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## **Approximating the long-term behaviour of a model for parasitic infection**

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**Abstract.** In a companion paper two stochastic models, useful for the initial behaviour of a parasitic infection, were introduced. Now we analyse the long term behaviour. First a law of large numbers is proved which allows us to analyse the deterministic analogues of the stochastic models. The behaviour of the deterministic models is analogous to the stochastic models in that again *three* basic reproduction ratios are necessary to fully describe the information needed to separate growth from extinction. The existence of stationary solutions is shown in the deterministic models, which can be used as a justification for simulation of quasi-equilibria in the stochastic models. Host-mortality is included in all models. The proofs involve martingale and coupling methods.

### **1. Introduction**

In Luchsinger (2001) [Ls] two *stochastic models* were introduced to model the spread of a parasitic disease. These models were more general versions of the non-linear model proposed in Barbour and Kafetzaki (1993) [BK] and the linear model of Barbour (1994) [Ba] respectively. The generalisation in [Ls] was to introduce host-mortality. One important result of these papers was that the natural candidate for the basic reproduction ratio  $R_0$  does not necessarily contain the information needed to separate growth from extinction of infection. In fact, another ratio,  $R_1$ , was also important in the models without host-mortality; and if host-mortality was included a third ratio  $R_2$  emerged. In Barbour, Heesterbeek and Luchsinger (1996) [BHL] a *linear deterministic model without host-mortality* was investigated. Similar phenomena are seen there, too.

In this paper, two associated *deterministic* models including host-mortality are introduced. Existence and uniqueness of solutions to the differential equations is shown in Theorem 2.1 (linear model) and Theorem 2.5 (non-linear model). The stochastic and deterministic models are linked by laws of large numbers (Theorem 2.3 for the linear models and Theorem 2.5 for the non-linear models). It is then not surprising that the deterministic models inherit the basic reproduction ratios from the stochastic models (Theorem 3.1 for the linear model and Theorem 3.7 for

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the non-linear model) - these threshold-results are of almost purely mathematical interest. In Theorem 3.3 (linear model) and Theorem 3.8 (non-linear model), stationary solutions are found for some parameter regions and ruled out for others. Convergence to these stationary solutions could only be proved for the linear model (Theorem 3.4).

The models in [Ls] have been developed for a disease (schistosomiasis), where endemic areas exist. As the epidemic dies out with probability one in the non-linear stochastic model (Theorem 2.2 in [Ls]), the use of that model for simulations could be questioned. But by Theorem 3.8 in this paper, there is a (non-trivial) stationary solution to the deterministic analogue of that stochastic model. By the law of large numbers (Theorem 2.5) we therefore have a justification to simulate a quasi-equilibrium in the non-linear stochastic model as long as the number of individuals  $M$  is large.

## 2. The models, and the links between the stochastic and deterministic models

The motivation for the following models can be found in [Ls], where two stochastic models, stochastic non-linear (SN)  $x^{(M)}$ , and stochastic linear (SL)  $X$  have been introduced. The definition of models SN and SL is repeated later in this section. In this paper deterministic models are introduced. In comparison to the stochastic models, they only mirror an “average” behaviour of the process. Let  $\xi_j(t)$ ,  $j \geq 0$ , denote the *proportion* of individuals at time  $t$ ,  $t \geq 0$ , who are infected with  $j$  parasites. We assume that  $\xi_j(0) \geq 0$  for all  $j \geq 0$  and that  $\sum_{j \geq 0} \xi_j(0) = 1$  (whereas the equation  $\sum_{j \geq 0} \xi_j(t) = 1$  for all  $t \geq 0$  has to be proved). The parasites have independent lifetimes, exponentially distributed with mean  $1/\mu$ . Each infected individual makes contacts with other individuals at rate  $\lambda$ ; but only those contacts that are with an uninfected individual lead to a new infection (concomitant immunity). Suppose that the infecting individual has  $j$  parasites. Then the result of a contact is to establish a newly infected individual with a random number  $S_j$  of parasites, where  $S_j := \sum_{i=1}^j Y_i$  and the  $Y_i$  are independent and identically distributed with mean  $\theta$  and variance  $\sigma^2 < \infty$ . Define  $p_{jk} := \mathbb{P}[S_j = k]$ , and note that  $\sum_{k \geq 0} p_{jk} = 1$  for each  $j$  and  $\sum_{k \geq 1} k p_{jk} = j\theta$ .

We assume that individuals have independent lifetimes, exponentially distributed with mean  $1/\kappa$ , no matter how high the parasite burden is. All parasites die if their host dies. We allow  $\kappa = 0$ , meaning that people can live for an infinite length of time in that case. The models studied in [BK], [Ba] and [BHL] have  $\kappa = 0$ . In the non-linear models we replace an individual that dies by an uninfected individual. The reader is referred to [Ls] for a critical discussion of the assumptions made so far and the set-up of equations (2.1) and (2.2) ahead. Besides, the reader should read this paper with [BK] and [BHL] at hand as many proofs are similar to the ones in those papers and only necessary changes have been mentioned. The following system of differential equations shows how  $\xi$  will evolve in time:

$$\begin{aligned} \frac{d\xi_j}{dt} &= (j + 1)\mu\xi_{j+1} - j\mu\xi_j + \lambda\xi_0 \sum_{l \geq 1} \xi_l p_{lj} - \kappa\xi_j; \quad j \geq 1, \\ \frac{d\xi_0}{dt} &= \mu\xi_1 - \lambda\xi_0 \left( 1 - \sum_{l \geq 0} \xi_l p_{l0} \right) + \kappa(1 - \xi_0). \end{aligned} \tag{2.1}$$

We call this model DN; this stands for **D**eterministic **N**on-linear.

The linear model, useful in modelling the initial phase of an epidemic outbreak, is defined as follows. Let  $\Xi_j(t)$ ,  $j \geq 1$ , denote the *number* of individuals at time  $t$ ,  $t \geq 0$ , who are infected with  $j$  parasites. We assume that  $\Xi_j(0) \geq 0$  for all  $j \geq 1$ . The following system of differential equations shows how  $\Xi$  will evolve in time:

$$\frac{d\Xi_j}{dt} = (j + 1)\mu\Xi_{j+1} - j\mu\Xi_j + \lambda \sum_{l \geq 1} \Xi_l p_{lj} - \kappa\Xi_j; \quad j \geq 1. \tag{2.2}$$

We call this model DL; this stands for **D**eterministic **L**inear. The difference between model DN and DL is the following: in model DL the contact rate is  $\lambda$  and there is no limiting factor in the model. In model DN the contact rate is altered from  $\lambda$  to  $\lambda\xi_0$ , because only those infectious contacts that are with an uninfected individual lead to a new infection. In DL we restrict our studies to solutions  $\Xi$  for which the following three conditions are satisfied:

$$\begin{aligned} &\sup_{0 \leq s \leq t} \sum_{j \geq 1} \Xi_j(s) < \infty \text{ for all } t \geq 0, \\ &\sum_{j \geq 1} j \Xi_j(0) < \infty, \\ &\text{there exists a } j \geq 1, \text{ such that } \Xi_j(0) > 0. \end{aligned} \tag{2.3}$$

We call these constraints conditions C. They are introduced for technical reasons. In what follows the initial values are at times more general than those specified above: if so, we make it clear.

We restrict our studies to *nonnegative* solutions of DN and DL, even if we do not mention this every time. For this whole paper we use the notation  $\Xi^{(0)}$  and  $\xi^{(0)}$  for a solution of DL and DN respectively if  $\kappa = 0$ .

We repeat the definition of the stochastic models from [Ls]. Consider a model with a fixed number  $M$  of individuals, each of which may carry parasites. Let  $x^{(M)}$  be an infinite dimensional Markov process  $x^{(M)}(\omega, t) : \Omega \times [0, \infty) \rightarrow \{[0, 1] \cap M^{-1}\mathbb{Z}\}^\infty$ . In what follows,  $x_j(t)$ ,  $j \geq 0$ , denotes the *proportion* of individuals at time  $t$ ,  $t \geq 0$ , that are infected with  $j$  parasites, so that  $\sum_{j \geq 0} x_j(t) = 1$  and  $x_j(t) \geq 0$ ,  $j \geq 0$ . We suppress the index  $M$  whenever possible. The rates with which  $x$  changes are as follows:

$$\begin{aligned} x &\rightarrow x + M^{-1}(e_{j-1} - e_j) \text{ at rate } jM\mu x_j; \quad j \geq 1, \\ x &\rightarrow x + M^{-1}(e_k - e_0) \text{ at rate } \lambda M x_0 \sum_{l \geq 1} x_l p_{lk}; \quad k \geq 1, \\ x &\rightarrow x + M^{-1}(e_0 - e_r) \text{ at rate } Mx_r \kappa; \quad r \geq 1, \end{aligned} \tag{2.4}$$

where  $e_i$  denotes the  $i$ -th co-ordinate vector in  $\mathbb{R}^\infty$ . We call this model SN; this stands for **S**tochastic **N**on-linear. We introduce a notation for the sigma-algebra too:  $\mathcal{F}_s := \sigma\{x(u), 0 \leq u \leq s\}$ .

The next model is defined as follows. Let  $X$  be an infinite dimensional Markov process  $X(\omega, t) : \Omega \times [0, \infty) \rightarrow \{[0, \infty) \cap \mathbb{Z}\}^\infty$ , where  $X_j(t)$ ,  $j \geq 1$ , denotes the number of individuals at time  $t$ ,  $t \geq 0$ , that are infected with  $j$  parasites. We assume that  $0 < \sum_{j \geq 1} X_j(0) = n < \infty$  and  $X_j(0) \geq 0$ ,  $j \geq 1$ . The rates at which  $X$  changes are as follows:

$$\begin{aligned} X &\rightarrow X + (e_{j-1} - e_j) \text{ at rate } j\mu X_j; \quad j \geq 2, \\ X &\rightarrow X - e_1 \text{ at rate } \mu X_1; \quad (j = 1), \\ X &\rightarrow X + e_k \text{ at rate } \lambda \sum_{l \geq 1} X_l p_{lk}; \quad k \geq 1, \\ X &\rightarrow X - e_r \text{ at rate } X_r \kappa; \quad r \geq 1. \end{aligned} \tag{2.5}$$

We call this model SL; this stands for **S**tochastic **L**inear. We introduce a notation for the sigma-algebra too:  $\mathcal{G}_s := \sigma\{X(u), 0 \leq u \leq s\}$ .

We first want to find the link between the deterministic linear models with  $\kappa = 0$  and  $\kappa > 0$  respectively. With the help of this link we will prove existence and uniqueness of the solutions to model DL.

It can easily be verified that the solutions  $\Xi^{(0)}$  of DL with  $\kappa = 0$  and the solution  $\Xi$  of DL with  $\kappa \geq 0$  are linked, in that the following equation is satisfied:

$$\Xi_j(t) = \Xi_j^{(0)}(t)e^{-\kappa t}, \tag{2.6}$$

for all  $j \geq 1$ . This should be understood in the sense that if one has a solution to either equation, one gets the solution to the other equation via formula (2.6).

The following theorem is just a translation of Theorem 2.3 in [BHL] and the remark following it using relation (2.6). The reader is therefore referred to [BHL] for further details. It shows that we have a unique nonnegative solution to system DL with  $\kappa \geq 0$ .

**Theorem 2.1.** *The system DL, with  $\Xi(0)$  such that  $0 < \sum_{j \geq 1} \Xi_j(0) < \infty$ , has a unique nonnegative solution satisfying  $\sup_{0 \leq s \leq t} \sum_{j \geq 1} \Xi_j(s) < \infty$  for all  $t \geq 0$ . The solution is given by*

$$\Xi_j(t) = j^{-1} \left( \sum_{l \geq 1} l \Xi_l(0) \mathbb{P}_l [Y(t) = j] \right) e^{(\lambda\theta - \mu - \kappa)t},$$

where  $Y$  is the unique pure jump Markov process defined in chapter 2 in [BHL] and  $\mathbb{P}_l$  denotes probability conditional on  $Y(0) = l$ .

