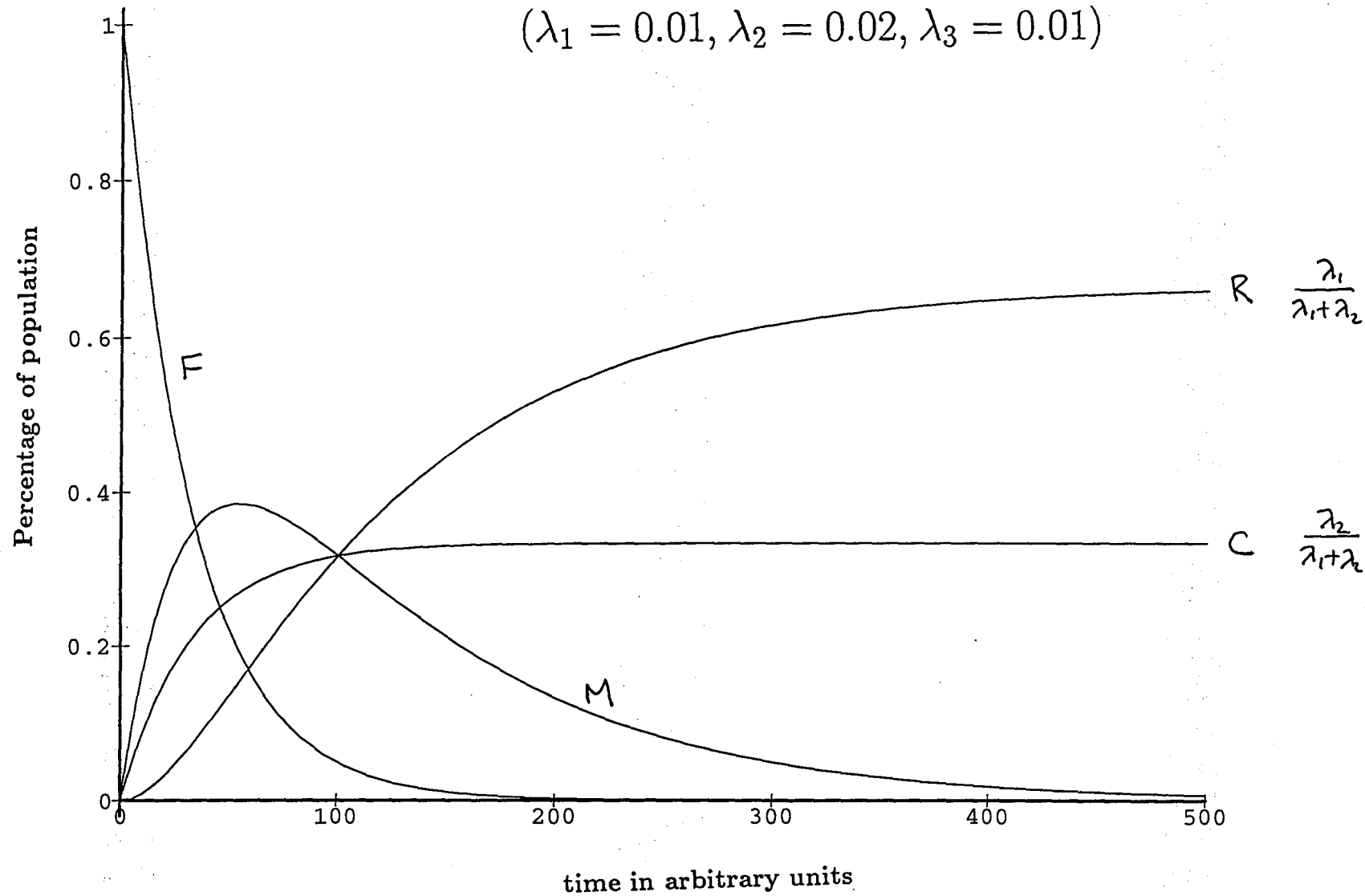


Figure 7

Estimate of N relative to true value

