# Transmission of infection along a dynamic sexual network with star-shaped components

K.Y. Leung (3130487)

Master's thesis Mathematical Sciences

Supervised by O. Diekmann & M. Kretzschmar

Department of Mathematics, Faculty of Science, Utrecht University.

Julius Centre for Health Sciences and Primary Care, University Medical Centre Utrecht.

Utrecht, 19th August 2011

### SUMMARY

Currently there is a debate in epidemiology about the contribution of overlapping sexual partnerships, and in particular polygamy, to the spread of HIV in sub-Saharan Africa. Motivated by this debate we formulate a mathematical model for the dynamic sexual network corresponding to polygamy. Consider the following situation. Suppose we have a heterosexual population where men may have multiple wives and women at most one husband. If we also assume men and women to be faithful to each other, then this gives rise to a sexual network with multiple star-shaped components. This network is dynamic as partnerships are formed and broken over time and individuals enter and leave the population due to demographic turnover. We can describe this network with a system of ordinary differential equations (ODEs). We analyse the system and study existence and uniqueness of solutions and the steady state of the system. We are interested in how sexually transmitted infections, such as HIV, spread along the network. Therefore, the next part of the research is to superimpose an S(usceptible)-I(nfectious) infection on the dynamic sexual network and describe the infection model with a set of ODEs. Using the interpretation of the model we determine epidemic thresholds for the system. The thresholds allow us to determine what the conditions are for an infection to become endemic in the population. We end the analysis by comparing the basic reproduction numbers of the infectious disease models for the polygynous population with that of a monogamous population.

**Keywords**: Mathematical modelling; dynamical systems; dynamic sexual network; polygyny (polygamy); S-I infection; HIV; epidemic thresholds

# Contents

1	Intr	oduction	3
<b>2</b>	Pair	Formation	9
	2.1	Pair-formation model	9
	2.2	Existence and uniqueness of solutions	13
	2.3	Semiflow	20
	2.4	Steady state: dependence on parameters	20
		2.4.1 Calculating an explicit expression	20
		2.4.2 Mean value analysis	26
		2.4.3 Dependence on parameters: numerical results	29
		2.4.4 Extreme situations	34
	2.5	Stability of the steady state	40
3	Infe	ctious disease	<b>53</b>
	3.1	Infectious-disease model	53
	3.2	Steady states	59
	3.3	Determining $R_0$	59
		3.3.1 The basic reproduction number $R_f$	60
		3.3.2 The basic reproduction number $R_m$	62
		3.3.3 $R_0$ revisited	67
	3.4	Another threshold	67
	3.5	$R_0$ and $\widetilde{R}_0$ : threshold parameters	69
	3.6	Monogamy vs polygyny	72
4	Disc	cussion	79
Bi	bliog	raphy	83

# Chapter 1

# Introduction

### Infectious diseases

Infectious diseases, such as HIV, influenza, and measles, are a part of modern life. Some diseases, such as measles, cause relatively small harm in the developed world, while others, such as HIV, form serious problems for public health. Other recent infectious disease outbreaks, such as SARS and swine flu (H1N1), remind us of the serious threat they pose to world health. Effective control measures require an understanding of how infectious diseases spread.

Mathematically modelling the transmission of diseases has proven to be very useful in this respect [1, 2]. Already in the beginning of the previous century, Sir Ronald Ross used a mathematical model to describe the spread of malaria [3, 4]. This allowed him to deduce that malaria could be eradicated in a region by reducing the density of mosquitoes below a certain threshold; it was not necessary to exterminate all mosquitoes. The qualitative insights gained from a mathematical analysis of the model were most important in providing ways to control malaria.

In recent years, mathematical modelling has played an increasingly important role in supporting decisions in infectious-disease control by providing insights into transmission dynamics and possible effects of intervention measures [5, 6].



Figure 1.1: Network structure of adolescent students in a romantic or sexual relationship with another student in a 'typical' high school in a midsized town in the midwest of the United States. [7, Fig. 2]

### Dynamic sexual networks

In studying the transmission of an infectious disease in a population, an important modelling component is the contact pattern; each contact generates a possibility to transmit the disease. We can suppose any two individuals in a population may contact each other: random contacts. This simplifying assumption of a randomly mixing population is often used in epidemiological research (often referred to as homogeneous mixing) and has proven to be successful for e.g. host-vector diseases such as malaria and respiratory infections like influenza [8]. For other infections, such as sexually transmitted infections (STIs), the contact patterns deviate strongly from the random mixing assumption. In these cases, the random mixing assumption does not allow us to capture the spread of an STI in a population.

In case of an STI, a connection between two individuals is established by sexual contact. As a rule, individuals engage in partnerships with other individuals and have multiple sexual contacts before separation: contacts do *not* occur at random. Such contact patterns can be described by networks in which vertices represent individuals and edges represent partnerships (Figure 1.1).

To understand the transmission dynamics of an STI we need to analyse the spread of it in a dynamic sexual contact network. This network describes all existing sexual partnerships in a population. It is dynamic since partnerships are formed and broken over time and individuals enter and leave due to demographic turnover in the population. The dynamic sexual network needs to be taken into account in order to really capture the dynamics of an STI in a population.



Figure 1.2: Components of the sexual network of Likoma Island, Malawi. Black (grey) nodes represent males (females), lines represent sexual partnerships. All sexual connections (a) in three years preceding the survey; all sexual connections of the 'giant component' (b) within one year and (c) at the time of the survey. [9, Fig. 2]

#### Mathematical modelling

In theory, if we know every sexual partnership of every individual in a population, we would be able to construct the dynamic sexual network. In practice, this is very cumbersome and almost impossible. A network quickly becomes very complicated (Figure 1.2) and determining the influence of the network on the disease dynamics even more so. This is where mathematical modelling comes into play. Rather than taking all possible details into account, we consider abstractions of reality using mathematical modelling. This allows us to gain insights into an idealized sexual network and the influence of structural properties of the network on the spread of infectious diseases.



Figure 1.3: The sexual network of a population that is strictly monogamous on the left and one that is not strictly monogamous on the left.

As every community has its own social and cultural values, there exist many different types of sexual networks. Therefore a wide variety of idealized dynamic sexual networks can be considered. By specifying different characteristics, we can obtain many different idealized networks; compare e.g. the sexual network of a population that is strictly monogamous to one that is not (Figure 1.3) and the romantic and sexual network of a 'typical' high school in a midsized town in the midwest of the United States (Figure 1.1) with the sexual network of a population at Likoma Island, Malawi (Figure 1.2).

So, how does one start studying dynamic sexual networks? Ideally, we would like to know what network characteristics have what effect on the disease dynamics. So if we would have a network with some specific characteristics, then we would investigate what the disease dynamics along this network would be. As we are still far away from understanding relations between network topologies and disease dynamics, this will not be the goal in this thesis. Rather we will study a specific sexual network, motivated by real-life problems.



Figure 1.4: The sexual network of a polygynous population. Multiple star-shaped components arise from men having multiple wives and women at most one husband.



Figure 1.5: HIV prevalence among adults aged 15-49 years old across the world in 2009 [10].

### Polygyny and HIV in sub-Saharan Africa

We find a motivation for this thesis in the HIV epidemic in sub-Saharan Africa. This epidemic has great social and economic impact, and its scale is enormous (Figure 1.5), especially in sub-Saharan Africa. It is estimated that in 2009, 2.6 million individuals were newly infected with HIV and HIV/AIDS caused 1.8 million deaths, a disproportionate amount (1.8 and 1.3 million, respectively) occurring in sub-Saharan Africa [10].

In heterosexual populations in sub-Saharan Africa, in contrast to elsewhere, polygyny, a form of polygamy, is commonly practised: men may have multiple wives while women have at most one husband. If we also assume men and women to be faithful, this gives rise to a network with multiple star-shaped components (Figure 1.4). A possible route of transmission is displayed in Figure 1.6. How does this sexual network influence the spread of STI such as HIV?



Figure 1.6: Possible route of transmission in a star-shaped union. In the last frame, the man has died, leaving two infectious women to potentially infect other men.

The influence of the sexual network in sub-Saharan Africa on the spread of HIV is most pertinent to study, both from a mathematical and an epidemiological point of view. In this region, HIV is widespread among the heterosexual population. This is very different from the rest of the world, where HIV mostly remains concentrated in specific high-risk groups such as injecting drug-users, prostitutes, and homosexual men [11].

Can we explain the pervasive HIV transmission among the heterosexual population in sub-Saharan Africa by the sexual network corresponding to polygyny? Currently, there is much debate in the epidemiological literature about the contribution of overlapping partnerships (concurrency) on HIV-transmission in sub-Saharan Africa [11]. While some (empirical researchers) argue that concurrency is an important factor in the rapid spread [12], others hypothesized that some forms of concurrency, such as the practice of polygyny, may be protective [13].

Motivated by the debate we will use mathematical modelling to study a dynamic sexual network with multiple star-shaped components and the transmission of an infection along the network. In a way, the models we consider here will be extensions of the model of Kretzschmar and Dietz [14]. In this paper, they considered the pair-formation process of a completely monogamous homosexual population and the spread of an infection. Now we will not make the restriction of the population being completely monogamous, but only impose this condition on one type of individuals, namely the women.

### Outline of the text

This thesis is set up in the following way. First, as a preparation, we consider the pair-formation model corresponding to an idealized polygamous population. This dynamic network is interesting in its own right and we will spend some time studying it, not avoiding the technical parts. Moreover, analysis of the dynamic sexual network allows us to make some simplifying assumptions when studying the transmission of infection along the network. The steady state of the pair-formation model will be used to simplify the statistical description of the dynamic sexual network in the next part of our investigation. In this second part, we will study the spread of an infection along the dynamic sexual network. Here, the emphasis will be on working with the interpretation of the model, and less on technical details.

In Chapter 2, we will describe the pair-formation model with an infinitedimensional system of nonlinear ordinary differential equations (ODEs) and then analyse this system. We will prove existence and uniqueness of solutions of the dynamical system and consider its steady state. Concerning this steady state, we will determine an explicit expression for it. This explicit expression will then be analysed numerically to understand the behaviour of the steady state as a function of the parameters.

In order to understand the behaviour of the system near the steady state we will consider its stability. Inspired by [15, 16], we will prove the stability of the steady statevia a compact attractor of an appropriate set. We will be able to prove that the steady state is a compact attractor, in particular it will be globally asymptotically stable.

Proving the existence and uniqueness of solutions and the stability of the steady state will comprise the largest part of Chapter 2. The topic of infinitedimensional systems of ODEs in Banach spaces, which we are dealing with here, has been dealt with before [17, 18, 19, 20]. In our situation, the system has a biological interpretation, e.g. we consider the fraction of single women in the population. We specifically need solutions to be nonnegative at any point of time in the future. Therefore, we can not simply use general results on existence and uniqueness of solutions such as presented in e.g. [17]. Fortunately, we are not the first to consider infinite-dimensional systems in modelling biological phenomena, and we will be able to use a lot of theory and ideas already developed, especially those presented in [16].

In Chapter 3 we superimpose an STI on our dynamic sexual network. We consider an S-I infection that can be transmitted through sexual contact. Individuals can then be either <u>S</u>usceptible or <u>Infectious</u>. One should think of this STI as describing the virus HIV in a much idealized way. Obviously, the actual virus is much more complex than this simple representation. We will however ignore most of the biological aspects of HIV in our model. Again this model can be described with an infinite-dimensional dynamical system. We are interested in the endemic steady state and criteria for the infection-free state to be asymptotically stable.

Using the interpretation of the model, we will determine the basic reproduction number  $R_0$ . This number can be interpreted as the expected number of secondary cases that one 'typical' infectious individual does cause in an otherwise susceptible population. It is one of the most important quantities of interest in infectious disease epidemiology as it determines whether an infection dies out when introduced in the population.

We will consider a threshold parameter  $\tilde{R}_0$  different from  $R_0$ . This  $\tilde{R}_0$  will again be determined using the interpretation of the model. This threshold parameter will just be a different way of bookkeeping. It will be shown that a relationship between  $R_0$  and  $\tilde{R}_0$  exists. Both have the threshold value 1.

Next, we will compare the  $R_0$  we have found for the polygynous population with the basic reproduction number of a monogamous population. This allows us to draw some conclusions on the effect of the polygynous structure on the initial spread of an infection (compared to a monogamous population).

Finally, in Chapter 4 we will give a short summary of our most important findings and some conclusions based on our investigation. We will also point out the challenges that we have not dealt with in this thesis. This is mainly due to time constraints. But for future work, it will be interesting to look into them. Furthermore, we will give an outlook on some ideas to further develop and extend the models presented here.

### Chapter 2

# **Pair Formation**

In this chapter, we will start by introducing the model for the dynamic sexual network corresponding to a polygamous population and discuss some of the assumptions we make. Next, we will describe the model using an infinite set of ODEs. We will concern ourselves with proving the existence and uniqueness of the solutions of the dynamical system.

We are interested in the long run behaviour of the system. Therefore, we study the steady state of the system. First, we will calculate an explicit expression for the steady state. Next, we will perform some numerical experiments and also consider the effect on the steady state of some extreme cases for the parameters. Finally, we will prove that the steady state is globally asymptotically stable.