In the linear case the solution to the deterministic model is the expectation of the stochastic model:

**Theorem 2.2.** *Let  $X$  be a Markov process with rates given in SL and with initial state  $X(0)$  satisfying  $\sum_{j \geq 1} X_j(0) =: n < \infty$ , and set  $\Xi(0) := n^{-1}X(0)$ . Then  $y$  defined by*

$$y_j(t) := n^{-1} \mathbb{E}\{X_j(t) | X(0) = n\Xi(0)\}$$

*satisfies the differential equations DL with  $y(0) = \Xi(0)$ , as well as conditions C.*

*Proof.* Theorem 2.2 was proved in [BHL, Theorem 2.2] in the case  $\kappa = 0$ . The proof of Theorem 2.2 is the same mutatis mutandis; introduction of host mortality does not cause any problems. □

**Remark.** There is no exact counterpart of Theorem 2.2 in the non-linear case. However, there is an asymptotic analogue. If we take the expectation of the Markov process  $x^{(M)}$  in model SN and then let  $M$  tend to infinity, the limit is the solution to the differential equations DN, because the sequence of Markov processes  $(x^{(M)})_{M \geq 1}$  converge weakly towards the solutions of the differential equations (as is seen in Theorem 2.5 (to come)), and each coordinate is bounded by 1.

The stochastic linear process  $X$  and the deterministic linear process  $\Xi$  are linked to each other in the following way: the (normalised) stochastic process SL converges weakly towards the solution to the deterministic system DL. We need sequences of processes behaving according to SL. We denote them with  $(X^{(n)}, n \geq 1)$ .

**Theorem 2.3.** *Let  $(X^{(n)}, n \geq 1)$  be a sequence of Markov branching processes as specified in SL. We assume that the initial state  $X^{(n)}(0)$  is such that  $\sum_{j \geq 1} X_j^{(n)}(0) < \infty$  and  $n^{-1}X^{(n)}(0) \rightarrow y^{(0)}$ , where  $0 < \sum_{j \geq 1} j y_j^{(0)} < \infty$ . Then  $n^{-1}X^{(n)}$  converges weakly in  $D^\infty[0, T]$  for each  $T > 0$  to the (unique) non-random, nonnegative process  $\Xi$ , which evolves according to the differential equations DL with initial state  $\Xi(0) = y^{(0)}$ , and satisfies conditions C.*

**Remark.** We can loosen the condition  $0 < \sum_{j \geq 1} j y_j^{(0)} < \infty$  to  $0 < \sum_{j \geq 1} y_j^{(0)} < \infty$ . Then conditions C are not necessarily satisfied and all we can guarantee is that  $\sup_{0 \leq s \leq t} \sum_{j \geq 1} \Xi_j(s) < \infty$  for all  $t \geq 0$  and that there exists a  $j \geq 1$  such that  $\Xi_j(0) > 0$ .

*Proof.* The proof for  $\kappa = 0$  can be found in [BHL] as Theorem 2.1. The proof of Theorem 2.3 follows the same lines. Therefore we only mention the few changes necessary. For all  $j \geq 1$  and  $x \in \mathbb{R}_+^\infty$ , define the functions

$$a_j(x) := (j + 1)\mu x_{j+1} - j\mu x_j + \lambda \sum_{l \geq 1} x_l p_{lj} - \kappa x_j;$$

$$b_j(x) := (j + 1)\mu x_{j+1} + j\mu x_j + \lambda \sum_{l \geq 1} x_l p_{lj} + \kappa x_j,$$

and the random processes

$$\begin{aligned}
 U_j^n(t) &:= x_j^n(t) - x_j^n(0) - \int_0^t a_j(x^n(u))du; \\
 V_j^n(t) &:= U_j^n(t)^2 - \frac{1}{n} \int_0^t b_j(x^n(u))du,
 \end{aligned}$$

where  $x^n(t) := n^{-1}X^{(n)}(t)$ .

The following Lemma 2.4 corresponds to Lemma 3.5 in [BHL] and the proof of this lemma is given completely. For Lemmas 3.6, 3.7, 3.8 and 3.9 respectively in [BHL] only the necessary changes of the proofs are summarized: Use *our* definitions above for  $a_j, b_j, U_j^n$  and  $V_j^n$  and replace  $(\lambda \vee \mu)$  by  $(\lambda \vee \mu \vee \kappa)$  everywhere. Instead of  $h$  and  $h_k$  respectively define  $\tilde{h}$  and  $\tilde{h}_k$  respectively such that  $\tilde{h}(x)(t) := h(x)(t) - \int_0^t \kappa x_j(u)du$  and  $\tilde{h}_k(x)(t) := h_k(x)(t) - \int_0^t \kappa x_j(u)du$ .  $\square$

**Lemma 2.4.**  $U_j^n(t)$  and  $V_j^n(t)$  are  $\mathcal{G}_t^n$ -martingales.

*Proof.* We apply Theorem A1 in the Appendix to prove that  $U_j^n$  is a martingale in the following way: choose  $S = \{\mathbb{Z}_+\}^\infty$  and  $f : \{\mathbb{Z}_+\}^\infty \rightarrow \mathbb{R}_+$  such that  $f(v) = v_j$ . Now choose  $Z$  to be  $x^n$ . By Lemma 3.1 in [Ls]  $x^n$  is regular. By definition we have

$$\begin{aligned}
 U_j^n(t) &:= x_j^n(t) - x_j^n(0) - \int_0^t a_j(x^n(u))du \\
 &= f(x^n(t)) - f(x^n(0)) \\
 &\quad - \int_0^t \rho(x^n(u)) \int [f(x^n(u) + y) - f(x^n(u))] \pi(x^n, dy)du
 \end{aligned}$$

where  $y, f(y)$  and  $\rho\pi$  take the following values for  $j \geq 1$ :

**Table 1.** The values for  $y, f(y)$  and  $\rho\pi$  in the infinitesimal generator.  $\rho\pi$  is a purely atomic measure and in Table 1 we only mention the positive values of that measure.

$y$	$f(x + y) - f(x)$	$\rho(x)\pi(x, \{y\})$
$-e_j n^{-1}$	$-n^{-1}$	$j\mu x_j$
$e_j n^{-1}$	$n^{-1}$	$(j + 1)\mu x_{j+1} + \lambda \sum_{l \geq 1} x_l p_{lj}$
$-e_j n^{-1}$	$-n^{-1}$	$\kappa x_j$

Choose  $F(z) := (\lambda + 2(j + 1)\mu + \kappa) \sum_{l \geq 1} z_l$ . Condition (B) is then satisfied because

$$b_j(x) \leq (\lambda + 2(j + 1)\mu + \kappa) \sum_{l \geq 1} x_l,$$

and for any  $T > 0$

$$\mathbb{E} \left[ \sup_{0 \leq t \leq T} \sum_{l \geq 1} x_l^n(t) \right] \leq e^{\lambda T}. \tag{2.7}$$

The latter is true, because  $\sum_{j \geq 1} X_j^{(n)}(t)$  only increases at an infection, and infections occur at a total rate of  $\lambda \sum_{j \geq 1} \sum_{k \geq 1} X_j^{(n)} p_{jk} \leq \lambda \sum_{j \geq 1} X_j^{(n)}$ ; thus, by comparison with a pure birth process with per capita rate  $\lambda$ , (2.7) follows.

With these choices, we can directly apply Theorem A1:  $N^f = U_j^n$  is a martingale.

Now let us proceed to prove that  $V_j^n$  is a martingale too. We apply Corollary A3 in the following way: by definition and using the notation introduced in the Appendix for Corollary A3 ( $N_i^g = U_j^n$  here) we have

$$\begin{aligned} V_j^n(t) &:= U_j^n(t)^2 - \frac{1}{n} \int_0^t b_j(X^{(n)}(u)) du \\ &= (N_i^g)^2 - \int_0^t \rho(X^{(n)}(u)) m_2(X^{(n)}(u)) du. \end{aligned}$$

Here,  $m_2(X^{(n)}(u)) = 1/n \sum_{i=-1}^1 i^2 \pi(X^{(n)}, i e_j)$ , and we can choose the same  $F(z) = (\lambda + 2(j + 1)\mu + \kappa) \sum_{l \geq 1} z_l$  as above. As  $(N_i^g)^2 - [N^g, N^g]_t$  is a martingale we may replace  $(N_i^g)^2$  by  $[N^g, N^g]_t$  and deduce by Corollary A3 that  $V_j^n$  is a martingale itself.  $\square$

The stochastic non-linear process  $x^{(M)}$  and the deterministic non-linear process  $\xi$  are linked to each other in the following way: the stochastic process  $x^{(M)}$  converges weakly towards  $\xi$ . With regard to this result, we prove the existence and uniqueness of the non-negative solution  $\xi$  to the system DN in the following theorem.

**Theorem 2.5.** Fix  $T > 0$ . Let  $C_1[0, T]$  denote the space of continuous functions  $f$  on  $[0, T]$  which satisfy  $0 \leq f(t) \leq 1$  for all  $t$ , and let  $C_T^\infty := (C_1[0, T])^\infty$ . Suppose that  $y \in [0, 1]^\infty$  and that  $\sum_{j \geq 0} y_j = 1$ . Then there is a unique element  $\xi \in C_T^\infty$  satisfying the equations DN such that  $\xi(0) = y$  and, for all  $t \in [0, T]$ ,  $\sum_{j \geq 0} \xi_j(t) \leq 1$ . Furthermore, if  $x^{(M)}(0) = y^M$  a.s., where  $y^M \rightarrow y$  in  $[0, 1]^\infty$ , then  $x^{(M)}$  converges weakly towards  $\xi \in C_T^\infty$ .

**Remark.** Since  $T$  is arbitrarily chosen, it follows that  $x^{(M)}$  converges weakly towards  $\xi$  in  $(C_1[0, \infty))^\infty$ , where  $C_1[0, \infty)$  has the projective limit topology. It is also in order to allow the initial values  $x^{(M)}(0)$  to be random, provided that the sequence of random elements  $x^{(M)}(0)$  of  $[0, 1]^\infty$  converges weakly to  $y$ .

The proof of Theorem 2.5 consists of several parts. The proof where  $\kappa = 0$  can be found in [BK] as Theorem 3.2, but the following proof works too if  $\kappa = 0$ . We first prove Lemma 2.6, because it is interesting in its own right, and already proves one part of Theorem 2.5; we also need it to prove the rest of Theorem 2.5.

**Lemma 2.6.** Given the initial values  $\xi(0)$  of a possible solution of DN, there is at most one solution of DN which satisfies  $\sum_{l \geq 0} \xi_l(t) \leq 1$  for all  $t \geq 0$ .

