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## **On the variance-to-mean ratio in models of parasite distributions**

Barbour, Andrew D ; Pugliese, Andrea

**Abstract:** We study the variance-to-mean ratio of the distributions of parasites among hosts for some models of parasite infection, using the cohort approach. We consider a model with density dependence in parasite mortality, and two different formulations of disease induced host mortality. We show that the distributions of parasites, conditional on host survival, converge to quasi-stationary distributions as host age increases. When there is density dependence in parasite mortality, the limiting variance-to-mean ratio is less than 1 (an 'underdispersed' distribution). In contrast, the two modes of disease induced host mortality show that either over- or underdispersed distributions may result.

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On the variance-to-mean ratio  
in models of parasite distributions

Andrew D. Barbour<sup>1</sup>

and

Andrea Pugliese<sup>\*2</sup>

<sup>1</sup>Universität Zürich <sup>2</sup>Dipartimento di Matematica - Università di

Trento

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## Abstract

we have studied the variance-to-mean ratio of the distributions of parasites among hosts for some models of parasite infection following the framework of [12]. In particular, we considered a model with density-dependence in parasite mortality, and two special rules for disease-induced host mortality. we proved that the distributions of parasites, conditional to host survival, converge, as host age increases, to a quasi-stationary distributions. we proved that the variance-to-mean ratio is less than 1 (an ‘under-dispersed’ distribution) when there is density-dependence in parasite mortality. By comparing the two special cases, we have shown that disease-induced host mortality may yield either over- or under-dispersed distributions.

## 1 Introduction

Distributions of parasites in host populations have been collected and fitted to probability distributions for several decades [11]. A standard method in statistical ecology is the comparison of empirical distributions with distributions arising from null models. Since we consider distributions of organisms and their possible values are the nonnegative integers, the prototype null model is a ‘random’ distribution of organisms in the units of observation, i.e. a Poisson distribution. Therefore it is usual [16] to distinguish distributions of counts as being ‘random’, ‘uniform’ (meaning that organisms are more uniformly spread than due to chance only) and ‘aggregated’ (meaning that most organisms are concentrated in few spots).

Often, when distributions are ‘aggregated’, the negative binomial has been used to fit empirical distributions; its parameter  $\kappa$  has been used [5] as a measure of the ‘aggregation’ of the distribution.

Another more general measure is the ratio of the (empirical) variance to the mean [16]: of course this ratio is equal to 1 for a Poisson distribution. Distributions with ratios greater than 1 will be considered here ‘over-dispersed’ (the usual term in the probabilistic literature corresponding to ‘aggregated’ of the ecological literature); those with ratios smaller than 1 ‘under-dispersed’.

Practically all observations of parasite burdens in animal hosts have yielded ‘over-dispersed’ distributions, generally with a very high ratio of the variance to the mean [20]. It is therefore of interest to elucidate the processes leading to this kind of pattern.

The first stochastic model considering the infection process in a cohort of host is due to Tallis and Leyton [22, 23]; the distributions yielded by their model was Poisson, in contrast with empirical

data.

The problem has been further studied by [1] through simulations. Their models considered a cohort of animals being born free of parasites; afterwards, they are subjected to a constant inflow of parasites. Moreover, both the animal hosts, and the individual parasites within them, may die.

Among others, they considered two models: in the first, the death rate of parasites in a host increased linearly with the number of parasites present in that host ('density-dependence' in parasites' death rate); in the second model, the death rate of hosts increased linearly with the number of parasites present in that host ('parasite-induced mortality'). From the simulations they concluded that both models yielded under-dispersed distributions, although that conclusion was based on very few observations for the second model.

More recently, [18] and [12] continued this study with a more theoretical approach. In particular, Isham showed (as was basically implicit in the work of previous authors) that, if the death rate of hosts increased linearly with the number of parasites present in that host while death rate and inflow of parasites were constant, parasites are subjected to a defective immigration-and-death process, and thus the parasite distribution is Poisson at each age  $a$  of the cohort. She then proceeded to study complications of the model that yielded different distributions (see also [15, 9, 7, 10]).

It remains, however, to see whether the claim that 'density-dependence' in parasites' death rate yields under-dispersed distributions is theoretically justified. Furthermore, the study of the effect of parasites on hosts' death rate has been limited to the case of a linear law; it would be interesting to consider more general laws.

The purpose of the present paper is to study the above problems. Precisely, in Section 2 three different models are presented: a general 'density-dependence' in parasites' death rates, and two different laws for the parasite-induced mortality. In Section 3 a general criterion for the under- or over-dispersion of a distribution is proved; this criterion might have some independent interest. In Section 4, it will be proved that the asymptotic distributions yielded by the three models satisfy

the conditions of the criterion of Section 3.

The variance to mean ratio has been recently studied for a large class of Markov chains and point processes [6]; however, as discussed at the end of the paper, their results do not seem to be directly applicable to the models considered here. Thus the present results seem to be new.

## 2 The models and their quasi-stationary distributions

Let us consider a cohort of hosts being born at time 0; thus, age and time will be equivalent. The state of a host of age  $a$ , conditioning on its survival to age  $a$ , will be a single random variable,  $M(a)$ , the number of parasites infecting that host. The main assumptions of the model (compare to [12]) are the following:

1. Hosts are born free of parasites, i.e.  $M(0) = 0$ .
2. For each host, new infections occur as a Poisson process of rate  $\varphi$ .
3. Let  $\sigma(m)$  be the *per capita* mortality rate of parasites, generally dependent by the number  $m$  of parasites present in the host.
4. Let  $\mu(m)$  be the mortality rate of hosts, generally dependent by the number  $m$  of parasites present in the host.

Thus, for a host of age  $a$  and such that  $M(a) = m$ , there are three possible transitions:

- to  $m + 1$  at rate  $\varphi$ ;
- to  $m - 1$  at rate  $m\sigma(m)$ ;
- the host may die at rate  $\mu(m)$ .

Let now:

$$q_m(a) = \mathbf{P}(\text{the host survives to age } a \text{ and } M(a) = m) \tag{2.1}$$

and

$$p_m(a) = \mathbf{P}(M(a) = m \mid \text{the host survives to age } a) = \frac{q_m(a)}{S(a)} \quad (2.2)$$

where

$$S(a) = \mathbf{P}(\text{the host survives to age } a) = \sum_{m \geq 0} q_m(a). \quad (2.3)$$

Note that this process can be formulated as a continuous-time Markov chain, whose states are all non-negative integers (the number of parasites a host harbours) plus an extra (absorbing) state corresponding to a dead host. The probabilities  $p_m(a)$  are the probabilities conditional to non-absorption, as discussed for instance in [19, 25, 24].