This chapter can be seen as a preparation for what we are really interested in: the transmission of an infection along the dynamic sexual network. Luckily for us, the preparations give rise to some interesting mathematics (which also explains why this chapter comprises the largest part of the entire text).

### 2.1 Pair-formation model

We consider a heterosexual population where the sex ratio is 1 : 1. In this population, each woman can be in a relationship with at most one man, while a man may have multiple partners, without any restriction on the number of partners for these men. Note that the situation is asymmetric for men and women. The network arising from this consists of star-shaped components, with men in the 'centre' of each star (Figure 1.4). We say that a star consisting of one man and his j wives has star size  $j, j = 0, 1, \ldots$  By definition, stars of size zero will consist of single men or single women.

The pair-formation process will be described with a deterministic model. We justify this deterministic setting by assuming the population to be large. Therefore, stochastic fluctuations are of relatively minor importance.

We make the following assumptions on the pair-formation process. A man with more than one partner does not distinguish between any of his wives; his first wife will not be of more or less importance than his potential third as far as sexual contacts and inclination to divorce his wife are concerned. The same goes for the women; the inclination to divorce her husband will not depend on the number of co-wives a woman has. Couples separate at a constant rate  $\sigma > 0$ , regardless of the number of partners of the man.

Women do not have any preference for the status of the man when 'looking' for a husband. Therefore a man with e.g. 10 wives acquires a new partner at the same rate as a single man. Men and women form new relationships at a per pair rate  $\rho > 0$ . The pair-formation function is derived from the mass-action principle. This means that if we have e.g. X single women and  $P_1$  men with one wife, then the rate of formation of partnerships between men with one wife and single women is  $\rho X P_1$ .

There is also demographic turnover due to birth and death. Since we are considering a pair-formation process, and eventually sexual contacts that generate possibilities to transmit an STI between individuals, birth of an individual should be interpreted as recruitment into the sexually active population. Individuals are recruited into the population as singles. The death of an individual may mean physical death or merely the individual leaving the sexually active population, we do not distinguish between these events. Note that a newly recruited individual may die before having any sexual contact with anyone in the population.

A partnership may dissolve if the individuals separate or if either of the two individuals involved in that partnership die. These dissolution events do not affect the emotional state of individuals, e.g. there is no mourning period after the loss of a partner. The woman whose partner dies, will be added to the single population, while the man, with more than one partner, whose partner dies will be left with j - 1 partners,  $j = 2, 3, \ldots$  The man will be added to the single population if he had one wife to begin with. If a man with j partners dies, j women will be added to the single population,  $j = 1, 2, \ldots$  Individuals will only remember the state they are in, not the states they may have visited in the past. So a single man may have been newly recruited into the population or he may have become single after losing his wife. Either way, his sexual behaviour will not depend on this.

A consequence of our assumptions is that once a partnership is dissolved, the two individuals involved never encounter each other again (in the sexual network): a partner, once lost, is lost forever. If the dissolution happens because one of the partners dies, this is obviously so. But if two individuals separate, they will also never have a sexual relationship again in our model. It is with probability zero that two individuals encounter each other again in our large population (and deterministic description) conform the standard case with massaction kinetics. So our population is randomly mixed in partner choice, but not in sexual contacts as these may occur (multiple times) within partnerships.

We include birth and death in the simplest way: there is a constant population birth rate and a constant per capita death rate. Since we want to maintain the sex ratio 1 : 1, we assume that the birth of males and females both happen at the same constant rate B > 0. We assume that each individual dies at rate  $\mu > 0$ , regardless of its sex or partnership status.<sup>1</sup>

Obviously, many of the above assumptions are arguable. For instance, the assumption that men acquire new partners regardless of the current number of partners is quite simplistic. In reality a man must have something to offer in

 $<sup>^{1}</sup>$ We may imagine that men will drop dead of exhaustion due to the obligation of entertaining too many wives. On the other hand it is not entirely realistic to assume there is no upper bound on the number of women a man may have.

return for the partnership, e.g. be able to provide for his wives or there is the law to abide to. In future work, we can extend the model by incorporating more sophisticated assumptions that reflect real life situations more accurately. However, we will focus on this idealized situation for this thesis.

We introduce the following variables.

- X: the number of single women,
- $P_j$ : the number of men with j partners,  $j \ge 0$ ,
- $N\colon$  the total population size.

Note that  $P_0$ , the number of men with zero partners, equals the number of single men in the population.

Due to demographic turnover, the total population size may change over time. Consistency requires the total population size to be the sum of all men and women, and the population of women to be equal to the population of men.

$$N = X + \sum_{j=0}^{\infty} (1+j)P_j,$$
  
$$\frac{1}{2}N = X + \sum_{j=1}^{\infty} jP_j = \sum_{j=0}^{\infty} P_j.$$

The set of ODE describing this model is given by the following:

$$\frac{dX}{dt} = B - \rho X \sum_{k=0}^{\infty} P_k + (\sigma + \mu) \sum_{k=1}^{\infty} k P_k - \mu X,$$

$$\frac{dP_0}{dt} = B - \rho X P_0 + \sigma P_1 + \mu P_1 - \mu P_0,$$

$$\frac{dP_j}{dt} = \rho X P_{j-1} - \left(\rho X + (\sigma + \mu)j\right) P_j + (\sigma + \mu)(j+1) P_{j+1} - \mu P_j,$$
(2.1)

 $j \ge 1.$ 

We are able to calculate the equilibrium population size. Since

$$\frac{d}{dt}\Big(X + \sum_{j=0}^{\infty} (1+j)P_j\Big) = 2B - \mu\Big(X + \sum_{j=0}^{\infty} (1+j)P_j\Big),$$

we see that the population size at equilibrium equals

$$N^* = \frac{2B}{\mu}.$$

For the population of women and the population of men we have

$$\frac{d}{dt}\left(X + \sum_{j=0}^{\infty} jP_j\right) = B - \mu\left(X + \sum_{j=0}^{\infty} jP_j\right),$$
$$\frac{d}{dt}\left(\sum_{j=0}^{\infty} P_j\right) = B - \mu\left(\sum_{j=0}^{\infty} P_j\right),$$

so the population of women and men in equilibrium is  $N_f = N_f^* = \frac{1}{2}N^*$  and  $N_m = N_m^* = \frac{1}{2}N^*$ , respectively. From now on we will assume the population is in equilibrium, i.e.  $N = N^*$ , and  $N_f = N_m = N_m^* = \frac{1}{2}N^*$ . We can consider fractions rather than numbers. We will use small letters to

We can consider fractions rather than numbers. We will use small letters to denote fractions, i.e.

$$x \coloneqq \frac{X}{N}$$
: the fraction of single women,  
 $p_j \coloneqq \frac{P_j}{N}$ : the fraction of men with  $j$  partners,  $j \ge 0$ .

The set of ODEs describing the model then becomes:

$$\frac{dx}{dt} = \frac{\mu}{2} - \frac{2B\rho}{\mu} x \sum_{k=0}^{\infty} p_k + (\sigma + \mu) \sum_{k=1}^{\infty} k p_k - \mu x,$$

$$\frac{dp_0}{dt} = \frac{\mu}{2} - \frac{2B\rho}{\mu} x p_0 + (\sigma + \mu) p_1 - \mu p_0,$$

$$\frac{dp_j}{dt} = \frac{2B\rho}{\mu} x p_{j-1} - \left(\frac{2B\rho}{\mu} x + (\sigma + \mu)j\right) p_j$$

$$+ (\sigma + \mu)(j+1) p_{j+1} - \mu p_j,$$
(2.2)

 $j \geq 1.$  We write the above system in a more condensed form by introducing the following coefficients. Let

$$r\coloneqq \frac{2B\rho}{\mu}$$

and

$$\begin{cases} \alpha_{0j} = \mu, & j = 1, 2, \dots, \\ \alpha_{jj} = -((\sigma + \mu)j + \mu), & j = 1, 2, \dots, \\ \alpha_{j-1,j} = (\sigma + \mu)j, & j = 1, 2, \dots, \\ \alpha_{jk} = 0, & \text{otherwise, } j, k = 0, 1, \dots \end{cases}$$
(2.3)

Furthermore, introduce

$$\begin{cases} \gamma_{jj} = -r, & j = 0, 1, \dots, \\ \gamma_{j+1,j} = r, & j = 1, 2, \dots, \\ \gamma_{jk} = 0, & \text{otherwise, } j, k = 0, 1, \dots \end{cases}$$
(2.4)

Since we assume a sex ratio 1:1, i.e.

$$x + \sum_{j=1}^{\infty} jp_j = \sum_{j=0}^{\infty} p_j = \frac{1}{2},$$
(2.5)

we may also write the birth rate for the fraction of women as  $\mu(x + \sum_{j=1}^{\infty} jp_j)$ and the birth rate for the fraction of men as  $\mu \sum_{j=0}^{\infty} p_j$ . The set of differential equations (2.2) can then be written as

$$x' = -rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j,$$
  
$$p'_j = \sum_{k=0}^{\infty} \alpha_{jk} p_k + x \sum_{k=0}^{\infty} \gamma_{jk} p_k,$$
  
(2.6)

with the coefficients  $\alpha_{jk}$  and  $\gamma_{jk}$ ,  $j, k = 0, 1, \ldots$  given by (2.3) and (2.4). For later use, it is also convenient to introduce the functions  $f: \mathbb{R}_+ \times \ell_+^{11} \to \mathbb{R}$  and  $g: \mathbb{R}_+ \times \ell_+^{11} \times \ell^{11}$ , with

$$f(x,p) = -rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j,$$
  
$$g_j(x,p) = x \sum_{k=0}^{\infty} \gamma_{jk} p_k, \quad j = 0, 1, \dots.$$
 (2.7)

### 2.2 Existence and uniqueness of solutions

This section (and Section 2.5) will rely on the paper by Martcheva and Thieme [16]. In this section, we will be dealing with the mathematical question of existence and uniqueness of solutions of (2.6) given appropriate initial conditions. We would like to prove that, with initial data  $(x(0), p(0)) = (\tilde{x}, \tilde{p})$  there exist unique solutions of (2.6) for all positive times t. In order to do this, we need to understand what a solution is in our setting. Recall the Banach space

$$\ell^{1} = \left\{ p = (p_{j})_{j \ge 0} \colon p_{j} \in \mathbb{R}, \ j = 0, 1, \dots, \ \sum_{j=0}^{\infty} |p_{j}| < \infty \right\},\$$

endowed with norm

$$||p|| = \sum_{j=0}^{\infty} |p_j|, \qquad p = (p_j)_{j \ge 0}.$$
(2.8)

We introduce the subspace

$$\ell^{11} = \left\{ p = (p_j)_{j \ge 0} \colon p_j \in \mathbb{R}, \ j = 0, 1, \dots, \ \sum_{j=0}^{\infty} j |p_j| < \infty \right\} \subset \ell^1.$$

By introducing the norm

$$||p||_1 = \sum_{j=0}^{\infty} (1+j)|p_j|, \qquad p = (p_j)_{j \ge 0},$$

this subspace  $\ell^{11}$  becomes a Banach space itself.

If we now write

$$\ell_{+}^{11} \coloneqq \left\{ p = (p_j)_{j \ge 0} \in \ell^{11} \colon p_j \ge 0, \ j = 0, 1, \ldots \right\},\$$

then it is natural to require solutions  $(x(t), p_0(t), p_1(t), \ldots) = (x(t), p(t))$  of (2.6) to lie in  $\mathbb{R}_+ \times \ell_+^{11} \subset \mathbb{R} \times \ell^{11}$ . The space  $\mathbb{R} \times \ell^{11}$  is endowed with the natural product-norm, which we will also denote with  $\|\cdot\|$ , i.e.

$$||(x,p)|| = |x| + ||p||_1, \qquad (x,p) \in \mathbb{R} \times \ell^{11}.$$
(2.9)

*Remark* 2.1. Recall the definition of a  $C_0$ -semigroup  $(S(t))_{t\geq 0}$  on a Banach space X; see e.g. [17, 18, 19, 20]. The family  $(S(t))_{t\geq 0}$  is a family of bounded linear operators on X such that

$$S(t+s) = S(t)S(s), \quad t,s \ge 0,$$
$$\lim_{t \to 0} S(t)x = S(0)x, \quad x \in X.$$

The operator A, the infinitesimal generator of the  $C_0$ -semigroup  $(S(t))_{t\geq 0}$  is defined by

$$A = \lim_{h \downarrow 0} \frac{S(h)x - x}{h}, \quad x \in D(A),$$

where D(A) is the set of all  $x \in X$  for which the above limit exists; D(A) is called the domain of A.