*Proof.* System DN can be rewritten in integral form as equations (2.8):

$$\begin{aligned} \xi_j(t) &= \xi_j(0) + \int_0^t \left\{ (j+1)\xi_{j+1}(u)\mu - j\xi_j(u)\mu \right. \\ &\quad \left. + \lambda\xi_0(u) \sum_{l \geq 1} \xi_l(u)p_{lj} - \kappa\xi_j(u) \right\} du, \quad j \geq 1; \tag{2.8} \\ \xi_0(t) &= \xi_0(0) + \int_0^t \left\{ \xi_1(u)\mu - \lambda\xi_0(u) \left( 1 - \sum_{l \geq 0} \xi_l(u)p_{l0} \right) + \kappa(1 - \xi_0(u)) \right\} du. \end{aligned}$$

We multiply the  $j$  equation in (2.8) by  $e^{-js}$ , for any fixed  $s > 0$ , and add over  $j \geq 0$ , obtaining

$$\begin{aligned} \phi(s, t) &= \phi(s, 0) + \int_0^t \left\{ \mu(1 - e^s) \frac{\partial \phi(s, u)}{\partial s} \right. \\ &\quad \left. + \lambda\phi(\infty, u)[\phi(-\log \psi(s), u) - 1] + \kappa - \kappa\phi(s, u) \right\} du; \end{aligned}$$

where  $\phi(s, t) := \sum_{j \geq 0} e^{-js} \xi_j(t)$  and  $\psi(s) := \sum_{j \geq 0} e^{-js} p_{1j}$ ;  $\phi(\infty, t)$  is just another way of writing  $\xi_0(t)$ . Differentiating with respect to  $t$  leads to the partial differential equation

$$\frac{\partial \phi(s, t)}{\partial t} = \mu(1 - e^s) \frac{\partial \phi(s, t)}{\partial s} + \lambda\phi(\infty, t)[\phi(-\log \psi(s), t) - 1] + \kappa - \kappa\phi(s, t). \tag{2.9}$$

Equation (2.9) can be integrated in  $s > 0, t \geq 0$ , using the method of characteristics, leading to

$$\begin{aligned} \phi(s, t) &= \phi(S_{s,t}(v), v) + \int_v^t \lambda\phi(\infty, u)[\phi(-\log \psi(S_{s,t}(u)), u) - 1] \\ &\quad + \kappa - \kappa\phi(S_{s,t}(u), u) du; \tag{2.10} \end{aligned}$$

for any  $v$ , and in particular for  $v = 0$ , where

$$S_{s,t}(u) = -\log\{1 - (1 - e^{-s})e^{-\mu(t-u)}\}.$$

Now if  $\xi_1$  and  $\xi_2$  are two different solutions of (2.8), they give rise to functions  $\phi_1$  and  $\phi_2$  satisfying (2.10), and such that  $0 \leq \phi_i \leq 1, i = 1, 2$ . Suppose that, for any  $v \geq 0, \phi_1(s, v) = \phi_2(s, v)$  for all  $s$  (as is certainly the case for  $v = 0$ ). Let

$$d_{v,w}(\phi_1, \phi_2) := \sup_{v \leq t \leq w} \sup_{s > 0} |\phi_1(s, t) - \phi_2(s, t)| \leq 1.$$



Then, from (2.10), for  $t \in [v, w]$ ,

$$\begin{aligned}
 &|\phi_1(s, t) - \phi_2(s, t)| \\
 &= \left| \int_v^t \left\{ \lambda \phi_1(\infty, u) [\phi_1(-\log \psi(S_{s,t}(u)), u) - 1] + \kappa - \kappa \phi_1(S_{s,t}(u), u) \right. \right. \\
 &\quad \left. \left. - \lambda \phi_2(\infty, u) [\phi_2(-\log \psi(S_{s,t}(u)), u) - 1] - \kappa + \kappa \phi_2(S_{s,t}(u), u) \right\} du \right| \\
 &\leq (\kappa + 2\lambda)(w - v)d_{v,w}.
 \end{aligned}$$

But then we have

$$d_{v,w} \leq (\kappa + 2\lambda)(w - v)d_{v,w}.$$

But this in turn implies that  $d_{v,w} = 0$  if  $w < v + (\kappa + 2\lambda)^{-1}$ . Iterating this procedure, starting with  $v = 0$  and continuing in steps of  $(2(\kappa + 2\lambda))^{-1}$  shows that  $\phi_1(s, t) = \phi_2(s, t)$ , for all  $s > 0, t \geq 0$  which completes the proof of Lemma 2.6.  $\square$

It is convenient to define the following functions and random variables to use in what follows:

$$\begin{aligned}
 a_j(x) &:= (j + 1)\mu x_{j+1} - j\mu x_j + \lambda x_0 \sum_{l \geq 1} x_l p_{lj} - \kappa x_j; \quad j \geq 1, \\
 a_0(x) &:= \mu x_1 - \lambda x_0 \left( 1 - \sum_{l \geq 0} x_l p_{l0} \right) + \kappa(1 - x_0), \\
 b_j(x) &:= (j + 1)\mu x_{j+1} + j\mu x_j + \lambda x_0 \sum_{l \geq 1} x_l p_{lj} + \kappa x_j; \quad j \geq 1, \\
 b_0(x) &:= \mu x_1 + \lambda x_0 \left( 1 - \sum_{l \geq 0} x_l p_{l0} \right) + \kappa(1 - x_0), \tag{2.11} \\
 a_j^* &:= \sup_x |a_j(x)| \leq (j + 1)\mu + \lambda + \kappa < \infty; \quad j \geq 1, \\
 b_j^* &:= \sup_x |b_j(x)| \leq 2(j + 1)\mu + \lambda + \kappa < \infty; \quad j \geq 1,
 \end{aligned}$$

$$U_j(x(t)) := x_j(t) - x_j(0) - \int_0^t a_j(x(u))du; \quad j \geq 0,$$

$$V_j^M(t) := U_j^M(t)^2 - \frac{1}{M} \int_0^t b_j(x^{(M)}(u))du; \quad j \geq 0,$$

$U_j^M := U_j(x^{(M)})$ ,  $j \geq 0$ , and  $U_j^* := U_j(x^*)$ ,  $j \geq 0$ , where  $x^*$  is defined in Lemma 3.7 in [BHL]. We need the following lemma to prove Theorem 2.5.

**Lemma 2.7.**  $U_j^M(t)$  and  $V_j^M(t)$  are  $\mathcal{F}_t^M$ -martingales.

*Proof.* The proof of Lemma 2.7 uses the same ideas as the proof of Lemma 2.4. Choose  $S = \{[0, 1] \cap M^{-1}\mathbb{Z}\}^\infty$  and  $f : \{[0, 1] \cap M^{-1}\mathbb{Z}\}^\infty \rightarrow [0, 1] \cap M^{-1}\mathbb{Z}$  such that  $f(v) = v_j$ . Then choose  $Z$  to be  $x^{(M)}$ . By Theorem 2.2 of [LS]  $x^{(M)}$  is regular. As  $f$  is bounded we can choose  $F := \lambda + 2(j + 1)\mu + \kappa$  which makes the proof even simpler.  $\square$

*Proof of Theorem 2.5.* Take  $y$  as in the statement of the theorem, and choose a sequence  $y^M$  of deterministic initial conditions for  $x^{(M)}$  such that  $y^M \rightarrow y$  in  $[0, 1]^\infty$ . Fix any  $j$ , and consider the uniform modulus of continuity

$$w(x_j^{(M)}; \delta) := \sup_{0 \leq s \leq t \leq T; t-s < \delta} \left| x_j^{(M)}(t) - x_j^{(M)}(s) \right|$$

of the random elements  $x_j^{(M)}$  of the space  $D[0, T]$ , given the Skorohod topology. The proof of Theorem 2.5 follows almost the same lines as the proof of Theorem 2.1 in [BHL]. For Lemmas 3.6, 3.7 and 3.9 respectively in [BHL] only the necessary changes of the proofs are summarized: Use *our* definitions above for  $a_j, b_j, U_j^M$  and use the boundedness of  $a_j^*$  in [BHL, equation (3.8)] and of  $b_j^*$  in [BHL, equation (3.9)], making [BHL, equation (3.10)] unnecessary. Because  $x^{(M)}$  converges weakly towards  $x^*$  we have  $\sum_{j \geq 0} x_j^*(t) \leq 1$ ; for all  $t$  a.e.. The proof of Lemma 2.8 differs from the proof of Lemma 3.8 in [BHL], that is why we state it completely:

**Lemma 2.8.**  $U_j^M$  converges weakly towards  $U_j^*$  in  $D[0, T]$ ,  $M \in \mathbb{N}$ ,  $j \geq 0$ .

*Proof.* We prove Lemma 2.8 by showing that  $U_j$  (see (2.11)) is continuous at  $x^*$ . Let  $(z_n, n \geq 0)$  be a sequence of elements of  $(D[0, T])^\infty$ , such that  $\lim_{n \rightarrow \infty} z_n = z \in C_T^\infty$  and  $0 \leq z_{nj}(t) \leq 1$  for all  $(n, j, t)$ . Then, since convergence in  $D[0, T]$  to an element of  $C[0, T]$  implies uniform convergence we have:  $\lim_{n \rightarrow \infty} \sup_{0 \leq t \leq T} |z_{nl}(t) - z_l(t)| = 0$ ; for all  $l \geq 0$ . So all we have to concentrate on to show continuity of  $U_j$  is the part  $z_{n0}(t) \sum_{l \geq 0} z_{nl}(t) p_{lj}$  of the integral. But here we can proceed in the following way:

$$\begin{aligned} & \sup_{0 \leq t \leq T} \left| z_{n0}(t) \sum_{l \geq 0} z_{nl}(t) p_{lj} - z_0(t) \sum_{l \geq 0} z_l(t) p_{lj} \right| \\ & \leq \left\{ \sup_{0 \leq t \leq T} |z_{n0}(t) - z_0(t)| \sum_{l \geq 0} p_{lj} \right\} + \left\{ \sum_{l \geq 0} \sup_{0 \leq t \leq T} |z_{nl}(t) - z_l(t)| p_{lj} \right\}. \end{aligned} \tag{2.12}$$

But by equation (2.2) in [BK] we have  $\sum_{l \geq 0} p_{lj} < \infty$ , and using the dominated convergence theorem, we see that (2.12) converges to 0 as  $n \rightarrow \infty$ . This ends the proof of Lemma 2.8 and therefore of Theorem 2.5. □

The behaviour of the stochastic process *in a finite time interval* is much the same as the behaviour of the solution of the corresponding differential equations, if the number of individuals is large. The following result is stronger than Theorem 2.5 because even the *sum* of absolute differences in all coordinates converges to zero. As a drawback, slight restrictions have to be imposed on the initial value  $y$  of  $\xi$

**Theorem 2.9.** Suppose that  $y \in [0, 1]^\infty$  is such that  $\sum_{j \geq 0} y_j = 1$  and  $s_\alpha := \sum_{j \geq 1} j^\alpha y_j < \infty$  for some  $\alpha > 0$ . Then, if  $\xi$  is the solution of DN with  $\xi(0) = y$ ,  $\sum_{j \geq 0} \xi_j(t) = 1$  for all  $t$ . If also  $x^{(M)}(0) = y^M \rightarrow y$  in such a way that  $\lim_{M \rightarrow \infty} \sum_{j \geq 0} j^\alpha y_j^M = s_\alpha$ , then

$$\lim_{M \rightarrow \infty} \mathbb{P} \left[ \sup_{0 \leq t \leq T} \sum_{j \geq 0} |x_j^{(M)}(t) - \xi_j(t)| > \epsilon \right] = 0$$

for any  $T, \epsilon > 0$ .

We first need to prove a lemma which is going to be used frequently in this and the next section. We define the following functions, where still  $x^{(M)}$  is the Markov Process behaving according to SN:

$$m_\alpha^M(t) := \sum_{j \geq 1} j^\alpha x_j^{(M)}(t), \text{ and } m_\alpha^\infty(t) := \sum_{j \geq 1} j^\alpha \xi_j(t),$$

$$c_\alpha(x) := \sum_{j \geq 1} j \mu x_j \{(j - 1)^\alpha - j^\alpha\} + \lambda x_0 \sum_{k \geq 1} \sum_{j \geq 1} x_j p_{jk} k^\alpha - \kappa \sum_{j \geq 1} j^\alpha x_j,$$

$$W_\alpha^M(t) := m_\alpha^M(t) - m_\alpha^M(0) - \int_0^t c_\alpha(x^{(M)}(u)) du.$$

**Lemma 2.10.** For  $\alpha \in (0, 1]$   $W_\alpha^M(t)$  is an  $\mathcal{F}_t$ -martingale. If additionally  $y$  is such that  $s_\alpha := \sum_{j \geq 1} j^\alpha y_j < \infty$  and  $\xi$  is a solution of DN with  $\xi(0) = y$ , then

$$m_\alpha^\infty(t) = m_\alpha^\infty(0) + \int_0^t c_\alpha(\xi(u)) du, \tag{2.13}$$

for  $t \geq 0$ .