Under the present assumptions (the rate of up-transitions is a constant  $\varphi$ ), the Markov process will be regular [8]. Thus  $q_m(a)$  will satisfy the forward Kolmogorov equations:

$$\frac{d}{da} q_m(a) = -(\mu(m) + \varphi + m\sigma(m)) q_m(a) + \varphi q_{m-1}(a) + (m+1)\sigma(m+1) q_{m+1}(a) \quad (2.4)$$

with the convention  $q_{-1}(a) \equiv 0$  and the initial conditions:

$$q_0(0) = 1 \quad q_m(0) = 0, \quad m \geq 1. \quad (2.5)$$

One has to add an equation for the absorption probability; in the previous notation, it easier to add all equations (2.4) and obtain

$$S'(a) = - \sum_{m=0}^{\infty} \mu(m) q_m(a). \quad (2.6)$$

Finally, noting that

$$\frac{d}{da} p_m(a) = \frac{q'_m(a)}{S(a)} - \frac{S'(a)}{S(a)} p_m(a), \quad (2.7)$$

we can obtain a system of equations for  $p_m(a)$ , the quantities of our interest. This will be done explicitly for the models considered below.

It is expectable that  $p_m(a)$  converge, as  $a$  goes to infinity, to a limiting distribution. This problem has been extensively studied by several authors [19, 25, 17, 24]. In the terminology of [24], a quasi-stationary distribution is a probability distribution  $\{\bar{p}_n\}$  such that, if  $p_n(0) = \bar{p}_n$ ,  $p_n(a) = \bar{p}_n$  for all

$a > 0$ . As proved in Theorem 5 by [25],  $\{\bar{p}_n\}$  will satisfy the eigenvector equation:

$$-(\varphi + \mu(0))\bar{p}_0 + \sigma(1)\bar{p}_1 = -r\bar{p}_0 \quad (2.8)$$

$$\varphi\bar{p}_{m-1} - (\varphi + \mu(m) + m\sigma(m))\bar{p}_m + (m+1)\sigma(m+1)\bar{p}_{m+1} = -r\bar{p}_m \quad m \geq 1 \quad (2.9)$$

where

$$r = -\lim_{a \rightarrow \infty} a^{-1} \log S(a). \quad (2.10)$$

Here we will study (2.8) only in three submodels of the general model (2.4); for these cases we will prove directly existence and uniqueness of solutions of (2.8), and will also prove the convergence of  $p_n(a)$ . Then we will consider the ratio of the variance to the mean (the *dispersion index*) for these quasi-stationary distributions  $\{\bar{p}_n\}$ .

For the sake of comparison, we start by considering the basic model studied by [12]. There  $\sigma(m) \equiv \sigma$  (no density-dependence in parasites' death rate), while  $\mu(m) = \mu + \alpha m$  (linear law for parasite-induced mortality). Then

$$\frac{d}{da} S(a) = -(\mu + \alpha \bar{m}(a)) S(a) \quad (2.11)$$

where

$$\bar{m}(a) = \mathbf{E}(M(a) | \text{host survival to age } a),$$

and

$$\frac{d}{da} p_m(a) = -(\varphi + m(\sigma + \alpha) - \alpha \bar{m}(a)) p_m(a) + \varphi p_{m-1}(a) + (m+1)\sigma p_{m+1}(a). \quad (2.12)$$

It can be seen, for instance by the use of the generating function [12], that the solution of (2.12) is a Poisson distribution of parameter

$$\lambda(a) = \frac{\varphi}{\sigma + \alpha} (1 - e^{-(\sigma + \alpha)a}).$$

Thus, at each age  $a$ , its dispersion index is 1.

## 2.1 Model 1. Density-dependence in parasites' death rate

In the first model we make the following assumptions:

$$\text{H1) } \sigma(m+1) \geq \sigma(m) > 0 \text{ for all } m \geq 1.$$

$$\text{H2) } \mu(m) \equiv \mu > 0 \text{ for all } m \geq 0.$$

From (2.6), we see that  $S(a) = e^{-\mu a}$  so that in (2.8)  $r = \mu$ . Then (2.8) becomes

$$0 = -\varphi p_0 + \sigma(1)p_1 \tag{2.13}$$

$$0 = \varphi p_{m-1} - (\varphi + m\sigma(m)) p_m + (m+1)\sigma(m+1)p_{m+1}. \tag{2.14}$$

Starting from  $p_0$  one obtains iteratively, using (2.13)

$$p_n = p_0 \frac{\varphi^n}{n! \prod_{i=1}^n \sigma(i)} \quad n \geq 1. \tag{2.15}$$

Since  $\sum_{n=0}^{\infty} p_n$  converges, one can normalize  $p_n$  to obtain a unique probability distribution solution of (2.13).

One may note that the conditional probabilities  $p_n(a)$  satisfy the system

$$\frac{d}{da} p_m(a) = -(\varphi + m\sigma(m)) p_m(a) + \varphi p_{m-1}(a) + (m+1)\sigma(m+1)p_{m+1}(a). \tag{2.16}$$

They are thus identical to the probabilities of a birth-and-death process with up-rate  $\varphi$  and down-rate  $n\sigma(n)$  and no absorbing state. It then follows from standard theory [8] that  $p_n(a)$  will converge to a limiting distribution, that must be (2.15) normalized.

## 2.2 Model 2. Threshold parasite-induced mortality

In the second model, we assume that parasites do not induce any mortality on hosts as long as they are not above a threshold level  $N$ ; as a host harbours  $N+1$  parasites, its mortality becomes infinite. Furthermore, we assume no density-dependence in parasites' death rate.

Without invoking explicitly infinite transition rates, the model can be described as follows:



The possible values of  $M(a)$ , the number of parasites a host that has survived to age  $a$  harbours, are  $0, 1, \dots, N$ .

If  $M(a) = m$ , the possible transitions are:

- to  $m + 1$  at rate  $\varphi$ , if  $m < N$ ;
- to  $m - 1$  at rate  $m\sigma$ ;
- the host dies at rate  $\mu$  if  $m < N$ , at rate  $\mu + \varphi$  if  $m = N$ .

Like the previous ones, this model can be formulated as a (finite) Markov chain with  $N + 1$  states plus an extra absorbing state corresponding to a dead host.

