EXTINCTION AND QUASI-STATIONARITY IN THE VERHULST LOGISTIC MODEL: WITH DERIVATIONS OF MATHEMATICAL RESULTS

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Abstract. We formulate and analyze a stochastic version of the Verhulst deterministic model for density dependent growth of a single population. Three parameter regions with qualitatively different behaviours are identified. Explicit approximations of the quasi-stationary distribution and of the expected time to extinction are presented in each of these regions. The quasi-stationary distribution is approximately normal, and the time to extinction is long, in one of these regions. Another region has a short time to extinction and a quasi-stationary distribution that is approximately geometric. A third region is a transition region between these two. Here the time to extinction is moderately long and the quasi-stationary distribution has a more complicated behaviour. Numerical illustrations are given.

1. Introduction

Early models in population biology were largely deterministic, and serious work on stochastic models started only after the theory of stochastic processes had reached some maturity. A major difference between deterministic and stochastic models lies in the state space, which is continuous in the deterministic setting and discrete for stochastic models. In this regard the stochastic models are more realistic than the deterministic ones, since counts of individuals are always discrete.

Date: September 5, 2007.

1991 *Mathematics Subject Classification.* 60J27,92D40.

Key words and phrases. Quasi-stationary distribution, time to extinction, asymptotic approximation, transition region, logistic model, SIS model, demographic stochasticity, stochastic fade-out.

The work reported here was stimulated by a study circle on biological models at the University of Stockholm during the spring term of 1998, initiated by Håkan Andersson. The study circle was focused on the 1991 book by Renshaw. An early version of this paper was presented at the 1998 Conference on Mathematical Population Dynamics in Zakopane, Poland. I thank Charles Mode for inviting me to this conference.

This manuscript is an extended version of the paper "Extinction and Quasi-stationarity in the Verhulst Logistic Model", which appeared in J. Theor. Biol., vol. 211, 11–27, 2001. The manuscript contains mathematical derivations and proofs that are largely absent in the paper. The manuscript can be found on the webpage www.math.kth.se/~ingemar/forsk/verhulst/verhulst.html.

Each deterministic model can be viewed as an approximation of a corresponding stochastic one. A major task for a mathematical model builder is to derive the conditions under which the deterministic model gives an acceptable approximation of the stochastic one. A known requirement is that the population size be sufficiently large; the explicit task is to quantify what is meant by the term "sufficiently large".

Deterministic modelling has been very successful in many areas of population biology. The important results are qualitative in nature, and are derived from nonlinear deterministic models. The long-term or steady-state behaviour of the models is often important. It is related to stationary solutions of the deterministic models.

The success of the work with nonlinear deterministic models does however not mean that all problems of a qualitative nature can be solved in a deterministic setting. It is noteworthy that there are problem areas where deterministic and stochastic models disagree qualitatively! Important examples are given by the phenomenon of persistence and its complement extinction. There are simple examples of situations where the deterministic model predicts that a population approaches a positive stationary level, while the corresponding stochastic model predicts that extinction will occur with certainty. In such a situation it becomes important to estimate the time required for extinction. This problem can only be handled in a stochastic framework.

Stochastic models are more difficult to handle mathematically than deterministic ones. The difficulty is enhanced when the deterministic model is nonlinear. An additional source of difficulty is associated with models where extinction is possible. Extinction corresponds mathematically to the existence of an absorbing state. It is natural to take a clue from the deterministic model and study the counterpart to its stationary solution, namely the stationary distribution of the stochastic model. This distribution is however degenerate and uninformative when the stochastic model has an absorbing state. One is therefore led to consider the more intricate concept of quasi-stationarity. It is not possible to find explicit expressions for the quasi-stationary distribution or for the time to extinction of a stochastic model whose deterministic counterpart is nonlinear. Progress with the analysis rests on finding good approximations.

The following analysis of the stochastic logistic model shows the importance of deriving approximations of interesting quantities. Approximations will be derived even when explicit expressions are available. This approach is typically taken when the explicit expressions are too complicated to give a feeling for their behaviour. Thus, mathematical progress is aided by the search for heuristic understanding. The approximation methods that we use are analytical in character. Whenever it is possible we shall derive approximations that have the mathematically desirable property of being asymptotic as the population size grows large, but we shall not hesitate to use other types of approximation when we are unable to find approximations that are asymptotic.

The deterministic version of the logistic model that we study in this paper was introduced by Verhulst [37] in 1838, and later rediscovered by Pearl and Reed (1920) [27]. It accounts for density dependence in the growth of a single population. The model is based on the hypothesis that the net birth rate per individual (i.e. the difference between the birth rate and the death rate) is a linearly decreasing function of the population size. This implies that the net population birth rate is a quadratic function of the population size. The model is closed in the sense that no immigration or emigration is supposed to take place. Mathematically the deterministic model leads to a nonlinear differential equation that can be solved explicitly.

A stochastic counterpart to the logistic model was formulated by Feller (1939) [12] as a finite-state birth-and-death process. Our model formulation is essentially the same as that of Feller. In particular, we follow Feller by accounting separately for the density dependence of the birth rate and the death rate. The origin is an absorbing state in the model, eventual absorption at the origin is certain, all states except the origin are transient, and the stationary distribution is degenerate with probability one at the origin. Two qualitatively different behaviours are possible at any given time. Either the process is extinct after having reached the absorbing state at the origin, or the process remains in the set of transient states. In the latter case, the distribution of the process can be found by conditioning on the event that absorption has not occurred. The resulting conditional distribution is approximated by a stationary conditional distribution, the so-called quasi-stationary distribution.

The quasi-stationary distribution poses subtle problems since it cannot be evaluated explicitly. One goal of our study is to derive approximations of this distribution. A second goal is to find out for how long time the quasi-stationary distribution is a good approximation of the distribution of the process. This goal is reached by studying the time to extinction. Important roles in the study are played by two auxiliary processes that lack absorbing states and that have non-degenerate stationary distributions that can be determined explicitly.

In [12], Feller derives the Kolmogorov forward equations for the state probabilities. One of the results in his paper is that the solution of the deterministic model does not agree with the expectation of the solution of the stochastic model, when both are studied as functions of time. (The difference can, however, be shown to be asymptotically small as the maximum population size becomes large.) We claim that the long-term behavior of the model is of considerably larger interest for the applications than the short-term time dependence. We shall therefore only study the behavior of the model in the situation where the population has been subjected to the hypothesized birth- and death-rates for a long time. This corresponds to a study of the counterpart in the stochastic model to the stationary solution (the so-called carrying capacity) in the deterministic model. This leads us to apply the very useful concept of quasi-stationarity.

A slight variation of this stochastic model is studied by Kendall [17]. He introduces the restriction that the state space is strictly positive. By excluding zero from the state space he establishes a related process without an absorbing state. Thus the difficulty of dealing with an absorbing state is avoided, at the expense of being unable to deal with the phenomenon of extinction. The resulting process has a nondegenerate stationary distribution that is determined explicitly. The Kendall process is closely related to the auxiliary process $\{X^{(0)}\}$ that we introduce below.

Whittle [39] discusses an approximation method based on the assumption that random variables that appear in the model are normally distributed. The method is applied to the Kendall model. Good agreement is reached in a specific numerical example between Whittle's approximation and the explicitly known exact expression for the stationary distribution. Our findings below indicate that Whittle's method can be expected to give good results in the parameter region where the time to extinction is long, but not where the time to extinction is moderately long or short.

Another variation of the logistic model has been proposed by Prendiville [31]. He suggests that the population birth rate λ_n and the population death rate μ_n, which are quadratic functions in n in the model that we deal with, be replaced by quantities that are linear functions of n, and where the birth rate is linearly decreasing and the death rate linearly increasing in n. As in the Kendall case, the state space excludes the state zero, and the phenomenon of extinction is absent also from this model. One reason for studying this process is that explicit evaluation of state probabilities is possible when the transition rates are linear in n. The stationary distribution is nondegenerate and can be determined explicitly. Takashima [35] has studied this model and found an explicit expression for the time-dependent probability generating function. The time dependence of the solution is however of less applied interest than the quasi-stationary distribution, which is the limiting distribution as time becomes large, conditional on not being absorbed.

The term "logistic process" is used by Ricciardi [33] to refer to the Prendiville process. Like Takashima, Ricciardi derives the probability generating function for the state of the process at time t. The stationary distribution is given as a special case. Bharucha-Reid [7] gives a brief discussion of what he calls the stochastic analogue of the logistic law of growth. He accounts for the work on the models formulated by Kendall and Prendiville. Iosifescu-Tautu [15] also discuss these early contributions. Another treatment of the Prendiville process is given in the review paper by Ricciardi [33]. Kijima [18] also refers to the Prendiville process as a logistic process. In fact, all of the authors mentioned after Feller analyze a stochastic process that they refer to with some variation of the term "logistic process", but neither of them deals with the process that we are concerned with here. The appropriate stochastic version of the Verhulst model has an absorbing state at the origin, and its deterministic version is nonlinear.

Goel and Richter-Dyn [14] use a stochastic version of a special case of the Verhulst model to study extinction of a colonizing species. Extinction times are studied, as well as the probability that a population will reach a certain size M, starting from an initial size m, before going extinct. Some conclusions are also reached for the SIS model, which is another special case of the Verhulst model (see below), with $\alpha_1 = 1$ and $\alpha_2 = 0$. Quasi-stationarity is not studied.

An important consequence of the existence of an absorbing state is that extinction becomes possible. The stationary distribution is then degenerate with probability one at the origin. The interesting mathematical questions for such a process are to determine the time to extinction, and the distribution of states conditional on non-extinction. It turns out that there exists a stationary conditional distribution, the so-called quasi-stationary distribution, which serves the role of approximating the state of the process if it is known that the process has been going on for a long time, and that extinction has not occurred. One of the earliest uses ot the term "quasi-stationarity" was by the eminent British mathematician Bartlett, [5] and [6]. Early theoretical papers devoted to quasi-stationary distributions, published by Darroch and Seneta, [9] and [10], were influenced by Bartlett. A bibliography of papers and books on quasi-stationarity is given by Pollett on the website `www.maths.uq.edu.au/~pkp/papers/qsds/qsds.html`. A modern presentation of the theory is given in textbook form by Kijima [18].

The concept of quasi-stationarity is used by Pielou [28] in a study of the stochastic logistic model. In her discussion, Pielou describes a recursive numerical method for determining what she describes as the quasi-stationary distribution. However, it is easy to see that the distribution determined by her method is the stationary distribution of the auxiliary process that we introduce below and denote by $\{X^{(0)}\}$.

The importance of quasi-stationarity in stochastic population models is emphasized in the book by Nisbet and Gurney [24]. They describe an iterative numerical method for determining the quasi-stationary distribution. Furthermore, they discuss the phenomenon of extinction and give exact, although unwieldy, expressions for the expected time to extinction from a fixed state n. This work is continued by Renshaw [32]. He also emphasizes the importance of the concept of quasi-stationarity in modelling biological populations, and he derives relations between the time to extinction and the quasi-stationary distribution. He uses the stationary distribution of the auxiliary process $\{X^{(0)}\}$ to represent the quasi-stationary distribution, without noting that this is an approximation. His results can not be used in the parameter regions where the time to extinction is moderately long or short.

The theoretical work based on the papers by Darroch and Seneta, and the applied work by Pielou, Nisbet-Gurney, and Renshaw appear to have gone on independently of each other, since neither group makes any reference to the work of the other group.

A special case of the Verhulst model is mathematically identical to a classical model in mathematical epidemiology, the so-called SIS-model. The stochastic version of this model was first described by Weiss and Dishon [38]. The same mathematical model has since then appeared in several contexts. Bartholomew [4] has applied it to study the transmission of rumours, Oppenheim *et al.* [26] use it as a model for chemical reactions, Cavender [8] uses it as an example of a birth-and-death process, Norden [25] describes it as a stochastic logistic model, while Kryscio and Lefèvre [19], Nåsell [21], and Andersson and Djehiche [2] return to the epidemic context. Kryscio and Lefèvre summarize and extend the work of the previous authors. An important contribution of this paper is its introduction of the concept of quasi-stationarity into the area of mathematical epidemiology. Nåsell provides further extensions of the results of Kryscio and Lefévre. Nåsell emphasizes asymptotic expansions throughout his 1996 paper as a means of deriving useful results. He introduces the transition region (see below) into the study.

The general approach used in Nåsell [21] is followed here. One difference is, however, that the ambition in the 1996 paper of deriving uniformly valid asymptotic approximations is abandoned. A second difference is that results for a general finite-state birth-and-death process with absorbing state at the origin are here developed before they are used to study the specific case represented by the transition rates associated with the Verhulst model. The approximation of the quasi-stationary distribution in the transition region that we give here is an improvement over the corresponding results in the 1996 paper. The corresponding improvement for the SIS model is treated by Nåsell [22].

Both the SIS model and the Verhulst model include an intriguing phase transition phenomenon. It takes the form that there are three parameter regions with qualitatively different behaviours. Epidemiologically (in the SIS model) it corresponds to a threshold phenomenon with important epidemiological intrepretations. Ecologically (in the

Verhulst model) it corresponds to three different orders of magnitude for the time to extinction: long, moderately long, and short. The three different parameter regions are identified, and an analysis of the quasi-stationary distribution and of the time to extinction is carried out in each of them.

The study of the Verhulst model is undertaken in Section 3. We prepare for this study in Section 2, where we derive some general results for a birth-death process with finite state space, and for which the origin is an absorbing state. Two auxiliary processes are introduced, and their stationary distributions are shown to be important for both the quasi-stationary distribution and for the time to extinction.

Asymptotic approximations are derived throughout Section 3, both for the quasi-stationary distribution and for the expected time to extinction. The results rest heavily on asymptotic approximations of the stationary distributions of the two auxiliary processes. We emphasize the importance of deriving asymptotic approximations of these two distributions even though we have exact expressions for them. Numerical illustrations are given, and some brief comments are given on numerical methods for evaluation of quasi-stationary distributions.

2. A univariate birth-death process with finite state space and with absorbing state at the origin

In Subsection 2.1 we formulate a birth-death process with finite state space, and for which the origin is an absorbing state. Two auxiliary processes without absorbing states are then formulated in Subsection 2.2, and their stationary distributions are determined. The quasi-stationary distribution of the original process is studied in Subsection 2.3. It is shown to satisfy a recursion relation where the coefficients can be interpreted in terms of the stationary distributions of the two auxiliary processes. The time to extinction is studied in Subsection 2.4 for an arbitrary initial distribution. We show that the time to extinction from the quasi-stationary distribution has an exponential distribution. This distribution is completely determined by its expectation, which in turn is determined by the quasi-stationary distribution. The expected time to extinction from an arbitrary initial distribution is determined by an explicit expression whose coefficients can be interpreted in terms of the stationary distributions of the two auxiliary processes.

Several of the results that we give are known before for the special case of the SIS model; see Nåsell [21], [22]. The importance of the stationary distributions of the two auxiliary processes was pointed out in the context of the SIS model by Kryscio and Lefèvre [19]. Recognition of this importance allows a useful structuring of the approximation problem for any specific case. The way this is done is exemplified by the Verhulst model treated in Section 3.

2.1. **Formulation of the birth-death process.** We study a birth-death process $\{X(t), t \geq 0\}$ with finite state space $\{0, 1, \ldots, N\}$ and where the origin is an absorbing state. Transitions in the process are only allowed to neighboring states. The rate of transition from state n to state $n+1$ (the population birth rate) is denoted λ_n, and the rate of transition from the state n to the state $n-1$ (the population death rate) is denoted by μ_n. It is convenient to also have notation for the sum of λ_n and μ_n: we put $\kappa_n = \lambda_n + \mu_n$. We assume that μ_0 and λ_N are equal to zero, to be consistent with the assumption that the state space is limited to $\{0, 1, \ldots, N\}$. Furthermore, we assume that λ_0 also equals zero, to be consistent with the assumption that the origin is an absorbing state. All other transition rates are assumed to be strictly positive.

The Kolmogorov forward equations for the state probabilities $p_n(t) = P\{X(t) = n\}$ can be written

$$p_n'(t) = \mu_{n+1} p_{n+1}(t) - \kappa_n p_n(t) + \lambda_{n-1} p_{n-1}(t), \quad n = 0, 1, \ldots, N. \tag{2.1}$$

(Put $\mu_{N+1} = \lambda_{-1} = p_{N+1}(t) = p_{-1}(t) = 0$, so that (2.1) makes sense formally for all n-values indicated.) The state probabilities depend on the initial distribution $p_n(0)$.

An alternative way of writing this system of equations is in the form

$$p' = pA, \tag{2.2}$$

where $p(t) = (p_0(t), p_1(t), \ldots, p_N(t))$ is the row vector of state probabilities and the matrix A contains the transition rates as follows: The nondiagonal element a_{mn} of this matrix equals the rate of transition from state m to state n, and the diagonal element a_{nn} equals the rate κ_n multiplied by -1. The matrix A can be written as follows:

$$A = \begin{pmatrix} -\kappa_0 & \lambda_0 & 0 & \ldots & 0 \\ \mu_1 & -\kappa_1 & \lambda_1 & \ldots & 0 \\ 0 & \mu_2 & -\kappa_2 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & -\kappa_N \end{pmatrix}$$

Note that A is a tridiagonal matrix with all row sums equal to 0. Thus the determinant of A equals zero, so A is noninvertible. Note also that $\lambda_0 = \kappa_0 = 0$, so the first row of A is a row of zeros.

A stationary distribution is found by putting the time derivative equal to zero, i.e. by solving $pA = 0$. It is readily shown that the process $\{X(t)\}$ has a degenerate stationary distribution $p = (1, 0, \ldots, 0)$. The distribution of $\{X(t)\}$ approaches the stationary distribution as time t approaches infinity. This says that ultimate absorption is certain. In many cases, the time to absorption is long. It is therefore of interest to study the distribution of $\{X(t)\}$ before absorption has taken place. This is done via the concept of quasi-stationarity, which is introduced in Subsection 2.3.

2.2. **Two auxiliary processes.** In this subsection we study two birth-death processes $\{X^{(0)}(t)\}$ and $\{X^{(1)}(t)\}$ that both are close to the original process $\{X(t)\}$, but lack absorbing states. The state space of each of the two auxiliary processes concides with the set of transient states $\{1, 2, \ldots, N\}$ for the original process. We determine the stationary distribution of each of the two auxiliary processes.

The process $\{X^{(0)}(t)\}$ can be described as the original process with the origin removed. Its death rate $\mu_1^{(0)}$ from the state 1 to the state 0 is equal to 0, while all other transition rates are equal to the corresponding rates for the original process.

The process $\{X^{(1)}(t)\}$ is found from the original process by allowing for one immortal individual. Here, each death-rate μ_n is replaced by $\mu_n^{(1)} = \mu_{n-1}$, while each of the birth rates $\lambda_n^{(1)}$ equals the corresponding birth rate for the original process.

The state probabilities for the two processes are denoted by $p^{(0)}(t) = (p_1^{(0)}(t), p_2^{(0)}(t), \ldots, p_N^{(0)}(t))$ and $p^{(1)}(t) = (p_1^{(1)}(t), p_2^{(1)}(t), \ldots, p_N^{(1)}(t))$, respectively.

Stationary distributions are easy to determine explicitly for both of the auxiliary processes. In order to describe them we introduce two sequencies ρ_n and π_n as follows:

$$\rho_1 = 1, \quad \rho_n = \frac{\lambda_1 \lambda_2 \cdots \lambda_{n-1}}{\mu_1 \mu_2 \cdots \mu_{n-1}}, \quad n = 2, 3, \ldots, N, \tag{2.3}$$

$$\pi_n = \frac{\mu_1}{\mu_n} \rho_n, \quad n = 1, 2, \ldots, N. \tag{2.4}$$

The two stationary distributions can be simply expressed in terms of these sequencies. The stationary distribution of the process $\{X^{(0)}(t)\}$ equals

$$p_n^{(0)} = \pi_n p_1^{(0)}, \quad n = 1, 2, \ldots, N, \quad \text{where} \quad p_1^{(0)} = \frac{1}{\sum_{n=1}^{N} \pi_n}, \tag{2.5}$$

while the stationary distribution of the process $\{X^{(1)}(t)\}$ equals

$$p_n^{(1)} = \rho_n p_1^{(1)}, \quad n = 1, 2, \ldots, N, \quad \text{where} \quad p_1^{(1)} = \frac{1}{\sum_{n=1}^{N} \rho_n}. \tag{2.6}$$

Both of these stationary distributions will serve as approximations of the quasi-stationary distribution defined in the next subsection. Furthermore, the related sequencies ρ_n and π_n play important roles in a recursion relation for the quasi-stationary distribution, and in an explicit expression for the expected time to extinction from an arbitrary inital distribution.

2.3. **The quasi-stationary distribution q.** We define and study the quasi-stationary distribution q of the process $\{X(t)\}$.