*Proof.* To prove that  $W_\alpha^M$  is an  $\mathcal{F}_t$ -martingale we can apply Theorem 2 in Hamza and Klebaner (1995) [HK], version for general state space. Choose  $f(z) := \sum_{j \geq 1} j^\alpha z_j$  and  $c := (2\mu + \lambda\theta + \kappa)$ , then  $|L|f(z) \leq c(1 \vee |f(z)|)$  is satisfied, where  $L$  is the infinitesimal generator of the Markov process  $x^{(M)}$ .

So we only have to prove equation (2.13). But this can be shown using exactly the same steps as the proof of Lemma 3.5 in [BK]. Note that the inequality

$$\mathbb{E} \left[ m_\alpha^M(t) \right] \leq m_\alpha^M(0) K(t), \tag{2.14}$$

where the monotonically increasing function  $K(t)$  is finite for all  $t \in (0, \infty)$ , can be shown more easily, as we know that  $W_\alpha^M$  is an  $\mathcal{F}_t$ -martingale.  $\square$

*Proof of Theorem 2.9.* The proof for  $\kappa = 0$  can be found in [BK] as Theorem 3.6 and the proof for  $\kappa > 0$  follows the same steps; use Theorem 2.5 and equation (2.14).  $\square$

### 3. Analysing the deterministic models

We first analyse the deterministic linear model DL. Using (2.9) in [BHL] and (2.6) we gain

$$\Xi_j(t) = \frac{1}{j} \left( \sum_{l \geq 1} l \Xi_l(0) \right) e^{(\lambda\theta - \mu - \kappa)t} \mathbb{P}^0[Y(t) = j], \tag{3.1}$$

for all  $j \geq 1$ , where  $\mathbb{P}^0$  denotes probability conditional on the initial distribution

$$\mathbb{P}^0[Y(0) = j] = j \Xi_j(0) / \left( \sum_{l \geq 1} l \Xi_l(0) \right).$$

We first want to study the threshold behaviour of model DL. Introduce  $R_0 := \lambda\theta/(\mu + \kappa)$ ,  $R_0^{(0)} := \lambda\theta/\mu$ ,  $R_1 := \lambda e \log \theta / (\mu\theta^{\frac{\kappa}{\mu}})$  and  $R_2 := \lambda/\kappa$ . For an interpretation of these ratios see [Ls]. By the expression ‘‘threshold behaviour’’ we *usually* denote general statements of the following type: if  $R_0 > 1$  the epidemic develops in deterministic systems and if  $R_0 < 1$  the epidemic dies out. As we have already seen in the stochastic approach (see [Ls]), the situation is more complex in our models. The next theorem makes a statement about the asymptotic behaviour of the number of infected individuals in DL and in Remark 1) following the theorem we derive the threshold result:

**Theorem 3.1.** *Assume that  $\sum_{j \geq 1} j \Xi_j(0) < \infty$ . Then the limit:*

$$\lim_{t \rightarrow \infty} t^{-1} \log \sum_{j \geq 1} \Xi_j(t) =: c^+(\lambda, \mu, \theta, \kappa) =: c^+$$

*exists and is given by:*

$$c^+ = \begin{cases} \lambda\theta - \mu - \kappa & \text{if } R_0^{(0)} \log \theta \leq 1 \\ \frac{\lambda\theta}{R_0^{(0)} \log \theta} (1 + \log(R_0^{(0)} \log \theta)) - \mu - \kappa & \text{if } 1 < R_0^{(0)} \log \theta \leq \theta \\ \lambda - \kappa & \text{if } R_0^{(0)} \log \theta > \theta. \end{cases}$$

**Remarks.** 1) Using Theorem 3.1, elementary although quite complicated calculations lead to the following threshold behaviour, which only involves determining whether  $c^+ < 0$  or  $c^+ > 0$ . In the region  $\log \theta \leq (1 + (\kappa/\mu))^{-1}$  we have:  $c^+ < 0$  if and only if  $R_0 < 1$ . In the region  $(1 + (\kappa/\mu))^{-1} < \log \theta \leq \mu/\kappa$  we have:  $c^+ < 0$  if and only if  $R_1 < 1$ . In the region  $\log \theta > \mu/\kappa$  we have:  $c^+ < 0$  if and only if  $R_2 < 1$ .

2) If  $\kappa = 0$ , these results stay true with the following adjustments: the third region for  $\theta$  is shifted away to infinity. So we have only two regions for  $\theta$  if  $\kappa = 0$ , namely:  $\theta < e$  and  $\theta \geq e$ , and the basic reproduction ratios simplify to  $R_0 = \lambda\theta/\mu$  and  $R_1 = \lambda e \log \theta / \mu$ . Then Theorem 3.1 and Remark 1) are Theorem 2.6 and Remark 2.7 in [BHL].

3) The stochastic analogue of the threshold behaviour of Remark 1) is Theorem 2.1 in [Ls].

*Proof.* Use (2.6) to see that from the definition of  $c$  in [BHL], Theorem 2.6, we have

$$c^+ = c - \kappa. \tag{3.2}$$

Then Theorem 3.1 follows from Theorem 2.6 in [BHL]. □

We can use equation (2.10) in [BHL] and (2.6) to compute the development of the number of parasites in the entire system:

$$\sum_{j \geq 1} j \Xi_j(t) = \left( \sum_{l \geq 1} l \Xi_l(0) \right) e^{(\lambda\theta - \mu - \kappa)t}. \tag{3.3}$$

Therefore  $R_0 = \lambda\theta / (\mu + \kappa) = 1$  is the threshold for the development of the number of parasites in DL. The stochastic analogue is equation (2.4) in [Ls].

We now prove Lemma 3.2 which enables us to simplify many of the following proofs. The Markov process  $Y$  and the probability measure  $\mathbb{P}^0$  are as defined in chapter 2 of [BHL].

**Lemma 3.2.** *Suppose that in DL we have  $R_0 = 1$ . The initial values are such that  $0 < K := \sum_{l \geq 1} l \Xi_l(0) < \infty$ . Then the following result holds:*

*Case (1):  $\log \theta < 1/(1 + \kappa/\mu)$ . Then there exists a unique infinite vector of positive real numbers  $v$  (the stationary distribution of  $Y$ ) such that  $\sum_{j \geq 1} v_j = 1$  and*

$$\lim_{t \rightarrow \infty} \Xi_j(t) = v_j K j^{-1} \quad \text{for all } j \geq 1.$$

*Case (2):  $\log \theta \geq 1/(1 + \kappa/\mu)$ . Then we have*

$$\lim_{t \rightarrow \infty} \Xi_j(t) = 0 \quad \text{for all } j \geq 1.$$

*Proof.* As  $R_0 = 1$ , (3.1) simplifies to

$$\Xi_j(t) = \frac{1}{j} \left( \sum_{l \geq 1} l \Xi_l(0) \right) \mathbb{P}^0[Y(t) = j],$$

for all  $j \geq 1$ . Looking at case (1), we have  $\log \theta < 1/(1 + \kappa/\mu)$ . Hence,

$$R_0^{(0)} \log \theta < \frac{\lambda\theta}{\mu} \frac{1}{1 + \kappa/\mu} = \frac{\lambda\theta}{\mu + \kappa} = R_0 = 1.$$

Thus, if  $p_{10} + p_{11} < 1$ ,  $Y$  is positive recurrent by Theorem 2.5 in [BHL]. Therefore by general theory of Markov processes we have a unique infinite vector of positive real numbers  $v$  such that  $\sum_{j \geq 1} v_j = 1$  and  $\lim_{t \rightarrow \infty} \mathbb{P}^0[Y(t) = j] = v_j$  for all  $j \geq 1$ . If  $p_{10} + p_{11} = 1$ ,  $Y$  is eventually absorbed in state 1. Then Lemma 3.2 is satisfied by choosing  $v_1 = 1$ .

Looking at case (2), we have  $\log \theta \geq 1/(1 + \kappa/\mu)$ . We can apply Theorem 2.5 in [BHL] again: here it is impossible that  $p_{10} + p_{11} = 1$  because then  $\log \theta > 1/(1 + \kappa/\mu) > 0$  and  $p_{11} = \theta < 1$  in that case.  $Y$  is either null recurrent or transient because

$$R_0^{(0)} \log \theta \geq \frac{\lambda \theta}{\mu} \frac{1}{1 + \kappa/\mu} = \frac{\lambda \theta}{\mu + \kappa} = 1.$$

But in both cases we have  $\lim_{t \rightarrow \infty} \mathbb{P}^0[Y(t) = j] = 0$  for all  $j \geq 1$ . This ends the proof of Lemma 3.2. □

Call  $\bar{\Xi}(t)$  a stationary solution of DL, if  $\bar{\Xi}_j(t) \geq 0$  for all  $j \geq 0$ , and putting  $\Xi = \bar{\Xi}$  in the right hand side of (2.2) gives zero: the solution to DL with  $\Xi(0) = \bar{\Xi}$  is then  $\Xi(t) = \bar{\Xi}$  for all  $t$ . It is clear that in the non-linear models  $e_0$  and in the linear models 0 are automatically stationary solutions. We call these stationary solutions *trivial* in comparison to the *nontrivial*. We mention these trivial solutions throughout, although they do not satisfy conditions C in the linear case, because conditions C ask for at least one co-ordinate  $j \geq 1$  such that  $\Xi_j(0) > 0$ . In reality we may assume that  $\kappa < \mu$ , meaning that the death rate of parasites is larger than the death rate of their hosts. Assuming this, we know about the stationary solutions in both models DL and DN that, for each  $j \geq 1$ , the following inequality must hold:

$$\bar{\Xi}_{j+1} < \bar{\Xi}_j.$$

This result follows immediately from the differential equations as for example in model DL via

$$\bar{\Xi}_j = \frac{(j + 1)\mu}{j\mu + \kappa} \bar{\Xi}_{j+1} + \frac{\lambda}{j\mu + \kappa} \sum_{l \geq 1} \bar{\Xi}_l p_{lj} > \bar{\Xi}_{j+1}.$$

The results about stationary solutions in DL are summarised in the following theorem:

- Theorem 3.3.** *a) For every choice of parameters  $(\lambda, \theta, \mu, \kappa)$  there exists the trivial stationary solution  $\bar{\Xi} = 0$ .*  
*b) There is no nontrivial stationary solution of DL with finite number of parasites if  $\log \theta \geq (1 + \kappa/\mu)^{-1}$ .*  
*c) If  $\log \theta < (1 + \kappa/\mu)^{-1}$  and  $R_0 = 1$ , then up to scalar multiplication there exists exactly one nontrivial stationary solution of DL with finite number of parasites.*  
*d) Suppose that  $\kappa = 0$ ,  $R_0^{(0)} = R_0 = 1$  and that  $\theta < e$ , and let  $\bar{\Xi}^{(0)}$  be a stationary solution of DL with finite number of parasites. Then, for any  $\alpha > 1$  the following statements hold:*

*If  $\theta \geq \alpha^{1/(\alpha-1)}$ , then  $\sum_{j \geq 1} j^\alpha \bar{\Xi}_j^{(0)} = \infty$ ;*

*If  $\theta < \alpha^{1/(\alpha-1)}$  and  $\sum_{j \geq 1} j^\alpha p_{1j} < \infty$ , then  $\sum_{j \geq 1} j^\alpha \bar{\Xi}_j^{(0)} < \infty$ .*

*Proof.* a) is clear.

b) Suppose we have a nontrivial stationary solution of DL with finite number of parasites. As the number of parasites is finite and the solution is nontrivial, conditions C are satisfied. In a stationary solution the number of parasites is constant. By (3.3) this requires that  $R_0 = 1$ . So we can apply Lemma 3.2, Case (2) which finishes the proof of part b).

c) A candidate for a nontrivial stationary solution with finite number of parasites can be found through Lemma 3.2 as follows: suppose we have  $\log \theta <$

$1/(1 + \kappa/\mu)^{-1}$ ,  $R_0 = 1$  and choose a fixed, finite number  $K$  (the (initial) number of parasites). Then for all  $j \geq 1$  we define:

$$\bar{\Xi}_j(t) := j^{-1} K v_j \tag{3.4}$$

for all  $t \geq 0$ , where  $v$  denotes the unique stationary distribution of  $Y$ . We now have to show that this is indeed a solution of DL. Consider a solution  $y$  of DL with initial values as in (3.4). By Theorem 2.1 that solution  $y$  exists and is unique. We now have to show that the solution  $y$  is equal to (3.4) for all  $t \geq 0$ . Now  $y$  has a representation of the form (3.1). As  $R_0 = 1$  we have  $\lambda\theta - \mu - \kappa = 0$  and so we only have to ensure that if we start with  $\mathbb{P}^{(0)}[Y(0) = j] = v_j$ , then we have  $\mathbb{P}^{(0)}[Y(t) = j] = v_j$  for all  $t \geq 0$ . But this is so because  $v$  is the stationary distribution of  $Y$ .