Note that the system of differential equations for p in system (2.6) consists of a linear part  $\sum_{k=0}^{\infty} \alpha_{jk} p_k$ , which is independent of x, and a nonlinear part  $x \sum_{k=0}^{\infty} \gamma_{jk} p_k$ . The coefficients  $\alpha_{jk}$  in (2.6) give rise to an infinitesimal generator  $A_1$  of a  $C^0$ -semigroup  $S_1$  on  $\ell^{11}$ ; see [16, Section 2.2]. The domain of  $A_1$  is given by  $D(A_1) = \{p \in \ell^{11} \cap D_0 : \check{A}p \in \ell^{11}\}$ , where  $D_0 = \{p \in \ell^1 : \sum_{j=0}^{\infty} |\alpha_{jj}| |p_j| < \infty\}$  and  $\check{A}$  is the linear operator with  $\check{A}p = (\sum_{k=0}^{\infty} \alpha_{jk} p_k)_{j\geq 0}, p \in D_0$ . We have

$$\sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j |\alpha_{jk}| |p_k| < \infty \quad \text{for all } p \in D(A_1);$$

see [16, Lemma 2] for a proof. This shows that the double series  $\sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j \alpha_{jk} p_k$  exists absolutely and we may interchange the order of summation. We will use this property several times to make estimates or for rewriting expressions, e.g. in the proof of Theorem 2.3.

The pair of continuous functions  $x: \mathbb{R}_+ \to \mathbb{R}_+$  and  $p: \mathbb{R}_+ \to \ell_+^{11}$  is called an integral solution of (2.6) with initial conditions  $x(0) = \tilde{x}, p(0) = \tilde{p}$  if it is a solution of

$$x' = -rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j, \quad t \in \mathbb{R}_+, \quad x(0) = \tilde{x},$$
  
$$p_j(t) = \tilde{p}_j + \sum_{k=0}^{\infty} \alpha_{jk} \int_0^t p_k(s) ds + \int_0^t x(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k(s) ds, \quad t \in \mathbb{R}_+,$$
  
(2.10)

 $j = 0, 1, \ldots$ , with the understanding that  $\int_0^t p(s) ds \in D(A_1)$  for all  $t \in \mathbb{R}_+$ .

Equivalently to the equation for p in (2.10), p is an integral solution of (2.6) if it satisfies

$$p(t) = S_1(t)\tilde{p} + \int_0^t S_1(t-s)g(x(s), p(s))ds, \quad t \in [0, \tau),$$

where  $g(x(s), p(s)) = (x(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k(s))_{j \ge 0}$  and  $S_1$  is the  $C_0$ -semigroup generated by  $A_1$  on  $\ell^{11}$ ; see Remark 2.1. This equivalence is stated in [16] without a proof given. We choose not to check the equivalence and believe that it holds.

If (x, p) is a pair of continuously differentiable functions that satisfies (2.6), then we say (x, p) is a classical solution. If such a classical solution exists, then it must also be an integral solution.

In this section, we will focus on the existence and uniqueness of integral solutions rather than classical solutions of (2.6). This allows us to apply the theory of [16]. Obviously, we could have chosen to only write down (2.10) to describe the model, and then such a distinction between classical and integral solutions does not have to be made.

We will prove that (2.10) has a unique solution by showing that we can apply [16, Theorem 7]. This theorem's statement is exactly that unique solutions exist to infinite systems such as (2.10) provided that certain assumptions are satisfied. We will write down the assumptions we need in their general form as they can be found in [16] and we will show that our system satisfies these assumptions.<sup>2</sup> These allow us to prove existence and uniqueness but also later on when dealing with stability of the steady state.

The following few pages will mainly be a list of assumptions from [16] that we need and propositions showing that our functions f and g (see (2.7)) and coefficients  $\alpha_{jk}$ ,  $\gamma_{jk}$ ,  $j, k = 0, 1, \ldots$  (see (2.3) and (2.4)) satisfy these assumptions.

Assumption 1 (Assumption 1 of [16]). The coefficients  $\alpha_{jk}$ , j, k = 0, 1, ... satisfy the following conditions.

- (a)  $\alpha_{jj} \leq 0 \leq \alpha_{jk}, k \neq j.$
- (b)  $\alpha^{\diamond} \coloneqq \sum_{k=0}^{\infty} \sum_{j=0}^{\infty} \alpha_{jk} < \infty.$
- (c) There exist constants  $c_0$ ,  $c_1 > 0$ ,  $\epsilon > 0$  such that

$$\sum_{j=1}^{\infty} j\alpha_{jk} \le c_0 + c_1k - \epsilon |\alpha_{kk}|, \quad k = 0, 1, \dots$$

**Proposition 1.** The coefficients  $\alpha_{jk}$ , j, k = 0, 1, ... of our system (2.10) as given by (2.3) satisfy Assumption 1.

*Proof.* (a)  $\alpha_{jj} \leq 0, j = 0, 1, 2, \dots$  and  $\alpha_{jk} \geq 0$  for  $j \neq k$ .

(b)  $\alpha_{00} = 0$  and for  $k \ge 1$  we get

$$\sum_{j=0}^{\infty} \alpha_{jk} = \alpha_{0k} + \alpha_{kk} + \alpha_{k-1,k} = 0,$$

so  $\alpha^{\diamond} = 0$ .

<sup>&</sup>lt;sup>2</sup>The notation in our text has been chosen such that it corresponds with the notation used in [16], the exception being (x, p) in our text which corresponds to (w, x) in [16]. A minor modification can also be found in the functions f and g (see (2.7)), these do not depend on time t and therefore we write  $f: \mathbb{R}_+ \times \ell_+^{11} \to \mathbb{R}_+, g: \mathbb{R}_+ \times \ell_+^{11} \to \ell^{11}$  instead of  $f: \mathbb{R}_+^2 \times \ell_+^{11} \to \mathbb{R}_+,$  $g: \mathbb{R}_+^2 \times \ell_+^{11} \to \ell^{11}$  in [16], where they may depend on time.

(c) Let  $c_0 = c_1 = 1$  and  $\epsilon = 1$ . Then  $\sum_{j=1}^{\infty} j\alpha_{j0} = 0 \le 1$  and for  $k \ge 1$  we find

$$\sum_{j=1}^{\infty} j\alpha_{jk} = k\alpha_{kk} + (k-1)\alpha_{k-1,k} = -(\sigma+2\mu)k$$
$$\leq -|\alpha_{kk}|$$
$$\leq c_0 + c_1k - \epsilon |\alpha_{kk}|.$$

Assumption 2 (Assumption 4 of [16]).  $f: \mathbb{R}_+ \times \ell_+^{11} \to \mathbb{R}$  and  $g: \mathbb{R}_+ \times \ell_+^{11} \to \ell^{11}$  are continuous and have the following properties:

- (a)  $f(0,p) \ge 0$  for all  $x \in \ell_+^{11}$ .
- (b) For every  $j = 0, 1, \dots, g_j(x, p) \ge 0$  whenever  $x \ge 0, p \in \ell_+^{11}$ , and  $p_j = 0$ .
- (c) For every R > 0 there exists a Lipschitz constant  $\Lambda_R$  such that

$$\frac{|f(x, p - f(\tilde{x}, \tilde{p}))|}{\|g(x, p) - g(\tilde{x}, \tilde{p})\|_{1}} \} \leq \Lambda_{R}(|x - \tilde{x}| + \|p - \tilde{p}\|_{1})$$

**Proposition 2.** The functions f and g given by (2.7) satisfy Assumption 2.

*Proof.* Obviously  $(x,p) \mapsto -rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j$  and  $(x,p) \mapsto (x \sum_{k=0}^{\infty} \gamma_{jk} p_k)_j$  are continuous on  $\mathbb{R}_+ \times \ell_+^{11}$ . Furthermore

- (a)  $-rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j \Big|_{x=0} = (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j \ge 0$ for all  $p \in \ell_+^{11}$ .
- (b) Let j = 0, 1, 2, ... Then  $x \sum_{k=0}^{\infty} \gamma_{jk} p_k = 0$  for all  $x \ge 0, p \in \ell_+^{11}$ , and  $p_j = 0$ .
- (c) Let  $R > 0, x, \tilde{x} \in [0, R], p, \tilde{p} \in \ell_+^{11}, \|p\|_1, \|\tilde{p}\|_1 \le R$ . Then we can estimate

$$\left| rx \sum_{j=0}^{\infty} p_j - (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j - r\tilde{x} \sum_{j=0}^{\infty} \tilde{p}_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} j\tilde{p}_j \right|$$
  
 
$$\leq r \left( |x - \tilde{x}| + ||p - \tilde{p}||_1 \right) + (\sigma + 2\mu) ||p - \tilde{p}||_1,$$

and

$$\sum_{j=0}^{\infty} (1+j) \Big| \sum_{k=0}^{\infty} \alpha_{jk} p_k + x \sum_{k=0}^{\infty} \gamma_{jk} p_k - \sum_{k=0}^{\infty} \alpha_{jk} \tilde{p}_k - \tilde{x} \sum_{k=0}^{\infty} \gamma_{jk} \tilde{p}_k \Big|$$
$$\leq 2rR \Big( |x - \tilde{x}| + ||p - \tilde{p}||_1 \Big).$$

If we let  $\Lambda_R \coloneqq 2rR + \sigma + 2\mu$ , then we obtain the desired estimate

$$\left| rx \sum_{j=0}^{\infty} p_j - (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j - r\tilde{x} \sum_{j=0}^{\infty} \tilde{p}_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} j\tilde{p}_j \right|$$

$$\sum_{j=0}^{\infty} (1+j) \left| \sum_{k=0}^{\infty} \alpha_{jk} p_k + x \sum_{k=0}^{\infty} \gamma_{jk} p_k - \sum_{k=0}^{\infty} \alpha_{jk} \tilde{p}_k - \tilde{x} \sum_{k=0}^{\infty} \gamma_{jk} \tilde{p}_k \right|$$

$$\leq \Lambda_R \left( |x - \tilde{x}| + ||p - \tilde{p}||_1 \right) \square$$

Assumption 3 (Assumption 6 of [16]). There exist constants  $c_2, c_3 \ge 0$  such that for all  $x \ge 0$  and  $p \in \ell^{11}$ 

(a) ∑<sub>j=0</sub><sup>∞</sup> g<sub>j</sub>(x, p) ≤ c<sub>3</sub> ||p||, with ||p|| the norm of p in the space l<sup>1</sup>; see (2.8).
(b) f(x, p) + ∑<sub>i=1</sub><sup>∞</sup> jg<sub>j</sub>(x, p) ≤ c<sub>2</sub>(x + ||p||<sub>1</sub>).

**Proposition 3.** The functions f and g given by (2.7) satisfy Assumption 3. *Proof.* For all  $x \ge 0$  and  $p \in \ell_+^{11}$  we have the following:

(a) 
$$\sum_{j=0}^{\infty} x \sum_{k=0}^{\infty} \gamma_{jk} p_k = -rxp_0 + x \sum_{j=1}^{\infty} rp_{j-1} - x \sum_{j=1}^{\infty} rp_j = 0,$$
  
(b)

$$-rx\sum_{j=0}^{\infty}p_{j} + (\sigma + 2\mu)\sum_{j=1}^{\infty}jp_{j} + \sum_{j=1}^{\infty}x\sum_{k=0}^{\infty}\gamma_{jk}p_{k}$$
$$= -rx\sum_{j=0}^{\infty}p_{j} + (\sigma + 2\mu)\sum_{j=1}^{\infty}jp_{j} - rx\sum_{j=1}^{\infty}jp_{j} + rx\sum_{j=1}^{\infty}jp_{j-1}$$
$$= (\sigma + 2\mu)\sum_{j=1}^{\infty}jp_{j}$$
$$\leq (\sigma + 2\mu)||p||_{1}.$$

The final assumption we need will be used in Section 2.5.

Assumption 4 (Assumption 10 of [16]). There exist constants  $c_4, c_5, \epsilon_4 > 0$  such that, for all  $x \ge 0, p \in \ell_+^{11}$ 

$$f(x,p) + \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk} p_k + \sum_{j=1}^{\infty} jg_j(x,p) \le c_4 ||p|| + c_5 - \epsilon_4 \left( x + \sum_{j=1}^{\infty} jp_j \right).$$

**Proposition 4.** The functions f and g given by (2.7) satisfy Assumption 4.

*Proof.* Using (2.7) for f and g in Assumption 4 we find the following relation.

$$f(x,p) + \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk}p_k + \sum_{j=1}^{\infty} jg_j(x,p) - rx \sum_{j=0}^{\infty} p_j + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j + \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk}p_k + \sum_{j=1}^{\infty} jx \sum_{k=0}^{\infty} \gamma_{jk}p_k = (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j - \sum_{k=1}^{\infty} (\sigma + 2\mu)kp_k = 0.$$

We have used the calculation in the proof of Proposition 3 to find that the sum of the first, second, and last term in the first line is equal to  $(\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j$ . By Remark 2.1 the series  $\sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk}p_k$  exists and is equal to  $-\sum_{k=1}^{\infty} (\sigma + 2\mu)kp_k$ . We have now written down the ingredients needed to prove existence and uniqueness of solutions of (2.10). Let's formulate this in a theorem.

**Theorem 2.2.** Let  $(\tilde{x}, \tilde{p}) \in \mathbb{R}_+ \times \ell_+^{11}$ . Then there exists a unique continuous solution (x, p):  $\mathbb{R}_+ \to \mathbb{R}_+ \times \ell_+^{11}$  of (2.10).