We partition the state space into two subsets, one containing the absorbing state 0, and the other equal to the set of transient states

$\{1, 2, \ldots, N\}$. Corresponding to this partition, we write the equation (2.2) in block form. The vector $p(t)$ is expressed as $p(t) = (p_0(t), p_Q(t))$, where $p_Q(t) = (p_1(t), \ldots, p_N(t))$ is the row vector of state probabilities in the set of transient states. The corresponding block form of the matrix A contains four blocks. The first row of A gives rise to two blocks of row vectors of zeroes. The remaining two blocks contain a column vector a of length N and a square matrix A_Q of order N. The first entry of a equals μ_1, while all other entries are equal to 0. The matrix A_Q is formed be deleting the first row and the first column from A. With this notation one can rewrite (2.2) in the form

$$(p_0'(t), p_Q'(t)) = (p_0(t), p_Q(t)) \begin{pmatrix} 0 & 0 \\ a & A_Q \end{pmatrix}.$$

By carrying out the product on the right-hand side and equating the block components of the two sides of the equation, we are led to the following two differential equations:

$$p_0'(t) = p_Q(t)a = \mu_1 p_1(t) \tag{2.7}$$

and

$$p_Q'(t) = p_Q(t)A_Q. \tag{2.8}$$

Before absorption, the process takes values in the set of transient states. The state of the process at time t is restricted to this set if two conditions are fulfilled. One is that the initial distribution is supported on this set, i.e. that $P\{X(0) > 0\} = 1$. The second condition is that absorption at the origin has not occurred at time t, i.e. that $X(t) > 0$. The corresponding conditional state probabilities are denoted $\tilde{q}_n(t)$. It is also useful to put $\tilde{q}(t) = (\tilde{q}_1(t), \ldots, \tilde{q}_N(t))$ to denote the row vector of conditional state probabilities. We note that $\tilde{q}(t)$ depends on the initial distribution $\tilde{q}(0)$. The conditioning on non-absorption at time t leads to the relation

$$\tilde{q}_n(t) = P\{X(t) = n | X(t) > 0\} = \frac{p_n(t)}{1 - p_0(t)}. \tag{2.9}$$

Hence the vector of conditional state probabilities $\tilde{q}(t)$ can be determined from the vector $p_Q(t)$ of state probabilities on the set of transient states via the relation

$$\tilde{q}(t) = \frac{p_Q(t)}{1 - p_0(t)}. \tag{2.10}$$

By differentiating this relation and using expressions (2.7) and (2.9) we get

$$\tilde{q}'(t) = \frac{p_Q'(t)}{1 - p_0(t)} + \mu_1 \tilde{q}_1(t) \frac{p_Q(t)}{1 - p_0(t)}. \tag{2.11}$$

By using (2.8) and (2.10) we get the following differential equation for the vector of conditional state probabilities $\tilde{q}$:

$$\tilde{q}'(t) = \tilde{q}(t)A_Q + \mu_1\tilde{q}_1(t)\tilde{q}(t).$$

The quasi-stationary distribution q can now be defined. It is the stationary solution of this equation. Thus, it satisfies the equation

$$qA_Q = -\mu_1 q_1 q. \tag{2.12}$$

This shows that the quasi-stationary distribution q is a left eigenvector of the matrix A_Q corresponding to the eigenvalue $-\mu_1 q_1$. This result is useful for numerical evaluations. One can show that the eigenvalue $-\mu_1 q_1$ is the maximum eigenvalue of the matrix A_Q.

We show that the probabilities q_n that determine the quasi-stationary distribution satisfy the following relation:

$$q_n = \pi_n \sum_{k=1}^{n} \frac{1 - \sum_{j=1}^{k-1} q_j}{\rho_k} q_1, \quad n = 1, 2 \ldots, N, \quad \sum_{n=1}^{N} q_n = 1. \tag{2.13}$$

Note that the sequencies π_n and ρ_n are known explicitly in terms of the transition rates λ_n and μ_n. It is useful to note that they are related to the two stationary distributions of the previous section, since $\pi_n = p_n^{(0)}/p_1^{(0)}$ and $\rho_n = p_n^{(1)}/p_1^{(1)}$.

In order to derive this result we note from relation (2.12) that the probabilities q_n satisfy the following difference equation of order two:

$$\mu_{n+1}q_{n+1} - \kappa_n q_n + \lambda_{n-1}q_{n-1} = -\mu_1 q_1 q_n, \quad n = 1, 2, \ldots, N. \tag{2.14}$$

Furthermore, boundary conditions are given by

$$q_0 = 0 \quad \text{and} \quad q_{N+1} = 0. \tag{2.15}$$

We derive two difference equations of order 1. Put

$$f_n = \mu_n q_n - \lambda_{n-1}q_{n-1}, \quad n = 1, 2, \ldots, N+1. \tag{2.16}$$

Then (2.14) can be written

$$f_{n+1} - f_n = -\mu_1 q_1 q_n, \quad n = 1, 2, \ldots, N,$$

with the final condition

$$f_{N+1} = 0.$$

By solving for f_n we find that

$$f_n = \mu_1 q_1 \sum_{i=n}^{N} q_i, \quad n = 1, 2, \ldots, N+1.$$

The second difference equation of order one is given by

$$\mu_n q_n = \lambda_{n-1}q_{n-1} + \mu_1 q_1 \sum_{i=n}^{N} q_i, \quad n = 1, 2, \ldots, N+1.$$

with the initial condition

$$q_0 = 0.$$

It is straightforward to verify (2.13) from this initial value problem.

We emphasize that the relation in (2.13) is not an explicit solution. It can be used to successively determine the values of q_2, q_3 etc. if q_1 is known. But the crux is that q_1 can only be determined from the relation $\sum_{n=1}^{N} q_n = 1$, which requires knowledge of all the q_n.

Two iteration methods for determining the quasi-stationary distribution can be based on (2.13). One of these methods uses iteration for determining q_1. It starts with an initial guess for q_1, determines successively all the q_n from (2.13), computes the sum of the q_n, and determines the result of the first iteration as the initial guess divided by this sum. The process is repeated until successive iterates are sufficiently close. Nisbet and Gurney [24] describe essentially the same iteration method, based on the recurrence relation (2.14), and use it for numerical evaluations.

The second method uses iteration on the whole distribution. It starts with an initial guess for the quasi-stationary distribution ($p^{(0)}$ and $p^{(1)}$ discussed in the previous subsection are candidates), uses this distribution as input in the numerators of the terms that are summed over k, and solves (2.13) for the q_n, under recognition of the requirement that $\sum_{n=1}^{N} q_n = 1$. The process is repeated until successive iterates are sufficiently close. The iteration of the second numerical method can be formally described as follows:

$$q_n^{(i+1)} = \pi_n \sum_{k=1}^{n} \frac{1 - \sum_{j=1}^{k-1} q_j^{(i)}}{\rho_k} q_1^{(i+1)}, \tag{2.17}$$

where the quasi-stationary distribution of iteration number i is denoted $q^{(i)}$. Both numerical evaluations and analytical approximations of the quasi-stationary distribution for the Verhulst model in Section 3 are based on this method.

The quasi-stationary distribution for a birth-death process can be determined explicitly in a few cases. Thus, the linear birth-death process determined by $\lambda_n = n\lambda$ and $\mu_n = n\mu$ has its quasi-stationary distribution equal to the geometric distribution $q_n = (1-R)R^{n-1}$ when $R = \lambda/\mu < 1$. Furthermore, the random walk in continuous time with absorbing barrier at the origin, determined by $\lambda_n = \lambda$ and $\mu_n = \mu$ for $n \geq 1$ and $\lambda_0 = \mu_0 = 0$, has the quasi-stationary distribution $q_n = (1-\sqrt{R})^2 n(\sqrt{R})^{n-1}$, $n = 1, 2, \ldots$, again under the assumption that $R < 1$. These results have been derived by a number of authors with different methods; see Seneta [34], Cavender [8], Pollett [29, 30], van Doorn [36]. It is straightforward to verify these results from (2.13).

These examples of explicit expressions for quasi-stationary distributions have two limitations. One is that they deal with birth-death processes where the transition rates λ_n and μ_n are at most linear functions of the state n, and another one is that they are confined to a parameter region where the time to extinction is short. The main applied interest in quasi-stationarity is, however, with models that account for density dependence so that one (or both) of the transition rates λ_n and μ_n depends nonlinearly on n. Furthermore, the parameter regions where the time to extinction is very long and moderately long are more interesting than the region where the time to extinction is short. It does not appear possible to determine the quasi-stationary distribution in explicit form in these cases. A fruitful strategy is then to search for approximations. The two stationary distributions $p^{(0)}$ and $p^{(1)}$ both serve as approximations of the quasi-stationary distribution q. Actually, $p^{(0)}$ provides the better approximation when the time to extinction is long, while $p^{(1)}$ does better when the time to extinction is short, as noted for the SIS model by Kryscio and Lefèvre [19]. The approximations are claimed to hold in the body of the distribution but not in its tails. This has important consequences with regard to time to extinction. We show in the next subsection that the probabilities q_1 and $p_1^{(0)}$ are important for determining the times to extinction from different initial conditions. These probabilities lie in the left tail of the corresponding distribution when the time to extinction is very long, but in the body of the distribution when the time to extinction is moderately long or short.

The processes $\{X(t)\}$ and $\{X^{(0)}(t)\}$ have the same transition rates as long as the first process has not gone extinct. This is probably the reason why several authors, as mentioned above, refer to the stationary distribution $p^{(0)}$ of the second of the processes as the quasi-stationary distribution q of the first one.

2.4. **The time to extinction.** The time to extinction τ is a random variable that clearly depends on the initial distribution. We denote this random variable by τ_Q when the initial distribution $p(0)$ equals the quasi-stationary distribution q, and by τ_n when $X(0) = n$.

If absorption has occurred at time t, then clearly the waiting time to extinction τ is at most equal to t and also the state of the process $X(t)$ is equal to 0. Hence the events $\{\tau \leq t\}$ and $\{X(t) = 0\}$ are identical. By computing the probabilities of these events we get

$$P\{\tau \leq t\} = P\{X(t) = 0\} = p_0(t). \tag{2.18}$$

We study first τ_Q. The reason why this is interesting is as follows. One can show that the distribution of the process, conditioned on non-extinction, approaches the quasi-stationary distribution as time increases, see van Doorn [36]. This holds for arbitrary initial distributions that are supported on the set of transient states. If the process has been going on for a long time, and it is known that it has not been absorbed, then its distribution is approximated by the quasi-stationary distribution.

It turns out to be possible to get a simple form for the state probabilities p in this case. To derive this we note from (2.11) that

$$p'_Q(t) = -\mu_1 q_1 p_Q(t), \quad p_Q(0) = q. \tag{2.19}$$

This says essentially that probability is leaking from each transient state with the same rate. This equation has the solution

$$p_Q(t) = q \exp(-\mu_1 q_1 t). \tag{2.20}$$

From this solution one can also determine $p_0(t)$, since (2.7) gives a differential equation for p_0 in terms of p_1, and the initial value is $p_0(0) = 0$. Thus p_0 satisfies the initial value problem

$$p'_0(t) = \mu_1 p_1(t), \quad p_0(0) = 0,$$

with solution

$$p_0(t) = 1 - \exp(-\mu_1 q_1 t). \tag{2.21}$$

The expressions in (2.20) and (2.21) combine to give the solution of the Kolmogorov forward equations in this case. It is noteworthy that it is possible to get such a simple expression for this solution. The solution is, however, not explicit, since we have no explicit expression for q_1.

We conclude, using (2.18), that the time to extinction from the quasi-stationary distribution, τ_Q, has an exponential distribution with the expectation

$$\mathrm{E}\tau_Q = \frac{1}{\mu_1 q_1}. \tag{2.22}$$

The distribution of τ_Q is thus completely determined from the probability q_1.

The distribution of the time to extinction τ from an arbitrary initial distribution is more complicated. Some insight into its behaviour may be gained by considering its expectation. It is a standard result for birth-death processes that this expectation can be determined explicitly when $X(0) = n$. Expressions for the result are given e.g. by Karlin and Taylor [16], Gardiner [13], Nisbet and Gurney [24], and Renshaw [32]. We show below that the result can be expressed as follows in terms of the notation that we have introduced above:

$$\mathrm{E}\tau_n = \frac{1}{\mu_1} \sum_{k=1}^{n} \frac{1}{\rho_k} \sum_{j=k}^{N} \pi_j = \frac{1}{\mu_1} \sum_{j=1}^{N} \pi_j \sum_{k=1}^{\min(n,j)} \frac{1}{\rho_k}. \tag{2.23}$$

The second expression follows from the first one by changing the order of summation. Note that the two parameter sequencies ρ_n and π_n that appear here are related to the stationary distributions $p^{(1)}$ and $p^{(0)}$ of the two auxiliary processes $\{X^{(0)}(t)\}$ and $\{X^{(1)}(t)\}$. Approximations of these stationary distributions can hence be used to derive approximations of $\mathrm{E}\tau_n$.

By putting $n = 1$ in the above formula we find that the expected time to extinction from the state 1 can be written as follows:

$$\mathrm{E}\tau_1 = \frac{1}{\mu_1}\sum_{j=1}^{N}\pi_j = \frac{1}{\mu_1 p_1^{(0)}}. \tag{2.24}$$

The expected time to extinction from state n can therefore be written in the alternative form

$$\mathrm{E}\tau_n = \mathrm{E}\tau_1 \sum_{k=1}^{n}\frac{1}{\rho_k}\sum_{j=k}^{N} p_j^{(0)}. \tag{2.25}$$

The expected time to extinction from an arbitrary initial distribution $\{p_n(0)\}$ can be derived from the above expression for $\mathrm{E}\tau_n$. The result can be written

$$\mathrm{E}\tau = \frac{1}{\mu_1}\sum_{j=1}^{N}\pi_j \sum_{k=1}^{j}\frac{1}{\rho_k}\sum_{n=k}^{N} p_n(0). \tag{2.26}$$

This assumes that the initial distribution is supported on the set of transient states, i.e. that $\sum_{n=1}^{N} p_n(0) = 1$.

Both Nisbet and Gurney [24] and Renshaw [32] describe the exact analytic expression that they give for $\mathrm{E}\tau_n$ as cumbersome and claim that it does not allow an intuitive understanding. Our different notation and our interpretation of ρ_n and π_n in terms of the stationary distributions $p^{(1)}$ and $p^{(0)}$ improves this situation. Additional improvement will be reached when we have derived approximations of ρ_n and π_n for the Verhulst process, as is done in the next section of the paper.

It is useful to note that our expressions for expected times to extinction are dimensionally correct. Each expectation is proportional to $1/\mu_1$, which is a natural time constant for the process.

We proceed to derive the first expression for $\mathrm{E}\tau_n$ in (2.23). The derivation is based on the recurrence relation of order two

$$\mathrm{E}\tau_n = \frac{1}{\kappa_n} + \frac{\lambda_n}{\kappa_n}\mathrm{E}\tau_{n+1} + \frac{\mu_n}{\kappa_n}\mathrm{E}\tau_{n-1}, \quad n = 1, 2, \ldots, N, \tag{2.27}$$

with boundary values

$$\mathrm{E}\tau_0 = 0 \quad \text{and} \quad \mathrm{E}\tau_N = \frac{1}{\mu_N} + \mathrm{E}\tau_{N-1}. \tag{2.28}$$

To solve this recursion relation we put $g_n = \rho_n(\mathrm{E}\tau_n - \mathrm{E}\tau_{n-1})$. It follows then that g_n satisfies the recursion relation of order one

$$g_n - g_{n+1} = \frac{\rho_n}{\mu_n} = \frac{\pi_n}{\mu_1}, \quad n = 1, 2, \ldots, N, \tag{2.29}$$

with final value

$$g_N = \frac{\rho_N}{\mu_N} = \frac{\pi_N}{\mu_1}, \tag{2.30}$$

and solution

$$g_n = \frac{1}{\mu_1} \sum_{j=n}^{N} \pi_j. \tag{2.31}$$

By solving the recursion of order one

$$\mathrm{E}\tau_n - \mathrm{E}\tau_{n-1} = \frac{1}{\mu_1} \frac{1}{\rho_n} \sum_{j=n}^{N} \pi_j, \quad n = 1, 2, \ldots, N, \tag{2.32}$$

with initial value

$$\mathrm{E}\tau_0 = 0, \tag{2.33}$$

we establish the first expression for $\mathrm{E}\tau_n$ in (2.23).

It remains for us to derive the expression (2.26) for $\mathrm{E}\tau$ for an arbitrary initial distribution supported on the set of transient states. Clearly we have

$$\mathrm{E}\tau = \sum_{n=1}^{N} p_n(0) \mathrm{E}\tau_n. \tag{2.34}$$

By using the second expression for $\mathrm{E}\tau_n$ in (2.23) and interchanging the order of summation between n and j we get

$$\mathrm{E}\tau = \frac{1}{\mu_1} \sum_{j=1}^{N} \pi_j \sum_{n=1}^{N} p_n(0) \sum_{k=1}^{\min(n,j)} \frac{1}{\rho_k}. \tag{2.35}$$

The result follows by interchanging the order of summation between n and k.

It is instructive to confirm that the results in (2.22) and (2.23) can be derived from (2.26). The derivation of (2.22) from (2.26) makes use of the relation (2.13) for the proabilities q_n in terms of the sequencies π_n and ρ_n.

3. The Verhulst logistic model

This section is devoted to an analysis of the Verhulst logistic model for population growth. The deterministic version of the model leads to a nonlinear differential equation that commonly is expressed in the form

$$Y' = r \left(1 - \frac{Y}{K}\right) Y. \tag{3.1}$$

Here the state variable Y can be interpreted as the population size. Its time development $Y(t)$ depends on its initial value $Y(0)$ and on the two parameters r and K, where r is called the intrinsic growth rate of the population and K is referred to as the carrying capacity of the environment.

A stochastic version of the model is formulated in Subsection 3.1. It takes the form of a finite-state birth-death process with an absorbing state at the origin.

The deterministic version of the model is briefly analysed in Subsection 3.2. The most important property is a bifurcation phenomenon. It defines a partition of the parameter space into two subsets with qualitatively different behaviours. The model predicts that the population size will in one of the parameter sets approach a positive level as time increases, and that it will approach zero in the other one.

A counterpart to this qualitative behaviour is established for the stochastic version of the model analyzed in this paper. It is shown to exhibit three qualitatively different behaviours in three subsets of parameter space. We identify these subsets and analyze both the quasi-stationary distribution and the time to extinction in each of them. Briefly, the time to extinction is long, moderately long, and short in each of these subsets.

The analysis of the stochastic version of the model proceeds by applying the results derived in the previous section for a finite-state birth-death process with an absorbing state at the origin. Notation that is used in this analysis is summarized in Subsection 3.3. Asymptotic approximations for the parameter sequences ρ_n and π_n are derived in Subsections 3.4 and 3.5. Approximations of the stationary distributions $p^{(1)}$ and $p^{(0)}$ of the two auxiliary processes when the time to extinction is long are derived in Subsections 3.6 and 3.7. Corresponding approximations of the quasi-stationary distribution and of the time to extinction are derived in Subsections 3.8 and 3.9. Approximations of the same quantities when the time to extinction is short are given in Subsection 3.10.

The remainder of the section is devoted to an analysis in the so-called transition region where the time to extinction is moderately long. This case is the most intricate of the three. Its treatment requires a rescaling of the parameters that is derived in Subsection 3.11. Approximations of the parameter sequencies ρ_n and π_n are given in Subsection 3.12. Approximations of the stationary distributions $p^{(1)}$ and $p^{(0)}$ of the two auxiliary processes are derived in Subsections 3.13 and 3.15, respectively. The derivation of the approximation of the latter of these two distributions requires a uniform approximation that is derived in Subsection 3.14. Finally, approximations of the quasi-stationary distribution and of the time to extinction are derived in Subsections 3.16 and 3.17.

Numerical illustrations of our results are given in each of the three subsets of the parameter space.

3.1. **Formulation of the stochastic Verhulst model.** The formulation of a stochastic version of the Verhulst model requires us to define transition rates λ_n and μ_n as functions of n. We note that the right-hand side of (3.1) divided by Y can be interpreted as the net birth rate per individual, i.e. as the difference between the birth rate per individual and the death rate per individual. Furthermore, the net birth rate per individual is seen to be a linearly decreasing function of the population size. This is the way in which the model acounts for density dependence.

In a stochastic setting we can achieve this dependence on the population size of the net birth rate per individual by assuming either that the birth rate per individual is a linearly decreasing function of the population size, or that the death rate per individual is a linearly increasing function of the population size, or that both of these rates depend on the population size in the postulated way. We are therefore led to the following specification of the two transition rates λ_n and μ_n:

$$\lambda_n = \begin{cases} \lambda \left(1 - \alpha_1 \dfrac{n}{N}\right) n, & n = 0, 1, \ldots, N-1, \\ 0, & n = N, \end{cases} \tag{3.2}$$

and

$$\mu_n = \mu \left(1 + \alpha_2 \frac{n}{N}\right) n, \quad n = 0, 1, \ldots, N. \tag{3.3}$$

This definition of λ_n and μ_n defines implicitly five parameters N, λ, μ, α_1, and α_2. Among these, the maximum population size N is a large positive integer, the rates λ and μ are strictly positive, while the parameters α_1 and α_2 obey the following inequalities: $0 \leq \alpha_1 \leq 1$ and $\alpha_2 \geq \max\{0, (1-\alpha_1)R_0 - 1\}$, with $R_0 = \lambda/\mu$. The upper bound for α_1 is necessary to ensure that the transition rate λ_n is nonnegative, while the second lower bound for α_2 guarantees that the quantity K defined in the next subsection is smaller than or at most equal to N. In order to assure density dependence we assume that at least one of α_1 and α_2 is strictly positive. Norden [25] analyzes this model with $\alpha_1 = 1$. Note that the SIS model corresponds to $\alpha_1 = 1$ and $\alpha_2 = 0$. The sum of α_1 and α_2 is denoted α:

$$\alpha = \alpha_1 + \alpha_2. \tag{3.4}$$

The ratio λ/μ is important in what follows. As already noted above we denote it by

$$R_0 = \lambda/\mu$$

and refer to it as the basic reproduction ratio. The parameter region where the time to extinction is long (short), is identified by the condition that $R_0 > 1$ is fixed ($R_0 < 1$ is fixed) as $N \to \infty$. We refer to the corresponding parameter region by saying that R_0 is distinctly above (distinctly below) the deterministic threshold value 1. The third parameter region where the time to extinction is moderately long is characterized by values of R_0 close to 1. This region is a transition region between the other two. The R_0-values that determine the boundaries between the three parameter regions depend on N, α_1, and α_2. They are derived in Subsection 3.11.