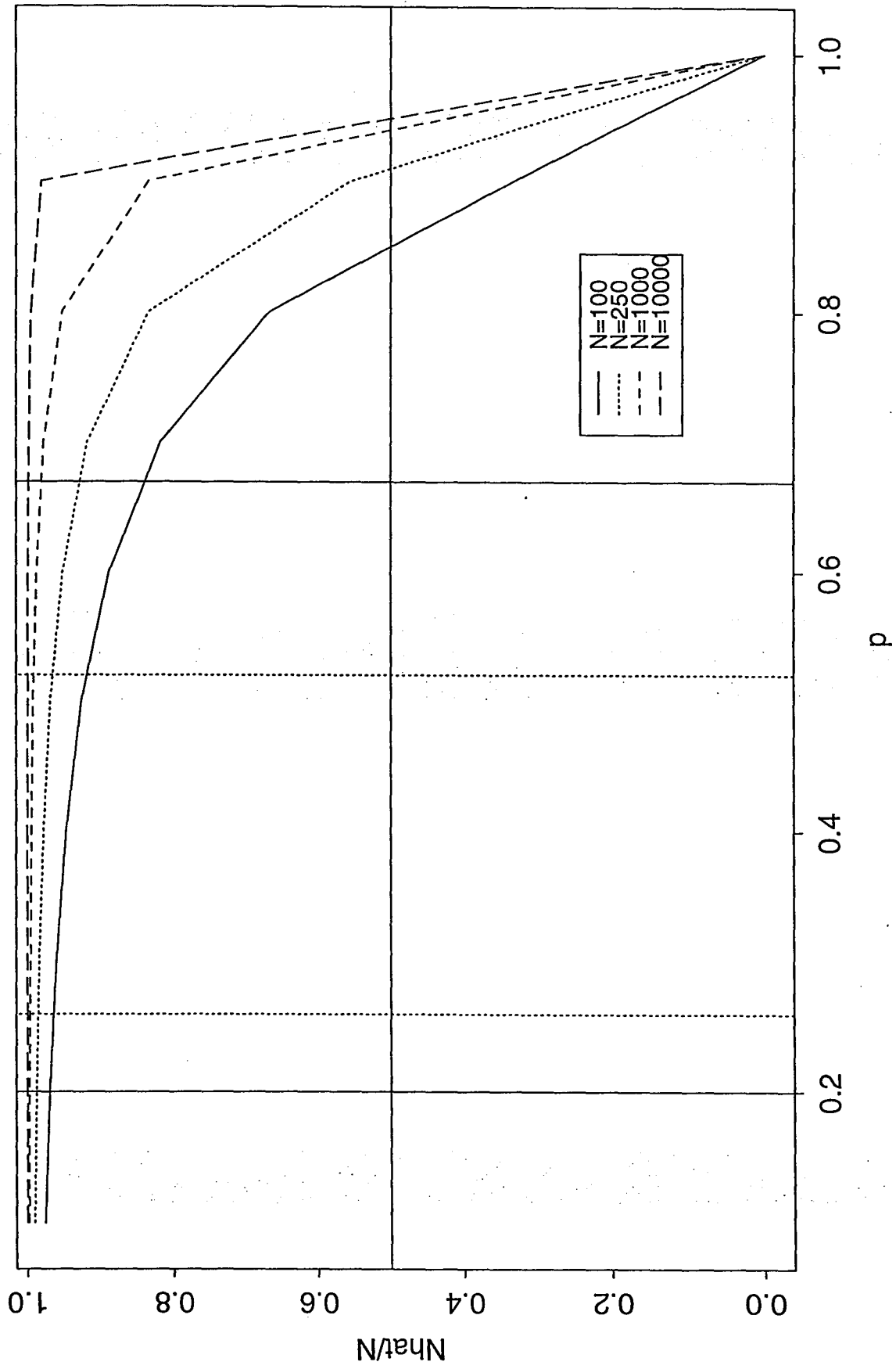
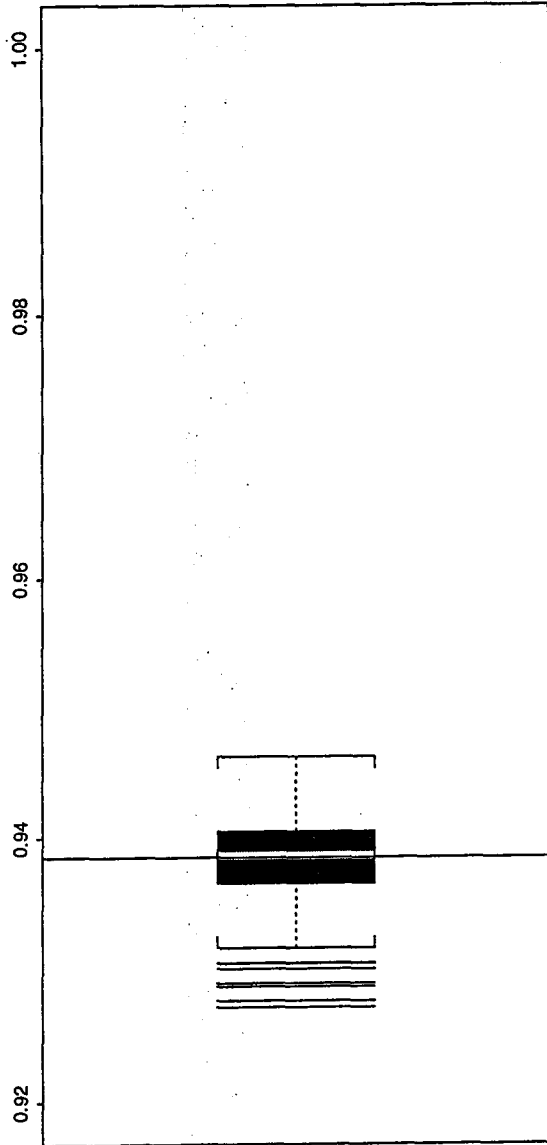