Now we show that (3.4) is (up to scalar multiplication) the unique stationary solution of DL according to the way we defined such solutions. All co-ordinates of (3.4) are nonnegative (even positive). We have to show that if we put our solution (3.4) in the right side of DL we get zero. We therefore need

$$\mu v_{j+1} - \mu v_j + \lambda \sum_{i \geq 1} \frac{v_i}{i} p_{ij} - \frac{\kappa v_j}{j} = 0,$$

for all  $j \geq 1$ . By equation (2.6) in [BHL] we see that this is equivalent to  $vS = 0$  as  $\theta = (\mu + \kappa)/\lambda$ . But this is true as  $v$  is the unique stationary distribution of the Markov process associated with the Q-matrix  $S$ .

Uniqueness follows through contradiction. If  $z$  is an other stationary solution of DL and  $z$  is not a scalar multiple of  $\bar{\Xi}$ , we argue as follows:  $z$  must have a representation in the form of (3.1) too. We may assume without loss of generality that the initial total number of parasites is the same in  $z$  and  $\bar{\Xi}$ , because in the linear models, every scalar multiple of a stationary solution is a stationary solution too. But then, looking at (3.1) there must be two stationary distributions of  $Y$ , which is not possible.

d) For  $\kappa = 0$  we compare the stationary solutions of DL and DN with each other and make contradictions using Theorem 4.4 in [BK]. Choose an arbitrary  $g_0 \in (0, 1)$ . If  $\theta \geq \alpha^{1/(\alpha-1)}$ , we assume we have a stationary solution  $\bar{\Xi}^{(0)}$  of DL such that  $\sum_{j \geq 1} j^\alpha \bar{\Xi}_j^{(0)} < \infty$ . Without loss of generality we may choose that

$$\sum_{j \geq 1} \bar{\Xi}_j^{(0)} + g_0 = 1, \tag{3.5}$$

because in the linear models, every scalar multiple of a stationary solution is a stationary solution too. Now we define  $\lambda' := \lambda/g_0$ . As  $R_0 = 1$ , we have  $\lambda'\theta > \mu$ . Therefore, by Theorem 4.2 of [BK] (included in Theorem 3.8, see later) we have a (unique), nontrivial stationary solution of DN  $\bar{\xi}^{(0)}$  with parameters  $(\lambda', \theta, \mu)$  with finite average number of parasites per individual. Now we compare the two systems DN (with  $(\lambda', \theta, \mu)$ ) and DL (with  $(\lambda, \theta, \mu)$ ) with each other for  $j \geq 1$ . The two systems are:

$$\frac{d\xi_j^{(0)}}{dt} = (j + 1)\mu\xi_{j+1}^{(0)} - j\mu\xi_j^{(0)} + \lambda'\xi_0^{(0)} \sum_{l \geq 1} \xi_l^{(0)} p_{lj}; \quad j \geq 1, \tag{DN}$$

and

$$\frac{d\Xi_j^{(0)}}{dt} = (j + 1)\mu\Xi_{j+1}^{(0)} - j\mu\Xi_j^{(0)} + \lambda \sum_{l \geq 1} \Xi_l^{(0)} p_{lj}; \quad j \geq 1. \tag{DL}$$

The only difference between DN and DL is in the infection process: we have  $\lambda'\xi_0^{(0)}$  in DN and only  $\lambda$  in DL. But, again by Theorem 4.2 of [BK] we know that  $\xi_0^{(0)} = \mu/\lambda'\theta = \mu g_0/\lambda\theta = g_0$ . Additionally we have by definition that  $\lambda = \lambda'g_0$ . So if we only want to look at stationary solutions (where  $\xi_0^{(0)}$  is constant in time and equal to  $g_0$ ), the two systems are in fact equal and both linear! We define:  $g_j := \bar{\Xi}_j^{(0)}$  for  $j \geq 1$ . By (3.5) and the equivalence of DN and DL the vector  $(g_j)_{j \geq 0}$  is the unique stationary solution of DN with parameters  $(\lambda', \theta, \mu)$ . So we have constructed a stationary solution  $g$  of DN where for  $\theta \geq \alpha^{1/(\alpha-1)}$  we have  $\sum_{j \geq 1} j^\alpha g_j < \infty$ . This is a contradiction to Theorem 4.4 of [BK].

On the other hand, if  $\theta < \alpha^{1/(\alpha-1)}$ , we assume we have a solution  $\bar{\Xi}^{(0)}$  of DL such that  $\sum_{j \geq 1} j^\alpha \bar{\Xi}_j^{(0)} = \infty$ . But then we can construct such a solution of DN too as shown above in the first part of d) which is again a contradiction to Theorem 4.4 of [BK]. □

By convergence towards a stationary solution  $\bar{\xi}$  we mean that all components of the converging function  $y(t)$  must satisfy  $\lim_{t \rightarrow \infty} y_i(t) = \bar{\xi}_i$  for all  $i \geq 1$  (convergence in  $\mathbb{R}^\infty$ ). In the next theorem we prove convergence of a solution of DL to a stationary solution under some obviously necessary assumptions.

**Theorem 3.4.** *If  $\log \theta < (1 + \kappa/\mu)^{-1}$  and if  $R_0 = 1$  then every solution  $y$  of DL which satisfies conditions C converges towards that unique stationary solution  $\bar{\Xi}$  of DL which satisfies  $\sum_{j \geq 1} j \bar{\Xi}_j = \sum_{j \geq 1} j y_j(0)$ .*

*Proof.* We can use Lemma 3.2 to see that each solution of DL that satisfies conditions C converges to some infinite positive vector  $(v_j K j^{-1})_{j \geq 1}$ . As in the proof of Theorem 3.3 c) we see that this is the unique stationary solution of DL. □

Call a solution  $\Xi$  periodic if there exists a  $\tau > 0$  such that  $\Xi(t + \tau) = \Xi(t)$  for all  $t$ .

**Theorem 3.5.** *In the linear system DL there are no periodic solutions which satisfy conditions C except stationary solutions.*

*Proof.* In a periodic solution the number of parasites must be periodically the same too. But in view of (3.3) this means that  $R_0 = 1$  is necessary. Now we can apply Lemma 3.2: but the behaviour suggested in both cases rules out periodic solutions which are not stationary solutions. □



We now analyse the non-linear deterministic model DN. Intuitively it is clear, that if a parasite has less than one offspring under ideal conditions, that is if  $R_0 < 1$ , then the epidemic must die out. That is precisely the following result:

**Theorem 3.6.** *If  $R_0 < 1$  and if  $\xi(0) = y$  is such that  $s_1 := \sum_{j \geq 1} j y_j < \infty$ , then  $\lim_{t \rightarrow \infty} \xi(t) = e_0$  and  $\sum_{j \geq 1} j \xi_j(t) \leq s_1 e^{-(\mu + \kappa - \lambda \theta)t}$ .*

*Proof.* From Lemma 2.10, recalling that  $m_1^\infty(t) := \sum_{j \geq 1} j \xi_j(t)$ , it follows that

$$m_1^\infty(t) = s_1 + \int_0^t (\theta \lambda \xi_0(u) - \mu - \kappa) m_1^\infty(u) du.$$

Hence

$$m_1^\infty(t) = s_1 e^{\int_0^t [\lambda \xi_0(u) \theta - \mu - \kappa] du}, \tag{3.6}$$

proving the theorem. □

Next we derive the threshold results for system DN:

**Theorem 3.7.** *Let  $\xi(0)$  in DN be such that  $0 < \sum_{j \geq 0} j \xi_j(0) < \infty$ . Then the following statements hold:*

*Case 1)  $\log \theta \leq (1 + \kappa/\mu)^{-1}$ : Then  $\lim_{t \rightarrow \infty} \xi(t) = e_0$  if  $R_0 < 1$ , and if  $R_0 > 1$  then  $\xi(t) \not\rightarrow e_0$  as  $t \rightarrow \infty$ .*

*Case 2)  $(1 + \kappa/\mu)^{-1} < \log \theta \leq \mu/\kappa$ : Then  $\lim_{t \rightarrow \infty} \xi(t) = e_0$  if  $R_1 < 1$ , and if  $R_1 > 1$  then  $\xi(t) \not\rightarrow e_0$  as  $t \rightarrow \infty$ .*

*Case 3)  $\log \theta > \mu/\kappa$ : Then  $\lim_{t \rightarrow \infty} \xi(t) = e_0$  if  $R_2 < 1$ , and if  $R_2 > 1$  then  $\xi(t) \not\rightarrow e_0$  as  $t \rightarrow \infty$ .*

**Remarks.** 1. The stochastic analogue of Theorem 3.7 in [Ls] is Theorem 2.3, but the reader should notice Theorem 2.2 in [Ls] too.

2. Again, as in Remark 2) following Theorem 3.1, if  $\kappa = 0$ , these results stay true with the interpretation that the third region for  $\theta$  is shifted away to infinity.

*Proof.* We first prove the results where the disease dies out (the relevant  $R_i$  must be smaller than 1). Then we prove that the infection does not die out if the relevant  $R_i$  is larger than one.

We use the notation of section 2 for  $c_\alpha$  and  $m_\alpha^\infty(t)$ . The function  $f(x) = x^\alpha$  is concave if  $\alpha \in [0, 1]$ . So

$$c_\alpha(\xi) \leq (\lambda \theta^\alpha \xi_0 - \mu \alpha - \kappa) \sum_{j \geq 1} j^\alpha \xi_j.$$

Using (2.13) we therefore have for  $0 \leq v \leq t$

$$m_\alpha^\infty(t) \leq m_\alpha^\infty(v) - \int_v^t (\mu \alpha + \kappa - \lambda \theta^\alpha \xi_0) m_\alpha^\infty(u) du. \tag{3.7}$$

The case where  $\kappa = 0$  was proved in [BK] as Theorems 4.1 and 4.6. If  $R_0 < 1$  we can use Theorem 3.6 which is valid for all  $\theta$  and so we may assume that  $R_0 \geq 1$ . We

want to find an  $\alpha \in (0, 1]$  such that  $g(\alpha) := \kappa + \mu\alpha - \lambda\theta^\alpha > 0$ . Then we can apply the Gronwall-inequality to (3.7) because then  $\lim_{t \rightarrow \infty} m_\alpha^\infty(t) = 0$  which ends the proof. Let us first analyse this function  $g$ :  $g(0) = \kappa - \lambda$  and  $g(1) = \kappa + \mu - \lambda\theta$  ( $\leq 0$  because  $R_0 \geq 1$ ). So if  $\kappa - \lambda > 0$  (that is  $R_2 < 1$ ) we easily find an  $\alpha \in (0, 1]$  such that  $g(\alpha) > 0$  ( $\alpha \rightarrow 0$  finally gives us such an  $\alpha$ ). So the third case where  $R_2 < 1$  is already satisfied. We may therefore assume that  $\kappa \leq \lambda$ . We therefore only have to show the second case:  $1/(1 + \kappa/\mu) < \log \theta \leq \mu/\kappa$ ,  $R_1 < 1$ . Elementary calculations show that  $g$  takes the maximum with respect to  $\alpha$  at

$$\alpha_0 := \frac{1}{\log \theta} \log \left( \frac{\mu}{\lambda \log \theta} \right).$$

Under the assumptions above it can be shown through elementary though partly tedious calculations that  $\alpha_0 \in (0, 1]$  and  $g(\alpha_0) > 0$ . This ends the proof of the first directions ( $R_i < 1$ ).