With the previous definitions of  $q_m(a)$ ,  $p_m(a)$  and  $S(a)$ , one obtains the following differential equations:

$$\frac{d}{da}q_m(a) = -(\mu + \varphi + m\sigma)q_m(a) + \varphi q_{m-1}(a) + (m+1)\sigma q_{m+1}(a) \quad (2.17)$$

$$\text{for } m = 0, \dots, N-1 \quad (2.18)$$

$$\frac{d}{da}q_N(a) = -(\mu + \varphi + N\sigma)q_N(a) + \varphi q_{N-1}(a) \quad (2.19)$$

with initial conditions (2.5);

$$S'(a) = -\mu S(a) - \varphi q_N(a). \quad (2.20)$$

From (2.7), one then obtains:

$$\frac{d}{da}p_m(a) = -(\varphi + m\sigma - \varphi p_N(a))p_m(a) + \varphi p_{m-1}(a) + (m+1)\sigma p_{m+1}(a) \quad (2.21)$$

$$\text{for } m = 0, \dots, N-1 \quad (2.22)$$

$$\frac{d}{da}p_N(a) = -(\varphi + N\sigma - \varphi p_N(a))p_N(a) + \varphi p_{N-1}(a) \quad (2.23)$$

A quasi-stationary distribution will be a solution of

$$-rp_m = -(\varphi + m\sigma)p_m + \varphi p_{m-1} + (m+1)\sigma p_{m+1} \quad m = 0, \dots, N-1 \quad (2.24)$$

$$-rp_N = -(\varphi + N\sigma)p_N + \varphi p_{N-1} \quad (2.25)$$

for an appropriate  $r$  (note that the term  $-rp_m$  on the left hand side includes a term  $-\mu p_m$  originally on the right hand side of (2.8)).

In other words,  $p$  must be a positive eigenvector of

$$A = \begin{pmatrix} -\varphi & \sigma & 0 & \dots & 0 \\ \varphi & -\varphi - \sigma & 2\sigma & \ddots & \vdots \\ 0 & \ddots & \ddots & \ddots & 0 \\ \vdots & \ddots & \varphi & -\varphi - (N-1)\sigma & N\sigma \\ 0 & \dots & 0 & \varphi & -\varphi - N\sigma \end{pmatrix} \quad (2.26)$$

corresponding to a negative eigenvalue  $-r$ .

Since  $A$  has nonnegative entries in all non-diagonal terms, we can apply Perron-Frobenius theory (see, for instance, [4]) to  $A + cI$  for  $c$  large enough. Clearly, the eigenvectors of  $A + cI$  are the same as those of  $A$ , while its eigenvalues are shifted of the quantity  $c$ ; hence the results for  $A + cI$  translate directly into results for  $A$ . Since  $A + cI$  is irreducible,  $A$  has a unique (apart from multiplicative constants) positive eigenvector. Setting  $v_n = \frac{\varphi^n}{\sigma^n n!}$ ,  $n = 0, \dots, N$ , we see that  $Av \leq 0$ ; hence (Th. 2.1.11 in [4]), the corresponding eigenvalue is negative. It follows that there exists a unique quasi-stationary distribution solution of (2.25).

Since the state space is finite, applying the results of [19], one has that  $p_n(a)$  converge to this unique quasi-stationary distribution.

### 2.3 Model 3. Constant parasite-induced mortality

In the third model, we assume that the value of parasite-induced mortality is a constant  $\alpha$ , as long as a host has at least one parasite. Thus, starting from equations (2.4), we make the following assumptions:

H1')  $\sigma(m) \equiv \sigma > 0$  for all  $m \geq 0$ .

H2')  $\mu(0) = \mu > 0$ ;  $\mu(m) = \mu + \alpha > \mu$  for all  $m \geq 1$ .

Then from (2.7), we obtain:

$$\frac{d}{da} p_m(a) = -(\varphi + \alpha + m\sigma - \alpha T_1(a)) p_m(a) + \varphi p_{m-1}(a) + (m+1)\sigma p_{m+1}(a) \quad m \geq 1 \quad (2.27)$$

$$\frac{d}{da}p_0(a) = -(\varphi - \alpha T_1(a))p_0(a) + \sigma p_1(a) \quad (2.28)$$

where

$$T_1(a) = \sum_{i \geq 1} p_i(a). \quad (2.29)$$

One may note that  $p_m(a)$  satisfy the same equations as the (unconditional) probabilities of an immigration–and–death–and–catastrophe process with catastrophe rate  $\alpha p_0(a)$ . In order to prove convergence of  $p_m(a)$  to a quasi-stationary distribution for this model, we study some properties of immigration–and–death–and–catastrophe processes, starting from their definition.

**Definition 1** *An immigration–and–death–and–catastrophe process with catastrophe rate  $c(t)$  is a non-stationary Markov process on the nonnegative integers with transition rates  $\varphi$  from  $n$  to  $n + 1$ ,  $\sigma n$  from  $n$  to  $n - 1$ ,  $c(t)$  from  $n$  to  $0$ .*

**Remark 1** *Following standard method, an immigration–and–death–and–catastrophe process  $X(t)$ ,  $t \geq 0$  with the given rates and initial distribution at time  $t = 0$  equal to  $\pi_0$ , can be constructed as follows: on a sample space  $\Omega$  we define, all independent of each other,:*

- *a Poisson process  $Z_0(t)$  of rate  $\varphi$ , whose jump times will be defined  $\tau_1, \tau_2 \dots$*
- *a Poisson process  $Z_1(t)$  of rate  $c(t)$ .*
- *two sequences  $\{E_1, E_2, \dots\}$  and  $\{\tilde{E}_1, \tilde{E}_2, \dots\}$  of independent random variables with exponential distribution of parameter  $\sigma$ .*
- *a random variable  $X_0$  on the nonnegative integers with distribution  $\pi_0$ .*

Let then be

$$I_j(t) = I[\tau_j \leq t]I[\tau_j + E_j > t]I[Z_1(t) = Z_1(\tau_j)] \quad (2.30)$$

$$\tilde{I}_j(t) = I[\tilde{E}_j > t]I[Z_1(t) = 0] \quad (2.31)$$

where  $I[A]$  denotes the indicator function of the set  $A$ .

Then

$$X(t) = \sum_{j=1}^{X_0(\omega)} \tilde{I}_j(t) + \sum_{j \geq 1} I_j(t) \quad (2.32)$$

is a Markov process that satisfies the given rules on the rates. Note than in (2.32) the sums are finite w.p. 1.

The first result on immigration–and–death–and–catastrophe processes is a monotonicity result. We first recall a stochastic ordering between probability measures on  $\mathbf{N}$ . We remind the following

**Definition 2** If  $\mathbf{p} = \{p_n, n \geq 0\}$  and  $\tilde{\mathbf{p}} = \{\tilde{p}_n, n \geq 0\}$  are two probability measures on  $\mathbf{N}$ ,  $\mathbf{p} \leq \tilde{\mathbf{p}}$  if

$$T_n = \sum_{i=n}^{\infty} p_i \leq \tilde{T}_n = \sum_{i=n}^{\infty} \tilde{p}_i \quad \text{for all } n \geq 0. \quad (2.33)$$

This definition is a special case of the general ordering between probability measures on ordered spaces (see for instance [14]) and is discussed in [13].