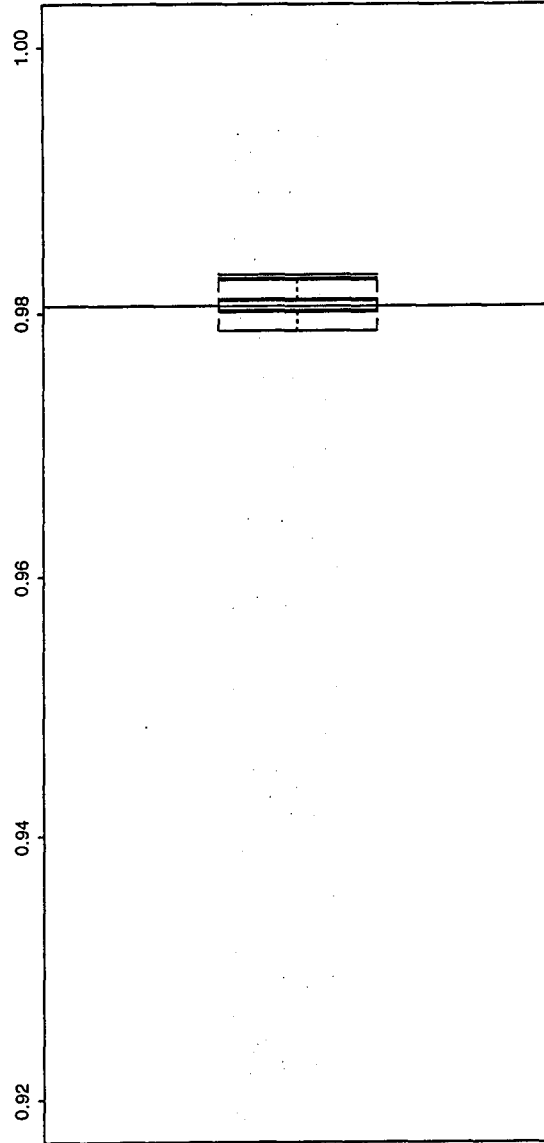
Figure 8

Simulations (500 trials) each individual has its own probability of being captured or marked, $\pi = \exp(-\lambda t)$, $\lambda \sim N(1, 0.2)$