Brief description of how the result relates to statements in [16]. We have shown in Propositions 1, 2, and 3 that Assumptions 1, 2, and 3 are satisfied (which correspond to Assumptions 1, 4, and 6 of [16]). Therefore we may apply [16, Theorem 7], which states exactly that there exists a unique continuous solution for a system of the form (2.10) that satisfies Assumptions 1, 4, and 6 of [16].

The proof of this theorem uses approximating solutions of (2.10), which we mention later on in the text in Lemma 1 on page 41 in this text. The proof uses local existence of solutions, which is stated and proven in [16, Theorem 5]. It is shown that the solutions to the approximating system (2.29) exist globally. Next, it is proven that the solutions (x, p) that exist locally on  $[0, \tau)$  are the uniform limit of the approximating solutions on the interval  $[0, \tau)$ . Then finally, it is proven that it must hold that  $\tau = \infty$ , so continuous solutions (x(t), p(t))exist and are unique on  $\mathbb{R}_+$ .

Recall the interpretation of x and  $p = (p_0, p_1, p_2, ...)$ . The fraction of single women is given by x, and the fraction of men with j partners is given by  $p_j$ , j = 0, 1, 2, ... If we have a solution (x(t), p(t)) of (2.10) with initial data  $(x(0), p(0)) = (\tilde{x}, \tilde{p})$ , then we can prove that, at all times  $t \ge 0$ , the fraction of women and the fraction of men are equal to the initial fractions. In particular, the solutions satisfy the consistency condition (2.5) if the initial conditions also satisfy (2.5). Note that this is also what we would expect based on the modelling assumptions. We have assumed that the death rate does not depend on the gender of the individual, and we have assumed the population birth rate to be equal for men and women. Therefore it makes sense that the fractions of men and women do not change over time. Let's formulate this in a theorem. This theorem will be helpful to us when proving the stability of the steady state  $(x^*, p^*)$  in Section 2.5.

**Theorem 2.3.** Let  $(x(0), p(0)) = (\tilde{x}, \tilde{p}) \in \mathbb{R}_+ \times \ell_+^{11}$ . Then the solutions (x(t), p(t)) of (2.10) satisfy the following:

$$\sum_{j=0}^{\infty} p_j(t) = \sum_{j=0}^{\infty} \tilde{p}_j, \quad and \quad x(t) + \sum_{j=1}^{\infty} j p_j(t) = \tilde{x} + \sum_{j=1}^{\infty} j \tilde{p}_j.$$

In other words, the fraction of men (women) in the population is, for all times  $t \ge 0$ , equal to the initial fraction of men (women).

*Proof.* For the first equality, note that p solves the integral equation

$$p_j(t) = \tilde{p}_j + \sum_{k=0}^{\infty} \alpha_{jk} \int_0^t p_k(s) ds + \int_0^t x(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k(s) ds.$$

We can use this equation for p(t) to determine its norm in  $\ell^1$  and show it is equal to the norm of  $\tilde{p}$  in  $\ell^1$ , i.e., for all  $t \in \mathbb{R}_+$ ,

$$\sum_{j=0}^{\infty} p_j(t) = \sum_{j=0}^{\infty} \tilde{p}_j.$$
(2.11)

This uses explicitly that  $\sum_{j=1}^{\infty} \alpha_{jk} = 0$ , as shown in Proposition 1,  $\sum_{j=0}^{\infty} \sum_{k=0}^{\infty} x \gamma_{jk} p_k = 0$ , as shown in Proposition 3a, and Proposition 4. For the details on the derivation see [16, Corollary 1].

Note that, formally, x solves

$$x(t) = \tilde{x} + \int_0^t \left( -rx(s) \sum_{j=0}^\infty p_j(s) + (\sigma + 2\mu) \sum_{j=1}^\infty jp_j(s) \right) ds.$$
(2.12)

If p is a solution of (2.10), then we find, for  $t \in \mathbb{R}_+$ ,

$$\begin{aligned} x(t) + \sum_{j=1}^{\infty} jp_j(t) \\ &= \tilde{x} + \sum_{k=1}^{\infty} j\tilde{p}_j + \int_0^t \left( -rx(s) \sum_{j=0}^{\infty} p_j(s) + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j(s) \right) ds \\ &+ \int_0^t \left( \sum_{j=1}^{\infty} jx(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k(s) \right) ds + \sum_{j=1}^{\infty} \sum_{k=0}^{\infty} j\alpha_{jk} \int_0^t p_k(s) ds \\ &= \tilde{x} + \sum_{k=1}^{\infty} j\tilde{p}_j + (\sigma + 2\mu) \int_0^t \sum_{j=1}^{\infty} jp_j(s) ds + \sum_{j=1}^{\infty} \sum_{k=0}^{\infty} j\alpha_{jk} \int_0^t p_k(s) ds \\ &= \tilde{x} + \sum_{k=1}^{\infty} j\tilde{p}_j. \end{aligned}$$

The last equality holds because of the following. By the absolute convergence of the double series  $\sum_{j=1}^{\infty} \sum_{k=0}^{\infty} j\alpha_{jk} \int_{0}^{t} p_{k}(s) ds$  we may interchange the order of summation; see Remark 2.1. Since  $p_{k} \geq 0$  we may also interchange the order of summation and integration. Therefore

$$\sum_{j=1}^{\infty} \sum_{k=0}^{\infty} j\alpha_{jk} \int_0^t p_k(s) ds = \int_0^t \left( \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk} p_k(s) \right) ds$$
$$= -\int_0^t \sum_{k=0}^{\infty} (\sigma + 2\mu) k p_k(s) ds,$$

where the second equality has been calculated in the proof of Proposition 1(c).  $\hfill \square$ 

Let initial conditions  $(\tilde{x}, \tilde{p}) \in C$ , where

$$C := \left\{ (x, p) \in \mathbb{R}_+ \times \ell_+^{11} \colon x + \sum_{j=1}^\infty j p_j = \sum_{j=0}^\infty p_j = \frac{1}{2} \right\}.$$
 (2.13)

Theorem 2.3 tells us that system (2.10) is defined on C, which is exactly what we would like. Obviously, C is bounded in norm in the space  $\mathbb{R} \times \ell^{11}$ : if  $(x, p) \in C$ , then ||(x, p)|| = 1. We will use this later on in Section 2.5.

### 2.3 Semiflow

As a reminder, a map  $\Phi \colon \mathbb{R}_+ \times \mathbb{R}_+ \times \ell_+^{11} \to \mathbb{R}_+ \times \ell_+^{11}$  is called a semiflow on  $\mathbb{R}_+ \times \ell_+^{11}$  if

$$\Phi(t+s,(\tilde{x},\tilde{p})) = \Phi(t,\Phi(s,(\tilde{x},\tilde{p}))), \quad t,s \ge 0,$$
  
$$\Phi(0,(\tilde{x},\tilde{p})) = (\tilde{x},\tilde{p}),$$

for  $(\tilde{x}, \tilde{p}) \in \mathbb{R}_+ \times \ell_+^{11}$ . If  $\Phi$  is also continuous, we call  $\Phi$  a continuous semiflow. For our system (2.10) we have the following useful theorem.

**Theorem 2.4.** The map  $\Phi \colon \mathbb{R}_+ \times \mathbb{R}_+ \times \ell_+^{11} \to \mathbb{R}_+ \times \ell_+^{11}$  defined by

$$\Phi(t, (\tilde{x}, \tilde{p})) = (x(t), p(t)),$$

with (x, p) being the solution of (2.10), is a continuous semiflow.

Description of how the result relates to statements in [16]. Apply [16, Theorem 8]. This makes exactly the statement in the theorem written down above. In order to apply this theorem, we need that Assumptions 1, 4, and 6 of [16] are satisfied, something we have checked with Proposition 1, 2, and 3. Furthermore, we need the coefficients  $\alpha_{jk}$  (see (2.3)) and  $\gamma_{jk}$  (see (2.4)) not to depend on time, which is the case.

We will use this semiflow later on to prove stability of the steady state  $(x^*, p^*)$ . Introduce the notation

$$\Phi_t(\tilde{x}, \tilde{p}) \coloneqq \Phi(t, (\tilde{x}, \tilde{p})), \tag{2.14}$$

for  $t \ge 0$  and  $(\tilde{x}, \tilde{p}) \in \mathbb{R}_+ \times \ell_+^{11}$ .

### 2.4 Steady state: dependence on parameters

In this section the focus will be on the steady state of the system. First we will establish that there exists such a steady state by explicitly calculating an expression for it. This explicit expression enables us to investigate a few things. We can see how the steady state depends on the parameters B,  $\rho$ ,  $\sigma$ ,  $\mu$  of the system.

The steady state will also enable us to determine the mean star size, variance in star size, and higher moments of the probability distribution of the stars.

We will start with some calculations to determine the steady state.

### 2.4.1 Calculating an explicit expression

Suppose  $B, \mu, \rho, \sigma > 0$ . To find the steady state of the system (2.2), we set  $dx/dt = dp_j/dt = 0, j = 0, 1, \ldots$  The consistency conditions (2.5) turn the right-hand side of dx/dt into a linear equation of x. Indeed,

$$\frac{\mu}{2} - \frac{r}{2}x + \sigma\left(\frac{1}{2} - x\right) + \mu\left(\frac{1}{2} - x\right) - \mu x = 0.$$
(2.15)

Hence

$$x^* = \frac{\mu + \sigma/2}{\frac{r}{2} + \sigma + 2\mu} = \frac{\mu(\sigma + 2\mu)}{2\left(B\rho + \mu(\sigma + 2\mu)\right)} \le \frac{1}{2}.$$
(2.16)

We see that this does not require any restrictions on the parameters B,  $\mu$ ,  $\rho$ , and  $\sigma$ . Using this expression for  $x^*$ , we define

$$\nu = \nu(B, \rho, \sigma, \mu) \coloneqq rx^* = \frac{B\rho(\sigma + 2\mu)}{B\rho + \mu(\sigma + 2\mu)}.$$
(2.17)

Setting  $dp_0/dt = 0$  allows us to express  $p_1$  as a function of  $p_0$ :

$$\frac{\mu}{2} - p_0(\nu + \mu) + p_1(\sigma + \mu) = 0,$$

 $\mathbf{SO}$ 

$$p_1^* = \frac{(\nu + \mu)p_0^* - \mu/2}{\sigma + \mu}.$$

Define

$$G(z) \coloneqq \sum_{j=0}^{\infty} p_j z^j,$$

the generating function of the  $p_j$ . We see that  $G(1) = \sum_{j=0}^{\infty} p_j$ , the fraction of all men in the population. Consistency (2.5) show us that we need to have

$$G(1) = \frac{1}{2}.$$
(2.18)

We will let G(z) be a function of the unknown  $p_0$  and then use (2.18) to solve for  $p_0$  and find  $p_0^*$ . By setting  $dp_j/dt = 0, j = 1, 2, ...$ , we obtain the equality

$$0 = \nu p_{j-1} - (\nu + j\sigma + (j+1)\mu)p_j + (\mu + \sigma)(j+1)p_{j+1}, \quad j = 1, 2, \dots$$

Multiplying this with  $z^j$ , j = 1, 2, ..., and taking the sum over all  $j \ge 1$ , we get

$$\begin{split} 0 &= \nu \sum_{j=1}^{\infty} p_{j-1} z^j - \nu \sum_{j=1}^{\infty} p_j z^j - \sigma \sum_{j=1}^{\infty} j p_j z^j - \mu \sum_{j=1}^{\infty} (j+1) p_j z^j \\ &+ (\mu + \sigma) \sum_{j=1}^{\infty} (j+1) p_{j+1} z^j \\ &= \nu z G(z) - \nu \big( G(z) - p_0 \big) - \sigma z G'(z) - \mu \big( z G'(z) + G(z) - p_0 \big) \\ &+ (\sigma + \mu) (G'(z) - p_1) \\ &= -G(z) \big( (1-z)\nu + \mu \big) + G'(z) (1-z) (\sigma + \mu) + (\nu + \mu) p_0 - (\sigma + \mu) p_1 \\ &= -G(z) \big( (1-z)\nu + \mu \big) + G'(z) (1-z) (\sigma + \mu) + \frac{\mu}{2}. \end{split}$$

In the last equality we have used the relation between  $p_0$  and  $p_1$  found by setting the right-hand side of  $dp_0/dt = 0$ . Together with the boundary condition  $G(0) = p_0$ , the first order linear nonhomogeneous differential equation

$$G'(z) = \left(\frac{\nu}{\sigma + \mu} + \frac{\mu}{(\sigma + \mu)(1 - z)}\right)G(z) - \frac{\mu}{2(\sigma + \mu)(1 - z)}$$

has a unique solution. Variation of constants gives us

$$G(z) = e^{\frac{\nu}{\mu + \sigma} z} (1 - z)^{-\frac{\mu}{\sigma + \mu}} \left( p_0 - \frac{\mu}{2(\sigma + \mu)} \int_0^z e^{-\frac{\nu}{\sigma + \mu} \xi} (1 - \xi)^{-\frac{\sigma}{\sigma + \mu}} d\xi \right).$$