Given two random variables  $X_1$  and  $X_2$  with distributions  $\pi_1$  and  $\pi_2$ , we say that  $X_1 \stackrel{\leq}{\mathbf{d}} X_2$  (in words,  $X_1$  is *distributionally smaller* than  $X_2$ ) if  $\pi_1 \leq \pi_2$  according to the previous definition [21]. Under such circumstances, one can construct a random variable  $X = (X_1, X_2)$  on a probability space  $\Omega$  such that  $X_1 \leq X_2$  w.p. 1, and  $X_i$  has distribution  $\pi_i$  [14].

**Lemma 1** Let  $X_1(t)$  and  $X_2(t)$  be immigration–and–death–and–catastrophe processes with the same immigration and death rate ( $\varphi$  and  $\sigma$ ) and with catastrophe rate  $c_1(t)$  and  $c_2(t)$ . Let

$$c_1(t) \leq c_2(t) \text{ for } t \geq 0 \quad \text{and} \quad X_2(0) \stackrel{\leq}{\mathbf{d}} X_1(0). \quad (2.34)$$

Then  $X_2(t) \stackrel{\leq}{\mathbf{d}} X_1(t)$  for all  $t \geq 0$ .

**Proof** The proof is by a coupling argument, repeating the construction of Remark 1. Let  $\pi_i$  be the distribution of  $X_i(0)$ . Assume we have on a sample space  $\Omega$ , all independent of each other:

- a Poisson process  $Z_0(t)$  of rate  $\varphi$ , whose jump times will be defined  $\tau_1, \tau_2, \dots$
- a Poisson process  $Z_1(t)$  of rate  $c_1(t)$ .
- a Poisson process  $Z_2(t)$  of rate  $c_2(t) - c_1(t)$ .
- two sequences  $\{E_1, E_2, \dots\}$  and  $\{\tilde{E}_1, \tilde{E}_2, \dots\}$  of independent random variables with exponential distribution of parameter  $\sigma$ .
- a random variable  $X_0 = (X_0^1, X_0^2) : \Omega \rightarrow \mathbf{N}^2$  such that  $X_0^2 \leq X_0^1$  w.p. 1, and  $X_0^i$  has distribution  $\pi_i$ .

Let then be

$$I_j^1(t) = I[\tau_j \leq t]I[\tau_j + E_j > t]I[Z_1(t) = Z_1(\tau_j)] \quad (2.35)$$

$$I_j^2(t) = I_j^1(t)I[Z_2(t) = Z_2(\tau_j)] \leq I_j^1(t) \quad (2.36)$$

$$\tilde{I}_j^1(t) = I[\tilde{E}_j > t]I[Z_1(t) = 0] \quad (2.37)$$

$$\tilde{I}_j^2(t) = \tilde{I}_j^1(t)I[Z_2(t) = 0] \leq \tilde{I}_j^1(t). \quad (2.38)$$

Then setting

$$X_1(t) = \sum_{j=1}^{X_0^1(\omega)} \tilde{I}_j^1(t) + \sum_{j \geq 1} I_j^1(t) \geq \sum_{j=1}^{X_0^2(\omega)} \tilde{I}_j^2(t) + \sum_{j \geq 1} I_j^2(t) = X_2(t) \quad (2.39)$$

we see  $X_1(t)$  and  $X_2(t)$  are Markov processes that satisfy the given rules on the rates. ■

**Corollary 2** *If  $X(t)$  is an immigration-and-death-and-catastrophe process such that  $X(0) = 0$ , then its distribution  $p(t)$  satisfies, for all  $t \geq 0$ ,  $p(t) \leq P(\frac{\varphi}{\sigma})$  in the sense of (2.33) where  $P(\lambda)$  denotes a Poisson distribution of parameter  $\lambda$ .*

**Proof** Use Lemma 1 with  $X_2(t) = X(t)$  and  $X_1(t)$  an immigration-and-death process ( $c(t) \equiv 0$ ) such that  $X_1(0) = 0$ . It is well known [3] that  $X_1(t)$  has a Poisson distribution of parameter  $\frac{\varphi}{\sigma}(1 - e^{-\sigma t})$  which is clearly smaller than  $P(\frac{\varphi}{\sigma})$ .

We now consider immigration–and–death–and–catastrophe processes with constant catastrophe rate  $c$ . As stated above, such processes are regular, hence there exists a unique stationary probability distribution denoted as  $\bar{p}(c)$ , stressing the dependence on the catastrophe rate  $c$ .  $\bar{p}(c)$  are solution of

$$0 = -\varphi\bar{p}_0 + \sigma\bar{p}_1 + c \sum_{m=1}^{\infty} \bar{p}_m \quad (2.40)$$

$$0 = \varphi\bar{p}_{m-1} - (\varphi + c + m\sigma)\bar{p}_m + (m+1)\sigma\bar{p}_{m+1} \quad m \geq 1 \quad (2.41)$$

Since  $\sum_{m=0}^{\infty} \bar{p}_m = 1$ , the first equation may be rewritten also as

$$0 = -\varphi\bar{p}_0 + \sigma\bar{p}_1 + c(1 - \bar{p}_0). \quad (2.42)$$

We state a comparison principle for limiting distributions of immigration–and–death–and–catastrophe processes.

**Lemma 3** *Consider an immigration–and–death–and–catastrophe process  $X(t)$  with catastrophe rate  $c(t)$  such that*

$$\underline{c} \leq c(t) \leq \bar{c} \text{ for } t \geq T. \quad (2.43)$$

Let  $p_0(t) = \mathbf{P}(X(t) = 0)$ . Then

$$\bar{p}_0(\underline{c}) \leq \liminf p_0(t) \leq \limsup p_0(t) \leq \bar{p}_0(\bar{c}). \quad (2.44)$$

**Proof** Let  $\underline{V}$  be a Poisson random variable of parameter  $\frac{\underline{c}}{\sigma}$ . Letting  $X^{\underline{c}}(t)$  and  $X^{\bar{c}}(t)$  be immigration–and–death–and–catastrophe processes with constant catastrophe rates  $\underline{c}$  and  $\bar{c}$ , respectively we have, by Lemma 1 restricted to  $t \geq T$ , using also Corollary 2,

$$\mathbf{P}(X^{\underline{c}}(t) = 0 | X^{\underline{c}}(T) = V) \leq p_0(t) \leq \mathbf{P}(X^{\bar{c}}(t) = 0 | X^{\bar{c}}(T) = 0). \quad (2.45)$$

Standard results on Markov chains imply that, when  $t$  goes to  $\infty$ , the rightmost term tends to  $\bar{p}_0(\bar{c})$ , yielding the right inequality in (2.44).