N=100



N=1000



N=10000

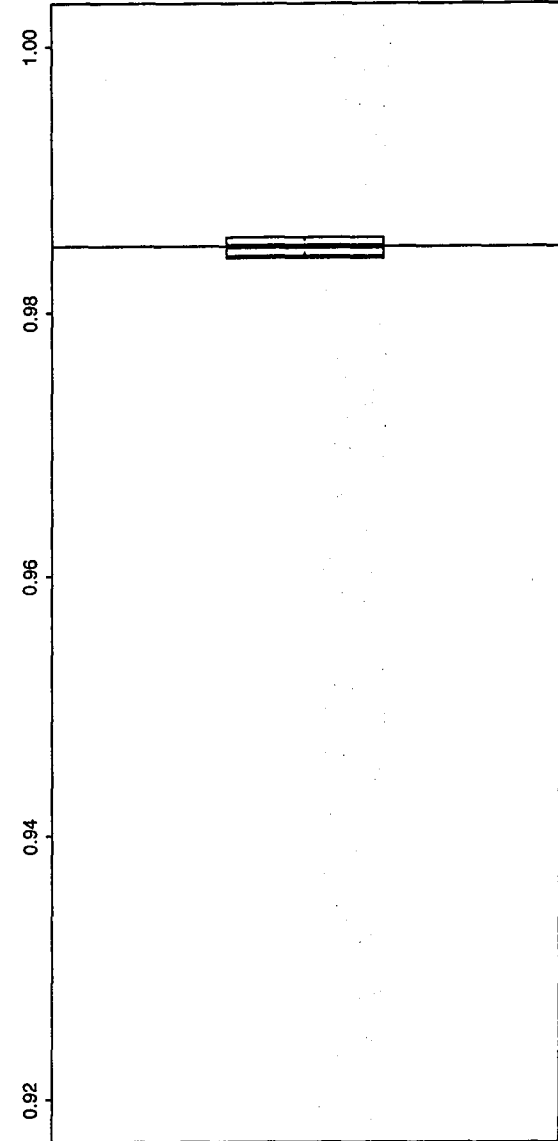
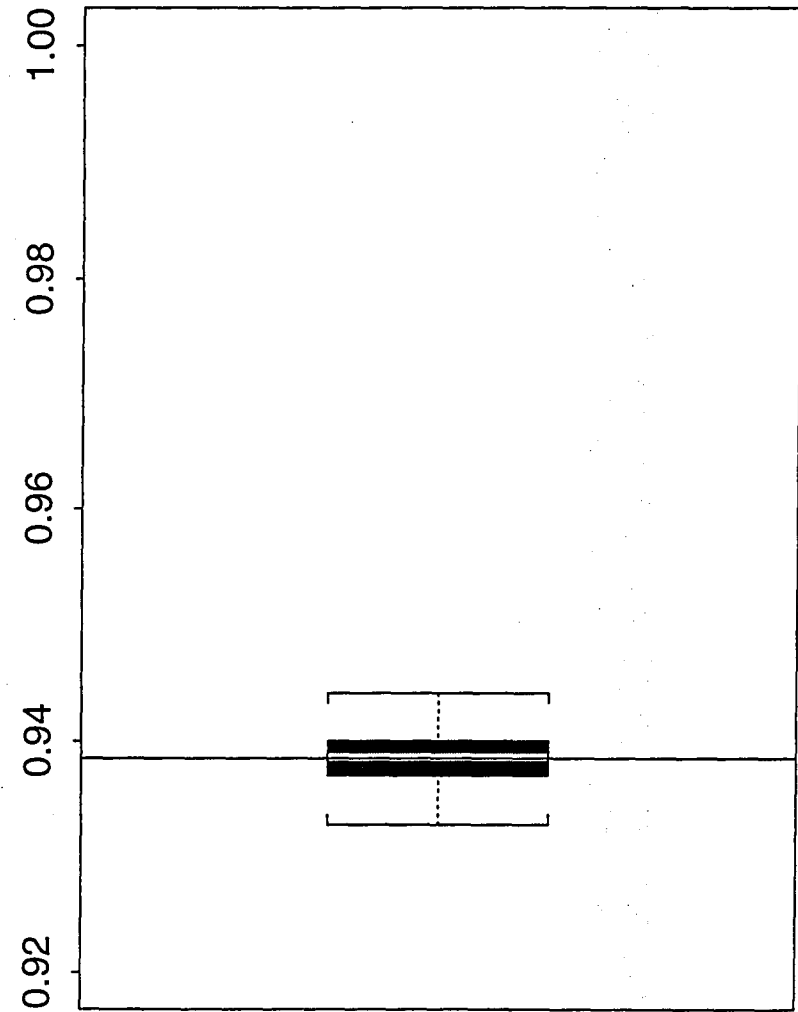
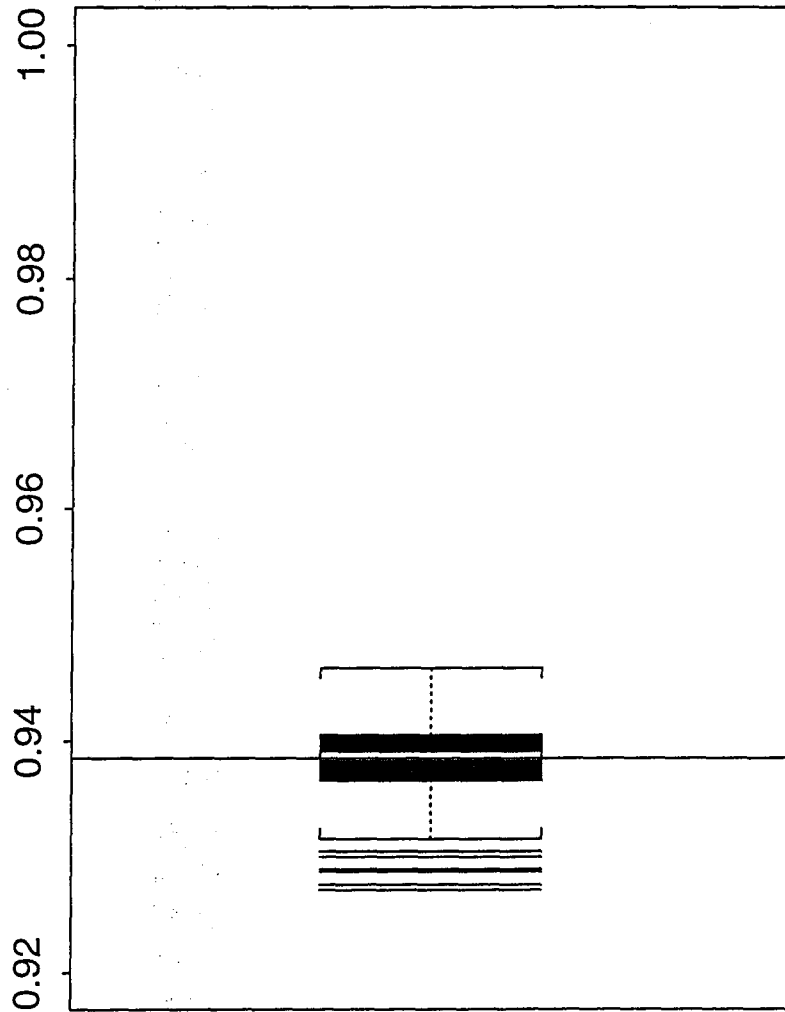


Figure 9

Simulations (500 trials) each individual has its own probability of being captured or marked, $\pi = \exp(-\lambda t)$

$\lambda \sim \text{normal}(1, 0.2)$

$\lambda \sim \text{uniform}(0.65359, 1.34641)$



True $N = 100$ individuals