3.2. **The deterministic version of the Verhulst model.** One can gather some useful information about the stochastic model formulated in the previous subsection by studying its deterministic approximation. We let $Y(t)$ denote the population size at time t. It follows then that Y satisfies the following differential equation:

$$Y' = \lambda\left(1 - \alpha_1 \frac{Y}{N}\right) Y - \mu\left(1 + \alpha_2 \frac{Y}{N}\right) Y.$$

This equation can be rewritten in the form

$$Y' = \mu\left(R_0 - 1 - (\alpha_1 R_0 + \alpha_2)\frac{Y}{N}\right) Y.$$

For $R_0 = 1$ this equation can be written

$$Y' = -\frac{\mu\alpha}{N} Y^2, \quad R_0 = 1,$$

while it takes the well-known form

$$Y' = r\left(1 - \frac{Y}{K}\right) Y, \quad R_0 \neq 1,$$

for R_0 different from 1. Here,

$$r = \mu(R_0 - 1) \tag{3.5}$$

is the intrinsic growth rate per individual at low population density, and

$$K = \frac{(R_0 - 1)N}{\alpha_1 R_0 + \alpha_2} \tag{3.6}$$

is referred to as carrying capacity when it is positive. Note that both K and r are negative if $R_0 < 1$.

We study the asymptotic behaviour of the solution $Y(t)$ of the differential equation for Y as $t \to \infty$ with the initial value $Y(0) \geq 0$. It is straightforward to show that $Y(t)$ approaches the positive carrying capacity K as $t \to \infty$ if $Y(0) > 0$ and $R_0 > 1$, while $Y(t)$ approaches 0 as $t \to \infty$ for all nonnegative initial values if $R_0 \leq 1$. Thus, a positive population size is predicted for $R_0 > 1$ if $Y(0) > 0$, while the population size approaches 0 for large t if $R_0 \leq 1$. This constitutes the bifurcation result for the deterministic version of the model.

The deterministic version of the model can be viewed as an approximation of the stochastic one as $N \to \infty$. With finite N we shall find that the time to extinction is always finite and that it can be studied in the stochastic model, while extinction in finite time is impossible for the deterministic model.

It is customary to study the deterministic version of the Verhulst model only for the case $R_0 > 1$, but this has the disadvantage that it will hide the interesting bifurcation phenomenon. We study the stochastic version of the model without this restriction.

3.3. **Notation.** For ease of reference we summarize here some of the notation that is used in the rest of the paper. Several quantities are defined as functions of the four basic parameters N, R_0, α_1, and α_2.

The first four quantities, K_1, $\bar{\sigma}_1$, γ_1, and β_1, are important for describing the results when the time to extinction is long, i.e. when $R_0 > 1$. The quantities K_1 and $\bar{\sigma}_1$ then serve as mean and standard deviation, respectively, of the approximation of the quasi-stationary distribution, while γ_1 appears in approximating expressions for the expected time to extinction, and β_1 appears in an expression that approximates the left tail of the quasi-stationary distribution. Note that K_1 equals the carrying capacity.

The quantities K_1 and $\bar{\sigma}_1$ are defined as follows:

$$K_1 = \frac{R_0 - 1}{\alpha_1 R_0 + \alpha_2} N, \tag{3.7}$$

$$\bar{\sigma}_1 = \frac{\sqrt{\alpha R_0}}{\alpha_1 R_0 + \alpha_2} \sqrt{N}, \tag{3.8}$$

When both α_1 and α_2 are strictly positive we define γ_1 as follows:

$$\begin{aligned} \gamma_1 &= \frac{1}{\alpha_2}\left(\frac{\alpha}{\alpha_1}\log\frac{\alpha_1 R_0 + \alpha_2}{\alpha} - \log R_0\right) \\ &= \frac{1}{\alpha_1}\left(\log R_0 - \frac{\alpha}{\alpha_2}\log\frac{\alpha R_0}{\alpha_1 R_0 + \alpha_2}\right), \\ &\qquad\qquad\qquad\qquad 0 < \alpha_1 \le 1, \quad 0 < \alpha_2. \end{aligned} \tag{3.9}$$

In case one of α_1 and α_2 is equal to zero, the definition of γ_1 is instead given by the following expressions:

$$\gamma_1 = \begin{cases} \dfrac{1}{\alpha_2}\left(R_0 - 1 - \log R_0\right), & \alpha_1 = 0, \\ \dfrac{1}{\alpha_1}\left(\log R_0 - \dfrac{R_0 - 1}{R_0}\right), & \alpha_2 = 0. \end{cases} \tag{3.10}$$

Furthermore, β_1 is defined in terms of γ_1 as follows:

$$\beta_1 = \operatorname{sign}(R_0 - 1)\sqrt{2N\gamma_1}. \tag{3.11}$$

It is straightforward to show that the two expressions given for γ_1 when α_1 and α_2 both are positive are equal. Furthermore, γ_1 is a continuous function of α_1 and α_2; it is decreasing in both of these arguments; it is nonnegative so β_1 is well defined. Both γ_1 and β_1 are equal to zero when $R_0 = 1$.

In showing these properties of the function γ_1, it is useful to define six auxiliary functions as follows:

$$\begin{aligned}
f_1(R_0) &= \frac{R_0-1}{R_0},\\
f_2(R_0,\alpha_1,\alpha_2) &= \frac{\alpha_1+\alpha_2}{\alpha_2}\log\frac{(\alpha_1+\alpha_2)R_0}{\alpha_1R_0+\alpha_2},\\
f_3(R_0) &= \log R_0,\\
f_4(R_0,\alpha_1,\alpha_2) &= \frac{\alpha_1+\alpha_2}{\alpha_1}\log\frac{\alpha_1R_0+\alpha_2}{\alpha_1+\alpha_2},\\
f_5(R_0) &= R_0-1,\\
f(R_0,\alpha_1,\alpha_2) &= \frac{(\alpha_1+\alpha_2)(R_0-1)}{\alpha_1R_0+\alpha_2}.
\end{aligned}$$

The domains of definition of these functions are $R_0 > 0$, $0 < \alpha_1 < 1$, and $\alpha_2 > 0$. One can then show that the following inequalities hold:

$$\begin{aligned}
&f_1(R_0) \le f_2(R_0,\alpha_1,\alpha_2) \le f_3(R_0) \le f_4(R_0,\alpha_1,\alpha_2) \le f_5(R_0),\\
&f_2(R_0,\alpha_1,\alpha_2) \le f(R_0,\alpha_1,\alpha_2) \le f_4(R_0,\alpha_1,\alpha_2).
\end{aligned}$$

These inequalities are strict except when $R_0 = 1$. All six functions are increasing in R_0. In addition, $f_2(R_0,\alpha_1,\alpha_2)$ approaches $f_3(R_0)$ and $f_4(R_0,\alpha_1,\alpha_2)$ approaches $f_5(R_0)$ as $\alpha_1 \to 0$, while $f_4(R_0,\alpha_1,\alpha_2)$ approaches $f_3(R_0)$ and $f_2(R_0,\alpha_1,\alpha_2)$ approaches $f_1(R_0)$ as $\alpha_2 \to 0$.

The next three quantities appear at several places in the paper. In particular, they serve a role in describing the approximations of the left tails of the stationary distributions $p^{(0)}$ and $p^{(1)}$ with R_0 distinctly above the threshold value one. These quantities carry the subscript 2. The definitions are as follows:

$$\begin{aligned}
\bar{\mu}_2 &= \log R_0\frac{N}{\alpha},\\
\bar{\sigma}_2 &= \sqrt{\frac{N}{\alpha}},\\
\beta_2 &= \frac{\bar{\mu}_2}{\bar{\sigma}_2} = \log R_0\sqrt{\frac{N}{\alpha}}.
\end{aligned}$$

The study of the transition region requires a rescaling of R_0 in terms of N and α. The rescaling is derived in Subsection 3.11. It leads to an alternate parameter ρ defined by

$$\rho = (R_0-1)\sqrt{\frac{N}{\alpha}}. \tag{3.12}$$

This parameter is used to identify the three parameter regions. The transition region is characterized by finite values of ρ as $N \to \infty$. Clearly, this means that R_0 approaches the value 1 as $N \to \infty$. For practical purposes we note the rule of thumb that sets the boundary between the transition region and the region where R_0 is distinctly larger than one at $\rho = 3$. This choice of value of ρ is related to the fact that a normally distributed random variable takes values smaller than three standard deviations below its mean with small probability.

The next three quantities are used to describe the approximation of the quasi-stationary distribution in the transition region. The definitions are

$$\begin{aligned}
\bar{\mu}_3 &= \rho\sqrt{\frac{N}{\alpha}}, \\
\bar{\sigma}_3 &= \bar{\sigma}_2 = \sqrt{\frac{N}{\alpha}}, \\
\beta_3 &= \frac{1}{\sqrt{R_0}}\frac{K_1}{\bar{\sigma}_1} = \frac{R_0 - 1}{R_0}\sqrt{\frac{N}{\alpha}}.
\end{aligned}$$

The description of the results in the transition region makes use of the three functions H, H_0, and H_1. The first two of these functions are defined in (3.55) and (3.50), respectively, while the last one is defined by

$$H_1(x) = \frac{\Phi(x)}{\varphi(x)}, \tag{3.13}$$

where φ denotes the normal density function $\varphi(x) = \exp(-x^2/2)/\sqrt{2\pi}$, and Φ denotes the normal distribution function $\Phi(x) = \int_{-\infty}^{x} \varphi(x)\, dx$.

Finally, it is useful to define the following three functions of n, one corresponding to each of the three subscripts 1, 2 and 3:

$$\begin{aligned}
y_1(n) &= \frac{n - K_1}{\bar{\sigma}_1}, \\
y_2(n) &= \frac{n - \bar{\mu}_2}{\bar{\sigma}_2}, \\
y_3(n) &= \frac{n - \bar{\mu}_3}{\bar{\sigma}_3}.
\end{aligned}$$

3.4. **Approximations of ρ_n.** By inserting the expressions (3.2) for the transition rates λ_n and μ_n into (2.3) and (2.4) we arrive at explicit expressions for the sequencies ρ_n and π_n in terms of n and the four parameters N, R_0, α_1, and α_2. Our method for deriving approximations of the quasi-stationary distribution and of the time to extinction starts with deriving approximations of these explicit expressions for ρ_n and π_n.

Three approximations of ρ_n, $n = 1, 2, \ldots, N$, are derived in this subsection. The results are as follows:

$$\rho_n \sim \frac{1}{\sqrt{R_0}} \frac{\varphi(y_1(n))}{\varphi(\beta_1)}, \quad y_1(n) = \mathrm{O}(1), \quad 1 \le n \le N, \quad N \to \infty, \tag{3.14}$$

$$\rho_n \sim \frac{1}{R_0} \frac{\varphi(y_2(n))}{\varphi(\beta_2)}, \quad n = \mathrm{O}(\sqrt{N}), \quad 1 \le n, \quad N \to \infty, \tag{3.15}$$

$$\rho_n \sim R_0^{n-1}, \quad n = \mathrm{o}(\sqrt{N}), \quad 1 \le n, \quad N \to \infty. \tag{3.16}$$

Here, $\varphi(x) = \exp(-x^2/2)/\sqrt{2\pi}$ denotes the normal density function.

Note that the first approximation of ρ_n is proportional to a normal density function with the argument $y_1(n)$. The definition $y_1(n) = (n - K_1)/\bar{\sigma}_1$ shows that the corresponding distribution has its mean equal to the carrying capacity K_1, and its standard deviation equal to $\bar{\sigma}_1$. The condition that $y_1(n)$ is $O(1)$ describes the body of this normal distribution, but excludes its tails. The restriction of n to positive integer values has the consequence that the range of n-values for which the first approximation is valid varies strongly with the parameter R_0. Thus, if R_0 has a fixed value larger than 1, then K_1 is of the order of N and actually equal to a fixed proportion of N. Since $\bar{\sigma}_1$ is of the order of $\sqrt{N}$ we conclude that the n-values of the body of the distribution belong to the interval from 1 to N. Thus, the first approximation holds throughout the body of the normal distribution. However, if R_0 is fixed at a value in the interval from 0 to 1, then K_1 is negative, and the body of the distribution has negative n-values. In this case, the first approximation does not hold for any value of n. In the transition region, finally, $K_1 = \rho\sqrt{N/\alpha}$ is of the order of $\sqrt{N}$, and $K_1/\bar{\sigma}_1 = \rho$ is finite as $N \to \infty$. The body of the distribution will then contain both positive and negative values of n. The first approximation is then valid for that portion of the body of the distribution where n is positive.

The second approximation of ρ_n is seen to be proportional to a normal density function with the argument $y_2(n)$. In this case, the corresponding distribution has its mean equal to $\bar{\mu}_2$ and its standard deviation equal to $\bar{\sigma}_2$. The range of n-values for which this approximation is valid lies in the left tail of the normal distribution if $R_0 > 1$, in the right tail if $R_0 < 1$, and in the body for the transition region. The third approximation is a special case of the second one. It holds for a smaller range of n-values. This approximation is of value in deriving an approximation of the quasi-stationary distribution in the transition region.

In order to derive these results we note first that ρ_n can be expressed in the following explicit form:

$$\rho_n = \frac{(N-\alpha_1)(N-2\alpha_1)\cdots(N-(n-1)\alpha_1)}{(N+\alpha_2)(N+2\alpha_2)\cdots(N+(n-1)\alpha_2)} R_0^{n-1}, \quad n = 2, 3, \ldots, N. \tag{3.17}$$

For $\alpha_1 > 0$ we express the numerator of the fraction on the right hand side as $\alpha_1^{n-1}(N/\alpha_1 - (n-1))_{n-1} = \alpha_1^{n-1}\Gamma(N/\alpha_1)/\Gamma(N/\alpha_1 - (n-1))$. Similarly, for $\alpha_2 > 0$ the denominator equals $\alpha_2^{n-1}(N/\alpha_2+1)_{n-1} = \alpha_2^{n-1}\Gamma(N/\alpha_2+n)/\Gamma(N/\alpha_2+1)$. The expression for ρ_n can therefore be rewritten as follows when both α_1 and α_2 are positive:

$$\rho_n = \frac{1}{R_0}\frac{1}{1-\alpha_1 n/N}\frac{\Gamma(N/\alpha_1)\Gamma(N/\alpha_2)}{\Gamma(N/\alpha_1 - n)\Gamma(N/\alpha_2+n)}\left(\frac{\alpha_1 R_0}{\alpha_2}\right)^n, \qquad 0 < \alpha_1 \le 1, \quad \alpha_2 > 0.$$

On the other hand, if either α_1 or α_2 is equal to zero, the expressions for ρ_n are as follows:

$$\rho_n = \begin{cases} \dfrac{1}{R_0}\dfrac{\Gamma(N/\alpha_2)}{\Gamma(N/\alpha_2+n)}\left(\dfrac{R_0 N}{\alpha_2}\right)^n, & \alpha_1 = 0, \\ \dfrac{1}{R_0}\dfrac{1}{1-\alpha_1 n/N}\dfrac{\Gamma(N/\alpha_1)}{\Gamma(N/\alpha_1 - n)}\left(\dfrac{\alpha_1 R_0}{N}\right)^n, & \alpha_2 = 0. \end{cases}$$

We proceed to approximate the gamma functions in these expressions with Stirling's formula: $\Gamma(x) \sim (x/e)^x\sqrt{2\pi/x}$ as $x \to \infty$. We require that $\alpha_2 = \mathrm{O}(1)$ as $N \to \infty$ if $\alpha_2 > 0$. The conditions for applying Stirling's formula are then satisfied as $N - n \to \infty$ if $0 < \alpha_1 \le 1$ and as $N \to \infty$ if $\alpha_2 > 0$. The resulting asymptotic approximation of ρ_n can be expressed as follows:

$$\rho_n \sim g(n)\exp(h(n)), \quad n = 1, 2, \ldots, N, \quad N \to \infty, \quad \text{and} \quad N - n \to \infty \quad \text{if} \quad 0 < \alpha_1 \le 1, \tag{3.18}$$

where

$$g(n) = \frac{1}{R_0}\frac{\sqrt{1+\alpha_2 n/N}}{\sqrt{1-\alpha_1 n/N}}, \tag{3.19}$$

and where the expression for $h(n)$ takes different forms depending on whether α_1 or α_2 equals zero. When both of these parameters are positive we get

$$h(n) = n\log R_0 - \left(\frac{N}{\alpha_2}+n\right)\log\left(1+\frac{\alpha_2 n}{N}\right) - \left(\frac{N}{\alpha_1}-n\right)\log\left(1-\frac{\alpha_1 n}{N}\right), \quad 0 < \alpha_1 \le 1, \quad \alpha_2 > 0. \tag{3.20}$$

When $\alpha_2 = 0$ the expression for $h(n)$ takes the form

$$h(n) = n\log R_0 - n - \left(\frac{N}{\alpha_1}-n\right)\log\left(1-\frac{\alpha_1 n}{N}\right), \qquad 0 < \alpha_1 \le 1, \quad \alpha_2 = 0. \tag{3.21}$$

Finally, $h(n)$ takes the following form when $\alpha_1 = 0$:

$$h(n) = n + n \log R_0 - \left(\frac{N}{\alpha_2} + n\right) \log\left(1 + \frac{\alpha_2 n}{N}\right), \qquad \alpha_1 = 0, \quad \alpha_2 > 0. \tag{3.22}$$

We shall use the approximation of ρ_n given in (3.18) to derive the three asymptotic approximations given in (3.14)-(3.16) by making further restrictions on n. The first approximation is derived for n-values in the vicinity of the n-value where $h(n)$ is maximum, while the other two hold for small n-values.

We determine the n-value for which $h(n)$ is maximum. In carrying out this step we allow n to be real-valued. By differentiation we find that

$$h'(n) = \log \frac{(1 - \alpha_1 n/N)R_0}{1 + \alpha_2 n/N}.$$

This expression holds for all three forms of $h(n)$ above. It is readily seen that derivative of h equals 0 for $n = K_1$. An evaluation of the second derivative shows that this corresponds to a maximum for the function h.

The approximation of ρ_n given in (3.14) is based on Taylor expansions of $g(n)$ and $h(n)$ about $n = K_1$, while the approximations in (3.15) and (3.16) are based on Taylor expansions about $n = 0$. We include one term in the expansions of $g(n)$ and three terms in the expansions of $h(n)$.

The sum of the first three terms of the Taylor expansion of $h(n)$ about K_1 gives the following asymptotic result, using the notation introduced in the previous subsection:

$$h(n) \sim \frac{1}{2}\beta_1^2 - \frac{1}{2}y_1^2(n), \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty. \tag{3.23}$$

The linear term in the expansion equals 0 since $h(n)$ has maximum at $n = K_1$. Note that β_1 and $\bar{\sigma}_1$ are defined from the relations $h(K_1) = \beta_1^2/2$ and $h''(K_1) = -1/\bar{\sigma}_1^2$.

The first (constant) term in the Taylor expansion of $g(n)$ about K_1 gives

$$g(n) \sim \frac{1}{\sqrt{R_0}}, \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty.$$

These approximations of $h(n)$ and $g(n)$ are asymptotic since succeeding terms in each Taylor expansion are of decreasing order in N when $y_1(n) = \mathrm{O}(1)$. By inserting these two approximations for $h(n)$ and $g(n)$ into the asymptotic approximation (3.18) for ρ_n we conclude that (3.14) holds.

The sum of the first three terms in the Taylor expansion of $h(n)$ about 0 gives the following result:

$$h(n) \sim n \log R_0 - \frac{\alpha}{2N} n^2 = \frac{1}{2}\beta_2^2 - \frac{1}{2} y_2^2(n), \qquad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

The constant term $h(0)$ equals 0 in this case. The parameters $\bar{\mu}_2$, $\bar{\sigma}_2$, and β_2 are determined by $\bar{\mu}_2 = -h'(0)/h''(0)$, $\bar{\sigma}_2^2 = -1/h''(0)$, and $\beta_2^2/2 = h(0) - (h'(0))^2/(2h''(0))$. The constant term in the Taylor expansion of $g(n)$ about 0 gives

$$g(n) \sim \frac{1}{R_0}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

Both of these approximations of $h(n)$ and $g(n)$ are asymptotic since succeeding terms in each of the Taylor expansions are of decreasing order in N when $n = \mathrm{O}(\sqrt{N})$. By inserting these two approximations of $h(n)$ and $g(n)$ into the asymptotic approximation (3.18) for ρ_n we find that (3.15) holds. If we impose the further restriction on n that it is asymptotically smaller than $\sqrt{N}$ we are led to the simpler result in (3.16).