The integral part of the above equation can be written as

$$\int_{0}^{z} e^{-\frac{\nu}{\sigma+\mu}\xi} (1-\xi)^{-\frac{\sigma}{\sigma+\mu}} d\xi$$
  
=  $\int_{0}^{\infty} e^{-\frac{\nu}{\sigma+\mu}\xi} (1-\xi)^{-\frac{\sigma}{\sigma+\mu}} d\xi - \int_{z}^{\infty} e^{-\frac{\nu}{\sigma+\mu}\xi} (1-\xi)^{-\frac{\sigma}{\sigma+\mu}} d\xi.$ 

Let's consider the first term of the right-hand side of the equation above. A change of variables  $t = -\frac{\nu}{\sigma + \mu}(1 - \xi)$  shows us it is equal to

$$-\left(-\frac{\nu}{\sigma+\mu}\right)^{\frac{\mu}{\sigma+\mu}}e^{-\frac{\nu}{\sigma+\mu}}\int_{-\frac{\nu}{\sigma+\mu}}^{\infty}e^t t^{\frac{\mu}{\mu+\sigma}-1}dt = \Gamma\left(\frac{\mu}{\sigma+\mu}, -\frac{\nu}{\sigma+\mu}\right),$$

where  $\Gamma(s, x)$  denotes the upper incomplete gamma function,

$$\Gamma(s,x) = \int_x^\infty e^{-t} t^{s-1} dt.$$

The same change of variables gives for the second term,

$$-\left(-\frac{\nu}{\sigma+\mu}\right)^{\frac{\mu}{\sigma+\mu}}e^{-\frac{\nu}{\sigma+\mu}}\int_{\frac{\nu(z-1)}{\sigma+\mu}}^{\infty}e^t t^{\frac{\mu}{\mu+\sigma}-1}dt = \Gamma\left(\frac{\mu}{\sigma+\mu},\frac{\nu(z-1)}{\sigma+\mu}\right).$$

Furthermore, the relation

$$\Gamma(s) = \gamma(s, x) + \Gamma(s, x)$$

holds, where  $\Gamma(s)$  denotes the gamma function,

$$\Gamma(s) = \int_0^\infty e^{-t} t^{s-1} dt,$$

and  $\gamma(s)$  denotes the lower incomplete gamma function,

$$\gamma(s,x) = \int_0^x e^{-t} t^{s-1} dt.$$

Hence

$$G(z) = \frac{e^{\frac{\nu}{\mu+\sigma}z}(p_0 + \delta(z))}{(1-z)^{\frac{\mu}{\sigma+\mu}}},$$
(2.19)

with  $\delta(z)$  given by

$$\begin{split} \delta(z) &= \frac{\mu e^{-\frac{\nu}{\sigma+\mu}}}{2(\sigma+\mu)} \left(-\frac{\nu}{\sigma+\mu}\right)^{\frac{-\mu}{\sigma+\mu}} * \\ &\quad * \left(\Gamma\left(\frac{\mu}{\sigma+\mu}, -\frac{\nu}{\sigma+\mu}\right) - \Gamma\left(\frac{\mu}{\sigma+\mu}\right) + \gamma\left(\frac{\mu}{\sigma+\mu}, \frac{\nu(z-1)}{\sigma+\mu}\right)\right) \\ &= \frac{\mu e^{-\frac{\nu}{\sigma+\mu}}}{2(\sigma+\mu)} \left(-\frac{\nu}{\sigma+\mu}\right)^{\frac{-\mu}{\sigma+\mu}} * \\ &\quad * \left(-\gamma\left(\frac{\mu}{\sigma+\mu}, -\frac{\nu}{\sigma+\mu}\right) + \gamma\left(\frac{\mu}{\sigma+\mu}, \frac{\nu(z-1)}{\sigma+\mu}\right)\right), \end{split}$$

and \* denotes the product sign. We also have the relationship

$$\gamma(s,x) = \Gamma(s)x^s e^{-x} \sum_{k=0}^{\infty} \frac{x^k}{\Gamma(s+k+1)}, \quad s \neq 0, -1, -2, \dots,$$
(2.20)

see e.g. [21, Formula 8.7.3]. Moreover the equality  $\Gamma(z+1) = z\Gamma(z)$  holds. In particular we find

$$\begin{split} \gamma\left(\frac{\mu}{\sigma+\mu},\frac{\nu(z-1)}{\sigma+\mu}\right) \\ &= (z-1)^{\frac{\mu}{\sigma+\mu}} \left(\frac{\nu}{\sigma+\mu}\right)^{\frac{\mu}{\sigma+\mu}} e^{-\frac{\nu(z-1)}{\sigma+\mu}} \Gamma\left(\frac{\mu}{\sigma+\mu}\right) * \\ &\quad * \left(\frac{1}{\Gamma\left(\frac{\mu}{\sigma+\mu}+1\right)} + \frac{\nu}{\sigma+\mu} \frac{z-1}{\Gamma\left(\frac{\mu}{\sigma+\mu}+2\right)} + \mathcal{O}(z-1)^2\right) \\ &= (z-1)^{\frac{\mu}{\sigma+\mu}} \left(\frac{\nu}{\sigma+\mu}\right)^{\frac{\mu}{\sigma+\mu}} e^{-\frac{\nu(z-1)}{\sigma+\mu}} * \\ &\quad * \left(\frac{\sigma+\mu}{\mu} + \frac{\nu(\sigma+\mu)(z-1)}{\mu(\sigma+2\mu)} + \mathcal{O}(z-1)^2\right). \end{split}$$

Using this, we can write the power series of the numerator of (2.19), i.e. the map  $z \mapsto e^{\frac{\nu}{\mu+\sigma}z}(p_0 + \delta(z))$ , around z = 1:

$$(z-1)^{\frac{\mu}{\sigma+\mu}}(-1)^{\frac{\mu}{\sigma+\mu}}\left(\frac{1}{2}+\mathcal{O}(z-1)\right) + p_0 e^{\frac{\nu}{\sigma+\mu}} - \frac{\mu}{2(\sigma+\mu)}\left(-\frac{\nu}{\sigma+\mu}\right)^{-\frac{\mu}{\sigma+\mu}}\gamma\left(\frac{\mu}{\sigma+\mu},-\frac{\nu}{\sigma+\mu}\right) + \mathcal{O}(z-1).$$

Recall that we want equation (2.18) to hold. Let us choose  $p_0^*$  such that the term independent of z - 1 equals zero:

$$p_0^* = \frac{\mu e^{-\frac{\nu}{\sigma+\mu}}}{2(\sigma+\mu)} \left(-\frac{\nu}{\sigma+\mu}\right)^{-\frac{\mu}{\sigma+\mu}} \gamma\left(\frac{\mu}{\sigma+\mu}, -\frac{\nu}{\sigma+\mu}\right).$$

Note that, since  $p_0^*$  has the interpretation of the fraction of single men in steady state, we require  $p_0^* \in [0, \frac{1}{2}]$ . The above formula for  $p_0^*$  gives us a restriction on the parameters. Both  $(-\frac{\nu}{\sigma+\mu})^{-\frac{\mu}{\sigma+\mu}} \in \mathbb{C}$  and  $\gamma\left(\frac{\mu}{\sigma+\mu}, -\frac{\nu}{\sigma+\mu}\right) \in \mathbb{C}$ . We need a combination of parameters such that their product is an element of  $\mathbb{R}$ . More specifically, we need to ensure  $p_0^* \in [0, \frac{1}{2}]$ .

By using (2.20) we see that

$$\begin{split} \gamma \left( \frac{\mu}{\sigma + \mu}, -\frac{\nu}{\sigma + \mu} \right) \\ &= \left( -\frac{\nu}{\sigma + \mu} \right)^{\frac{\mu}{\sigma + \mu}} e^{\frac{\nu}{\sigma + \mu}} \Gamma \left( \frac{\mu}{\sigma + \mu} \right) \sum_{k=0}^{\infty} \frac{\left( -\frac{\nu}{\sigma + \mu} \right)^k}{\Gamma \left( \frac{\mu}{\sigma + \mu} + k + 1 \right)}. \end{split}$$

Hence we see that

$$p_0^* = \frac{\mu}{2(\sigma+\mu)} \Gamma\left(\frac{\mu}{\sigma+\mu}\right) \sum_{k=0}^{\infty} \frac{\left(-\frac{\nu}{\sigma+\mu}\right)^k}{\Gamma\left(\frac{\mu}{\sigma+\mu}+k+1\right)} \in \mathbb{R}.$$

We can further simplify  $p_0^*$ . Note that the relation  $\Gamma(z+1) = z\Gamma(z)$  implies

$$\Gamma\left(\frac{\mu}{\sigma+\mu}+k+1\right) = \prod_{j=0}^{k} \left(\frac{\mu}{\sigma+\mu}+j\right) \Gamma\left(\frac{\mu}{\sigma+\mu}\right),$$

for all k = 0, 1, ... We can therefore rewrite the expression for  $p_0^*$  as follows.

$$p_0^* = \frac{\mu}{2(\sigma+\mu)} \sum_{k=0}^{\infty} \frac{\left(-\frac{\nu}{\sigma+\mu}\right)^k}{\prod_{j=0}^k \left(\frac{\mu}{\sigma+\mu}+j\right)}$$
$$= \frac{\mu}{2(\sigma+\mu)} \sum_{k=0}^{\infty} \left(-\frac{\nu}{\sigma+\mu}\right)^k \prod_{j=0}^k \frac{\sigma+\mu}{(\sigma+\mu)j+\mu}$$
$$= \frac{\mu}{2\nu} \sum_{k=0}^{\infty} (-1)^k \prod_{j=0}^k \frac{\nu}{(\sigma+\mu)j+\mu}.$$

Our generating function becomes

$$\begin{split} G(z) &= \frac{\mu(1-z)^{-\frac{\mu}{\sigma+\mu}} e^{\frac{\nu(z-1)}{\sigma+\mu}}}{2(\sigma+\mu)} \left(-\frac{\nu}{\sigma+\mu}\right)^{-\frac{\mu}{\sigma+\mu}} \gamma\left(\frac{\mu}{\sigma+\mu}, \frac{\nu(z-1)}{\sigma+\mu}\right) \\ &= \frac{\mu}{2(\sigma+\mu)} \Gamma\left(\frac{\mu}{\sigma+\mu}\right) \sum_{k=0}^{\infty} \frac{\left(\frac{\nu(z-1)}{\sigma+\mu}\right)^k}{\Gamma\left(\frac{\mu}{\sigma+\mu}+k+1\right)}. \end{split}$$

We can check that this choice of  $p_0$  implies  $\lim_{z\to 1} G(z) = \frac{1}{2}$ , i.e. equation (2.18) holds. Indeed we see that

$$G(1) = \frac{\mu}{2(\sigma + \mu)} \frac{\Gamma\left(\frac{\mu}{\sigma + \mu}\right)}{\Gamma\left(\frac{\mu}{\sigma + \mu} + 1\right)} = \frac{1}{2},$$

where we have used that  $\Gamma\left(\frac{\mu}{\sigma+\mu}+1\right) = \frac{\mu}{\sigma+\mu}\Gamma\left(\frac{\mu}{\sigma+\mu}\right)$ . Hence, the consistency (2.5) is satisfied.

We are now left to determine the  $p_j$ , j = 1, 2, ..., i.e. we want to find the power series expansion of G(z) around z = 0. We write G(z) as the product of three functions for which we can find the Taylor coefficients. Write

$$G(z) = C_1 f(z)g(z)h(z),$$

where

$$C_1 \coloneqq \frac{\mu}{2(\sigma+\mu)} e^{-\frac{\nu}{\sigma+\mu}} \left(-\frac{\nu}{\sigma+\mu}\right)^{-\frac{\mu}{\sigma+\mu}} f(z) \coloneqq e^{\frac{\nu}{\sigma+\mu}z},$$
$$g(z) \coloneqq (1-z)^{-\frac{\mu}{\sigma+\mu}},$$
$$h(z) \coloneqq \gamma\left(\frac{\mu}{\sigma+\mu}, \frac{\nu(z-1)}{\sigma+\mu}\right).$$

We can write  $f(z) = \sum_{n \ge 0} f_n z^n$ ,  $g(z) = \sum_{n \ge 0} g_n z^n$ , and  $h(z) = \sum_{n \ge 0} h_n z^n$ . It is easy to find expressions for the coefficients  $f_n$  and  $g_n$ :

$$f_n = \frac{\left(\frac{\nu}{\sigma+\mu}\right)^n}{n!}, \qquad n \ge 0,$$
  

$$g_0 = 1, \qquad (2.21)$$
  

$$g_n = \frac{1}{n!} \prod_{j=0}^{n-1} \left(\frac{\mu}{\sigma+\mu} + j\right), \qquad n \ge 1.$$

,

To find the coefficients  $h_n$  we note that  $h_0 = h(0) = \gamma\left(\frac{\mu}{\sigma+\mu}, \frac{-\nu}{\sigma+\mu}\right)$ , and

$$h'(z) = \frac{\nu}{\sigma + \mu} e^{-\frac{\nu(z-1)}{\sigma + \mu}} \left(\frac{\nu(z-1)}{\sigma + \mu}\right)^{-\frac{\sigma}{\sigma + \mu}} = (-1)^{\frac{\sigma}{\sigma + \mu}} \left(\frac{\nu}{\sigma + \mu}\right)^{\frac{\mu}{\sigma + \mu}} e^{\frac{\nu}{\sigma + \mu}} e^{\frac{-\nu}{\sigma + \mu}z} (1-z)^{-\frac{\sigma}{\sigma + \mu}} =: q(z).$$