Now we need to prove that in cases 1), 2) and 3) the infection does not die out if the relevant  $R_i$  is larger than 1. The proof runs through for  $\kappa = 0$  too. We prove all three cases in one. If we write “ $R_i$ ”, we mean  $R_0$  in the first case,  $R_1$  in the second case and  $R_2$  in the third case.

The strategy of the proof is as follows: in the non-linear model DN the contact rate  $\lambda$  is decreased to the effective contact rate  $\lambda\xi_0(t)$ . If the disease is near to extinction,  $\xi_0$  must be almost 1. So the non-linear process  $\xi$  is almost a linear process  $\Xi$  behaving according to DL. But by Remark 1 of Theorem 3.1 we know that the linear process  $\Xi$  does not die out under the conditions mentioned above. So we must show that there exists a linear process  $\Xi$  such that  $\Xi_j \leq \xi_j$  for  $j \geq 1$  at least until there is no danger for the process  $\xi$  to die out.

Let us define  $N(t) := \sum_{j \geq 1} \xi_j(t)$ . The expression  $\xi(t) \not\rightarrow e_0$  means that there exists an  $\epsilon > 0$  such that if at some time  $t_1$  we have  $N(t_1) < \epsilon$ , then there exists a  $t_2 > t_1$  such that  $N(t_2) \geq \epsilon$ . Without loss of generality we choose  $t_1 = 0$  and  $\epsilon$  such that  $(1 - \epsilon)R_i > 1$ . We therefore have to show that there exists a  $T^* > 0$  such that  $N(T^*) \geq \epsilon$ . Let us define  $\lambda' := \lambda(1 - \epsilon)$  and let  $\Xi$  be a solution of DL with parameters  $(\lambda', \theta, \mu)$ . We choose the initial values such that  $\Xi_j(0) = \xi_j(0)$  for all  $j \geq 1$ . Then we define  $L(t) := \sum_{j \geq 1} \Xi_j(t)$  and  $T := \inf\{t : L(t) \geq \epsilon\}$ .

By Remark 1 of Theorem 3.1 we have  $T < \infty$ . Now if there exists a  $v \in [0, T]$  such that  $N(v) \geq \epsilon$  we can choose  $T^* := v$  and nothing remains to be proved. Otherwise we have  $N(t) < \epsilon$  for all  $t \in [0, T]$ . If we can show that for all  $t \in [0, T]$  and  $j \geq 1$ ,

$$\Xi_j(t) \leq \xi_j(t) \tag{3.8}$$

we have finished the proof.

We have  $N(t) = 1 - \xi_0(t) < \epsilon$  for all  $t \in [0, T]$ . So we have  $\lambda' = \lambda(1 - \epsilon) < \lambda\xi_0$  for all  $t \in [0, T]$ . Although intuitively we might expect that we therefore can easily prove (3.8) by just comparing the two systems DN and DL with each other, such approaches seem difficult to carry through. We therefore look at stochastic processes ( $x^{(M)}$  and  $X$ ) where such a comparison is possible through the coupling method. Then we use Theorems 2.3 and 2.5 to finish the proof.

We now construct the two stochastic processes: the non-linear process  $x^{(M)}$  and the linear process  $X$ . We define the process  $x^{(M)}$  as in section 2, developing according to SN, where the initial values are to be suitably chosen later and  $1/M \ll \epsilon$ . For this we define a trivariate Markov process  $(x^{(M)}(t), X(t), x^{(r)}(t))$ . “ $r$ ” stands for residual. In fact, each of the components in  $(x^{(M)}(t), X(t), x^{(r)}(t))$  are themselves infinite dimensional: the first component is an infinite vector  $(x_j^{(M)}(t))_{j \geq 0}$  where the co-ordinates take values in  $\mathbb{Z}M^{-1} \cap [0, 1]$ , the second component is an infinite vector  $(X_k(t))_{k \geq 1}$  where the co-ordinates take values on the natural numbers and the third component is an infinite vector  $(x_j^{(r)}(t))_{j \geq 0}$  where the co-ordinates take values in  $\mathbb{Z}M^{-1} \cap [0, 1]$ . We choose the initial values to be such that  $x_0^{(M)}(0) = x_0^{(r)}(0)$ ,  $x_j^{(M)}(0) = M^{-1}X_j(0)$  for  $j \geq 1$  and  $x_k^{(r)}(0) = 0$  for  $k \geq 1$ .

We want the trivariate Markov process to satisfy the following requirements  $\mathcal{R}$ .

Our aim is to construct  $x^{(M)}$  and  $x^{(r)}$  such that  $x_j^{(M)} = M^{-1}X_j + x_j^{(r)}$  almost surely for  $j \geq 1$  at least in the beginning (as long as  $x_0^{(M)} > 1 - \epsilon$ ). Then we have  $x_j^{(M)}(t) \geq M^{-1}X_j(t)$  for  $j \geq 1$  too in the beginning. Additionally we want  $x^{(M)}$  to behave according to SN and  $X$  to behave according to SL.

We begin with  $x_0^{(M)} > 1 - \epsilon$ . Until  $x_0^{(M)} \leq 1 - \epsilon$  for the first time, we let these processes develop according to the following rates:

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_{j-1} - e_j), X + e_{j-1} - e_j, x^{(r)})$$

at rate  $j\mu X_j$ ;  $j \geq 2$ , (death of a parasite in the linear process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_0 - e_1), X - e_1, x^{(r)} + M^{-1}e_0)$$

at rate  $\mu X_1$ , (death of a parasite in an individual with only one parasite in the linear process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_0 - e_u), X - e_u, x^{(r)} + M^{-1}e_0)$$

at rate  $\kappa X_u$ ;  $u \geq 1$ , (death of an individual in the linear process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_{j-1} - e_j), X, x^{(r)} + M^{-1}(e_{j-1} - e_j))$$

at rate  $j\mu M x_j^{(r)}$ ;  $j \geq 1$ , (death of a parasite in the residual process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_0 - e_u), X, x^{(r)} + M^{-1}(e_0 - e_u))$$

at rate  $\kappa M x_u^{(r)}$ ;  $u \geq 1$ , (death of an individual in the residual process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_k - e_0), X + e_k, x^{(r)} - M^{-1}e_0)$$

at rate  $\lambda' \sum_{u \geq 1} X_u p_{uk}$ ;  $k \geq 1$ , (infection in the linear process)

$$(x^{(M)}, X, x^{(r)}) \rightarrow (x^{(M)} + M^{-1}(e_k - e_0), X, x^{(r)} + M^{-1}(e_k - e_0))$$

at rate  $\lambda x_0^{(M)} M \sum_{l \geq 1} x_l^{(r)} p_{lk} + (\lambda x_0^{(M)} - \lambda') \sum_{l \geq 1} X_l p_{lk}$ , (infection in the residual process due to infective force of the residual process itself (first part of the rate) and due to residual rate (difference between the linear and non-linear contact rate, second part of the rate)). Note that  $x_0^{(M)}(t) = x_0^{(r)}(t)$  until  $x_0^{(M)} \leq 1 - \epsilon$  for the first time. As soon as  $x_0^{(M)}(t) \leq 1 - \epsilon$  for the first time, we let the linear process  $X$  develop according to SL and independently of  $x^{(M)}$ . The reader should notice that we have to distinguish carefully between the processes  $x^{(M)}$  and  $x^{(r)}$  on the one side and  $X$  on the other side. The non-linear process and the residual process denote *proportions* of individuals while  $X$  denotes the *explicit number*. This has to be considered while dealing with rates. The reader can check that with our construction of the trivariate Markov process we meet all requirements  $\mathcal{R}$ . We show (3.8) through contradiction: suppose there is a  $u \in [0, T]$  and a  $J \in \mathbb{N} \setminus \{0\}$  such that

$$\Xi_J(u) > \xi_J(u). \tag{3.9}$$

As  $N = 1 - \xi_0$ ,  $N$  must be a continuous function. Therefore there exists  $q := \sup\{N(t) : t \in [0, T]\} < \epsilon$ .

Now let us define  $A_M := \{\omega : \sup_{0 \leq s \leq T} |x_0^{(M)}(s)(\omega) - \xi_0(s)| \leq \epsilon - q\}$ . As by definition  $q = \sup\{(1 - \xi_0(t)) : t \in [0, T]\}$ , we have  $A_M \subseteq \{\omega : x_0^{(M)}(t)(\omega) > (1 - \epsilon)$  for all  $t \in [0, T]\}$ . We now choose the initial values  $y^M$  of  $x^{(M)}$  such that  $y^M \rightarrow \xi(0)$  and  $\sum_{j \geq 1} j y_j^M \rightarrow \sum_{j \geq 1} j \xi_j(0)$ . By Theorem 2.9,  $\mathbb{P}[A_M]$  converges to 1. We now define

$$B_M(u) := x_J^{(M)}(u) I_{A_M}, \quad C_M(u) := \frac{1}{M} X_J(u) I_{A_M}.$$

As  $A_M \subseteq \{\omega : x_0^{(M)}(t)(\omega) > (1 - \epsilon)$ , for all  $t \in [0, T]\}$  we have by construction of the coupling  $B_M(u) \geq C_M(u)$ . But as  $M$  tends to  $\infty$ ,  $I_{A_M}$  converges weakly to 1,  $x_J^{(M)}(u)$  converges weakly to  $\xi_J(u)$  by Theorem 2.5 and  $(1/M) X_J(u)$  converges weakly to  $\Xi_J(u)$  by Theorem 2.3. But this is contradictory to (3.9) which finishes the proof. □

Let us now look at stationary solutions of DN. Call  $\bar{\xi}(t)$  a stationary solution of DN, if for all  $j \geq 0$  we have  $\bar{\xi}_j(t) \geq 0$  and  $\sum_{j \geq 0} \bar{\xi}_j(t) = 1$ , and putting  $\xi = \bar{\xi}$  in the right hand side of DN gives zero: the solution to DN with  $\xi(0) = \bar{\xi}$  is then  $\xi(t) = \bar{\xi}$  for all  $t$ . The next theorem summarises all results about stationary solutions in model DN:

- Theorem 3.8.** *a) In every non-linear system DN we always have the trivial stationary solution  $\bar{\xi} = e_0$  no matter which values the parameters take.*  
*b) There is no nontrivial stationary solution of DN with finite average number of parasites per individual if  $\log \theta \geq (1 + \kappa/\mu)^{-1}$ .*  
*c) Suppose that  $\log \theta < (1 + \kappa/\mu)^{-1}$  and  $R_0 > 1$ . Then there exists a unique stationary solution  $\bar{\xi}$  of DN with finite average number of parasites per individual. For this stationary solution we furthermore have  $\bar{\xi}_0 = R_0^{-1}$ .*  
*d) Assuming the conditions of c) and as long as  $R_0$  remains greater than 1, the ratios  $\bar{\xi}_j/(1 - \bar{\xi}_0)$  for  $j \geq 1$  do not change if the vector  $(\lambda, \mu, \kappa)$  is altered in such*

a way that the ratio  $\kappa/\mu$  remains constant. More, if  $p_{10} + p_{11} < 1$  then these ratios can not all stay the same if the ratio  $\kappa/\mu$  is altered.