3.5. **Approximations of π_n.** In this subsection we derive the following three asymptotic approximations of π_n:

$$\pi_n \sim \frac{1}{(R_0 - 1)\sqrt{R_0}\,\bar{\sigma}_1^2} \frac{\varphi(y_1(n))}{\varphi(\beta_1)}, \qquad R_0 > 1, \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty, \tag{3.24}$$

$$\pi_n \sim \frac{1}{nR_0} \frac{\varphi(y_2(n))}{\varphi(\beta_2)}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty, \tag{3.25}$$

$$\pi_n \sim \frac{1}{n} R_0^{n-1}, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty. \tag{3.26}$$

In addition, we show that π_n is asymptotically equal to an integral of ρ_n with respect to R_0. We emphasize the functional dependencies of ρ_n and π_n on R_0 by writing $\rho_n(R_0)$ and $\pi_n(R_0)$ instead of ρ_n and π_n. The relation to be established can then be written

$$\pi_n(R_0) \sim \frac{1}{R_0} \int_0^{R_0} \rho_n(x)\,dx, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty. \tag{3.27}$$

By using the definition (2.4) of π_n, the asymptotic expression (3.18) for ρ_n, and the expression (3.19) for $g(n)$, we find that π_n can be approximated as follows:

$$\pi_n \sim g_0(n) \exp(h(n)), \quad n = 1, 2, \ldots, N, \quad N \to \infty, \quad N - n \to \infty, \tag{3.28}$$

where

$$g_0(n) = \frac{1}{R_0} \frac{1+\alpha_2/N}{n\sqrt{(1-\alpha_1 n/N)(1+\alpha_2 n/N)}},$$

while $h(n)$ is given by (3.20)-(3.22).

The constant term in the Taylor expansion of $g_0(n)$ about K_1 gives the following approximation:

$$g_0(n) \sim \frac{1}{(R_0-1)\sqrt{R_0}\,\bar{\sigma}_1^2}, \quad R_0 > 1, \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty.$$

This approximation is asymptotic since succeeding terms in the Taylor expansion are of decreasing order in N for $y_1(n) = \mathrm{O}(1)$. By inserting this approximation of $g_0(n)$ and the approximation (3.23) of $h(n)$ into the asymptotic approximation (3.28) for π_n we conclude that (3.24) holds.

For small values of n we find from (2.4) that

$$\pi_n \sim \frac{1}{n}\rho_n, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty. \tag{3.29}$$

Combining this result with the approximations of ρ_n in (3.15) and (3.16) establishes (3.25) and (3.26).

The remaining relation to be established is based on the expression (3.17) for ρ_n. This expression has the important feature that the dependence on R_0 is simple. We write $\rho_n = \rho_n(R_0) = CR_0^{n-1}$, where C depends on N, n, α_1, and α_2, but not on R_0. By using (3.29) we find that $R_0\pi_n(R_0) \sim CR_0^n/n$ for $n = \mathrm{O}(\sqrt{N})$. It follows that $\pi_n(R_0)$ satisfies asymptotically the differential equation

$$\frac{d}{dR_0}(R_0\pi_n(R_0)) \sim CR_0^{n-1} = \rho_n(R_0), \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

The relation (3.27) follows since $R_0\pi_n(R_0)$ takes the value 0 if $R_0 = 0$.

3.6. **Approximation of the stationary distribution $p^{(1)}$ when R_0 is distinctly larger than the deterministic threshold value one.** In this and the following three subsections we study the Verhulst model under the condition that $R_0 > 1$ is fixed as $N \to \infty$. The scaling introduced in Subsection 3.11 will allow us to judge for any fixed value of R_0 larger than one how large N has to be in order for this condition to hold.

We derive three approximations of the distribution $p^{(1)}$ in this subsection. The first one is valid in the body of the distribution, and the other two in the left tail. The third one is valid for a smaller range of n-values than the second one.

The three approximations can be expressed as follows:

(3.30)

$$p_n^{(1)} \sim \frac{1}{\bar{\sigma}_1}\varphi(y_1(n)), \quad R_0 > 1, \quad R_0 \text{ fixed}, \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty,$$

$$p_n^{(1)} \sim \frac{\alpha_1 R_0 + \alpha_2}{R_0\sqrt{\alpha N}} \frac{\varphi(\beta_1)}{\varphi(\beta_2)} \varphi(y_2(n)), \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty, \tag{3.31}$$

and

$$p_n^{(1)} \sim \frac{\alpha_1 R_0 + \alpha_2}{\sqrt{\alpha N}} \varphi(\beta_1)\, R_0^{n-1}, \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty. \tag{3.32}$$

The first of these results shows that the distribution $p^{(1)}$ is approximately normal in its body. The second result shows that the left tail of the same distribution is approximated by the left tail of another normal distribution, multiplied by a known constant.

The derivations of these results are based on the expression (2.6) for the probability $p_n^{(1)}$. Since ρ_n is approximated in Subsection 3.4, it remains to find an approximation of $p_1^{(1)} = 1/\sum_{n=1}^{N} \rho_n$. The approximation (3.14) shows that ρ_n is proportional to the probability $\varphi(y_1(n))/\bar{\sigma}_1$ for a normally distributed random variable with mean K_1 and standard deviation $\bar{\sigma}_1$ to take the value n. This approximation is valid in the body of the distribution, where the argument of the function φ is $\mathrm{O}(1)$. Now the sum of all these probabilities over n from 1 to N is asymptotically equal to 1. The reason is that this range of n-values covers the body of the distribution. This follows since for $R_0 > 1$ we have $y_1(1) < 0$ and $y_1(N) > 0$ and furthermore $K_1 = \mathrm{O}(N)$ and $\bar{\sigma}_1 = \mathrm{O}(\sqrt{N})$, and therefore $y_1(1) = \mathrm{O}(\sqrt{N})$ and $y_1(N) = \mathrm{O}(\sqrt{N})$. We can therefore approximate the sum $\sum_{n=1}^{N} \rho_n$ as follows:

$$\sum_{n=1}^{N} \rho_n \sim \frac{1}{\sqrt{R_0}} \frac{1}{\varphi(\beta_1)} \sum_{n=1}^{N} \varphi(y_1(n)) \sim \frac{\bar{\sigma}_1}{\sqrt{R_0}\varphi(\beta_1)}.$$

Hence we find that

$$p_1^{(1)} = \frac{1}{\sum_{n=1}^{n=N} \rho_n} \sim \frac{\sqrt{R_0}\varphi(\beta_1)}{\bar{\sigma}_1} = \frac{\alpha_1 R_0 + \alpha_2}{\sqrt{\alpha N}} \varphi(\beta_1), \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

This result and the approximation (3.14) of ρ_n inserted into the expression (2.6) for $p_n^{(1)}$ establishes (3.30). If instead we use the approximation (3.15) or (3.16) of ρ_n we are led to (3.31) and (3.32), respectively.

3.7. **Approximation of the stationary distribution $p^{(0)}$ when R_0 is distinctly larger than the deterministic threshold value one.** We derive three approximations of the stationary distribution $p^{(0)}$, one in the body of the distribution, and two in the left tail. These approximations can be written as follows:

$$(3.33)\quad p_n^{(0)} \sim \frac{1}{\bar{\sigma}_1}\varphi(y_1(n)),\qquad R_0>1,\quad R_0 \text{ fixed},\quad y_1(n)=\mathrm{O}(1),\quad N\to\infty,$$

$$(3.34)\quad p_n^{(0)} \sim \frac{(R_0-1)\sqrt{\alpha N}}{\alpha_1 R_0+\alpha_2}\,\frac{\varphi(\beta_1)}{\varphi(\beta_2)}\,\frac{\varphi(y_2(n))}{n},\qquad R_0>1,\quad R_0 \text{ fixed},\quad n=\mathrm{O}(\sqrt{N}),\quad N\to\infty,$$

and

$$(3.35)\quad p_n^{(0)} \sim \frac{(R_0-1)\sqrt{\alpha N}}{\alpha_1 R_0+\alpha_2}\,\varphi(\beta_1)\,\frac{R_0^n}{n},\qquad R_0>1,\quad R_0 \text{ fixed},\quad n=\mathrm{o}(\sqrt{N}),\quad N\to\infty.$$

A comparison of the first of these expressions with (3.30) shows that the bodies of the two distributions $p^{(1)}$ and $p^{(0)}$ are approximated by the same normal distribution. The last of the expressions shows an unusual feature of the left tail of the distribution $p^{(0)}$. The probabilities $p_n^{(0)}$ will not all increase monotonically with n in the left tail of the distribution unless $R_0>2$. With $R_0<2$ we find from the asymptotic approximation above that $p_n^{(0)} < p_{n-1}^{(0)}$ holds (asymptotically) if $n < R_0/(R_0-1)$.

The derivation is based on the expression (2.5) for the probability $p_n^{(0)}$. We use the approximation (3.24) of π_n. As in the previous subsection we use the result $\sum_{n=1}^N \varphi(y_1(n))/\bar{\sigma}_1 \sim 1$ to evaluate the sum $\sum_{n=1}^N \pi_n$. It follows that $p_1^{(0)} = 1/\sum_{n=1}^N \pi_n$ is approximated as follows:

$$(3.36)\quad p_1^{(0)} \sim \frac{R_0(R_0-1)\sqrt{\alpha N}}{\alpha_1 R_0+\alpha_2}\,\varphi(\beta_1),\qquad R_0>1,\quad R_0 \text{ fixed},\quad N\to\infty.$$

Insertion of this approximation of $p_1^{(0)}$ and the approximation (3.24) of π_n into the expression (2.5) for $p_n^{(0)}$ establishes (3.33). If instead we use the approximation (3.25) or (3.26) of π_n we are led to (3.34) and (3.35), respectively.

3.8. **Approximation of the quasi-stationary distribution q for R_0 distinctly larger than the deterministic threshold value one.** It is a larger challenge to find an approximation of the quasi-stationary distribution q than to find approximations of the stationary distributions $p^{(1)}$ and $p^{(0)}$. The reason is of course that we have explicit expressions for the latter, but not for the former. The approximations that we derive for the quasi-stationary distribution q are weaker than those for the stationary distributions $p^{(1)}$ and $p^{(0)}$ in two ways. One weakness is that they are not claimed to be asymptotic. A second weakness is that the approximation of the left tail of q is valid for a shorter range of n-values than the corresponding approximations for $p^{(1)}$ and $p^{(0)}$.

The following results are derived:

(3.37)
$$q_n \approx \frac{1}{\bar{\sigma}_1}\varphi(y_1(n)), \quad R_0 > 1, \quad R_0 \text{ fixed}, \quad y_1(n) = \mathrm{O}(1), \quad N \to \infty,$$
and

(3.38)
$$q_n \approx \frac{(R_0-1)\sqrt{\alpha N}}{\alpha_1 R_0 + \alpha_2}\,\varphi(\beta_1)\,\frac{R_0^n - 1}{n}, \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty.$$

Our derivation is based on the relation (2.13). A basic problem is to determine the sum over k in (2.13). We note that the numerator in each term of this sum is a decreasing function of k, and that the denominator is an increasing function of k up to $k = [K_1]$, since the quantity ρ_k is proportional to the probability $p_k^{(1)}$, and these probabilities increase monotonically with k over this range of k-values. Thus we can conclude that the terms in the sum over k decrease monotonically in k at least up to $k = [K_1]$. Furthermore, the first term in the sum is equal to 1, while the term that corresponds to $k = [K_1]$ is very much smaller than 1. It may then be expected that the sum is dominated by the sum of the first several terms.

We consider k-values up to a value that grows toward infinity as $N \to \infty$, but for which the growth is slower than $\sqrt{N}$. For such k-values we make the assumption that $q_k = \mathrm{o}(1)$ as $N \to \infty$ for $k = \mathrm{o}(\sqrt{N})$. This implies that the numerator of each term is asymptotically equal to 1. We are therefore led to consider the problem of finding an approximation of the sum $\sum_{k=1}^n 1/\rho_k$. We note from (3.16) that $\rho_k \sim R_0^{k-1}$ if $k = \mathrm{o}(\sqrt{N})$ as $N \to \infty$. By using this approximation of each term, the sum itself is found to be approximated by

$$\sum_{k=1}^{n} \frac{1 - \sum_{j=1}^{k-1} q_j^{(0)}}{\rho_k} \sim \sum_{k=1}^{n} \frac{1}{R_0^{k-1}} = \frac{R_0}{R_0 - 1}\left(1 - \frac{1}{R_0^n}\right), \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty.$$

We note that the sum increases toward the constant value $R_0/(R_0-1)$ as n becomes large. We assume that the sum is approximated by this constant value for all larger n-values. From this assumption we get the following simple approximation of the quasi-stationary distribution:

(3.39)
$$q_n \approx \frac{R_0}{R_0 - 1}\left(1 - \frac{1}{R_0^n}\right)\pi_n q_1, \quad R_0 > 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Note that the factor $1 - 1/R_0^n$ is asymptotic to 1 as $n \to \infty$.

It remains to determine an approximation of q_1. We use the requirement that the sum of the probabilities q_n equals 1. This sum is approximated as follows:

$$\sum_{n=1}^{N} q_n \approx \frac{R_0}{R_0-1}\sum_{n=1}^{N}\left(1-\frac{1}{R_0^n}\right)\pi_n q_1 \sim \frac{R_0}{R_0-1}\sum_{n=1}^{N}\pi_n q_1$$
$$= \frac{R_0}{R_0-1}\frac{q_1}{p_1^{(0)}}, \quad R_0>1, \quad R_0 \text{ fixed}, \quad N\to\infty.$$

Here we have used the fact that the terms π_n that lie in the tail of the distribution $p^{(0)}$ are asymptotically small. By putting this approximation of the sum equal to 1 and applying the approximation (3.36) of $p_1^{(0)}$ we are led to the following approximation of the probability q_1:

$$q_1 \approx \frac{R_0-1}{R_0}p_1^{(0)} \sim \frac{(R_0-1)^2\sqrt{\alpha N}}{\alpha_1 R_0+\alpha_2}\,\varphi(\beta_1),$$
$$R_0>1, \quad R_0 \text{ fixed}, \quad N\to\infty. \tag{3.40}$$

The approximation (3.37) follows by inserting this approximation of q_1 and the approximation (3.24) of π_n into (3.39), and using the fact that $n = \mathrm{O}(\sqrt{N})$ when $y_1(n) = \mathrm{O}(1)$ and $R_0 > 1$. The approximation (3.38) follows if instead we insert the approximation (3.26) of π_n.

The tail probabilities are exponentially small as $N \to \infty$ because of the factor $\varphi(\beta_1)$. Hence the assumption made earlier that they are $\mathrm{o}(1)$ as $N \to \infty$ is satisfied.

In summary we note that the bodies of all three distributions $p^{(1)}$, $p^{(0)}$ and q are approximately normal with the mean equal to the carrying capacity K_1 and with standard deviation $\bar{\sigma}_1$ in the parameter region where $R_0 > 1$ is fixed as $N \to \infty$. We note also that the important left tails of these distributions are all different.

In this parameter region we find that K_1 is of the order $\mathrm{O}(N)$ and that $\bar{\sigma}_1$ is of the order $\mathrm{O}(\sqrt{N})$. The coefficient of variation of the quasi-stationary distribution is therefore of the order $\mathrm{O}(1/\sqrt{N})$. This supports the arguments by May [20] as a justification for using deterministic modelling for large populations in this parameter region.

A plot of the three distributions is shown in Figure 1. The stationary distributions $p^{(0)}$ and $p^{(1)}$ are computed from the exact expressions in (2.5) and (2.6) with the transition rates λ_n and μ_n given by (3.2). The quasi-stationary distribution q is computed by using the iteration procedure (2.17). We note that the quasi-stationary distribution is closer to $p^{(0)}$ than to $p^{(1)}$. The same observation was made by Kryscio and Lefèvre [19] for the SIS model with $\alpha_1 = 1$ and $\alpha_2 = 0$. The feature that the probabilities $p_n^{(0)}$ decrease as a function of n for small n-values when $R_0 < 2$ is evident from the figure. The left tails of the three distributions are shown in Figure 2, together with their approximations.

For $p^{(0)}$ and $p^{(1)}$ the figure shows the approximations that are valid for $n = \mathrm{O}(\sqrt{N})$, while the approximation for q is only valid for $n = \mathrm{o}(\sqrt{N})$.

It is straightforward to show that the mean of the quasi-stationary distribution K_1 is a decreasing function of α_1 and α_2, and that the standard deviation $\bar{\sigma}_1$ is a decreasing function of α_1, while it decreases as a function of α_2 only if $\alpha_2 > (R_0 - 2)/\alpha_1$. A possibly more interesting situation concerns the influence of the parameters α_1 and α_2 on the standard deviation $\bar{\sigma}_1$ when the carrying capacity K_1 is constant. To study this, we allow R_0 to be a function of α_1 and α_2 with the property that the ratio K_1/N is constant and equal to A. Thus, we get $R_0(\alpha_1, \alpha_2) = (1 + A\alpha_2)/(1 - A\alpha_1)$. The standard deviation $\bar{\sigma}_1$ is then determined as a function of α_1 and α_2 from the expression

$$\bar{\sigma}_1(\alpha_1, \alpha_2) = \frac{\sqrt{(1 - A\alpha_1)(1 + A\alpha_2)}}{\sqrt{\alpha_1 + \alpha_2}} \sqrt{N}. \tag{3.41}$$

It is straightforward to show that the standard deviation $\bar{\sigma}_1(\alpha_1, \alpha_2)$ is a decreasing function of α_1 and α_2. Norden [25] has studied the same question in the special case with $\alpha_1 = 1$. We conclude that a stronger density dependence in the situation where the carrying capacity K_1 is constant leads to a smaller standard deviation of the quasi-stationary distribution.

3.9. **Approximation of the time to extinction when R_0 is distinctly above the deterministic threshold value one.** We noted in Subsection 2.4 that the time to extinction τ_Q from quasi-stationarity for a birth-death process with finite state space and with absorbing state at the origin has an exponential distribution with expectation equal to $\mathrm{E}\tau_Q = 1/(\mu_1 q_1)$. An approximation for this expectation is found by inserting the approximation (3.40) for q_1 into this expression for $\mathrm{E}\tau_Q$. This approximation takes the following form:

$$\mathrm{E}\tau_Q \approx \frac{\sqrt{2\pi}}{\mu} \frac{\alpha_1 R_0 + \alpha_2}{(R_0 - 1)^2} \frac{\exp(\gamma_1 N)}{\sqrt{\alpha N}} \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad N \to \infty. \tag{3.42}$$

Note that this approximation of the expected time to extinction from quasi-stationarity grows exponentially with N.

The expected time to extinction from the state 1 can be expressed as follows, using the expression (2.24) for $\mathrm{E}(\tau_1)$ and the approximation (3.36) of $p_1^{(0)}$:

$$\mathrm{E}\tau_1 = \frac{1}{\mu_1 p_1^{(0)}} \sim \frac{\sqrt{2\pi}}{\mu} \frac{\alpha_1 R_0 + \alpha_2}{R_0(R_0 - 1)} \frac{\exp(\gamma_1 N)}{\sqrt{\alpha N}} \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Finally, we approximate the expected time to extinction from the state n. By using arguments similar to those of the previous subsection we can approximate the sum appearing in the expression (2.25) for $\mathrm{E}\tau_n$. The result is

$$\mathrm{E}\tau_n \approx \frac{\sqrt{2\pi}}{\mu} \frac{\alpha_1 R_0 + \alpha_2}{(R_0-1)^2} \left(1 - \frac{1}{R_0^n}\right) \frac{\exp(\gamma_1 N)}{\sqrt{\alpha N}} \qquad R_0 > 1, \quad R_0 \text{ fixed}, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty.$$

Note that this approximation of the expected time to extinction from the state n increases monotonically with n from the approximation of $\mathrm{E}\tau_1$ toward the approximation of $\mathrm{E}\tau_Q$. Note also that the approximation of the ratio $\mathrm{E}\tau_Q/\mathrm{E}\tau_1 \approx R_0/(R_0-1)$ for $R_0 > 1$ is bounded as $N \to \infty$.

It should be noted that the time to extinction from state n, τ_n, is a random variable whose location is poorly measured by its expectation $\mathrm{E}\tau_n$ for small values of n when $R_0 > 1$. The reason for this is that its distribution is bimodal. In fact, τ_n can be seen as a mixture of two random variables with widely different expectations. After starting in the state n, the process will either reach the absorbing state 0 very quickly, with probability $1/R_0^n$, or it will with the complementary probability reach the set of states where the quasi-stationary distribution describes its behaviour, and where the time to extinction is equal to τ_Q.