So we see that  $h_1 = h'(1) = e^{\frac{\nu}{\sigma+\mu}}(-1)^{\frac{\sigma}{\sigma+\mu}}(\frac{\nu}{\sigma+\mu})^{\frac{\mu}{\sigma+\mu}}$ . We write  $q(z) = C_2 r(z)s(z)$  with

$$C_2 \coloneqq e^{\frac{\nu}{\sigma+\mu}} (-1)^{\frac{\sigma}{\sigma+\mu}} (\frac{\nu}{\sigma+\mu})^{\frac{\mu}{\sigma+\mu}},$$
$$r(z) \coloneqq e^{-\frac{\nu}{\sigma+\mu}z} = \sum_{n=0}^{\infty} r_n,$$
$$s(z) \coloneqq (1-z)^{-\frac{\sigma}{\sigma+\mu}} = \sum_{n=0}^{\infty} s_n.$$

The coefficients  $r_n$  and  $s_n$  are given by

$$r_n = \frac{1}{n!} \left( -\frac{\nu}{\sigma + \mu} \right)^n, \qquad n = 0, 1, 2, \dots$$
  

$$s_0 = 1,$$
  

$$s_n = \frac{1}{n!} \prod_{j=0}^{n-1} \left( \frac{\sigma}{\sigma + \mu} + j \right), \qquad n = 1, 2, 3, \dots$$

Using these expressions for  $r_n$  and  $s_n$ ,  $n \ge 0$ , we find expressions for  $q_n$ ,  $n \ge 0$ :

$$q_0 = C_2,$$
  
 $q_n = C_2 \left( r_n + \sum_{k=0}^{n-1} r_k s_{n-k} \right), \qquad n = 1, 2, \dots.$ 

Now we find, for  $n \geq 2$ , that

$$h_{n} = \frac{h^{(n)}(0)}{n!} = \frac{q_{n-1}}{n}$$

$$= C_{2} \left( \frac{\left(\frac{-\nu}{\sigma+\mu}\right)^{n-1}}{n!} + \frac{1}{n} \sum_{k=0}^{n-2} \left[ \frac{\left(\frac{-\nu}{\sigma+\mu}\right)^{k}}{k!(n-1-k)!} \prod_{j=0}^{n-k-2} \left(\frac{\sigma}{\sigma+\mu} + j\right) \right] \right).$$
(2.22)

Now we have all the ingredients to find expressions for the  $p_j$ ,  $j \ge 1$ . For example we can write

$$p_j = \sum_{m=0}^{j} \left( \sum_{n=0}^{m} f_n g_{m-n} \right) h_{j-m}, \quad j = 1, 2, \dots,$$

or, by interchanging the summation, we can use some other order in combining the coefficients  $f_n$ ,  $g_n$ ,  $h_n$ . In theory, we now have an explicit expression for the  $p_j^*$ , j = 0, 1, ... In practice, this does not help much in gaining more insight in how the  $p_j^*$  behave as a function of the different parameters of the system. Therefore, we conclude our investigation of the explicit expression of the steady state of the system for now. In Section 2.4.3 we will conduct a short numerical investigation.

To summarize, the steady state  $(x^*, p^*)$  is given by

$$x^{*} = \frac{\mu(\sigma + 2\mu)}{2(B\rho + \mu(\sigma + 2\mu))},$$
  

$$p_{0}^{*} = \frac{\mu}{2\nu} \sum_{k=0}^{\infty} (-1)^{k} \prod_{j=0}^{k} \frac{\nu}{(\sigma + \mu)j + \mu},$$
  

$$p_{j}^{*} = \sum_{m=0}^{j} \left( \sum_{n=0}^{m} f_{n}g_{m-n} \right) h_{j-m}$$
  

$$j = 1, 2, \dots,$$
  
(2.23)

with

$$\nu = \frac{2B\rho}{\mu}x^* = \frac{B\rho(\sigma + 2\mu)}{B\rho + \mu(\sigma + 2\mu)},$$

and  $f_n$ ,  $g_n$ , and  $h_n$  given by (2.21) and (2.22).

### 2.4.2 Mean value analysis

From this point onwards we will assume the pair-formation process to be in equilibrium, so we have a fraction  $x^*$  of single women,  $p_0^*$  of single men,  $p_1^*$  of men with one wife, and so on. In Section 2.5 we will prove that the steady state  $(x^*, p^*)$  is globally asymptotically stable. This means that no matter how we choose the initial conditions (x(0), p(0)), as long as they satisfy (2.5), the solution (x(t), p(t)) converges to the steady state as  $t \to \infty$ . We assume the population to exist long enough for this to have happened before we take any interest in the population and its dynamic sexual network, allowing us to consider the system in equilibrium. Thus we have simplified its statistical description.

The steady state  $(x^*, p^*)$  can be translated in probabilities by normalizing. We have assumed the total fraction of women and men to be  $\frac{1}{2}$ , so if we are interested in the probability a woman is single, then this given by  $2x^*$  rather than  $x^*$  (and the probability a woman is part of a star of size j is given by  $2jp_j^*$ ). Similarly, up to a factor 2,  $p_j^*$  equals the probability that a man has j partners,  $j = 0, 1, 2, \ldots$  Let us denote the number of wives per man, or equivalently the star size of one star, with the random variable S, then

$$\mathbb{P}(S=j) = 2p_i^*, \quad j = 0, 1, \dots$$

In other words, the probability of a man to have j wives is equal to  $2p_j^*$ . Therefore, the mean number of partners of a man, or the mean star-size, is given by

$$\mathbb{E}(S) = 2\sum_{j=1}^{\infty} jp_j^* = 1 - 2x^*$$

$$= 1 - \frac{\mu(\sigma + 2\mu)}{B\rho + \mu(\sigma + 2\mu)} = \frac{B\rho}{B\rho + \mu(\sigma + 2\mu)}.$$
(2.24)

What implications does this have? First of all, we observe that the mean number of partners per man is always less than 1. This is to be expected. There are as many males as females present in the population, there is a positive fraction  $x^*$ of single women in equilibrium, and women can only be in a partnership with at most one man at once. Our second observation is that in order to determine the expected number of partners of a man we only need to know the fraction of single women  $x^*$ , and this fraction can be calculated without having explicit expressions for the  $p_j$ 's (recall (2.15)).

Note that the number of sexual partnerships in the population is equal to the mean number of women involved in a partnership, or equivalently, the total number of women minus the number of single women:

$$\frac{1}{2}N^* - X^* = N^* \left(\frac{1}{2} - x^*\right) = \frac{2B}{\mu} \frac{B\rho}{2(B\rho + \mu(\sigma + 2\mu))}.$$

Concerning the dependence on the parameters, we see that the mean starsize is increasing as a function of both the population birth rate and the pairformation rate, and it is a decreasing function in the death and the separation rate. Indeed

$$\begin{split} \frac{d}{dB} \, \mathbb{E}(S) &= \frac{\rho \mu (\sigma + \mu)}{\left(B\rho + \mu (\sigma + \mu)\right)^2} > 0, \\ \frac{d}{d\rho} \, \mathbb{E}(S) &= \frac{B\mu (\sigma + \mu)}{\left(B\rho + \mu (\sigma + \mu)\right)^2} > 0, \\ \frac{d}{d\sigma} \, \mathbb{E}(S) &= -\frac{\mu B\rho}{\left(B\rho + \mu (\sigma + \mu)\right)^2} < 0, \\ \frac{d}{d\mu} \, \mathbb{E}(S) &= -\frac{\left(\sigma + 4\mu\right)B\rho}{\left(B\rho + \mu (\sigma + \mu)\right)^2} < 0. \end{split}$$

Intuitively this also makes sense. An increased population birth rate means an increased population size since  $N^* = 2B/\mu$ , so there are more women to recruit. An increased pair-formation rate let men 'profit' from this more than women by the asymmetric situation. On the other hand, death and separation lead to men losing their partners, which decreases their star size.

Note that, because of the relation  $\mathbb{E}(S) = 1 - 2x^*$  we also see the opposite dependence of  $x^*$  on the parameters, i.e.  $x^*$  is a decreasing function in B and  $\rho$  and increasing as a function of  $\sigma$  and  $\mu$ .

Using the probability distribution for the number of wives per husband, we can also consider higher moments for S. Let  $k \in \mathbb{N}$ , then the k-th moment is given by

$$\mathbb{E}(S^k) = \sum_{j=1}^{\infty} j^k \, \mathbb{P}(S=j) = 2 \sum_{j=1}^{\infty} j^k p_j^*,$$

and we see that, contrary to  $\mathbb{E}(S)$ , we need the explicit expressions for the  $p_j$ 's in order to calculate  $\mathbb{E}(S^k)$ , k = 2, 3, ... In particular, we find the variance to be

$$\operatorname{Var}(S) = \mathbb{E}(S^2) - \mathbb{E}(S)^2 = 2\sum_{j=1}^{\infty} j^2 p_j^* - (1 - 2x^*)^2.$$

Beside the mean star-size we can also consider some other mean values, these will help us in choosing appropriate parameter values in Section 2.4.3.

The mean number of different partners one single man acquires in his life time is equal to

$$W = \frac{\rho X^*}{\mu}.\tag{2.25}$$

Indeed, (single) women arrive according to a Poisson stream with rate  $\rho X^*$ , with  $X^* = x^* N^*$  the number of single women in steady state, and the mean life length of this man is  $\frac{1}{\mu}$ . So in total, the mean number of women arriving in his life time is  $\frac{\rho X^*}{\mu}$ . Note that this uses that the acquisition of new partners is independent of the man's partnership status, so that we can indeed view the acquisition of new wives as a Poisson arrival process.

Since women are restricted by the fact that they may only have one husband at the time, the mean number of different partners a single woman acquires in her life time H needs to be derived in a different way than W. We can derive this quantity H using first step analysis. A single woman acquires a husband with probability  $\frac{\rho N_m^*}{\rho N_m^* + \mu}$ , where  $N_m^* = \frac{1}{2}N^*$  is the total male population size in equilibrium.<sup>3</sup> If she is to acquire more husbands, her original partnership must dissolve either by separation or by the death of her husband. This occurs with probability  $\frac{\sigma + \mu}{\sigma + 2\mu}$ . She is then again in the single state; see Figure 2.1 for the flow diagram of the process.

<sup>&</sup>lt;sup>3</sup>Note the asymmetry between men and women in our population. While a single woman acquires a new husband at rate  $\rho N_m^*$ , a man (either single or not) acquires a new wife at rate  $\rho X^* \leq \rho N_m^*$ . This has to do with women being able to choose a partner from all the men in the population, while men are only allowed to choose wives from the population of single women.



Figure 2.1: Flow diagram for the pair-formation process from the point of view of a woman. She is either single or in a partnership with a man, denoted with 0 and 1, respectively.

The memoryless property tells us that the expected number of partners she has at this point in time equals the expected number of partners she has at the beginning. Hence

$$H = \frac{\rho N_m^*}{\rho N_m^* + \mu} \left( 1 + \frac{\sigma + \mu}{\sigma + 2\mu} H \right).$$

Solving this equation for H yields

$$H = \frac{\rho N_m^*(\sigma + 2\mu)}{\mu(\rho N_m^* + \sigma + 2\mu)}.$$
 (2.26)

Comparing H with W, we see that H = W. This is what one should expect due to consistency reasons.

Furthermore, note that the mean life length of an individual equals

$$\frac{1}{\mu}$$
,

and for the mean duration of one partnership we reason as follows. Two individuals in a partnership separate at rate  $\sigma$  and each individual dies at rate  $\mu$ , so the partnership dissolves at rate  $\sigma + 2\mu$ , and we see that the mean duration of a partnership is given by

$$\frac{1}{\sigma + 2\mu}.$$

### 2.4.3 Dependence on parameters: numerical results

Let's consider a population with initial size  $N_0 = 10\,000$ . Then, as we assume the population to be in equilibrium we have  $B = \frac{1}{2}\mu N_0$ . We take one day as the time unit in our numerical analysis in this section.

We investigate the dependence of the steady state on the parameters by considering some parameter values. These will be chosen somewhat arbitrarily and will not be estimated from data. However, we will choose them in a range such that the expected number of partners of a single man W (see (2.25)) and the expected number of partners of a single woman H (see (2.26)), the expected duration of a partnership, and the expected duration of an individual's sexually active life are not completely ridiculous.