*Proof.* The proof of this theorem if  $\kappa = 0$  can be found in [BK] as Theorems 4.2 and 4.6.

a) is obvious.

b) In this part we assume that  $\log \theta \geq 1/(1 + \kappa/\mu)$ . We prove part b) by contradiction: we show that if we have a nontrivial stationary solution  $\bar{\xi}$  of DN with finite average number of parasites per individual, then we must have a nontrivial stationary solution  $\bar{\Xi}$  of DL which is contradictory to Theorem 3.3 b). So let us suppose that  $\bar{\xi}$  is a nontrivial stationary solution of DN with finite average number of parasites per individual. Therefore, if we put  $\bar{\xi}$  in the right side of DN we get zero. As we are only interested in a stationary solution, we have a constant  $\bar{\xi}_0$  in DN in the infection process. But then, if we choose  $\lambda' := \lambda \bar{\xi}_0$  in DL, the equations are the same in DN and DL for  $j \geq 1$ . So if we have a stationary solution  $\bar{\xi}$  of DN with finite average number of parasites per individual, then with the choice  $\bar{\Xi}_j := \bar{\xi}_j$  for  $j \geq 1$  we have a stationary solution for DL with finite average number of parasites per individual. This is contradictory to Theorem 3.3 b).

c) Let us first construct a candidate  $g$  for the unique nontrivial stationary solution of DN with finite average number of parasites per individual in the following way: we choose  $g_0 := R_0^{-1} (<1)$ . Then we define  $\lambda' := \lambda g_0$ . We now have

$$\frac{\lambda'\theta}{\mu + \kappa} = \frac{\lambda g_0 \theta}{\mu + \kappa} = 1$$

as  $g_0 = R_0^{-1}$ . We know by Theorem 3.3 c) that if  $\log \theta < 1/(1 + \kappa/\mu)$ , there exists a nontrivial stationary solution  $\bar{\Xi}$  of DL which is unique up to scalar multiplication. We choose that unique nontrivial stationary solution  $\bar{\Xi}^*$  of DL which is scaled such that

$$g_0 + \sum_{j \geq 1} \bar{\Xi}_j^* = 1.$$

Our candidate is the  $g$  such that  $g_0 = R_0^{-1}$  as chosen above and then we choose  $g_j := \bar{\Xi}_j^*$  for  $j \geq 1$ . We now have to check that this candidate satisfies our demands: from Theorem 3.3 c)  $g$  inherits nontriviality and that the number of parasites is finite. Additionally we have chosen  $g_0 = R_0^{-1}$  which solves one part of c). We therefore only have to prove that  $g$  is a stationary solution of DN and that it is unique under the constraints above. Let us look at the two systems DN and DL (repeated in the proof of part b)).  $g_j, j \geq 1$  is a stationary solution of DL. As  $\lambda'$  is by construction equal to  $\lambda g_0$  and  $g_0$  is constant, the two systems are even equivalent for  $j \geq 1$ . So  $g$  does satisfy all equations of DN for  $j \geq 1$  too. We have to check the  $j = 0$ -equation too. But as the right side of DN sums up to 0 this equation must be satisfied too. Therefore we have a stationary solution. We now have to show that it is unique amongst the nontrivial stationary solutions with finite average number of parasites per individual. We prove this through contradiction. Suppose we have two different nontrivial stationary solutions  $p$  and  $q$  of system

DN with finite average number of parasites per individual. We now construct two different nontrivial stationary solutions  $p'$  and  $q'$  of a system DL with parameters  $(\tilde{\lambda}, \theta, \mu, \kappa)$  where  $p'$  is not a scalar multiple of  $q'$ . But this is contradictory to Theorem 3.3 c). In fact we can simply choose  $p'_j := p_j$  for  $j \geq 1$  and  $q'_j := q_j$  for  $j \geq 1$ . We choose  $\tilde{\lambda} := \lambda p_0$ . Then  $p'$  is a stationary solution of system DL with parameters  $(\tilde{\lambda}, \theta, \mu, \kappa)$  because of the equivalence of systems DN and DL if we choose the  $\xi_0$  in the infection process of DN to be constant (as it is in a stationary solution). The same construction can be carried out with  $q'$ . We choose  $\tilde{\lambda} := \lambda q_0$ .  $q'$  is a stationary solution of system DL with parameters  $(\tilde{\lambda}, \theta, \mu, \kappa)$  because of the equivalence of systems DN and DL if we choose the  $\xi_0$  in the infection process of DN to be constant (as it is in a stationary solution). In system DL we can only have a nontrivial stationary solution if  $R_0 = 1$  because of equation (3.3). But this must be true for both combinations of parameters:

$$R_0 = \frac{\tilde{\lambda}\theta}{\mu + \kappa} = \frac{\tilde{\lambda}\theta}{\mu + \kappa} = 1,$$

and therefore we must have  $\tilde{\lambda} = \bar{\lambda}$  and  $p_0 = q_0$ . So in fact we have two different stationary solutions  $p'$  and  $q'$  of the same system DL with parameters  $(\tilde{\lambda}, \theta, \mu, \kappa)$ . They both sum up to  $(1 - p_0)$  which shows that neither is a scalar multiple of the other. So we have two nontrivial stationary solutions of DL with finite numbers of parasites where neither is a scalar multiple of the other, a contradiction to Theorem 3.3 c).

d) Let  $u$  be the unique stationary solution of DN with parameters  $(\lambda, \theta, \mu, \kappa)$  and let  $v$  be the unique stationary solution of DN with altered parameters  $(\alpha\lambda, \theta, \beta\mu, \gamma\kappa)$  where  $\alpha, \beta$  and  $\gamma$  are each positive. We define  $R_0 := \lambda\theta/(\mu + \kappa)$  and  $R_* := \alpha\lambda\theta/(\beta\mu + \gamma\kappa)$ . We want to show that  $u_j/(1 - u_0) = v_j/(1 - v_0)$  for all  $j \geq 1$  under the assumptions of Theorem 3.8 d) (if  $\beta = \gamma$ ). We show this by proving that the proportions amongst the  $u_j, j \geq 1$ , are the same as the proportions amongst the  $v_j, j \geq 1$ . In a stationary solution the derivatives are all 0. So  $u$  must satisfy

$$0 = (j + 1)\mu u_{j+1} - j\mu u_j + \frac{\mu + \kappa}{\theta} \sum_{l \geq 1} u_l p_{lj} - \kappa u_j, \tag{3.10}$$

for all  $j \geq 1$ , (we used  $u_0 = R_0^{-1} = (\mu + \kappa)/(\lambda\theta)$  from part c)) and  $v$  must satisfy

$$0 = (j + 1)\beta\mu v_{j+1} - j\beta\mu v_j + \frac{\beta\mu + \gamma\kappa}{\theta} \sum_{l \geq 1} v_l p_{lj} - \gamma\kappa v_j, \tag{3.11}$$

for all  $j \geq 1$  (we used  $v_0 = R_*^{-1} = (\beta\mu + \gamma\kappa)/(\alpha\lambda\theta)$  from part c) again). To assume that the ratio  $\kappa/\mu$  remains constant means that  $\beta = \gamma$ . So in fact, equation (3.11) is equation (3.10) multiplied by  $\beta \neq 0$ . But as we are looking at stationary solutions, and so the  $u_0$  and  $v_0$  respectively are constant, these equation are in fact both linear and so multiplying with a constant does not change their solutions. Therefore  $u$  satisfies equation (3.11) too. But stationary solutions of a system of

type DL are unique up to scalar multiplication by Theorem 3.3 c). So both solutions must be equal up to scalar multiplication, hence the proportions amongst their co-ordinates must be the same too. So the first part of Theorem 3.8 d) is proved: the ratios  $\bar{\xi}_j/(1 - \bar{\xi}_0)$  for  $j \geq 1$  do not change if the vector  $(\lambda, \mu, \kappa)$  is altered in such a way that the ratio  $\kappa/\mu$  remains constant and  $R_0$  remains larger than 1.

We are now going to rule out the possibility of other changes. So suppose that the equations  $u_j = v_j(1 - u_0)/(1 - v_0)$  hold for all  $j \geq 1$ , that means that the ratios  $u_j/(1 - u_0)$  do not change if the parameters are altered. We must now show that this implies  $\beta = \gamma$ . But the assumption  $u_j = v_j(1 - u_0)/(1 - v_0)$  for all  $j \geq 1$  means that  $u$  is a scalar multiple of  $v$ . So  $u$  must satisfy equations (3.11) too. We can write equations (3.10) and (3.11) in a more convenient form:

$$u_j = \frac{(j + 1)\mu u_{j+1} + \frac{\mu + \kappa}{\theta} \sum_{l \geq 1} u_l p_{lj}}{j\mu + \kappa}, \tag{3.12}$$

for all  $j \geq 1$ . In the same way  $v$  (and as we have just seen  $u$  too therefore) must satisfy the following equation:

$$v_j = \frac{(j + 1)\beta\mu v_{j+1} + \frac{\beta\mu + \gamma\kappa}{\theta} \sum_{l \geq 1} v_l p_{lj}}{j\beta\mu + \gamma\kappa}, \tag{3.13}$$

for all  $j \geq 1$ . Let us write  $A_j$  for  $\sum_{l \geq 1} u_l p_{lj}$ . As  $u$  satisfies (3.12) and (3.13) we have

$$\frac{(j + 1)\mu u_{j+1} + \frac{\mu + \kappa}{\theta} A_j}{j\mu + \kappa} = \frac{(j + 1)\beta\mu u_{j+1} + \frac{\beta\mu + \gamma\kappa}{\theta} A_j}{j\beta\mu + \gamma\kappa}$$

for all  $j \geq 1$ . Simple calculations lead to

$$\beta[\kappa\theta(j + 1)\mu u_{j+1} + A_j(\mu\kappa - j\mu\kappa)] = \gamma[\kappa\theta(j + 1)\mu u_{j+1} + A_j(\mu\kappa - j\mu\kappa)]$$

for all  $j \geq 1$ . But  $\kappa\theta(j + 1)\mu u_{j+1} + A_j(\mu\kappa - j\mu\kappa)$  is not 0 for all  $j \geq 1$  as can be seen in the equation for  $j = 1$  because  $u_2 > 0$  in a stationary solution of DL if  $p_{10} + p_{11} < 1$ . So  $\beta = \gamma$  must hold which finishes the proof.  $\square$

The results about convergence towards a nontrivial stationary solution of DN are summarised in the following

**Theorem 3.9.** *Let  $\log \theta \geq (1 + \kappa/\mu)^{-1}$  and  $\bar{\xi}$  be a nontrivial stationary solution of DN. For a solution  $\xi$  of DN with initial conditions  $\xi(0) = y$  where  $\sum_{j \geq 1} j y_j < \infty$  we have the following behaviour:*

*Case 1)  $(1 + \kappa/\mu)^{-1} \leq \log \theta \leq \mu/\kappa$ : If  $R_1 > 1$ , then  $\lim_{t \rightarrow \infty} \xi(t) = \bar{\xi}$  is only possible if  $\bar{\xi}_0 \geq 1/R_1$ .*

*Case 2)  $\mu/\kappa < \log \theta$ : If  $R_2 > 1$ , then  $\lim_{t \rightarrow \infty} \xi(t) = \bar{\xi}$  is only possible if  $\bar{\xi}_0 \geq 1/R_2$ .*

*Proof.* The proof for  $\kappa = 0$  can be found as Theorem 4.6 in [BK]. We use inequality (3.7) of the proof of Theorem 3.7. Let us assume that  $R_1 > 1$  (or  $R_2 > 1$  respectively in the third region for  $\theta$ ) and  $\lim_{t \rightarrow \infty} \xi(t) = \bar{\xi}$ . If there exists an  $\alpha \in [0, 1]$  such that  $g(\alpha) := (\mu\alpha + \kappa - \lambda\theta^\alpha \bar{\xi}_0) > 0$ , we can deduce by (3.7) and the Gronwall-inequality that  $m_\alpha^\infty(t)$  converges towards 0 for  $t \rightarrow \infty$ . Then  $\xi$  must converge towards the trivial solution  $e_0$  too which is a contradiction to our assumptions. In both cases we prove the existence of such an  $\alpha$  by using  $\bar{\xi}_0 < 1/R_1 < 1$  (or  $\bar{\xi}_0 < 1/R_2 < 1$  respectively in the third region for  $\theta$ ). With these contradictions we then have finished the proofs.