The approximations of the expected times to extinction $\mathrm{E}\tau_Q$ and $\mathrm{E}\tau_n$ are increasing functions of α_1 and α_2 when the ratio K_1/N is constant and equal to A. To prove this we insert $R_0(\alpha_1,\alpha_2) = (1 + A\alpha_2)/(1 - A\alpha_1)$ into the expression (3.9) for γ_1. We find that

$$\gamma_1 = -\frac{1}{\alpha_1}\log(1 - A\alpha_1) - \frac{1}{\alpha_2}\log(1 + A\alpha_2), \quad 0 < \alpha_1 \le 1, \quad 0 < \alpha_2.$$

It is straightforward to show that the partial derivatives of this expression with respect to α_1 and α_2 are positive. This proves that a stronger density dependence implies that the expected times to extinction $\mathrm{E}\tau_Q$ and $\mathrm{E}\tau_n$ become larger, since these expectations grow exponentially with N.

The approximation (3.42) is not new; it was essentially given by Barbour [3]. Indeed, Barbour's result shows that if T_N denotes the time to extinction, then

$$\lim_{N\to\infty} P[k_N T_N \ge x] = \exp(-x),$$

where

$$k_N = \frac{(\bar\alpha_1 - \bar\alpha_2)^2}{\bar\gamma_1 + \bar\gamma_2} \sqrt{\left(\frac{\bar\gamma_1}{\bar\alpha_1} + \frac{\bar\gamma_2}{\bar\alpha_2}\right)\frac{N}{2\pi}} \cdot \left(\frac{\bar\alpha_1\bar\gamma_2 + \bar\alpha_2\bar\gamma_1}{\bar\alpha_1(\bar\gamma_1 + \bar\gamma_2)}\right)^{N\bar\alpha_1/\bar\gamma_1} \left(\frac{\bar\alpha_1\bar\gamma_2 + \bar\alpha_2\bar\gamma_1}{\bar\alpha_2(\bar\gamma_1 + \bar\gamma_2)}\right)^{N\bar\alpha_2/\bar\gamma_2}.$$

Here, the parameters $\bar\alpha_1$, $\bar\gamma_1$, $\bar\alpha_2$, and $\bar\gamma_2$ are related to our transition rates λ_n and μ_n as follows:

$$\lambda_n = \bar\alpha_1 n - \bar\gamma_1 \frac{n^2}{N}, \qquad \mu_n = \bar\alpha_2 n + \bar\gamma_2 \frac{n^2}{N}.$$

Barbour's parameters can therefore be expressed in ours by the relations

$$\bar\alpha_1 = \lambda, \quad \bar\gamma_1 = \lambda\alpha_1, \quad \bar\alpha_2 = \mu, \quad \bar\gamma_2 = \mu\alpha_2.$$

Barbour's result for finite N is that the distribution of the time to extinction T_N is approximately exponential with the expected value $1/k_N$. This can be compared with our result that if the initial distribution equals the quasi-stationary distribution, then the distribution of $T_N = \tau_Q$ is exactly exponential with expectation approximated by (3.42). It is straightforward to use the above relations between Barbour's parameters and ours to show that Barbour's expression for $1/k_N$ is equal to our approximation (3.42) for $\mathrm{E}\tau_Q$. Our parametrization has the advantage of giving a better heuristic understanding for the N-dependence of $\mathrm{E}\tau_Q$.

3.10. **Approximations when R_0 is distinctly below the deterministic threshold value one.** The time to extinction decreases drastically for large N if R_0 is lowered from a fixed value larger than one to a fixed value smaller than one. We give approximations of the time to extinction and of the quasi-stationary distribution in the latter case.

It follows from (3.16) that the stationary distribution $p^{(1)}$ is approximated as follows:

$$p_n^{(1)} \sim (1-R_0)R_0^{n-1}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad 1 \le n, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty.$$

Thus, $p^{(1)}$ has a truncated geometric distribution. The expected number of individuals in stationarity is

$$\mathrm{E}X^{(1)} \sim \frac{1}{1-R_0}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Similarly it follows from (3.26) that the stationary distribution $p^{(0)}$ is approximated by the log series distribution:

$$p_n^{(0)} \sim \frac{R_0}{\log(1/(1-R_0))}\frac{1}{n}R_0^{n-1}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad 1 \le n, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty,$$

and that the expected number of individuals in stationarity is

$$\mathrm{E}X^{(0)} \sim \frac{R_0}{(1-R_0)\log(1/(1-R_0))}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

The quasi-stationary distribution in this case has the same approximation as the stationary distribution $p^{(1)}$:

$$q_n \approx (1-R_0)R_0^{n-1}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \qquad 1 \le n, \quad n = \mathrm{o}(\sqrt{N}), \quad N \to \infty.$$

The expected number of individuals in quasi-stationarity is therefore approximated by

$$\mathrm{E}X^{(Q)} \approx \frac{1}{1-R_0}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

To derive this result we assume that $q_n \sim (1-R_0)R_0^{n-1}$ for $n = \mathrm{o}(\sqrt{N})$ as $N \to \infty$. By applying (3.16) we find that each term in the sum over k in (2.13) is asymptotic to 1. We conclude that $q_n \sim n\pi_n q_1$ for $n = \mathrm{o}(\sqrt{N})$. The result follows by application of (3.26).

The expected time to extinction from quasi-stationarity is found to be asymptotically approximated as follows:

$$\mathrm{E}\tau_Q = \frac{1}{\mu_1 q_1} \sim \frac{1}{\mu}\frac{1}{1-R_0}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Similarly, we find that the expected time to extinction from the state 1 is asymptotically approximated by

$$\mathrm{E}\tau_1 = \frac{1}{\mu_1 p_1^{(0)}} \sim \frac{1}{\mu}\frac{\log(1/(1-R_0))}{R_0}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Note that these approximations of expectations of time to extinction are independent of N, while the results in Subsection 3.9 show that the corresponding approximations grow exponentially with N. Note also that these results are all independent of α_1 and α_2. This means that the approximations of both the quasi-stationary distribution and of the expected time to extinction are independent of the density dependence.

The three distributions $p^{(1)}$, $p^{(0)}$, and q are illustrated for R_0 distinctly below the deterministic threshold value one in Figure 3. Here, $p^{(1)}$ is seen to give a closer approximation of the quasi-stationary distribution than $p^{(0)}$, in line with our results above.

3.11. **Scaling of R_0 in the transition region.** We recall that the quasi-stationary distribution q is for $R_0 > 1$ and N sufficiently large approximated in its body by a normal distribution with mean K_1 and standard deviation $\bar{\sigma}_1$. The random variable having q as its distribution takes only positive values. The normal approximation can therefore be expected to be acceptable only if the ratio of K_1 to $\bar{\sigma}_1$ is large. We find from (3.7) and (3.8) that this ratio equals

$$\frac{K_1}{\bar{\sigma}_1} = \frac{R_0 - 1}{\sqrt{\alpha R_0}}\sqrt{N}.$$

The normal distribution is a good approximation if the ratio approaches infinity as $N \to \infty$, as it does in the parameter region defined by $R_0 > 1$ being constant as $N \to \infty$, but a poor approximation if the ratio is small. Smallness in an asymptotic analysis context is interpreted as not approaching infinity as $N \to \infty$, or, equivalently, as the condition $K_1/\bar{\sigma}_1 = \mathrm{O}(1)$. The expression for the ratio $K_1/\bar{\sigma}_1$ above shows that this ratio remains bounded if the quantity ρ defined by (3.12) remains bounded. The introduction of ρ represents a rescaling of R_0 that makes R_0 a function of N. If ρ remains bounded as $N \to \infty$ then R_0 approaches one. The parameter region described by the condition $\rho = \mathrm{O}(1)$ defines the transition region that will be studied in the following subsections. A natural condition that guarantees boundedness of ρ is that ρ is fixed. We note the rule of thumb that the boundary between the transition region and the region where R_0 is distinctly larger than one is for practical purposes approximately given by $\rho = 3$.

It is also useful to note that the quantities introduced in Subsection 3.3 obey the following simple asymptotic relations in the transition region:

$$(3.43)\quad K_1 \sim \bar{\mu}_3, \quad \bar{\sigma}_1 \sim \bar{\sigma}_3, \quad \beta_1 \sim \rho, \quad \rho \text{ fixed}, \quad N \to \infty,$$

$$(3.44)\quad \bar{\mu}_2 \sim \bar{\mu}_3, \quad \bar{\sigma}_2 = \bar{\sigma}_3, \quad \beta_3 \sim \rho, \quad \beta_2 \sim \rho, \quad \rho \text{ fixed}, \quad N \to \infty.$$

Furthermore, the functions y_1 and y_2 are asymptotically equivalent to the function y_3 in the sense that

$$(3.45)\qquad y_1(n) \sim y_3(n), \quad y_2(n) \sim y_3(n), \quad \rho \text{ fixed}, \quad N \to \infty.$$

3.12. **Approximations of ρ_n and π_n in the transition region.** The following simple asymptotic approximations of ρ_n and π_n hold in the transition region:

$$(3.46)\qquad \rho_n \sim \frac{\varphi(y_3(n))}{\varphi(\rho)}, \quad \rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty,$$

$$(3.47)\qquad \pi_n \sim \frac{\varphi(y_3(n))}{n\varphi(\rho)}, \quad \rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

To derive these expressions we note first that in the transition region the condition $y_3(n) = \mathrm{O}(1)$ is equivalent to $n = \mathrm{O}(\sqrt{N})$. By applying the asymptotic expressions for β_1 in (3.43) and for y_1 in (3.45) to the asymptotic expression (3.14) for ρ_n, (3.46) follows. An alternate way of deriving the same result is to apply the asymptotic expressions for β_2 in (3.44) and for y_2 in (3.45) to the asymptotic expression (3.15) for ρ_n. The same asymptotic approximations of β_2 and y_2 applied to the asymptotic expression for π_n in (3.25) establishes (3.47).

3.13. **Approximation of the stationary distribution $p^{(1)}$ in the transition region.** We show in this subsection that the stationary distribution $p^{(1)}$ is approximated by a truncated normal distribution in the transition region. The approximation can be expressed as follows:

$$p_n^{(1)} \sim \frac{\varphi(y_3(n))}{\bar{\sigma}_3 \Phi(\rho)}, \quad \rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty, \tag{3.48}$$

where Φ denotes the normal distribution function. The probability $p_1^{(1)}$ is approximated by

$$p_1^{(1)} \sim \frac{\varphi(\rho)}{\bar{\sigma}_3 \Phi(\rho)} = \frac{1}{H_1(\rho)} \sqrt{\frac{\alpha}{N}}, \quad \rho \text{ fixed}, \quad N \to \infty, \tag{3.49}$$

where the function $H_1 = \Phi/\varphi$ was defined in (3.13).

In order to derive the results in (3.48) and (3.49) we evaluate the sum $\sum_{n=1}^{N} \rho_n$, using the approximation (3.46) of ρ_n. We get

$$\sum_{n=1}^{N} \rho_n \sim \frac{1}{\varphi(\rho)} \sum_{n=1}^{N} \varphi(y_3(n)) \sim \frac{\bar{\sigma}_3(1 - \Phi(y_3(\frac{1}{2}))}{\varphi(\rho)} \sim \frac{\bar{\sigma}_3 \Phi(\rho)}{\varphi(\rho)},$$
$$\rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

The argument $y_3(1/2)$ of the function Φ results from the well-known continuity correction in the body of the normal distribution. In the last step we use the fact that $y_3(1/2) \sim -\rho$. By using (2.6) we conclude that the approximation of $p_1^{(1)}$ in (3.49) holds. The approximation of $p_n^{(1)}$ in (3.48) follows by inserting this approximation of $p_1^{(1)}$ and the approximation (3.46) of ρ_n into the expression (2.6) for $p_n^{(1)}$.

3.14. **Approximation of the stationary distribution $p^{(0)}$ in the transition region.** The results in this subsection are based on a function H_0, defined as follows:

$$H_0(\rho) = \begin{cases} H_a(\rho), & \rho \le -3, \\ H_a(-3) + \displaystyle\int_{-3}^{\rho} \frac{\Phi(y)}{\varphi(y)}\, dy, & \rho > -3, \end{cases} \tag{3.50}$$

where the auxiliary function H_a is given by

$$H_a(\rho) = -\log|\rho| - \frac{1}{2\rho^2} + \frac{3}{4\rho^4} - \frac{5}{2\rho^6}, \quad \rho \le -3.$$

The dependence of H_0 on ρ is illustrated in Figures 4 and 5. Note that the vertical scale is linear in Figure 4 and logarithmic in Figure 5.

We show in this subsection that the stationary distribution $p^{(0)}$ can be approximated as follows in the transition region:

$$p_n^{(0)} \approx \frac{1}{\frac{1}{2}\log(N/\alpha) + H_0(\rho)} \frac{1}{\varphi(\rho)} \frac{\varphi(y_3(n))}{n}, \tag{3.51}$$
$$\rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty.$$

and the probability $p_1^{(0)}$ by

$$p_1^{(0)} \approx \frac{1}{\frac{1}{2}\log(N/\alpha) + H_0(\rho)}, \quad \rho \text{ fixed}, \quad N \to \infty. \tag{3.52}$$

The approximations are not claimed to be asymptotic. Note that the expression $\frac{1}{2}\log(N/\alpha) + H_0(\rho)$ is asymptotically approximated by its first term for N sufficiently large. But the slow growth of the first term with N makes this one-term approximation useless for reasonable values of N, and necessitates the inclusion of both terms.

Two steps are needed to derive the approximation of the distribution above. The first one is taken by inserting the approximation (3.47) for π_n into the expression (2.5) for $p_n^{(0)}$, to get

$$p_n^{(0)} \sim \frac{1}{n}\frac{\varphi(y_3(n))}{\varphi(\rho)} p_1^{(0)}, \quad \rho \text{ fixed}, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty. \tag{3.53}$$

The second step is taken in Appendix B. It consists in deriving the following approximation of $\sum_{n=1}^{N} \pi_n$:

$$\sum_{n=1}^{N} \pi_n \approx \frac{1}{2}\log\frac{N}{\alpha} + H_0(\rho), \quad \rho \text{ fixed}, \quad N \to \infty. \tag{3.54}$$

This establishes the approximation (3.52), since (2.5) shows that $p_1^{(0)}$ is equal to the inverse of $\sum_{n=1}^{N} \pi_n$. The approximation (3.51) of $p_n^{(0)}$ follows by inserting this approximation of $p_1^{(0)}$ into (3.53).

3.15. **Approximation of the quasi-stationary distribution q in the transition region.** In this subsection the function H defined implicitly by the relation

$$H(\rho, \alpha) = \frac{1}{\rho\sqrt{\alpha} + 1/H(\rho, \alpha)} \int_{-1/H(\rho,\alpha)}^{\rho} \frac{\Phi(y)}{\varphi(y)}\, dy \tag{3.55}$$

plays an important role. Note that $H(\rho, 1)$ is the average of the function $H_1(\rho) = \Phi(\rho)/\varphi(\rho)$ over the interval $(-1/H(\rho, 1), \rho)$, whose left endpoint depends on $H(\rho, 1)$. We show in Appendix D that $H(\rho, \alpha) > 0$ is well defined by the requirement that it satisfy the above relation if one of the following two conditions holds: 1) $\rho \geq 0$ and $\alpha \geq 0$; 2) $\rho < 0$ and $0 \leq \alpha \leq 1$ and $H(\rho, \alpha) < -1/\rho$. The dependence of $H(\rho, \alpha)$ on ρ is illustrated in Figures 4 and 5.

It is convenient in what follows to introduce $\tilde{\rho}$ to denote the following function of ρ and α:

$$\tilde{\rho} = \frac{1}{\sqrt{\alpha} H(\rho, \alpha)}. \tag{3.56}$$

The domain of definition of the function H identifies a restricted parameter domain on which the quasi-stationary distribution q can be approximated as follows:

$$(3.57)\quad q_n \approx \frac{1}{\varphi(\rho)} \frac{\tilde{\rho}}{\rho+\tilde{\rho}} \frac{1}{n} \left(1 - \frac{1}{R_1^n}\right) \varphi(y_3(n)),$$
$$\rho \text{ fixed}, \quad \rho \geq 0 \text{ if } \alpha > 1, \quad n = \mathrm{O}(\sqrt{N}), \quad N \to \infty,$$

where we use R_1 to denote a function of N, ρ, and α defined by

$$(3.58)\qquad R_1 = 1 + \frac{\sqrt{\alpha}(\rho+\tilde{\rho})}{\sqrt{N}}.$$

The important probability q_1 is approximated by

$$(3.59)\qquad q_1 \approx \frac{1}{\sqrt{N} H(\rho,\alpha)}, \quad \rho \text{ fixed}, \quad \rho \geq 0 \text{ if } \alpha > 1, \quad N \to \infty.$$

The quasi-stationary distribution q is shown in the transition region together with the two stationary distributions $p^{(0)}$ and $p^{(1)}$ in Figure 6. The figure also shows the approximation (3.57) of the quasi-stationary distribution and the approximations (3.51) and (3.48) of the two stationary distributions. All three approximations appear to be acceptable. The expectations of the three distributions are shown as functions of ρ in Figure 7 together with their approximations. The approximations get poorer as ρ increases, and improve as N increases. We note that the expectation of the quasi-stationary distribution $\mathrm{E}X^{(Q)}$ is better approximated by the expectation $\mathrm{E}X^{(1)}$ than by the expectation $\mathrm{E}X^{(0)}$ when ρ is small, but that the roles of these two approximating expectations are reversed as ρ becomes large. This is in line with our earlier observation that the quasi-stationary distribution is best approximated by the stationary distribution $p^{(1)}$ when R_0 is distinctly less than one, but by $p^{(0)}$ when R_0 is distinctly larger than one.

The derivation of the approximation for the distribution is given in Appendix C.

3.16. **Approximation of the time to extinction in the transition region.** By inserting the approximation (3.59) of q_1 into the expression (2.22) for the expected time to extinction from quasi-stationarity, $\mathrm{E}\tau_Q$, we find that

$$(3.60)\quad \mathrm{E}\tau_Q = \frac{1}{\mu_1 q_1} \approx \frac{\sqrt{N} H(\rho,\alpha)}{\mu},$$
$$\rho \text{ fixed}, \quad \rho \geq 0 \text{ if } \alpha > 1, \quad N \to \infty.$$

Furthermore, insertion of the approximation (3.52) of $p_1^{(0)}$ into the expression (2.24) for the expected time to extinction from the state 1, $\mathrm{E}\tau_1$, gives the approximation

$$\mathrm{E}\tau_1 = \frac{1}{\mu_1 p_1^{(0)}} \approx \frac{1}{\mu} \left(\frac{1}{2} \log \frac{N}{\alpha} + H_0(\rho)\right), \quad \rho \text{ fixed}, \quad N \to \infty.$$

We note that the expected time to extinction from the state n, $\mathrm{E}\tau_n$, grows quite strongly with n in the transition region. The reason is based on our results that $\mathrm{E}\tau_Q$ is of the order $\sqrt{N}$, while $\mathrm{E}\tau_1$ is of the order $\log N$. Hence the relation $\mathrm{E}\tau_Q = \sum_{n=1}^{N} q_n \mathrm{E}\tau_n$ implies that there are n-values for which $\mathrm{E}\tau_n$ is at least of the order $\sqrt{N}$. This is turn implies that the ratio $\mathrm{E}\tau_n/\mathrm{E}\tau_1$ is at least of the order $\sqrt{N}/\log N$ for these values of n.

A numerical evaluation of the expected time to extinction from quasi-stationarity shows that it grows slowly with ρ when ρ is negative, and that it grows much faster with ρ when ρ is positive. An illustration with $N = 1000$ and $\alpha_1 = \alpha_2 = 0.5$ is given in Figure 8. The figure also shows two approximations, namely (3.42) and (3.60). The former of these is valid when R_0 is distinctly larger than one, while the latter one happens to be uniformly valid in the two parameter regions where R_0 is distinctly smaller than one, and in the transition region. This uniformity is valid in the special case $\alpha = \alpha_1 + \alpha_2 = 1$, but not for other values of the sum of the two parameters α_1 and α_2.

4. Concluding Comments

We have carried out a careful analysis of the quasi-stationary distribution and of the time to extinction in the three parameter regions that give qualitatively different results. The transition region presented the largest mathematical challenge. It is hoped that the insight that this has given will be of value in studying more realistic and more complicated population models.

One of the main outstanding problems in mathematical epidemiology is to understand the mechanisms that cause the combination of extinction and recurrence that has been observed in transmission of such infections as measles; see the discussion of critical community size by Dietz [11]. A model suited for the study of these questions takes the form of a bivariate birth-and-death process with absorbing states. It is shown by Nåsell [23] that this model exhibits qualitative behaviour similar to what we have derived for the Verhulst model. A notable difference is, however, that the transition region is very much wider for this model than for the Verhulst model. This has the consequence that the transition region is needed for the analysis of this model for a large range of reasonable parameter values and population sizes. There is therefore a very definite need to understand the behaviour of the quasi-stationary distribution in the transition region. This need is further emphasized by the fact that the study of the quasi-stationary distribution in this bivariate birth-and-death model presents appreciable mathematical difficulties in addition to those that are encountered in dealing with the univariate Verhulst model.