First, let's vary  $\mu$  in the range  $(\frac{1}{18240}, \frac{1}{3650})$  while keeping the remaining parameters fixed at  $\rho = \frac{1}{3000}$  and  $\sigma = \frac{1}{1000}$ ; see Figure 2.2 and Table 2.1 for

some results. Next, we vary  $\rho$  in the range  $(\frac{1}{30000}, \frac{1}{300})$  with  $\sigma = \frac{1}{1000}$  and  $\mu = \frac{1}{9120}$ ; see Figure 2.3 and Table 2.2 for some results. Finally, we vary  $\sigma$  in the range  $(\frac{1}{10000}, \frac{1}{100})$  with  $\rho = \frac{1}{3000}$ ,  $\mu = \frac{1}{9120}$ ; see Figure 2.4 and Table 2.3 for some results.

$\mu$	$\frac{1}{\mu}$	$\frac{1}{\sigma+2\mu}$	H = W	$x^*$	$p_0^*$	$p_1^*$
$\frac{1}{18240}$	50.0 years	2.5 years	20.2	0.003	0.187	0.180
$\frac{1}{9120}$	25.0 years	2.2 years	11.1	0.0003	0.189	0.177
$\frac{1}{3650}$	10.0 years	1.7 years	5.6	0.0004	0.195	0.171

**Table 2.1:** Table displaying some approximating values for among others the mean duration of one partnership when varying the death rate  $\mu$  from  $\mu = \frac{1}{18240}$  till  $\mu = \frac{1}{3650}$ , and letting  $\rho = \frac{1}{3000}$ ,  $\sigma = \frac{1}{1000}$ .

ρ	$\frac{1}{\mu}$	$\frac{1}{\sigma+2\mu}$	H = W	$x^*$	$p_0^*$	$p_{1}^{*}$
$\frac{1}{30000}$	25.0 years	2.2 years	11.0	0.003	0.191	0.177
$\frac{1}{3000}$	25.0 years	2.2 years	11.1	0.0003	0.189	0.177
$\frac{1}{300}$	25.0 years	2.2 years	11.1	0.00003	0.189	0.177

**Table 2.2:** Table displaying some approximating values for among others the mean duration of one partnership when varying the pair-formation rate  $\rho$  from  $\rho = \frac{1}{30000}$  till  $\rho = \frac{1}{300}$ , and letting  $\sigma = \frac{1}{1000}$ ,  $\mu = \frac{1}{9120}$ .

σ	$\frac{1}{\mu}$	$\frac{1}{\sigma+2\mu}$	H = W	$x^*$	$p_0^*$	$p_1^*$
$\frac{1}{10000}$	25.0 years	8.6 years	2.9	0.0001	0.201	0.159
$\frac{1}{1000}$	25.0 years	2.2 years	11.1	0.0003	0.189	0.177
$\frac{1}{100}$	25.0 years	3.3 months	92.6	0.003	0.186	0.183

**Table 2.3:** Table displaying some approximating values for among others the mean duration of one partnership when varying the separation rate  $\sigma$  from  $\sigma = \frac{1}{10000}$  till  $\sigma = \frac{1}{100}$ , and letting  $\rho = \frac{1}{3000}$ ,  $\mu = \frac{1}{9120}$ .



**Figure 2.2:** Exploring the dependence on  $\mu$ . The figure on the left shows the expected number of different partners of a single individual (H = W) in its life as a function of  $\mu$ . The figure on the right shows the fraction of single men  $p_0^*$  (purple) and the fraction of men with 1 partner  $p_1^*$  (orange, dashed) as functions of  $\mu$ . The remaining parameters are fixed at  $\rho = \frac{1}{3000}$  and  $\sigma = \frac{1}{1000}$ .



**Figure 2.3:** Exploring the dependence on  $\rho$ . The figure on the left shows the expected number of different partners of a single individual (H = W) in its life as a function of  $\rho$ . The figure on the right shows the fraction of single men  $p_0^*$  (purple) and the fraction of men with 1 partner  $p_1^*$  (orange, dashed) as functions of  $\rho$ . The remaining parameters are fixed at  $\sigma = \frac{1}{1000}, \mu = \frac{1}{9120}$ .



**Figure 2.4:** Exploring the dependence on  $\sigma$ . The figure on the left shows the expected number of different partners of a single individual (H = W) in its life as a function of  $\sigma$ . The figure on the right shows the fraction of single men  $p_0^*$  (purple) and the fraction of men with 1 partner  $p_1^*$  (orange, dashed) as functions of  $\sigma$ . The remaining parameters are fixed at  $\rho = \frac{1}{3000}$  and  $\mu = \frac{1}{9120}$ .

Typically,  $2p_n^*$ , i.e. the distribution of the number of wives per man, will have the following shape. A large fraction of men is single or has 1 partner. If we consider the fraction of men with more than 1 partner, then we find a sharp decrease in  $p_n$  as n gets larger. Typically, the fraction of men with more than 4 partners is next to zero. Moreover, if we compare this distribution with the Poisson distribution with parameter 1, then we see this is quite a good approximation; see Figures 2.6 and 2.7. In Table 2.4 we find a list with some numerical values.

Recall the Poisson distribution. Suppose we have a random variable Z which is Poisson distributed with rate  $\lambda$ , then

$$\mathbb{P}(Z=n) = \frac{e^{-\lambda}\lambda^n}{n!}, \quad n = 0, 1, 2, \dots$$

Concerning our situation of a population with demographic turnover we note the following. In the range of parameter values that we investigate in this section, the Poisson distribution with parameter 1 is quite a good approximation; see Figures 2.6 and 2.7. However, we can come up with parameter values for  $\rho$ ,  $\sigma$ ,  $\mu$ , where the Poisson distribution does not perform well as an approximation of  $2p_n^*$ ; see e.g. Figure 2.5. Note that this combination of parameter values will probably never be estimated from data of any real-life population. Based on these parameter values the expected number of sexually active years is approximately 2.7 years, the mean number of partners of a single woman will be approximately  $1 * 10^{-6}$  and a single man has an expected number of 0.0001 partners in his life time. Despite this, we can still use the Poisson distribution to approximate  $(2p_n^*)_n$ . Choose  $\lambda$  such that  $\mathbb{P}(Z = 0) = 2p_0^*$ , i.e. let  $\lambda = -\log(2p_0^*)$ . We can then improve approximations of Figures 2.6, 2.7, and 2.5 (see also Table 2.4). So it seems we can use the Poisson distribution to approximate  $(2p_i^*)_j$ .



**Figure 2.5:** The distribution  $(2p_n^*)$  of the number of wives per man (blue, dashed), n = 0, ..., 10, together with the Poisson distribution with parameter 1 (purple) and the Poisson distribution with parameter  $-\log(2p_0^*)$  (orange, dashed). For the pair-formation process we have used  $B = \frac{1}{2}\mu N_0$ ,  $N_0 = 10000$ ,  $\rho = 1/100000000$ ,  $\sigma = 1/100000$ , and  $\mu = 1/1000$ .



**Figure 2.6:** The distribution of the number of wives per man, n = 0, 1, ..., 10. The chosen parameter values are as follows:  $B = \frac{1}{2}\mu N_0$ ,  $\rho = \frac{1}{3000}$ ,  $\sigma = \frac{1}{100}$ ,  $\mu = \frac{1}{9120}$ . On the right, this distribution is compared with a Poisson distribution with parameter 1.
n	$2p_n^*$	$P(Z=n) - 2p_n^*,$	$P(Z=n) - 2p_n^*,$
		$Z \sim \text{Poisson}(1)$	$Z \sim \text{Poisson}(-\log(2p_0^*))$
0	0.3713	0.003497	0
1	0.3663	-0.001581	-0.001564
2	0.2926	-0.001355	0.0003936
3	0.06086	-0.0004547	0.0007027
4	0.01523	-0.00009359	0.0003380

**Table 2.4:** In the second column we have the distribution of the number of wives per man  $2p_n^*$ ,  $n = 0, \ldots 4$ , with parameters  $B = \frac{1}{2}\mu N_0$ ,  $N_0 = 10000$ ,  $\rho = 1/3000$ ,  $\sigma = 1/100$ , and  $\mu = 1/9120$ . In the third column we have the difference  $\mathbb{P}(Z = n) - 2p_n^*$ , where Z is a Poisson distributed random variable with parameter 1. In the fourth column we have again a difference  $\mathbb{P}(Z = n) - 2p_n^*$ , this time Z is Poisson distributed with parameter  $-\log(2p_0^*)$ . We see that the latter approximation of  $(2p_n^*)$  is slightly better.

Another observation we can make about the  $p_n^*$  is that nearly all men will have either 0, 1, 2, 3, or 4 partners, for e.g. the case  $\rho = \frac{1}{3000}$ ,  $\sigma = \frac{1}{100}$ ,  $\mu = \frac{1}{9120}$  we have

$$p_0^* + p_1^* + p_2^* + p_3^* + p_4^* \approx 0.498.$$

Note that this means that less than 1% of all men have more than 4 partners. Concerning the women in the population, we observe that, for the same set of parameter values  $\rho = \frac{1}{3000}$ ,  $\sigma = \frac{1}{100}$ ,  $\mu = \frac{1}{9120}$ , nearly all women are in a marriage with 0, 1, 2, 3, or 4 co-wives (so this means her husband has 1, 2,..., 5 wives). Indeed,

$$\sum_{n=1}^{5} np_n^* \approx 0.495.$$

We find the mean star size to equal

$$2\sum_{j=1}^{\infty} jp_j^* \approx 0.9939$$

We approximate the variance in the star size and find

$$2\sum_{j=1}^{\infty} j^2 p_j^* - (1 - 2x^*)^2 \approx 2\sum_{j=1}^{50} j^2 p_j^* - (1 - 2x^*)^2 \approx 0.9992.$$

So the average number of partners per man is almost 1, but the variance in the number of partners is also close to one. Compare with the the Poisson distribution with parameter 1, its mean and variance are both 1. If we disregard all men with more than four partners and all single men, we find that the mean star size is equal to

$$\frac{\sum_{j=1}^{4} j p_j^*}{\sum_{j=1}^{4} p_j^*} \approx 1.583$$

and the variance to be

$$\frac{\sum_{j=1}^{4} j^2 p_j^*}{\sum_{j=1}^{4} p_j^*} - \left(\frac{\sum_{j=1}^{4} j p_j^*}{\sum_{j=1}^{4} p_j^*}\right)^2 \approx 0.615.$$

On first sight, based on this limited numerical investigation, the pairformation model seems to be quite a good approximation of reality as far as the steady state of the system is concerned. After all, we would expect that in real life most men do not have more than one wife and certainly that almost none have more than 4 wives. We do find that the fraction of single women  $x^*$  is in general quite small in our model (see Tables 2.1, 2.2, and 2.3 for some numerical values), and this may be not very realistic.

Our pair-formation model only contains four parameters B,  $\mu$ ,  $\rho$ , and  $\sigma$ . Suppose we would have some data on a sexually active population. Information about the demography of the population, i.e. the total population size and the average number of years individuals are sexually active allow us to give an estimate for B and  $\mu$ . Information about the average duration of a partnership would give us an estimate for  $\sigma$ . Then we would be able to give an estimate for  $\rho$ by having data on the average number of partners of an individual in its lifetime (use the formula for H = W) or the average star size using formula (2.24).

That being said, we do not claim the above description of finding estimates for the parameters the 'correct' way. For example, the rate at which men acquire new wives is dependent on the number of single women, and this may make it difficult to find good estimates for some of the parameters. Whether or not one is able to estimate the parameters of course depends on the data available. Moreover, from the point of view of the theory on statistics, estimators should satisfy certain conditions such as being unbiased and consistent. We have not investigated whether we can find such estimators.



**Figure 2.7:** The fraction of men in the population with *n* partners (normalized to a probability distribution function), n = 0, 1, ..., 10. The chosen parameter values are as follows:  $B = \frac{1}{2}\mu N_0$ ,  $\rho = \frac{1}{500}$ ,  $\sigma = \frac{1}{1000}$ ,  $\mu = \frac{1}{9120}$ . On the right, this distribution is compared with a Poisson distribution with parameter 1.

#### 2.4.4 Extreme situations

Let us consider some extremes for the parameter values. We will consider the cases  $\rho = 0$ ,  $\sigma = 0$ ,  $\rho = \sigma = 0$ , and the situation without birth and death.

#### No partnership formation: $\rho = 0$

If we let  $B, \mu > 0, \sigma > 0$  and  $\rho = 0$ , then no partnerships can be formed and all existing partnerships will eventually dissolve. We expect the steady state to be globally asymptotically stable and to satisfy  $x^* = p_0^* = \frac{1}{2}, p_j^* = 0, j = 1, 2, ...$ Indeed, since partnerships can only dissolve, we expect that all individuals in the population will eventually become single. We can easily derive the steady state from our system of differential equations. The system becomes

$$\frac{dx}{dt} = \frac{\mu}{2} - (\sigma + \mu)x + \mu + \frac{1}{2}\sigma,$$
  
$$\frac{dp_0}{dt} = \frac{\mu}{2} + (\sigma + \mu)p_1 - \mu p_0,$$
  
$$\frac{dp_j}{dt} = -(\sigma + \mu)p_j - \mu p_j + (\sigma + \mu)(j+1)p_{j+1}, \qquad j \ge 1.$$

Letting dx/dt = 0, we see that indeed  $x^* = \frac{1}{2}$ . From  $dp_0/dt = 0$  we derive that

$$p_1^* = \frac{\mu}{\mu + \sigma} p_0^* - \frac{\mu}{2(\mu + \sigma)}.$$

Since the  $p_j$ ,  $j \ge 0$  must all be nonnegative,  $p_0^*$  must satisfy the inequality  $p_0^* \ge \frac{1}{2}$ . On the other hand, by the consistency conditions (2.5) we also have

$$x^* + p_0^* \le 1$$
,

from which the reverse inequality  $p_0^* \leq \frac{1}{2}$  follows. Therefore we see that  $p_0^* = \frac{1}{2}$ . Since  $\sum_{n\geq 0} p_n^* = \frac{1}{2}$ , it also follows that  $p_n^* = 0$  for all  $n \geq 1$ .