As for the leftmost term, it can be written as

$$\sum_{i=0}^{\infty} \pi_i p_{i0}^c(t - T) \quad (2.46)$$

where

$$\pi_i = \mathbf{P}(V = i) \quad \text{and} \quad p_{ij}^c(t) = \mathbf{P}(X^c(t) = j | X^c(0) = i). \quad (2.47)$$

Again standard Markov chain theory implies

$$p_{ij}^c(t) \rightarrow \bar{p}_0(\underline{c}) \text{ as } t \rightarrow \infty. \quad (2.48)$$

Then, since  $p_{i0}^c(t) < 1$ , we can apply Lebesgue's dominated convergence theorem to (2.46), and obtain that the leftmost term in (2.45) converges to  $\bar{p}_0(\underline{c})$ , yielding the left inequality in (2.44).

[Andrew: is the argument that simple? I seem to remember an argument like: Lemma 1 shows that  $p_{i0}^c(t)$  is monotonically decreasing, hence  $p_{i0}^c(t) \leq p_{00}^c(t)$  but this seems useless.] ■

Let us now define the function

$$G : [0, 1] \rightarrow [0, 1] \quad (2.49)$$

$$q \rightarrow \bar{p}_0(\alpha q) \quad (2.50)$$

We have

**Lemma 4** *G is a continuous function; there exists  $q^* \in (0, 1)$  such that  $G(q) < q$  for  $q \in (0, q^*)$ ,  $G(q) > q$  for  $q \in (q^*, 1)$ .*

**Proof** The continuity of  $G$  follows from standard results on Markov chains [Andrew: is that true?].

When  $q = 0$ , there are no catastrophes; hence the stationary distribution is Poisson of parameter  $\varphi/\sigma$  so that  $G(0) = e^{-\varphi/\sigma} > 0$ . On the other hand,  $\bar{p}_0(\alpha) < 1$ , so that  $G(1) < 1$ . From this it follows that there exists at least a fixed point  $q^*$  of  $G$ .

In order to prove the thesis, we only need to prove uniqueness of  $q^*$ .

Assume that  $q$  and  $\tilde{q}$  are fixed points of  $G$  with  $q < \tilde{q}$ . Let us denote  $p$  or  $\tilde{p}$  the solution of (2.41) with  $c = \alpha q$  or  $\tilde{c} = \alpha \tilde{q}$ . First note that from Lemma 1 it follows that, if  $c \leq \tilde{c}$ ,  $p_0 \leq \tilde{p}_0$ .

Let us define

$$u_n = p_n/p_{n-1} \quad n \geq 1 \quad (2.51)$$

and analogously  $\tilde{u}_n$ . From (2.41) or (2.42) we obtain:

$$u_1 = \frac{\varphi - \alpha q \frac{1-p_0}{p_0}}{\sigma} = \frac{\varphi - \alpha + \alpha q}{\sigma} \quad (2.52)$$

$$\tilde{u}_1 = \frac{\varphi - \alpha \tilde{q} \frac{1-\tilde{p}_0}{\tilde{p}_0}}{\sigma} = \frac{\varphi - \alpha + \alpha \tilde{q}}{\sigma} \quad (2.53)$$

$$\begin{aligned} u_{n+1} &= \frac{\varphi + \alpha q + n\sigma - \frac{\varphi}{u_n}}{(n+1)\sigma} \\ \tilde{u}_{n+1} &= \frac{\varphi + \alpha \tilde{q} + n\sigma - \frac{\varphi}{\tilde{u}_n}}{(n+1)\sigma} \end{aligned} \quad (2.54)$$

remembering that, by assumption,  $p_0(\alpha q) = q$  and  $p_0(\alpha \tilde{q}) = \tilde{q}$ .

Equations (2.54) show that  $u_1 < \tilde{u}_1$  and, from  $u_n < \tilde{u}_n$ , it follows  $u_{n+1} < \tilde{u}_{n+1}$ . Iteratively, we thus obtain  $u_n < \tilde{u}_n$  for all  $n$ ; hence, using also  $p_0 \leq \tilde{p}_0$ , we obtain  $p_n < \tilde{p}_n$  for all  $n$ , which is in contrast with  $\sum_{n=0}^{\infty} p_n = 1 = \sum_{n=0}^{\infty} \tilde{p}_n$ . ■

**Remark 2** Note that  $\bar{p}(\alpha q^*)$ , the quasi-stationary distribution corresponding to the fixed point of  $G$ , is an eigenvector of the infinite matrix

$$A = \begin{pmatrix} -\varphi & \sigma & 0 & \dots & \dots & \dots \\ \varphi & -\varphi - \alpha - \sigma & 2\sigma & \ddots & \ddots & \ddots \\ 0 & \ddots & \ddots & \ddots & \ddots & \ddots \\ \vdots & \ddots & \varphi & -\varphi - \alpha - n\sigma & (n+1)\sigma & \ddots \\ \vdots & \ddots & \ddots & \ddots & \ddots & \ddots \end{pmatrix} \quad (2.55)$$

with eigenvalue  $-r = -\alpha(1 - q^*)$ . It can also be proved that it is the unique (apart from a multiplicative factor) nonnegative eigenvector of  $A$ , but this is not needed.

We now are in the conditions to prove



**Theorem 1**  $p_n(a)$ , the solutions of (2.28) converge, as  $a$  goes to  $\infty$ , to a unique  $\mathbf{p}$ ;  $\mathbf{p} = \bar{p}(\alpha q^*)$  from Lemma 4, and is also the unique (normalized) positive eigenvector of the infinite matrix  $A$ . Moreover  $\mathbf{p} \leq P\left(\frac{\varphi}{\sigma}\right)$  in the sense of (2.33).

**Proof** Let

$$\underline{p}_0 = \liminf_{t \rightarrow \infty} p_0(t) \quad \text{and} \quad \bar{p}_0 = \limsup_{t \rightarrow \infty} p_0(t). \quad (2.56)$$

Assume  $\bar{p}_0 > r^*$ . Then, by Lemma 4,  $G(\bar{p}_0) < \bar{p}_0$ ; choose  $\varepsilon$  such that  $G(\bar{p}_0 + \varepsilon) < \bar{p}_0$ . Choose  $T$  such that

$$p_0(t) \leq \bar{p}_0 + \varepsilon \quad \forall t \geq T.$$

Considering  $p_0(t)$  to be a given function, we see that the solutions of (2.28) are those of an immigration-and-death-and-catastrophe process with catastrophe rate  $\alpha p_0(t)$ . We can then apply the right inequality of Lemma 3 to obtain

$$\limsup_{t \rightarrow \infty} p_0(t) \leq \bar{p}_0(\alpha(\bar{p}_0 + \varepsilon)) = G(\bar{p}_0 + \varepsilon) < \bar{p}_0 \quad (2.57)$$

in contradiction with the initial assumption. Hence

$$\limsup_{t \rightarrow \infty} p_0(t) \leq r^*. \quad (2.58)$$

Analogously, it can be proved

$$\liminf_{t \rightarrow \infty} p_0(t) \geq r^* \quad (2.59)$$

Hence  $\lim_{t \rightarrow \infty} p_0(t) = r^*$ .