Appendix A. A uniform approximation of $\sum_{n=1}^N \rho_n$

An approximation of the stationary distribution $p^{(0)}$ in the transition region is derived in Subsection 3.14. An important ingredient in this derivation is the approximation of $\sum_{n=1}^N \pi_n$ in the transition region derived in Appendix B, since by (2.5) $p_1^{(0)} = 1/\sum_{n=1}^N \pi_n$. The development in Appendix B is based on an approximation of the sum $\sum_{n=1}^N \rho_n$ that is uniformly valid in two adjoining parameter regions, namely the region where R_0 is fixed at a value between 0 and 1 and the transition region where ρ is fixed. This is derived in the present appendix. We derive the following result:

(A.1)
$$\sum_{n=1}^N \rho_n \sim \frac{\bar{\sigma}_2}{R_0}\frac{\Phi(\beta_3)}{\varphi(\beta_3)}, \quad R_0 < 1 \text{ and } R_0 \text{ fixed, or } \rho \text{ fixed}, \quad N \to \infty.$$

The first step in the derivation is to insert the approximation (3.15) for ρ_n into the sum $\sum_{n=1}^N \rho_n$. We note that this approximation of ρ_n is valid without restriction on R_0. Thus we get

$$\sum_{n=1}^N \rho_n \sim \frac{1}{R_0\varphi(\beta_2)} \sum_{n=1}^N \varphi(y_2(n)), \quad N \to \infty.$$

The evaluation of the sum $\sum_{n=1}^N \varphi(y_2(n))$ requires an extension of the continuity correction for the normal distribution from the body to the tails of the distribution. A result to this effect is established by Nåsell [21]. This result gives an asymptotic approximation of a sum of the form $\sum_{n=1}^N \varphi(y(n))$, where $y(n) = (n-\mu)/\sigma$, and where it is assumed that $\sigma = \mathrm{O}(\sqrt{N})$. The result can be written in the form

$$\sum_{n=1}^N \varphi(y(n)) \sim \sigma\left(\Phi\left(\frac{N + G(z(N)) - \mu}{\sigma}\right) - \Phi\left(\frac{G(z(1)) - \mu}{\sigma}\right)\right), \quad N \to \infty.$$

where $z(n) = y(n)/\sigma = (n-\mu)/\sigma^2$, and where the function G is defined by

$$G(z) = \begin{cases} \dfrac{1}{z}\log\dfrac{\exp(z)-1}{z}, & z \neq 0, \\ \dfrac{1}{2}, & z = 0. \end{cases}$$

The function G is continuous, monotonically increasing, takes values in the open interval $(0,1)$, and satisfies the relation $G(z) + G(-z) = 1$. It takes the value $1/2$ (corresponding to the well-known continuity correction in the body of a normal distribution) when its argument is equal to 0. Note that the result that the continuity correction equals $1/2$ actually holds asymptotically also in those parts of the tails of the distribution (where $|y(n)| \to \infty$) that lie so close to the body that $y(n) = \mathrm{o}(\sqrt{N})$.

By applying the continuity correction result we find that

$$\begin{aligned}\sum_{n=1}^{N} &\varphi(y_2(n)) \\ &\sim \bar{\sigma}_2 \left(\Phi \left(\frac{N + G(z_2(N)) - \bar{\mu}_2}{\bar{\sigma}_2} \right) - \Phi \left(\frac{G(z_2(1)) - \bar{\mu}_2}{\bar{\sigma}_2} \right) \right) \\ &\sim \bar{\sigma}_2 \Phi(B_2), \quad N \to \infty,\end{aligned}$$

where $z_2(n) = y_2(n)/\bar{\sigma}_2$ and where we use B_2 as short-hand notation for the following expression:

$$B_2 = \beta_2 - \frac{G(z_2(1))}{\bar{\sigma}_2}.$$

Hence we get

$$\sum_{n=1}^{N} \rho_n \sim \frac{\bar{\sigma}_2 \Phi(B_2)}{R_0 \varphi(\beta_2)}, \quad N \to \infty.$$

In order to prove that $\sum_{n=1}^{N} \rho_n$ has the asymptotic approximation (A.1), it suffices to show that

$$\text{(A.2)} \quad \frac{\Phi(B_2)}{\varphi(\beta_2)} \sim \frac{\Phi(\beta_3)}{\varphi(\beta_3)}, \quad R_0 < 1 \text{ and } R_0 \text{ fixed, or } \rho \text{ fixed}, \quad N \to \infty.$$

In the transition region where $\rho = \mathrm{O}(1)$ this follows from the results that all three arguments β_2, β_3, and B_2 are asymptotic to ρ.

The function $\Phi(y)/\varphi(y)$ is of importance at several places in this paper. A well-known asymptotic approximation as $y \to -\infty$, which is actually an upper bound for $y < 0$, will be used repeatedly. It can be stated as follows:

$$\text{(A.3)} \qquad \frac{\Phi(y)}{\varphi(y)} \sim -\frac{1}{y}, \quad y \to -\infty.$$

The result can be derived through integration by parts of $\varphi(t)$. Additional asymptotic approximations are given below by (B.3).

In the region where R_0 is fixed at a value smaller than 1 we note that $B_2 \to -\infty$ as $N \to \infty$. By using the asymptotic approximation of $\Phi(x)/\varphi(x)$ given above we find that

$$\frac{\Phi(B_2)}{\varphi(\beta_2)} \sim -\frac{1}{\beta_2} \frac{\varphi(B_2)}{\varphi(\beta_2)}, \quad R_0 < 1 \quad R_0 \text{ fixed}, \quad N \to \infty.$$

Here,

$$\begin{aligned}\frac{\varphi(B_2)}{\varphi(\beta_2)} &= \exp\left(\frac{\beta_2^2 - B_2^2}{2} \right) \sim \exp\left(\frac{\beta_2 G(z_2(1))}{\bar{\sigma}_2} \right) \\ &= \exp(-\log(1/R_0) G(z_2(1))), \quad R_0 < 1 \quad R_0 \text{ fixed}, \quad N \to \infty.\end{aligned}$$

Now

$$z_2(1) = \frac{1-\bar{\mu}_2}{\bar{\sigma}_2^2} \sim \log\frac{1}{R_0}, \quad R_0 < 1 \quad R_0 \text{ fixed}, \quad N \to \infty.$$

By using the definition of the function G we find that

$$\log\frac{1}{R_0}\, G(\log\frac{1}{R_0}) = \log\left(\frac{1-R_0}{R_0\log(1/R_0)}\right).$$

Hence we get

$$\frac{\varphi(B_2)}{\varphi(\beta_2)} \sim \frac{R_0\log(1/R_0)}{1-R_0}, \quad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

We conclude therefore that the left-hand side of (A.2) is approximated by

$$\frac{\Phi(B_2)}{\varphi(\beta_2)} \sim \frac{R_0\sqrt{\alpha}}{(1-R_0)\sqrt{N}} = -\frac{1}{\beta_3}, \qquad R_0 < 1, \quad R_0 \text{ fixed}, \quad N \to \infty.$$

This completes the derivation since the right-hand side of (A.2) is asymptotic to the same expression.

Appendix B. Approximation of $\sum_{n=1}^{N} \pi_n$ in the transition region

In this appendix we derive an approximation of the sum $\sum_{n=1}^{N} \pi_n$ in the transition region. The approximation is not asymptotic, and we shall therefore be concerned with the error involved in using this approximation. The approximation given in (3.54) is a special case of the results derived here.

By using the relation between π_n and ρ_n in (3.27) and the uniform approximation of $\sum_{n=1}^{N} \rho_n$ in (A.1) we find that

$$\sum_{n=1}^{N} \pi_n \sim \frac{1}{R_0}\int_0^{R_0} \sum_{n=1}^{N} \rho_n(x)\,dx \sim \frac{\bar{\sigma}_2}{R_0}\int_0^{R_0} \frac{1}{x}\frac{\Phi(y(x))}{\varphi(y(x))}\,dx, \qquad \rho \text{ fixed}, \quad N \to \infty.$$

Here, the argument of Φ and φ in the integrand is $\beta_2\sqrt{N} = \bar{\sigma}_2(R_0 - 1)/R_0$ with R_0 replaced by x. Hence $y(x) = \bar{\sigma}_2(x-1)/x$. The uniformity of the approximation of $\sum_{n=1}^{N} \rho_n$ derived in Appendix A is important here, since the integration interval covers both the parameter region where $R_0 < 1$ is fixed and the one where ρ is fixed as $N \to \infty$. The integral in the right-hand side of this expression can be rearranged by a change of integration variable. We get

$$\text{(B.1)}\quad \sum_{n=1}^{N}\pi_n \sim \frac{1}{R_0}\int_{-\infty}^{\rho/R_0}\frac{1}{1-y/\bar{\sigma}_2}\frac{\Phi(y)}{\varphi(y)}\,dy, \sim \int_{-\infty}^{\rho}\frac{1}{1-y/\bar{\sigma}_2}\frac{\Phi(y)}{\varphi(y)}\,dy,$$
$$\rho \text{ fixed}, \quad N\to\infty.$$

Here we have used the facts that the integrand is O(1) at the right end of the integration interval, that $R_0 \sim 1$, and that $\rho/R_0 \sim \rho$.

It remains to establish the following approximation:

$$\text{(B.2)}\quad \int_{-\infty}^{\rho}\frac{1}{1-y/\bar{\sigma}_2}\frac{\Phi(y)}{\varphi(y)}\,dy \approx \frac{1}{2}\log\frac{N}{\alpha}+H_0(\rho), \quad \rho \text{ fixed}, \quad N\to\infty,$$

where the function H_0 is defined below.

The derivation of the approximation given by the right-hand side of (B.2) is based on a partitioning of the integration interval $(-\infty,\rho)$ into the union of the two subintervals $(-\infty,\rho_b)$ and (ρ_b,ρ). Different approximations of the integrand are used in these two subintervals. In the first one, the function $\Phi(y)/\varphi(y)$ is replaced by its asymptotic approximation as $y\to-\infty$, while the factor $1/(1-y/\bar{\sigma}_2)$ is replaced by its asymptotic approximation 1 in the second subinterval.

We choose ρ_b to be a negative constant, independent of N. The approximation of the integrand in the first subinterval will then be asymptotic in part of the interval, but it will fail to be asymptotic at the right-hand end, since y is finite there. The resulting approximation of the corresponding integral will therefore also fail to be asymptotic. The error introduced in this way can however be kept acceptably small, as shown below.

The sum of the first m terms of the asymptotic approximation of the ratio $\Phi(y)/\varphi(y)$ as $y\to-\infty$ is denoted $S_m(y)$. It is defined by

(B.3)
$$S_m(y)=\sum_{k=1}^{m}\frac{a_k}{y^{2k-1}}=-\frac{1}{y}+\frac{1}{y^3}-\frac{1\cdot 3}{y^5}+\cdots+\frac{a_m}{y^{2m-1}}, \quad m=1,2,\dots,$$

where

$$\text{(B.4)}\qquad a_k=(-1)^k\frac{(2k-2)!}{2^{k-1}(k-1)!}, \quad k=1,2,\dots.$$

The result that $S_m(y)$ gives an asymptotic approximation of $\Phi(y)/\varphi(y)$ as $y\to-\infty$ extends (A.3), and can be established by integration by parts of $\varphi(t)$. The result is quoted by Abramowitz and Stegun [1], formula 26.2.12. The sum $S_m(y)$ also gives an upper bound (lower bound) of the ratio $\Phi(y)/\varphi(y)$ for $y<0$ if m is odd (even). By applying the bounds one finds that

$$\text{(B.5)}\qquad \left|\frac{\Phi(y)}{\varphi(y)}-S_m(y)\right| < -\frac{|a_{m+1}|}{y^{2m+1}}, \quad y<0.$$

We proceed to define the function H_0. Let ρ_b be a negative constant, independent of N, and put

$$H_0(\rho) = \begin{cases} H_a(\rho), & \rho \le \rho_b, \\ H_a(\rho_b) + \displaystyle\int_{\rho_b}^{\rho} \frac{\Phi(y)}{\varphi(y)}\,dy, & \rho > \rho_b, \end{cases} \tag{B.6}$$

where the auxiliary function H_a is defined by

$$H_a(\rho) = -\log|\rho| - \sum_{k=2}^{m_b} \frac{a_k}{2k-2}\frac{1}{\rho^{2k-2}}, \quad \rho < 0.$$

Here, m_b is an integer given by

$$m_b(\rho_b) = \left[\frac{\rho_b^2 - 1 + \sqrt{(\rho_b^2+1)^2 + 4\rho_b^2}}{4} \right]. \tag{B.7}$$

where the brackets denote the largest integer less than or equal to the quantity inside the brackets. Note that $m_b(\rho_b)$ is positive if $\rho_b \le -\sqrt{3/2}$. The definition of H_0 is complete after we specify ρ_b. The recommendation is to take ρ_b in the interval from -6 to -3. Further comments on the choice of ρ_b and on the corresponding value of $m_b(\rho_b)$ are given below.

Note that the definition of the function H_0 given in Subsection 3.14 corresponds to the choice $\rho_b = -3$.

With this preparation we turn to the derivation of the approximation (B.2). Assume first that $\rho > \rho_b$. The interval of integration in the integral in the left-hand side of (B.2) is written as the union of the two subintervals $(-\infty, \rho_b)$ and (ρ_b, ρ). The integral can then be written as a sum of three integrals as follows:

$$\int_{-\infty}^{\rho} \frac{1}{1 - y/\bar{\sigma}_2}\frac{\Phi(y)}{\varphi(y)}\,dy = I_1 + I_2 + I_3, \tag{B.8}$$

where

$$I_1 = \int_{-\infty}^{\rho_b} \frac{1}{1 - y/\bar{\sigma}_2} S_m(y)\,dy,$$
$$I_2 = \int_{-\infty}^{\rho_b} \frac{1}{1 - y/\bar{\sigma}_2}\left(\frac{\Phi(y)}{\varphi(y)} - S_m(y)\right)dy,$$
$$I_3 = \int_{\rho_b}^{\rho} \frac{1}{1 - y/\bar{\sigma}_2}\frac{\Phi(y)}{\varphi(y)}\,dy.$$

Here, m is a positive integer that depends on ρ_b and that will be determined later.

Among the three integrals above, the first one can be evaluated explicitly since the integrand is rational, the absolute value of the second one can be bounded with the help of the inequality (B.5), and the third one can be approximated since the factor $1/(1-y/\bar{\sigma}_2)$ is asymptotically equal to 1.

By applying the inequality (B.5) we find the following bound for the absolute value of I_2:

$$|I_2| < -|a_{m+1}| \int_{-\infty}^{\rho_b} \frac{1}{1-y/\bar{\sigma}_2} \frac{1}{y^{2m+1}}\, dy.$$

By partial fraction expansion, integration, substitution of the integration bounds, and leaving out the terms that are o(1) as $N \to \infty$, we find that the upper bound of $|I_2|$ is asymptotically approximated by

$$b_m = \frac{|a_{m+1}|}{2m\rho_b^{2m}}.$$

We determine m so that this asymptotic approximation of the upper bound is minimized. By using the definition of a_k we find that

$$\frac{b_{m+1}}{b_m} = \frac{(2m+1)m}{(m+1)\rho_b^2}.$$

The value of m that minimizes b_m is the largest integer $m_b = m_b(\rho_b)$ that is smaller than or equal to the positive root of the equation in m that results by putting $b_{m+1} = b_m$. This establishes the expression (B.7) for $m_b(\rho_b)$. The resulting asymptotic approximation of the error bound of $|I_2|$ is b_{m_b}.

Our results depend on the value of ρ_b. A guide to the choice of ρ_b is given by the following table. It lists the number of terms m_b and the asymptotic approximation b_{m_b} of the error bound for some possible values of ρ_b.

ρ_b	m_b	b_{m_b}
-3	4	$2 \cdot 10^{-3}$
-4	8	$3 \cdot 10^{-5}$
-5	12	$2 \cdot 10^{-7}$
-6	18	$6 \cdot 10^{-10}$

The table shows that the asymptotic approximation of the error bound for I_2 can be made acceptably small by choosing the absolute value of ρ_b sufficiently large.

We now turn to the integral I_1, with $m = m_b$. After partial fraction expansion, integration, substitution of the integration bounds, and leaving out the terms that are o(1) as $N \to \infty$ we find that

$$I_1 \sim \log \frac{\bar{\sigma}_2}{|\rho_b|} - \sum_{k=2}^{m_b} \frac{a_k}{2k-2} \frac{1}{\rho_b^{2k-2}} = \frac{1}{2} \log \frac{N}{\alpha} + H_a(\rho_b).$$

The integral I_3, finally, is found to have the following asymptotic approximation:

$$I_3 \sim \int_{\rho_b}^{\rho} \frac{\Phi(y)}{\varphi(y)}\, dy, \quad \rho \text{ fixed}, \quad N \to \infty.$$

It follows that

$$I_1 + I_3 \sim \frac{1}{2}\log\frac{N}{\alpha} + H_0(\rho)$$

for $\rho > \rho_b$. This establishes the approximation in (B.2) since I_2 is approximated by 0.

The development so far is based on the assumption that $\rho_b < \rho$. The treatment of the case $\rho \le \rho_b$ is closely similar. In this case the integral in the left-hand side of (B.8) is equal to the sum of two integrals corresponding to I_1 and I_2. These integrals are found from I_1 and I_2, respectively, by replacing the upper bounds of integration ρ_b by ρ. The integral corresponding to I_2 is, as above, approximated by 0, while the integral corresponding to I_1 is asymptotically equal to

$$\frac{1}{2}\log\frac{N}{\alpha} + H_a(\rho),$$

consistent with the definition of H_0 in (B.6).

Appendix C. Derivation of the approximation of the quasi-stationary distribution in the transition region

The derivation of the results in this appendix is based on the relation (2.13). We start with the assumption that

$$q_j \sim \frac{1}{H(\rho,\alpha)\sqrt{N}}, \quad j = \mathrm{o}(\sqrt{N}), \quad \rho \text{ fixed}, \quad N \to \infty,$$

where $H(\rho,\alpha)$ remains to be determined. This means that we are assuming that the j-dependence of q_j is determined by terms of smaller order of magnitude for the indicated range of j-values. By using our assumption and the approximation (3.16) of ρ_n we find that the terms in the sum in (2.13) are approximated as follows for $k = \mathrm{o}(\sqrt{N})$:

$$\frac{1 - \sum_{j=1}^{k-1} q_j}{\rho_k} \sim \frac{1 - (k-1)/(H(\rho,\alpha)\sqrt{N})}{1 + (k-1)\rho\sqrt{\alpha}/\sqrt{N}} \sim \frac{1}{R_1^{k-1}},$$
$$k = \mathrm{o}(\sqrt{N}), \quad \rho \text{ fixed}, \quad N \to \infty,$$

where R_1 is given by (3.58). Evaluation of the sum over k in (2.13) for $n = \mathrm{o}(\sqrt{N})$ leads to the expression

(C.1)
$$q_n \sim \frac{R_1}{R_1 - 1}\left(1 - \frac{1}{R_1^n}\right)\pi_n q_1, \quad n = \mathrm{o}(\sqrt{N}), \quad \rho \text{ fixed}, \quad N \to \infty.$$

By using the approximation (3.26) of π_n and noting that $R_1^n - 1 \sim n(\rho\sqrt{\alpha} + 1/H(\rho,\alpha))/\sqrt{N}$, $R_1^n \sim 1$, and $R_0^{n-1} \sim 1$ for $n = \mathrm{o}(\sqrt{N})$ we find that

$$q_n \sim q_1, \quad n = \mathrm{o}(\sqrt{N}), \quad \rho \text{ fixed}, \quad N \to \infty.$$

This result is consistent with our assumption above in the sense that the approximation is asymptotically independent of n for the indicated range of n-values.

The next step is to determine q_1 from the condition $\sum_{n=1}^N q_n = 1$. This step introduces an approximation that cannot be claimed to be asymptotic since we use our above approximation of q_n, and this approximation is not asymptotic for all n-values that satisfy $n = \mathrm{O}(\sqrt{N})$, but only for $n = \mathrm{o}(\sqrt{N})$. Inserting the approximation (C.1) of q_n into the sum $\sum_{n=1}^N q_n$ gives

$$\sum_{n=1}^N q_n \approx \frac{R_1}{R_1-1} q_1 \sum_{n=1}^N \pi_n \left(1 - \frac{1}{R_1^n}\right), \quad \rho \text{ fixed}, \quad N \to \infty. \tag{C.2}$$

The sum over n is written as a sum of two sums. The first of these is approximated by the use of the approximation (3.54) of $\sum_{n=1}^N \pi_n$. For emphasis, we write $\pi_n(R_0)$ instead of π_n. The result is

$$\sum_{n=1}^N \pi_n(R_0) \approx \frac{1}{2}\log\frac{N}{\alpha} + H_0(\rho), \quad \rho \text{ fixed}, \quad N \to \infty.$$

The terms in the second sum can be approximated for $n = \mathrm{o}(\sqrt{N})$ by using the approximation (3.26) of π_n. We get

$$\sum_{n=1}^N \frac{\pi_n(R_0)}{R_1^n} \approx \frac{1}{R_1}\sum_{n=1}^N \pi_n(R_0/R_1), \quad \rho \text{ fixed}, \quad N \to \infty.$$

Now

$$\frac{R_0}{R_1} \sim 1 - \frac{1/H(\rho,\alpha)}{\sqrt{N}}, \quad \rho \text{ fixed}, \quad N \to \infty.$$

Since $R_1 \sim 1$ we conclude, again using the approximation (3.54) of $\sum_{n=1}^N \pi_n$, that

$$\sum_{n=1}^N \frac{\pi_n(R_0)}{R_1^n} \approx \frac{1}{2}\log\frac{N}{\alpha} + H_0(-1/H(\rho,\alpha)), \qquad \rho \text{ fixed}, \quad N \to \infty.$$

By adding the approximations of the two sums we get

$$\sum_{n=1}^N \pi_n \left(1 - \frac{1}{R_1^n}\right) \approx H_0(\rho) - H_0(-1/H(\rho,\beta)) = \int_{-1/H(\rho,\alpha)}^{\rho} \frac{\Phi(y)}{\varphi(y)}\,dy, \quad \rho \text{ fixed}, \quad N \to \infty.$$

We next insert this approximation into the approximation (C.2) of $\sum_{n=1}^N q_n$, put $\sum_{n=1}^N q_n = 1$, and solve for q_1. The result is

$$q_1 \approx \frac{R_1 - 1}{R_1} \frac{1}{\int_{-1/H(\rho,\alpha)}^{\rho} \frac{\Phi(y)}{\varphi(y)}\,dy}, \quad \rho \text{ fixed}, \quad N \to \infty.$$

We insert the expression for R_1 from (3.58) and use the fact that $R_1 \sim 1$. By equating the resulting expression with the assumed form for q_n we find that H satisfies the relation (3.55), and that q_1 is approximated by (3.59). The approximation of q_n in (3.57) follows from the approximation (C.1) by using the approximation (3.59) of q_1 and the approximation (3.47) of π_n.