Let us first assume that  $1/(1 + \kappa/\mu) \leq \log \theta \leq \mu/\kappa$  and  $\bar{\xi}_0 < 1/R_1 < 1$ . We choose

$$\alpha_1 := \min \left( 1, \frac{1}{\log \theta} \log \left( \frac{\mu}{\lambda \bar{\xi}_0 \log \theta} \right) \right).$$

Let us first treat the case where  $\alpha_1 = (1/\log \theta) \log(\mu/(\lambda \bar{\xi}_0 \log \theta))$ . Then  $\alpha_1$  must be smaller or equal to 1 and because  $1/(1 + \kappa/\mu) \leq \log \theta \leq \mu/\kappa$  we have  $\alpha_1 \geq 0$ . We now must check that  $g(\alpha_1) > 0$ . We have

$$g(\alpha_1) = \frac{\mu}{\log \theta} \log \left( \frac{\mu}{\lambda \bar{\xi}_0 \log \theta} \right) + \kappa - \frac{\mu}{\log \theta}.$$

This is larger than 0 if

$$\log \left( \frac{\mu}{\lambda \bar{\xi}_0 \log \theta} \right) + \log(\theta^{\frac{\kappa}{\mu}}) > 1,$$

which is satisfied if

$$\frac{\mu \theta^{\kappa/\mu}}{\lambda \bar{\xi}_0 \log \theta} > e.$$

As  $R_1^{-1} > \bar{\xi}_0$  this inequality is satisfied. Now we treat the case where  $\alpha_1 = 1$  and therefore we may additionally use that  $(1/\log \theta) \log(\mu/(\lambda \bar{\xi}_0 \log \theta)) > 1$ . This is equivalent to  $\mu/(\lambda \theta \log \theta) > \bar{\xi}_0$ . Therefore  $\bar{\xi}_0 < \min(\mu/(\lambda \theta \log \theta), R_1^{-1})$ . Because  $\log \theta \geq 1/(1 + \kappa/\mu)$ , we have  $\mu/(\lambda \theta \log \theta) < R_1^{-1}$ . Hence

$$\bar{\xi}_0 < \frac{\mu}{\lambda \theta \log \theta}. \tag{3.14}$$

Let us now show that  $g(1) = \mu + \kappa - \lambda\theta \bar{\xi}_0 > 0$ . By (3.14) this is satisfied if  $\mu + \kappa \geq \mu/\log \theta$ . But this is satisfied because  $\log \theta \geq 1/(1 + \kappa/\mu)$  which ends the proof of the first case.

Now we assume that  $\log \theta > \mu/\kappa$  and  $\bar{\xi}_0 < 1/R_2 < 1$ . Define  $c := 1/R_2 - \bar{\xi}_0 > 0$ . Then we have

$$g(\alpha) = \mu\alpha + \kappa - \lambda\theta^\alpha \bar{\xi}_0 = \mu\alpha + \kappa - \lambda\theta^\alpha (\kappa/\lambda - c) = \mu\alpha + \kappa - \theta^\alpha \kappa + \lambda\theta^\alpha c,$$

where we used the definitions of  $c$  and  $R_2 = \lambda/\mu$ . This shows that there exists an  $\alpha \in [0, 1]$  such that  $g(\alpha) > 0$  (let  $\alpha$  tend to 0). This ends the proof of case 2).  $\square$



**Remark.** Suppose that in model DL  $\mu/\kappa \geq \log \theta > (1 + \kappa/\mu)^{-1}$ ,  $R_0 > 1$  and  $R_1 < 1$ . By Remark 1) to Theorem 3.1 the epidemic dies out; but by equation (3.3) the number of parasites tends to infinity. We have the same behaviour in models DN (Theorem 3.7 and equation (3.6)) and SL (Remark 3) to Theorem 2.1 in [Ls].

**Open questions.** 1. Having proved laws of large numbers (Theorems 2.3 and 2.5), can we prove a central limit theorem? There are various possibilities: single co-ordinates, a finite combination of co-ordinates or even the entire process (a measure-valued process). For one single co-ordinate  $j$  such a result could be that there is a diffusion limit for

$$\sqrt{M} \left( x_j^{(M)}(t) - \xi_j(t) \right)_{0 \leq t \leq T}$$

as  $M \rightarrow \infty$  if the initial values are suitable.

2. In view of Theorem 3.8 c), do we have convergence in DN towards that stationary solution  $\bar{\xi}$ ?

3. Are there stationary solutions with infinite average number of parasites per individual and under which conditions does a solution  $\xi$  converge to such a stationary solution? Is such a solution unique?

**Appendix**

In the Appendix we look at variations of results from [HK] which we used frequently in this paper. We consider a time-homogeneous Markov chain  $\{Z_t\}$  on a general state-space  $S$ . The process is defined by its times of jumps,  $\{\tau_n\}$  ( $\tau_0 = 0$ ,  $\tau_{n+1} = \inf\{t > \tau_n; \Delta Z_t := Z_t - Z_{t-} \neq 0\}$  and  $\tau_n = \infty$  if there are less than  $n$  jumps), and the sizes of its jumps,  $\{J_n\}$  ( $J_0 = 0$ ). By the Markov property, conditionally on  $\{Z(\tau_n) = z\}$ , for  $\tau_{n+1} < \infty$  a.s. we have

- a)  $\tau_{n+1} - \tau_n$  is exponentially distributed with mean, say  $\rho(z)^{-1}$ , and
- b)  $Z(\tau_{n+1}) - Z(\tau_n)$  has a law that depends on  $z$  only, say  $\pi(z, \cdot)$ .

Let  $\{\mathcal{F}_t\}$  be the natural filtration of the process  $Z_t$ . We have

$$\begin{aligned} Z(\tau_{n+1}) &= Z(\tau_n) + J_{n+1}, \\ Z_t &= Z_0 + \sum_{n \geq 1} J_n I[\tau_n \leq t]. \end{aligned} \tag{A1}$$

Let  $f$  be an arbitrary function and define

$$Lf(z) := \rho(z) \int [f(y + z) - f(z)]\pi(z, dy)$$

and

$$N_t^f := f(Z_t) - f(Z_0) - \int_0^t Lf(Z_s) ds$$

$L$  is the infinitesimal generator of the Markov process  $Z$ , see for example Ethier and Kurtz (1986) [EK], p. 376. In Theorem A1 and its corollaries, we investigate conditions under which  $N_t^f$  is a martingale. Additionally, a sufficient condition, condition (B), is given for the integrability of the process  $f(Z_t)$ .

**Theorem A1.** Assume that the process  $Z$  is regular and takes values on a general state-space  $S$ . Let  $f : S \rightarrow \mathbb{R}_+$  be a possibly unbounded function such that there exists a function  $F : S \rightarrow \mathbb{R}_+$  such that

$$|L|f(z) := \rho(z) \int |f(z+y) - f(z)|\pi(z, dy) \leq F(z), \tag{B}$$

where

$$\mathbb{E} \left[ \sup_{0 \leq u \leq s} F(Z_u) \right] < \infty$$

for all  $s \geq 0$ . If  $f(Z_0)$  is integrable, then so is  $f(Z_t)$ , moreover  $N^f$  is a martingale and

$$\mathbb{E}[f(Z_s)] = \mathbb{E}[f(Z_0)] + \int_0^t \mathbb{E}[Lf(Z_s)]ds.$$

*Proof.* The proof of Theorem A1 follows the same lines as the proof of Theorem 2 in [HK] with the following exceptions (notation and numbers of equations according to [HK]):

1. Equation (5) in step 1 becomes

$$\mathbb{E}[|Y|_T] \leq \mathbb{E}[|Y_0|] + \mathbb{E} \left[ \int_0^T F(Z_s)ds \right] < \infty,$$

proving immediately that the variation process  $|Y|_t = \int I[s \leq t]|x|\mu^f(ds, dx)$  is locally integrable.

2. The first equations in step 2 become

$$\mathbb{E}[|f(Z_t^{S_n})|] \leq \mathbb{E}[|Y_0|] + \mathbb{E} \left[ \int_0^t I[s \leq S_n]F(Z_s)ds \right] < \infty$$

independently of  $n$  which leads directly to (7).

3. In equation (8) we use again the upper bound  $F(Z_s)$  for  $|L|f(Z_s)$  which finishes the proof of Theorem A1. □

Again, let  $S$  be a general state-space such that the elements  $z$  of  $S$  are (infinite) vectors and  $f_j : S \rightarrow \mathbb{R}_+$  be a projection on the co-ordinate  $j$ :  $f_j(z) = z_j$ . Define  $m_k(z) := \int (f_j(x))^k \pi(z, dx)$  and  $|m|_k(z) := \int |f_j(x)|^k \pi(z, dx)$ . Applying the above theorem to the particular case of polynomials we get

**Corollary A2.** Assume that  $(f_j(Z_0))^k$  is integrable and that there exists a function  $F$  such that for all  $i = 1, \dots, k$

$$\rho(z)|m|_i(z) \leq F(z).$$

and  $\mathbb{E}[\sup_{0 \leq u \leq s} F(Z_u)] < \infty$ . Then  $(f_j(Z_t))^k$  is integrable and

$$(f_j(Z_t))^k - (f_j(Z_0))^k - \sum_{i=0}^{k-1} \binom{k}{i} \int_0^t \rho(Z_s) (f_j(Z_s))^i m_{k-i}(Z_s)ds$$

is a martingale.

Particular attention is, of course, given to the function  $g_1(z) := z_j$  for  $j \geq 0$  (so  $k = 1$  in Corollary A2) and to the process

$$N_t^g := g_1(Z_t) - g_1(Z_0) - \int_0^t \rho(Z_s)m_1(Z_s)ds.$$

It is, for example, clear that if we find an  $F$  such that  $\rho(z)|m_1(z)| \leq F(z)$  and  $\mathbb{E}[\sup_{0 \leq u \leq s} F(Z_u)] < \infty$  holds and  $g_1(Z_0)$  is integrable, then the process  $g_1(Z_t)$  is regular and integrable and  $N_t^g$  is a martingale. When a second-order condition is added, we obtain an expression for the predictable compensator of the quadratic variation process  $[N^g, N^g]_t$ .

**Corollary A3.** *Assume that the conditions of Corollary A2 with  $k = 2$  hold. Then the process*

$$[N^g, N^g]_t - \int_0^t \rho(Z_s)m_2(Z_s)ds$$

is a martingale.

*Proof.* Applying Corollary A2 to the function  $g_2(z) := z_j^2$  ( $k = 2$  in Corollary A2), we get that the process

$$g_2(Z_t) - g_2(Z_0) - \int_0^t \rho(Z_s)m_2(Z_s)ds - 2 \int_0^t \rho(Z_s)g_1(Z_s)m_1(Z_s)ds$$

is a martingale. Writing  $[N, N]_t$  in terms of the process  $g_1(Z_t)$  (and its jumps), shows that the process

$$g_2(Z_t) - g_2(Z_0) - 2 \int_0^t \rho(Z_s)g_1(Z_s)m_1(Z_s)ds - [N^g, N^g]_t$$

is a martingale. Then the statement follows by differencing the previous two equations. □

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