From the convergence of  $p_0(t)$ , the convergence of  $p_n(t)$  for all  $n \geq 1$  follows easily. [Andrew: is that true?]

The last claim of thesis follows from Corollary 2. ■

### 3 Under- or over-dispersion of the distributions considered

We start by considering a general criterion for the under- or over-dispersion of a distribution.

**Definition 3** Let  $X$  be a random variable (with distribution  $p$ ) taking values in the nonnegative integers. We say that  $X$  (or  $p$ ) is under-dispersed if

$$\mathbf{V}(X) < \mathbf{E}(X) < +\infty. \quad (3.1)$$

We say that  $X$  (or  $p$ ) is over-dispersed if

$$\mathbf{E}(X) < \mathbf{V}(X) \leq +\infty. \quad (3.2)$$

We state a criterion for the dispersion of distributions satisfying the following assumption:

(H) If  $p_n = 0$ , then  $p_{n+1} = 0$ .

In other words, under assumption (H), either  $p_n > 0$  for all  $n \geq 0$ ; or there exists  $N \geq 0$  such  $p_n > 0$  for  $n = 0, \dots, N$ ,  $p_n = 0$  for all  $n > N$ .

Given a probability distribution  $\mathbf{p} = \{p_n\}$  satisfying assumption (H), we define, as in (2.51), for  $n \geq 1$ ,

$$u_n = \begin{cases} p_n/p_{n-1} & \text{if } p_{n-1} > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (3.3)$$

Because of assumption (H) it is clear that

$$p_n = p_0 \prod_{i=1}^n u_i; \quad (3.4)$$

with the convention that  $\prod_{i=m}^n u_i = 1$  whenever  $m > n$ .

The criterion anticipated above is the following

**Theorem 2** Let  $X$  be a random variable with values on the nonnegative integers with distribution  $\mathbf{p} = \{p_n\}$  satisfying assumption (H). If the sequence  $\{nu_n\}$  is non-increasing and not constant, then  $X$  is under-dispersed. If  $\{nu_n\}$  is non-decreasing and not constant and  $\mathbf{E}(X)$  exists, then  $X$  is over-dispersed.

**Remark 3** Note that for a Poisson distribution, that is just the limiting case between under- and over-dispersion, the sequence  $\{nu_n\}$  is constant.

**Proof** Choose  $\lambda \in \mathbf{R}$  and a function  $g : \mathbf{N} \rightarrow \mathbf{R}$  such that the following expectations exist. Then

$$\lambda \mathbf{E}(g(X+1)) - \mathbf{E}(Xg(X)) = \sum_{n=1}^{\infty} g(n)(\lambda p_{n-1} - np_n) = \sum_{n=1}^{\infty} g(n)p_{n-1}(\lambda - nu_n). \quad (3.5)$$

If  $\{nu_n\}$  is non-increasing, choosing  $\lambda = u_1$  and  $g(n) = I_{[0, N]}$ , one obtains from (3.5)

$$\sum_{n=1}^N np_n \leq u_1 \sum_{n=0}^{N-1} p_n \leq u_1. \quad (3.6)$$

Hence  $\mathbf{E}(X) \leq u_1$ . In any case, it can then be assumed that  $\mathbf{E}(X)$  exists, since, when  $\{nu_n\}$  is non-decreasing, this is part of the assumptions.

Using then (3.5) with  $\lambda = \mathbf{E}(X)$  and  $g(n) \equiv 1$ , one obtains

$$0 = \sum_{n=1}^{\infty} p_{n-1}(\mathbf{E}(X) - nu_n). \quad (3.7)$$

Taking instead  $\lambda = \mathbf{E}(X)$  and  $g(n) = n$  in (3.5), one obtains

$$\mathbf{E}(X) - \mathbf{V}(X) = \sum_{n=1}^{\infty} np_{n-1}(\mathbf{E}(X) - nu_n). \quad (3.8)$$

If  $\{nu_n\}$  is non-increasing, choose  $a \in \mathbf{R}$  such that

$$\min_{n < a} (\mathbf{E}(X) - nu_n) \leq 0 \quad \text{and} \quad \sup_{n > a} (\mathbf{E}(X) - nu_n) \geq 0 \quad (3.9)$$

or the opposite inequalities if  $\{nu_n\}$  is non-decreasing. Such an  $a$  exists because of (3.7).

Subtracting (3.7) multiplied by  $a$  from (3.8), one obtains

$$\mathbf{E}(X) - \mathbf{V}(X) = \sum_{n=1}^{\infty} (n-a)p_{n-1}(\mathbf{E}(X) - nu_n). \quad (3.10)$$

Because of (3.9), (3.10) implies  $\mathbf{E}(X) > \mathbf{V}(X)$  if  $\{nu_n\}$  is non-increasing;  $\mathbf{E}(X) < \mathbf{V}(X)$  (the latter possibly infinite) if  $\{nu_n\}$  is non-decreasing. ■

**Remark 4** *Actually, under the assumption that  $\{nu_n\}$  is non-increasing [non-decreasing], a stronger statement can be obtained. Let*

$$\tilde{p}_n = \frac{np_n}{\mathbf{E}(X)} \quad (3.11)$$

and  $\tilde{X}$  a random variable with distribution  $\tilde{p}$ . Usually in our models,  $X$  represents the number of parasites in a randomly chosen host; then  $\tilde{X}$  represents the number of parasites present in the host that harbours a randomly chosen parasite.

Then (3.5) with  $\lambda = \mathbf{E}(X)$  can be read as

$$\mathbf{E}(g(X+1) - \mathbf{E}(g(\tilde{X}))) = \sum_{n=1}^{\infty} g(n)p_{n-1}(\lambda - nu_n). \quad (3.12)$$

If  $g$  is a non-decreasing function, with the same choice (3.9) of  $a$  used for (3.10), we have

$$\mathbf{E}(g(X+1) - \mathbf{E}(g(\tilde{X}))) = \sum_{n=1}^{\infty} (g(n) - g(a))p_{n-1}(\lambda - nu_n) > [<]0 \quad (3.13)$$

when  $\{nu_n\}$  is non-increasing [non-decreasing].

In other words, we have obtained that when  $\{nu_n\}$  is non-increasing [non-decreasing],  $\tilde{X} \stackrel{<}{\underset{d}{\leq}} [\stackrel{>}{\underset{d}{\geq}}] X + 1$ .