Appendix D. Proof that the function H is well defined

In this appendix we show that the function H defined implicitly by the relation

$$\text{(D.1)} \qquad H(\rho,\alpha) = \frac{1}{\rho\sqrt{\alpha} + 1/H(\rho,\alpha)} \int_{-1/H(\rho,\alpha)}^{\rho} \frac{\Phi(y)}{\varphi(y)}\,dy,$$

given in (3.55), is well defined for $\rho \geq 0$ and $\alpha \geq 0$, and also for $\rho < 0$ if $0 \leq \alpha \leq 1$. In both cases we require $H(\rho,\alpha) > 0$, and in the latter case we add the requirement that $H(\rho,\alpha) < -1/\rho$ if $0 < \alpha < 1$.

For brevity put $H_1(y) = \Phi(y)/\varphi(y)$. The function H_1 is important for the arguments in this appendix. We show that both H_1 and the function f_1 defined by $f_1(y) = yH_1(y)$ are completely monotonic, meaning that their derivatives of all orders are positive for all real values of their arguments.

To show this, note that the Laplace transform of the function which equals $\varphi(t)\sqrt{2\pi} = \exp(-t^2/2)$ for $t > 0$ is

$$G_1(s) = \int_0^\infty \exp(-st)\exp(-t^2/2)\,dt = H_1(-s).$$

It follows that the function G_1 is completely monotonic for all real values of the argument s, meaning that $(-1)^n G_1^{(n)}(s) > 0$. We conclude that the function H_1 is absolutely monotonic. See Widder [40] for further discussion of the concepts of complete and absolute monotonicity. Differentiation shows that $H_1'(x) = 1 + xH_1(x)$ and that $f_1'(x) = H_1''(x)$. We conclude that also f_1 is absolutely monotonic.

Define the function g as follows:

$$g(v) = \begin{cases} \dfrac{v}{v+\rho\sqrt{\alpha}} \displaystyle\int_{-v}^{\rho} H_1(y)\,dy, \quad v \geq 0, \quad \alpha \geq 0, \quad v \neq -\rho\sqrt{\alpha}, \\ -\rho H_1(\rho), \quad v = -\rho, \quad \alpha = 1, \quad \rho < 0, \\ 0, \quad \rho = 0. \end{cases}$$

Clearly, g depends also on ρ and α, but this dependence is omitted in the notation. It follows from its definition that g is a continuous function and that $H(\rho,\alpha)$ satisfies $g(1/H(\rho,\alpha)) = 1$.

The derivative of g with respect to v is equal to

$$g'(v) = \frac{1}{v+\rho\sqrt{\alpha}}\left(\frac{\rho\sqrt{\alpha}}{v+\rho\sqrt{\alpha}}\int_{-v}^{\rho} H_1(y)\,dy + vH_1(-v)\right), \qquad v>0, \quad \alpha \ge 0, \quad v \ne -\rho\sqrt{\alpha}. \tag{D.2}$$

We study first $g(v)$ for $\rho \ge 0$ and $\alpha \ge 0$. We get $g(0) = 0$ and $g(\infty) = \infty$, since $\int_{-\infty}^{\rho} H_1(y)\,dy = \infty$. Furthermore, $g'(v) > 0$. We conclude that $g(v)$ increases monotonically from 0 toward ∞ as v grows from 0 to ∞. Thus the equation $g(v) = 1$ has a unique solution, and $H(\rho,\beta)$ is well defined for $\rho \ge 0$ and $\alpha \ge 0$.

Next consider $\rho < 0$. The function g will then have a singularity at $v = -\rho\sqrt{\alpha}$ and zeroes at $v = 0$ and at $v = -\rho$. Exceptions occur for $\alpha = 0$ and for $\alpha = 1$, when the singularity is absorbed by one of the zeroes.

Thus, with $\alpha = 0$ we get

$$g(v) = \int_{-v}^{\rho} H_1(y)\,dy, \quad v \ge 0, \quad \rho < 0, \quad \alpha = 0.$$

Then $g(-\rho) = 0$, $g(\infty) = \infty$, and $g'(v) = H_1(-v) > 0$. Hence the equation $g(v) = 1$ has a unique solution, and $H(\rho,0)$ is well defined for $\rho < 0$.

Next we consider $\alpha = 1$. Note that $g(v)/v$ is the average of $H_1(y)$ over the interval $(-v,\rho)$ if $-v < \rho$ and over the interval $(\rho,-v)$ if $\rho < -v$. Since H_1 is an increasing function we conclude that $H_1(-v) < g(v)/v < H_1(\rho)$ in the first case and that $H_1(\rho) < g(v)/v < H_1(-v)$ in the second case. We show that $g(v) < 1$ for $0 < v \le -\rho$, and that therefore the v-value where g equals one is larger than $-\rho$.

The function H_1 satsfies the inequalities $yH_1(-y) < 1$ if $y > 0$ and $-\rho H_1(\rho) < 1$ for $\rho < 0$. This follows from the inequality $\Phi(y)/\varphi(y) < S_1(y) = -1/y$ for $y < 0$ noted after (B.4).

By applying the inequality $yH_1(-y) < 1$ for $y > 0$ we get $g(v) \le vH_1(-v) < 1$ for $0 < v \le -\rho$. We conclude that $g(v) < 1$ for $0 < v \le -\rho$. This means that the equation $g(v) = 1$ has no solution in this case.

Consider therefore $v \ge -\rho$ with $\rho < 0$. We then have $g(-\rho) = -\rho H_1(\rho) < 1$ and $g(\infty) = \infty$. We show below that $g'(v) > 0$ for $v > -\rho$. It follows that the equation $g(v) = 1$ has a unique solution with $v > -\rho$, and that therefore the function $H(\rho,\beta)$ is well defined for $\rho < 0$ and $\alpha = 1$.

It remains to prove that $g'(v) > 0$ for $v > -\rho$ when $\rho < 0$ and $\alpha = 1$. Since $g(v)/v < H_1(\rho)$, we find from (D.2) that the derivative

$g'(v)$ satisfies

$$g'(v) > \frac{1}{v+\rho}(\rho H_1(\rho) + vH_1(-v)) = \frac{1}{v+\rho}(f_1(\rho) - f_1(-v)) > 0,$$
$$v > -\rho, \quad \rho < 0, \quad \alpha = 1.$$

Here we have used the result established above that $f_1'(x) > 0$.

Now consider the case $0 < \alpha < 1$ and $\rho < 0$ with $v \geq 0$. The function g then has a singularity at $v = -\rho\sqrt{\alpha}$, and zeroes at $v = 0$ and at $v = -\rho$. Furthermore, $g(v)$ approaches ∞ as $v \to \rho\sqrt{\alpha}$ from the left, and also as $v \to \infty$. We show below that $g'(v) > 0$ both for $0 < v < -\rho\sqrt{\alpha}$ and for $v > -\rho$. It follows that there are two solutions to the equation $g(v) = 1$, but that only one of them satisfies $v > -\rho$.

Note that $g(v)$ is positive only for $0 < v < -\rho\sqrt{\alpha}$ and for $v > -\rho$, so it is only in these two intervals that it is possible for $g(v)$ to take the value one. Note furthermore that $\sqrt{\alpha}/(v + \rho\sqrt{\alpha})$ is an increasing function of α. Hence $\sqrt{\alpha}/(v + \rho\sqrt{\alpha}) < 1/(v + \rho)$ for $0 < \alpha < 1$. Applying this inequality in the expression (D.2) for $g'(v)$ gives

$$g'(v) > \frac{1}{v+\rho\sqrt{\alpha}}\left(\frac{\rho}{v+\rho}\int_{-v}^{\rho} H_1(y)\,dy + vH_1(-v)\right).$$

This inequality holds both for $0 < v < -\rho\sqrt{\alpha}$ and for $v > -\rho$ with $\rho < 0$ and $0 < \alpha < 1$. Now

$$\frac{1}{v+\rho}\int_{-v}^{\rho} H_1(y)\,dy < H_1(y) \quad -\rho < v, \quad \rho < 0, \quad 0 < \alpha < 1,$$

while the inequality is reversed if $v < -\rho$. In either case we find that

$$g'(v) > \frac{1}{v+\rho\sqrt{\alpha}}(f_1(\rho) - f_1(-v)) > 0.$$

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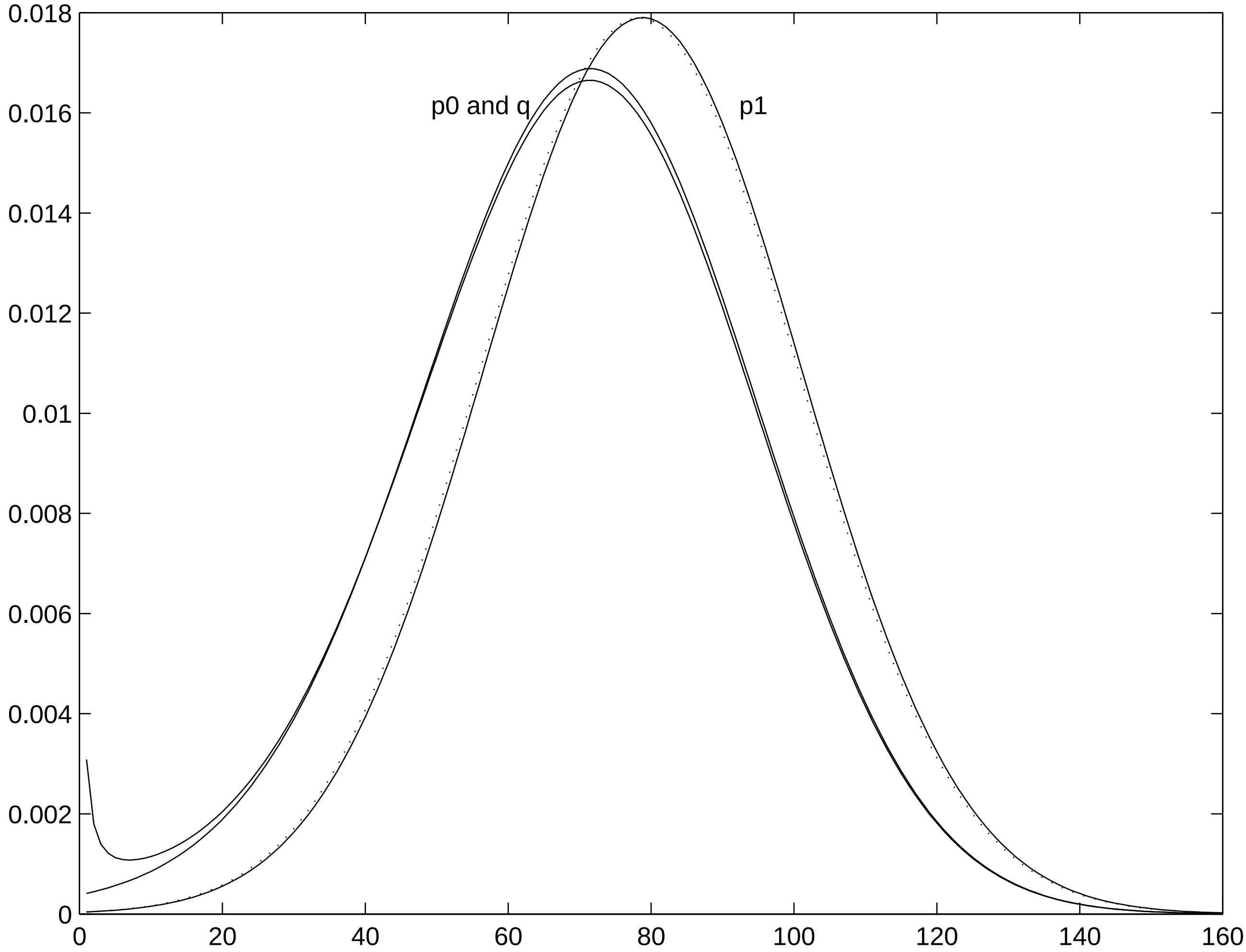

Figure 1. Numerical evaluations of the two stationary distributions $p^{(0)}$ and $p^{(1)}$ and of the quasi-stationary distribution qs are shown for R_0 distinctly above the deterministic threshold value 1. The parameters are $N = 1000$, $R_0 = 1.17$, and $\alpha_1 = \alpha_2 = 1$. The bodies of all three distributions are approximated by a normal distribution, shown dashed, that is practically indistinguishable from $p^{(1)}$. The approximations improve as N and/or R_0 are increased.

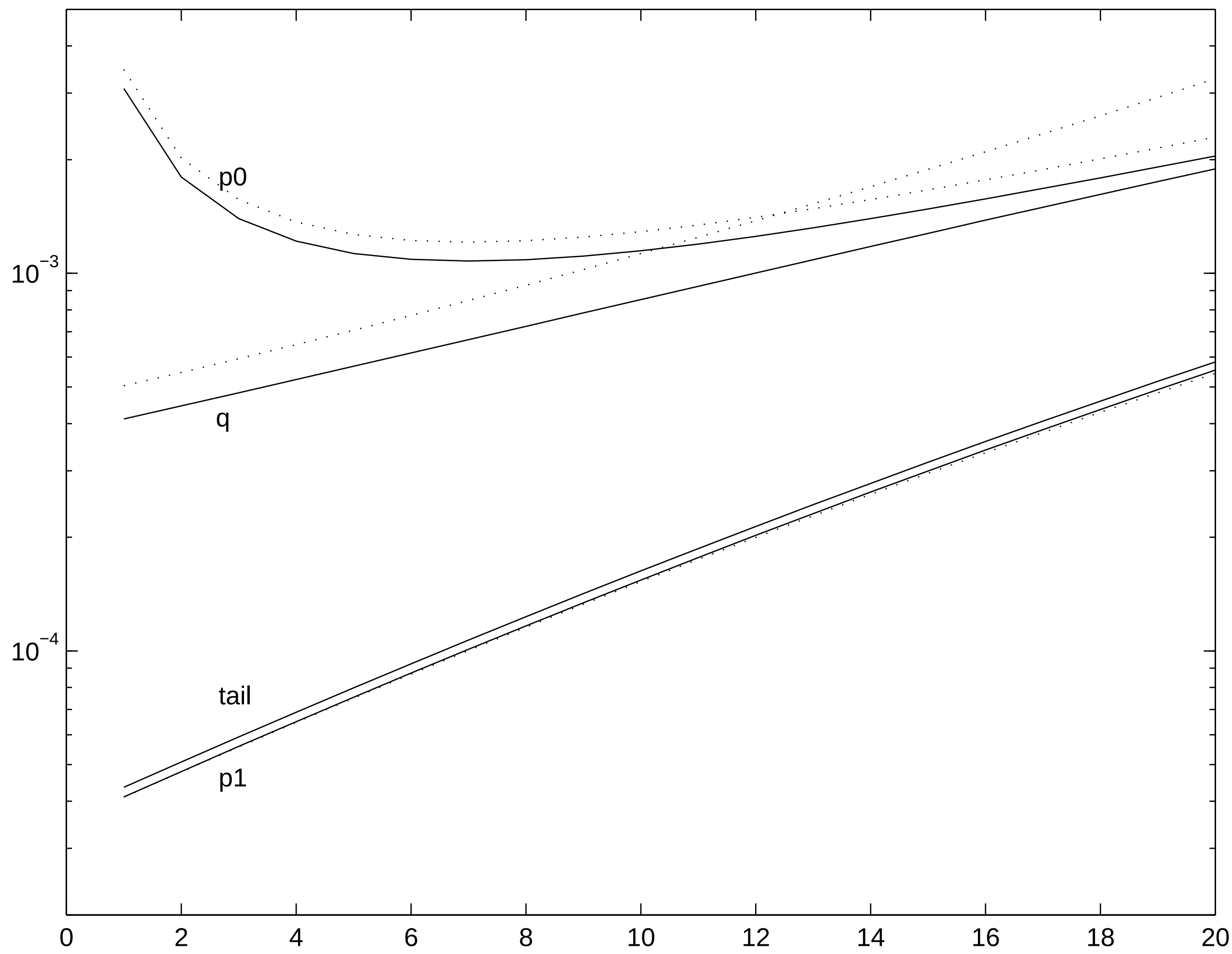

FIGURE 2. Numerical evaluations of the left tails of the two stationary distributions $p^{(0)}$ and $p^{(1)}$ and of the quasi-stationary distribution qs are shown for R_0 distinctly above the deterministic threshold value 1. The parameters are $N = 1000$, $R_0 = 1.17$, and $\alpha_1 = \alpha_2 = 1$ (same as in Figure 1). The approximations of the respective tails are shown dotted. The tail of the normal distribution that approximates the bodies of all three distributions is also shown.

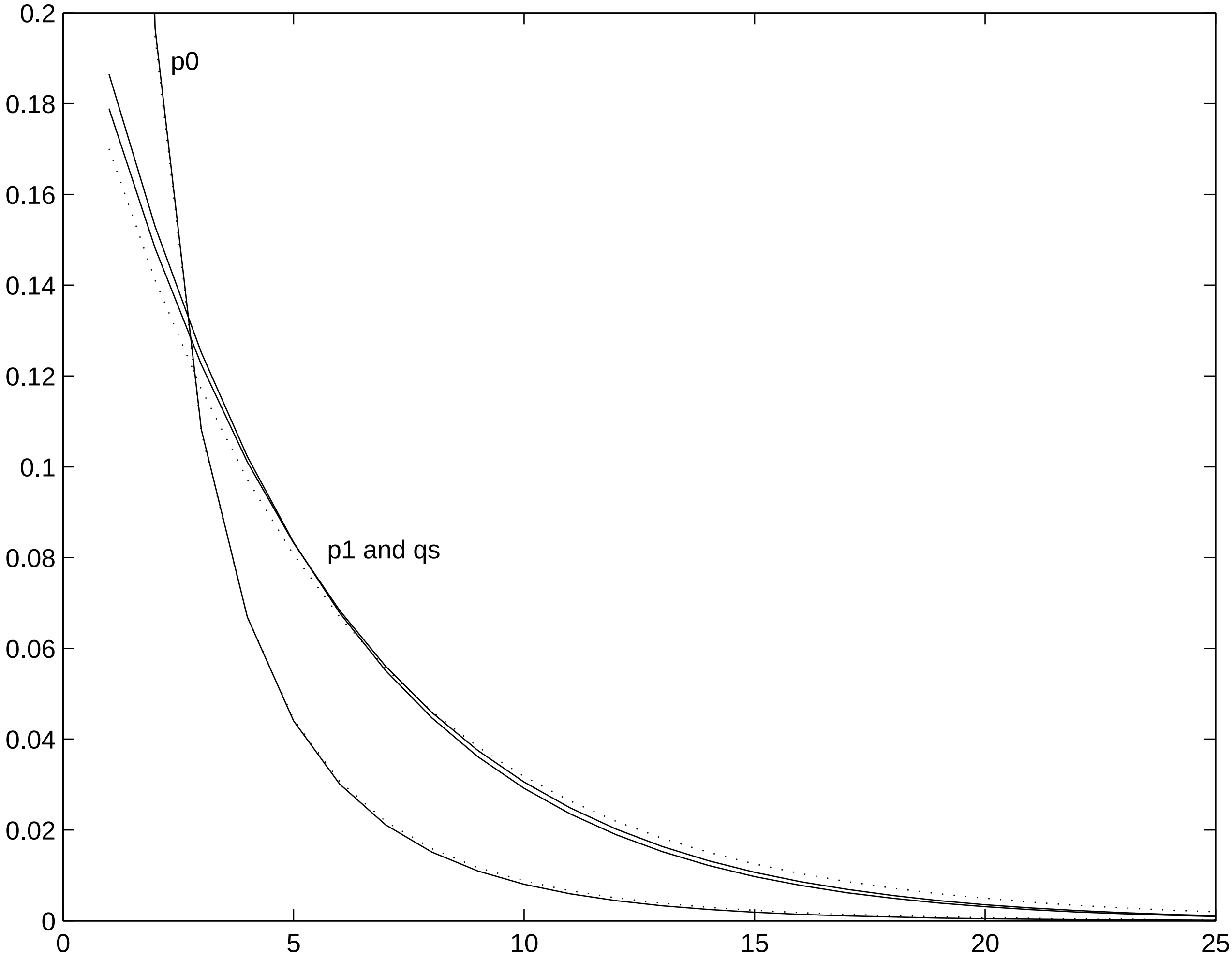

Figure 3. Numerical evaluations of the two stationary distributions $p^{(0)}$ and $p^{(1)}$ and of the quasi-stationary distribution qs are shown for R_0 distinctly below the deterministic threshold value 1. The parameters are $N = 1000$, $R_0 = 0.83$, and $\alpha_1 = \alpha_2 = 1$. The truncated geometric distribution that approximates $p^{(1)}$ and qs and the log series distribution that approximates $p^{(0)}$ are shown dotted.

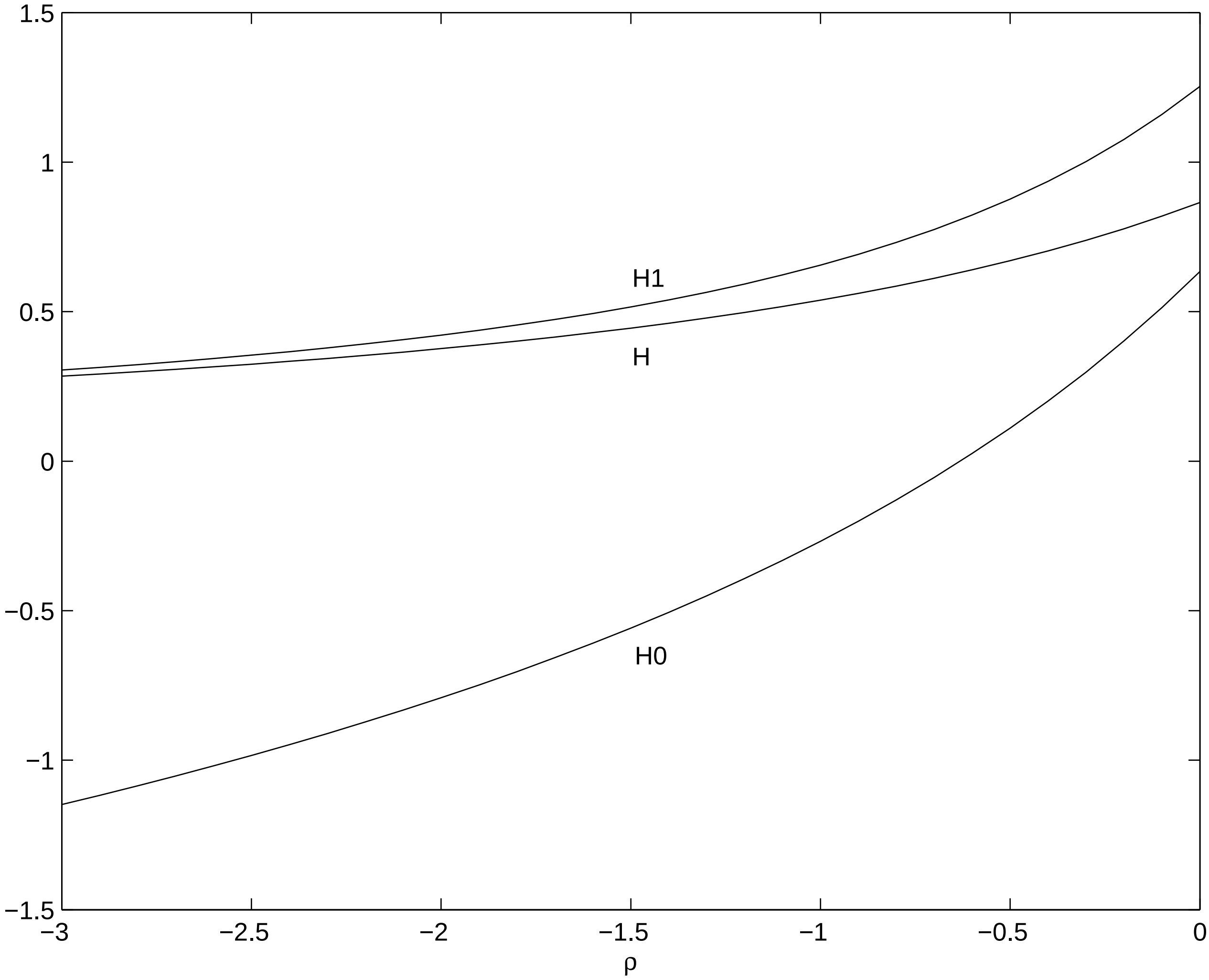

FIGURE 4. The functions $H(\rho, \alpha)$, $H_0(\rho)$, and $H_1(\rho) = \Phi(\rho)/\varphi(\rho)$ are shown as functions of ρ for negative values of ρ. The second argument of H is $\alpha = 1$.

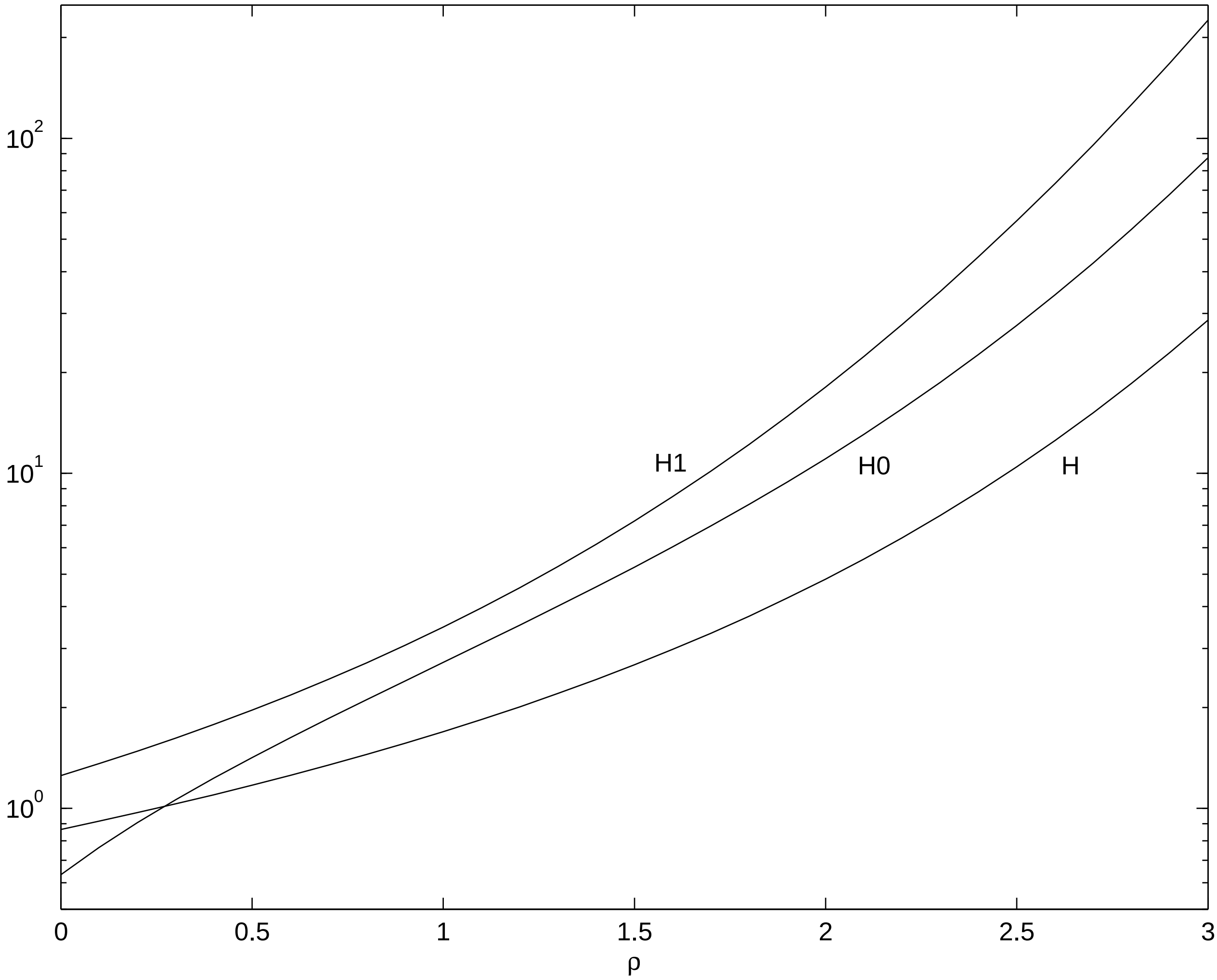

FIGURE 5. The functions $H(\rho, \alpha)$, $H_0(\rho)$, and $H_1(\rho) = \Phi(\rho)/\varphi(\rho)$ are shown as functions of ρ for positive values of ρ. The second argument of H is $\alpha = 1$. Note that the vertical scale is logarithmic.

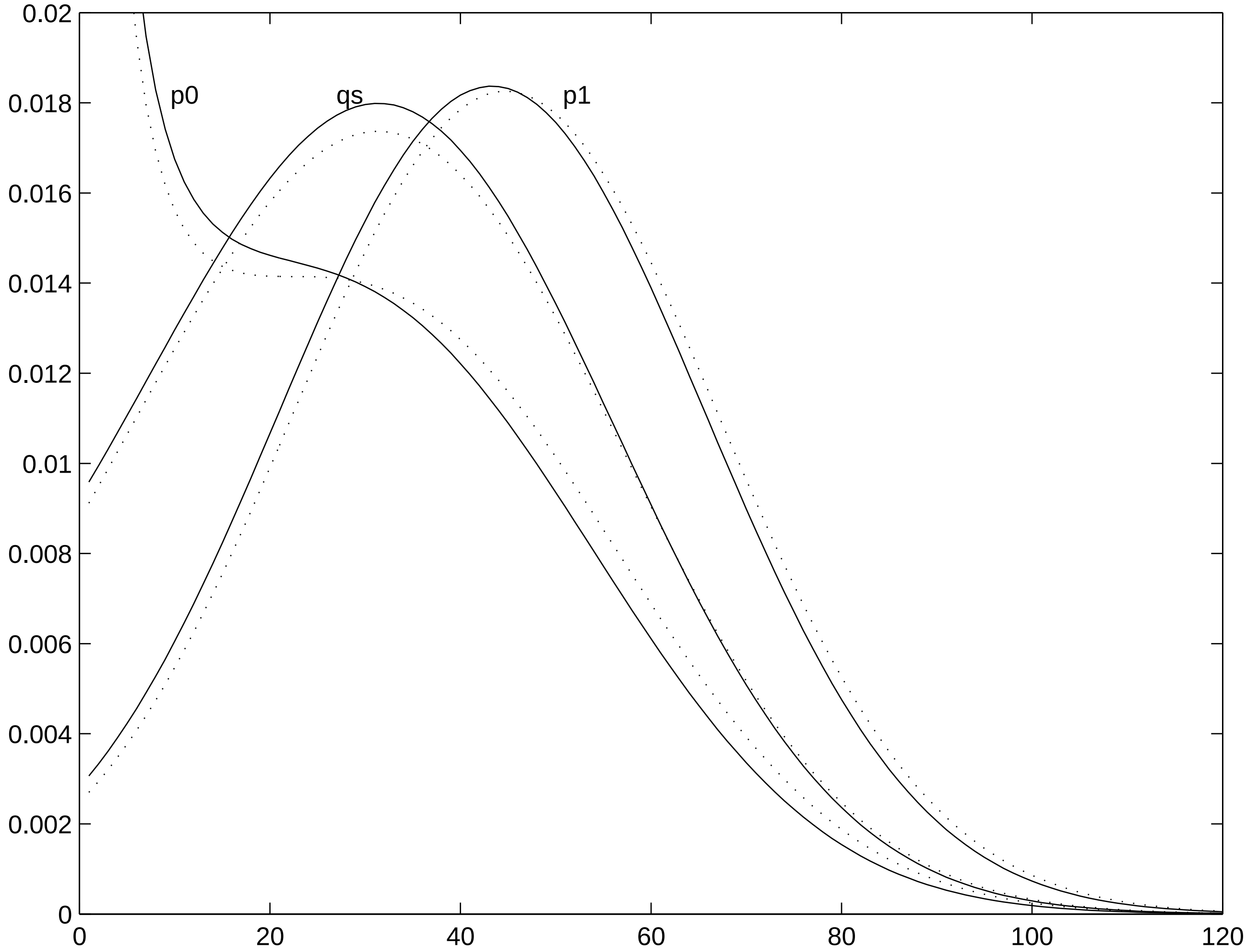

FIGURE 6. Numerical evaluations of the two stationary distributions $p^{(0)}$ and $p^{(1)}$ and of the quasi-stationary distribution qs are shown for R_0 in the transition region near 1. The parameters are $N = 1000$, $\rho = 2$, and $\alpha_1 = \alpha_2 = 1$. The approximations of the three distributions are shown dotted.

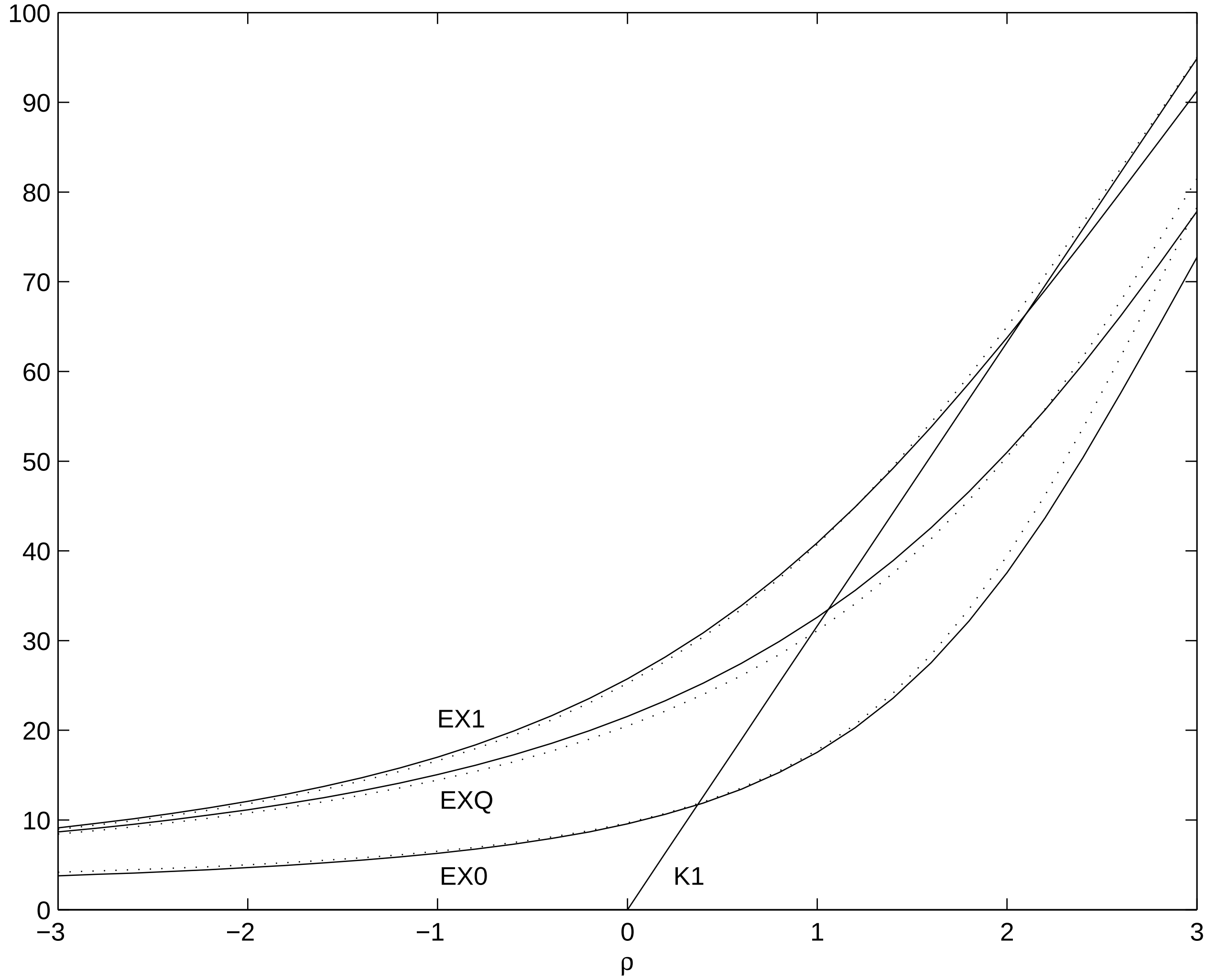

FIGURE 7. Numerical evaluations of the expectations of the two stationary distributions $p^{(0)}$ and $p^{(1)}$ and of the quasi-stationarity distribution qs are shown as functions of ρ for R_0 in the transition region near 1, together with the carrying capacity K_1. The parameters are $N = 1000$ and $\alpha_1 = \alpha_2 = 0.5$. The corresponding approximations are shown dotted.

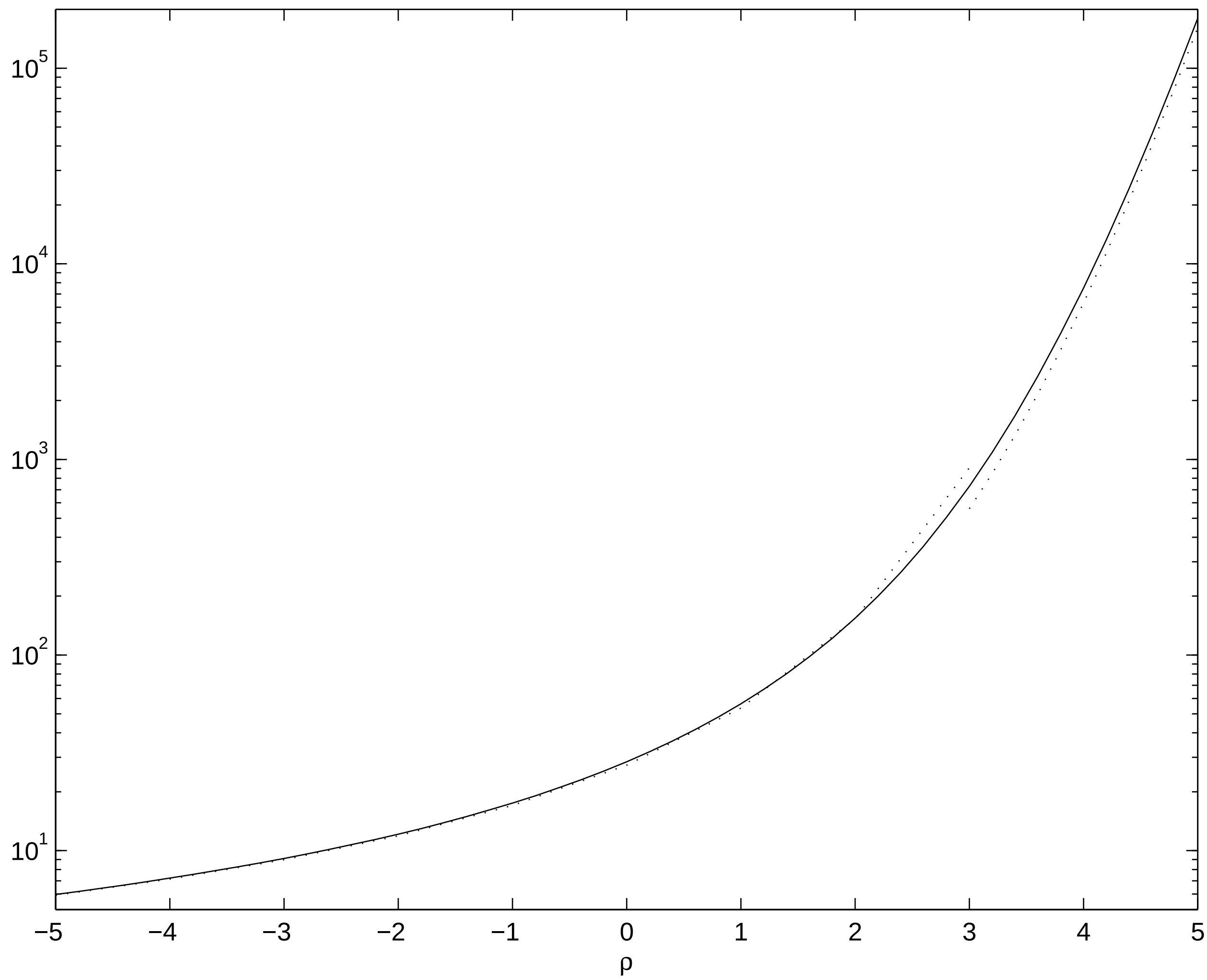

FIGURE 8. The expected time to extinction from quasi-stationarity is shown as a function of ρ with $N = 1000$ and $\alpha_1 = \alpha_2 = 0.5$, and $\mu = 1$. Two approximations are shown dotted. One of them holds for R_0 distinctly larger than 1, and the other one holds uniformly for R_0 distinctly smaller than 1, and for R_0 in the transition region.