From (3.13) one can obtain several consequences. For instance, choosing

$$g(n) = (n)_k = n(n-1)\cdots(n-k+1) \quad (3.14)$$

one obtains

$$\mathbf{E}((X)_k) = \mathbf{E}((\tilde{X}-1)_{k-1}) \cdot \mathbf{E}(X) \leq [\geq] \mathbf{E}((X)_{k-1}) \cdot \mathbf{E}(X) \quad (3.15)$$

when  $\{nu_n\}$  is non-increasing [non-decreasing]. (3.15) for  $k=2$  is just (3.10); using (3.15) iteratively yields

$$\mathbf{E}((X)_k) \leq [\geq] (\mathbf{E}(X))^k \quad (3.16)$$

for all  $k$ .

Remembering that, if  $X$  is a Poisson random variable,  $\mathbf{E}((X)_k) = (\mathbf{E}(X))^k$ , (3.16) shows that when  $\{nu_n\}$  is non-increasing [non-decreasing],  $X$  is factorially smaller [larger] than a Poisson variable with the same mean. The factorial order was introduced in [13].

Now we will use the criterion of Theorem 2 to the quasi-stationary distributions of the models considered in the previous Section.

### 3.1 Model 1

For this model we state

**Theorem 3** *The unique quasi-stationary distribution, solution of (2.13), is under-dispersed.*

**Proof** We start from (2.15) and compute the corresponding sequence  $\{u_n\}$ :

$$u_n = \frac{\varphi}{n\sigma(n)}. \quad (3.17)$$

Then hypothesis H1 says that the sequence  $\{nu_n\}$  is non-increasing. Theorem 2 then yields the thesis. ■

### 3.2 Model 2

For this model we state

**Theorem 4** *The quasi-stationary distribution, solution of (2.25), is under-dispersed.*

In order to study the dispersion pattern of  $\{p_n, n = 0, \dots, N\}$  (the unique positive eigenvector of  $A$  in (2.26)), we switch to the corresponding  $u_n$  obtaining

$$u_1 = \frac{\varphi - r}{\sigma} \quad (3.18)$$

$$u_{n+1} = \frac{\varphi - r + n\sigma - u_n}{(n+1)\sigma} \quad n = 1, \dots, N-1. \quad (3.19)$$

The two following lemmas show some properties of  $\{u_n, n = 1, \dots\}$ .

**Lemma 5**

$$u_n \leq \frac{\varphi}{n\sigma} \quad \forall n \geq 1 \quad (3.20)$$

**Proof** The thesis is true for  $n = 1$  from (3.19), since  $r > 0$ .

Let the thesis be true for  $n$ . Then  $u_{n+1} < \frac{\varphi - r}{(n+1)\sigma}$  which proves the thesis for  $n + 1$ . ■

We also have  $u_n > 0$  for  $n = 1, \dots, N$ . This could be proved from (3.19) using suitable bounds on  $r$ , but it is actually a trivial consequence of positivity of the vector  $p$ .

**Lemma 6**

$$n\sigma u_n > \varphi - r + n\sigma - \frac{\varphi}{u_n} \quad \forall n = 1, \dots, N-1. \quad (3.21)$$

**Proof** For  $n = 1$  the RHS of (3.21) is equal to

$$\varphi - r - \frac{\sigma r}{\varphi - r}$$

which is less than  $\varphi - r$ , the LHS of (3.21).

Let the thesis be true for  $n$ . Substituting (3.19) into the LHS of (3.21) for  $n+1$ , we see that the thesis for  $n+1$  is equivalent to

$$\varphi - r + n\sigma - \frac{\varphi}{u_n} > \varphi - r + (n+1)\sigma - \frac{\varphi}{u_{n+1}}.$$

We thus need to prove

$$\sigma - \frac{\varphi}{u_{n+1}} + \frac{\varphi}{u_n} < 0. \quad (3.22)$$

Now the LHS of (3.22) is equal to

$$\sigma - \frac{(n+1)\varphi\sigma}{(n+1)\sigma u_{n+1}} + \frac{\varphi}{u_n} = \frac{(\sigma + \frac{\varphi}{u_n})(\varphi - r + n\sigma - \frac{\varphi}{u_n}) - (n+1)\varphi\sigma}{\varphi - r + n\sigma - \frac{\varphi}{u_n}} \quad (3.23)$$

$$< \frac{(\sigma + \frac{\varphi}{u_n})n\sigma u_n - (n+1)\varphi\sigma}{(n+1)\sigma u_{n+1}} = \frac{\sigma(n\sigma u_n - \varphi)}{(n+1)\sigma u_{n+1}} < 0 \quad (3.24)$$

as was the thesis. The inequalities in (3.24) come from the inductive hypothesis and from (3.20).

■

**Proof of Theorem 4** Using (3.19), (3.21) just shows that the sequence  $\{nu_n\}$  is decreasing for  $n = 1, \dots, N$ ; after, it is identically equal to 0. Theorem 2 then yields the thesis. ■

### 3.3 Model 3

For this model we state

**Theorem 5** *The unique quasi-stationary distribution, eigenvector of  $A$  (see (2.55)), is over-dispersed.*

We start with the unique quasi-stationary distribution (Theorem 1)  $\mathbf{p} = \{p_n\}$ , switching to the corresponding sequence  $u_n$  given, as shown in (2.54), by:

$$u_1 = \frac{\varphi - r}{\sigma} \quad (3.25)$$

$$u_{n+1} = \frac{\varphi + \alpha - r + n\sigma - \frac{\varphi}{u_n}}{(n+1)\sigma} \quad (3.26)$$

where  $r = \alpha(1 - q^*)$ .

We will show that the sequence  $\{nu_n\}$  is non-decreasing. Let now  $v_n = \sigma nu_n$ . We will need several lemmas on this sequence.

**Lemma 7** *If  $v_n \geq \varphi$ , then  $v_{n+1} \geq \varphi + \alpha - r > \varphi$*

**Proof**

$$v_{n+1} = \varphi + \alpha - r + n\sigma \left(1 - \frac{\varphi}{v_n}\right). \quad (3.27)$$

The proof is completed, since  $r < \alpha$ . ■

Because of Lemma 7, either  $v_n < \varphi$  for all  $n$ ; or there exists  $N$  such that  $v_n > \varphi$  for all  $n > N$ .

The second case is dealt with first.

**Lemma 8** *If  $v_n \geq v_{n-1}$  and  $v_n \geq \varphi$ , then  $v_{n+1} \geq v_n$ .*

**Proof** We have

$$v_{n+1} - v_n = \varphi + \alpha - r + n\sigma - n\sigma \frac{\varphi}{v_n} - v_n \quad (3.28)$$

$$= \varphi + \alpha - r + n\sigma - n\sigma \frac{\varphi}{v_n} - \left(\varphi + \alpha - r + (n-1)\sigma - (n-1)\sigma \frac{\varphi}{v_{n-1}}\right) \quad (3.29)$$

$$= \sigma - n\sigma \frac{\varphi}{v_n} + (n-1)\sigma \frac{\varphi}{v_{n-1}} = \sigma \left(1 - \frac{\varphi}{v_n} + (n-1)\varphi \left(\frac{1}{v_{n-1}} - \frac{1}{v_n}\right)\right) \geq 0 \quad (3.30)$$

because of the two assumptions of the lemma. ■

We need to consider what happens when  $v_n < \varphi$ .

**Lemma 9** *If  $v_n \leq v_{n-1} < \varphi$ , then  $v_{n+1} < v_n$ .*

**Proof** Let

$$G_n(v) = \varphi + \alpha - r + n\sigma \left(1 - \frac{\varphi}{v}\right) - v. \quad (3.31)$$

One sees that  $v_{n+1} < \lfloor v_n$  if and only if  $G_n(v_n) < \lfloor 0$ . It is also easy to see that for each  $n$ , there exists  $v_n^* \in (0, \varphi)$  such that  $G_n(v) < \rfloor 0$  for  $v \in (0, \varphi)$  if and only if  $v < \rfloor v_n^*$ . Finally  $G_n(v) < G_{n-1}(v)$  if  $v \in (0, \varphi)$ . It follows that  $v_n^* > v_{n-1}^*$ .

Our assumptions imply that  $v_n \leq v_{n-1} \leq v_{n-1}^*$ . This, together with the previous inequality, yields  $v_n < v_n^*$ , i.e.  $G_n(v_n) < 0$ . ■

Improving on this lemma, we have

**Lemma 10** *If  $v_n \leq v_{n-1} < \varphi$ , then*

$$v_{n+1} - v_{n-1} \leq -\frac{1}{n-1}(\varphi - v_{n-1}). \quad (3.32)$$

**Proof** By assumption

$$\varphi + \alpha - r - (n-1)\sigma \left(\frac{\varphi}{v_{n-1}} - 1\right) \leq v_{n-1} \quad (3.33)$$

or

$$\frac{\varphi}{v_{n-1}} - 1 \geq \frac{\varphi + \alpha - r - v_{n-1}}{(n-1)\sigma} \quad (3.34)$$

Now

$$v_{n+1} = \varphi + \alpha - r - n\sigma \left(\frac{\varphi}{v_n} - 1\right) \leq \varphi + \alpha - r - n\sigma \left(\frac{\varphi}{v_{n-1}} - 1\right) \quad (3.35)$$

$$\leq \varphi + \alpha - r - \frac{n}{n-1}(\varphi + \alpha - r - v_{n-1}) = -\frac{1}{n-1}(\varphi + \alpha - r) + \frac{n}{n-1}v_{n-1}. \quad (3.36)$$

Hence

$$v_{n+1} - v_{n-1} \leq -\frac{1}{n-1}(\varphi + \alpha - r - v_{n-1}) < -\frac{1}{n-1}(\varphi - v_{n-1}). \quad (3.37)$$

■

**Proof of Theorem 5** Because of Lemma 8, it is impossible that there exists  $N$  such that  $v_{N+1} < v_N$  and  $v_N \geq \varphi$ . Assume there exists  $N$  such that  $v_{N+1} < v_N < \varphi$ . Because of Lemma 9  $v_{n+1} < v_n$  for



all  $n \geq N$ . Using now (3.32), we have

$$v_{N+2p} = v_N + \sum_{i=0}^{p-1} (v_{N+2i+2} - v_{N+2i}) \leq v_N - \sum_{i=0}^{p-1} \frac{1}{N+2i} (\varphi - v_N). \quad (3.38)$$

Letting  $p$  go to  $\infty$ , we would have  $v_{N+2p} \rightarrow -\infty$  against the condition  $v_i > 0$  for all  $i$ . Hence  $v_n$  and thus  $nu_n$  are non-decreasing sequences.

To apply Theorem 2, we need also to prove that  $\mathbf{E}(\mathbf{p})$  is finite. This follows from Theorem 1 that yields  $\mathbf{E}(\mathbf{p}) \leq \frac{\varphi}{\sigma}$ . We can thus apply Theorem 2 and prove Theorem 5. ■

**Remark 5** *Taking all the lemmas together, we have proved that either definitely  $v_n > \varphi$ , or  $v_n < \varphi$  for all  $n$ . However, using (3.28) repeatedly, one sees that in the first case, one would have  $\lim_{n \rightarrow \infty} v_n = +\infty$  which is incompatible with  $\mathbf{p} \leq P(\varphi/\sigma)$  (Theorem 1). Thus, we will have  $v_n < \varphi$  for all  $n$ .*

## 4 Discussion

In this paper, we have studied the variance-to-mean ratio of the quasi-stationary distributions for some models of parasite infection. In particular, we proved that the ratio is less than 1 when there is density-dependence in parasite mortality. By considering two special cases, we have shown that disease-induced mortality may yield either over- or under-dispersed distributions; this result is in contrast with what obtained under the linear law: no influence of disease-induced on the dispersion index. It is not clear from these examples whether one can establish a rule for over- or under-dispersion of the quasi-limiting distribution under a general law of parasite-induced mortality

Clearly processes others than those considered in the present model may have a much greater influence on the distribution of parasites among hosts. The reason for the over-dispersion of the distribution has often been ascribed to differences in the susceptibility to parasites among hosts [2]; another important factor might be the infections with several larvae at a time [12]. Here we simply aimed at better identifying the role of parasite-induced host mortality, and of density-dependence in parasite mortality.

It remains completely open the problem of the dispersion index for the conditional distributions at each time  $t > 0$ . Such a problem has been recently studied by [6] for general Markov chains, without absorbing states however. Even for Model 1 where, as stated above, the conditional probabilities  $p_n(a)$  are identical to the probabilities of a birth-and-death process, their results do not seem to be directly applicable. In fact, using their notation for the present Model 1,  $\lambda(n)m_1(n) = \varphi - n\sigma(n)$  is decreasing in  $n$ ; while

$$m_2(n) = 1 > \frac{\varphi - n\sigma(n)}{\varphi + n\sigma(n)} = m_1(n). \quad (4.1)$$

The two sufficient conditions for establishing over- or under-dispersion are thus mixed.

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Permanent address of authors:

Andrea Pugliese, Dipartimento di Matematica, Università di Trento, Via Sommarive 14, 38050, Povo (TN), Italy

e-mail: pugliese@science.unitn.it

fax: +39-0461881624