#### No partnership formation or separation: $\rho = \sigma = 0$

We can also take the (boring) extreme of  $\sigma = \rho = 0$ . Then new partnerships can not be formed, while existing partnerships will eventually dissolve due to the death of one of the partners. If we proceed as in the case of  $\sigma > 0$ ,  $\rho = 0$ , we find the same steady state  $x^* = p_0^* = \frac{1}{2}$ ,  $p_j^* = 0$  for all  $j \ge 1$ . This is also what one should expect. By setting  $\sigma = \rho = 0$ , all partnerships will eventually dissolve by natural death of partners. New individuals enter the population as singles and no new partnerships can be formed since  $\rho = 0$ . Hence, after enough time, the dynamics of the population are only influenced by birth and death. Since we assume the population to be in equilibrium and the sex ratio to be 1:1, we expect the number of single men to equal the number of single women in equilibrium.

#### No partnership separation: $\sigma = 0$

Note that if we take the romantic view of partnerships existing till one of the partners involved dies, i.e. if we let  $\sigma = 0$ , the calculation of the steady state  $(x^*, p^*)$  simplifies compared to Section 2.4.1. We also assume all other parameters to be strictly larger than zero.

First, by setting the right-hand side of (2.2) equal to zero, and by setting  $\sigma = 0$ , we find for  $x^*$  the following expression:

$$x^* = \frac{\mu^2}{\rho B + 2\mu^2}$$

If we again let  $\nu := \frac{2B\rho}{\mu}x^* = \frac{2\rho B\mu}{\rho B + 2\mu^2}$ , we can find, in exactly the same way as with  $\sigma > 0$ , explicit expressions for the  $p_j$ ,  $j = 0, 1, \ldots$  Indeed, our generating function G then solves the differential equation

$$G'(z) = \frac{\nu}{\mu}G(z) + \frac{G(z)}{1-z} - \frac{1}{2(1-z)},$$

and with initial condition  $G(0) = p_0$ , it gets the expression

$$G(z) = \frac{\mu}{2\nu} \frac{1 - e^{\frac{\nu}{\mu}z}}{1 - z} + p_0 \frac{e^{\frac{\nu}{\mu}z}}{1 - z}$$

We can again choose  $p_0$  such that the limit  $\lim_{z\to 1} G(z) = \frac{1}{2}$ . First, we expand the function  $z \mapsto \frac{\mu(1-e^{\frac{\nu}{\mu}}z)}{2\nu} + p_0 e^{\frac{\nu}{\mu}}z$  around the point z = 1, and set the zeroth order term equal to zero. Note that, contrary to before, we can now simply take the Taylor expansion. The zeroth order term is given by  $\frac{\mu}{2\nu}(1-e^{\frac{\nu}{\mu}})+p_0 e^{\frac{\nu}{\mu}}$ . We want this term to equal zero, thus we choose  $p_0$  as follows:

$$p_0 = \frac{\mu}{2\nu} \left( 1 - e^{-\frac{\nu}{\mu}} \right).$$
 (2.27)

This choice of  $p_0$  gives

$$G(z) = \frac{\mu}{2\nu} \frac{e^{\frac{\nu}{\mu}} - e^{\frac{\nu}{\mu}z}}{1 - z},$$

If we let z near 1, then we have

$$G(z) = \frac{-\frac{1}{2}e^{\frac{\nu}{\mu}}(z-1) + p_0\frac{\nu}{\mu}e^{\frac{\nu}{\mu}}(z-1) + \mathcal{O}(z-1)^2}{1-z}.$$

This shows us that

$$\lim_{z \to 1} G(z) = \frac{1}{2} e^{\frac{\nu}{\mu}} - p_0 \frac{\nu}{\mu} e^{\frac{\nu}{\mu}} = \frac{1}{2}$$

where we used the expression for  $p_0$  in the second equality. The explicit expression that we find for G shows us that the coefficients  $p_j$  of the power series expansion of G in z = 0 are given by

$$p_j = \frac{\mu}{2\nu} \left( 1 - e^{-\frac{\nu}{\mu}} \sum_{k=0}^j \left(\frac{\nu}{\mu}\right)^k \frac{1}{k!} \right), \quad j = 0, 1, 2, \dots$$

We see from this expression that  $j \mapsto p_j$  is a decreasing function of j and  $p_j \to 0$  as  $j \to \infty$ . Finally, we can check that indeed  $\sum_{j=0}^{\infty} p_j = \frac{1}{2}$ . First we rewrite  $p_j$ :

$$p_{j} = \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \left( e^{\frac{\nu}{\mu}} - \sum_{k=0}^{j} \left( \frac{\nu}{\mu} \right)^{k} \frac{1}{k!} \right)$$
$$= \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \left( \sum_{k=0}^{\infty} \left( \frac{\nu}{\mu} \right)^{k} \frac{1}{k!} - \sum_{k=0}^{j} \left( \frac{\nu}{\mu} \right)^{k} \frac{1}{k!} \right)$$
$$= \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \sum_{k=j+1}^{\infty} \left( \frac{\nu}{\mu} \right)^{k} \frac{1}{k!}.$$

If we now sum over all  $p_j$  we get

$$\sum_{j=0}^{\infty} p_j = \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \sum_{j=0}^{\infty} \sum_{k=j+1}^{\infty} \frac{(\nu/\mu)^k}{k!} = \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \sum_{k=1}^{\infty} \sum_{j=0}^{k-1} \frac{(\nu/\mu)^k}{k!}$$
$$= \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \sum_{k=1}^{\infty} \frac{k(\nu/\mu)^k}{k!} = \frac{\mu}{2\nu} e^{-\frac{\nu}{\mu}} \frac{\nu}{\mu} e^{\frac{\nu}{\mu}}$$
$$= \frac{1}{2}.$$

Note that we may interchange the summation over k and j since the sums are absolutely convergent.

If we compare the steady state found in this extreme case of  $\sigma = 0$  with the general case (2.23), then we see that (2.23) coincides with the extreme situation if we let  $\sigma = 0$  in (2.23). Indeed,  $x^*$  becomes  $\frac{\mu^2}{B\rho+2\mu^2}$ , and for  $p_0^*$  we obtain

$$p_0^* = \frac{1}{2} \sum_{k=0}^{\infty} \prod_{j=0}^k \frac{-\nu}{\mu(j+1)} = \frac{1}{2} \sum_{k=0}^{\infty} \left(-\frac{\nu}{\mu}\right)^k \frac{1}{(k+1)!} = -\frac{\mu}{2\nu} \left(e^{-\frac{\nu}{\mu}} - 1\right)$$
$$= \frac{\mu}{2\nu} \left(1 - e^{-\frac{\nu}{\mu}}\right).$$

For the remaining  $p_j$  we can also show the expressions coincide if we let  $\sigma = 0$  in (2.23). Indeed, we find

$$C_{1} = -\frac{\mu}{\nu}e^{-\frac{\nu}{\mu}}$$

$$f_{n} = \frac{\left(\frac{\nu}{\mu}\right)}{n!}, \qquad n = 0, 1, \dots$$

$$g_{n} = 1, \qquad n = 0, 1, \dots$$

$$h_{0} = \gamma \left(1, -\frac{\nu}{\mu}\right) = \int_{0}^{-\frac{\nu}{\mu}} e^{-t}dt = 1 - e^{\frac{\nu}{\mu}},$$

$$h_{1} = e^{\frac{\nu}{\mu}}\frac{\nu}{\mu},$$

$$h_{n} = -e^{\frac{\nu}{\mu}}\frac{\left(-\frac{\nu}{\mu}\right)^{n}}{n!}, \qquad n = 2, 3, \dots$$

If we express  $p_j = C_1 \sum_{m=0}^{j} f_{j-m} \left( \sum_{n=0}^{m} h_n g_{m-n} \right), \ j = 0, 1, \ldots$ , then we find the right expression. Indeed,

$$\sum_{n=0}^{m} h_n g_{n-m} = h_0 + h_1 + \sum_{n=2}^{m} h_n$$
$$= 1 - e^{\frac{\nu}{\mu}} + e^{\frac{\nu}{\mu}} \frac{\nu}{\mu} - e^{\frac{\nu}{\mu}} \sum_{n=2}^{m} \frac{\left(-\frac{\nu}{\mu}\right)^n}{n!}$$
$$= 1 - e^{\frac{\nu}{\mu}} \sum_{n=0}^{m} \frac{\left(-\frac{\nu}{\mu}\right)^n}{n!},$$

$$\sum_{m=0}^{j} f_{j-m} \left( \sum_{n=0}^{m} h_n g_{m-n} \right) = \sum_{m=0}^{j} \frac{\left(\frac{\nu}{\mu}\right)^{j-m}}{(j-m!)} - e^{\frac{\nu}{\mu}} \sum_{m=0}^{j} \sum_{n=0}^{m} \frac{\left(-\frac{\nu}{\mu}\right)^n \left(\frac{\nu}{\mu}\right)^{j-m}}{n!(j-m)!}$$
$$= \sum_{m=0}^{j} \frac{\left(\frac{\nu}{\mu}\right)^m}{m!} - e^{\frac{\nu}{\mu}}.$$

The last equality can be found as follows. The last summand of the above derivation can be rewritten:

$$\sum_{m=0}^{j} \sum_{n=0}^{m} \frac{\left(-\frac{\nu}{\mu}\right)^{n} \left(\frac{\nu}{\mu}\right)^{j-m}}{n!(j-m)!}$$
  
=  $\sum_{m=0}^{j} \frac{\left(-\frac{\nu}{\mu}\right)^{m} \left(\frac{\nu}{\mu}\right)^{j-m}}{m!(j-m)!} + \sum_{m=1}^{j} \frac{\left(-\frac{\nu}{\mu}\right)^{m-1} \left(\frac{\nu}{\mu}\right)^{j-m}}{(m-1)!(j-m)!}$   
+  $\dots + \sum_{m=j-1}^{j} \frac{\left(-\frac{\nu}{\mu}\right)^{m-(j-1)} \left(\frac{\nu}{\mu}\right)^{j-m}}{(m-(j-1))!(j-m)!} + 1$   
= 1.

Hence, we find

$$p_j = \frac{\mu}{2\nu} \left( 1 - \sum_{m=0}^j \frac{\left(\frac{\nu}{\mu}\right)^m}{m!} \right).$$

No demographic turnover:  $B = \mu = 0$ 

Finally, we can also consider the situation without birth and death, i.e.  $B = \mu = 0.^4$  We then obtain a pair-formation process in a closed population of fixed size N. This can be described by the following system.

$$\frac{dx}{dt} = -\rho N x \sum_{j=0}^{\infty} p_j + \sigma \sum_{j=1}^{\infty} j p_j$$
$$\frac{dp_0}{dt} = -\rho N x p_0 + \sigma p_1$$
$$\frac{dp_j}{dt} = \rho N x p_{j-1} - (\rho N x + \sigma j) p_j + \sigma (j+1) p_{j+1}, \qquad j \ge 1$$

It turns out to be quite simple to calculate the steady state of this system. Consistency conditions give us  $\sum_{j=0}^{\infty} p_j = \frac{1}{2}$  and  $\sum_{j=1}^{\infty} jp_j = \frac{1}{2} - x$ . By setting dx/dt = 0 we obtain a linear equation in x that we can solve:

 $-\rho \tfrac{1}{2}Nx + \sigma(\tfrac{1}{2} - x) = 0,$ 

and

 $<sup>^{4}</sup>$ Note that the situation with only birth or with only death is not interesting to consider. In the first case we will have exponential growth of the population whereas in the second case the population will decrease and eventually not contain any individuals.

hence  $x^* = \frac{\sigma}{\rho N + 2\sigma}$ . Let us write

$$\nu = \nu(\rho, \sigma, N) \coloneqq \rho N x^* = \frac{\rho N \sigma}{\rho N + 2\sigma}.$$

By setting the right-hand side of  $dp_0/dt$  equal to zero we can express  $p_1^*$  in terms of  $p_0^*$ . This gives  $-\nu p_0 + \sigma p_1 = 0$ , hence  $p_1^* = \frac{\nu}{\sigma} p_0^*$ .

For  $j \ge 1$  we have a recurrence relation that we solve by the generating function approach. Let  $G(z) := \sum_{j=0}^{\infty} p_j z^j$  be the generating function of the  $p_j$ . Note that  $G(0) = p_0$ . Now, by multiplying the right-hand side of  $dp_j/dt$  with  $z^n$  and summing over all  $n \ge 1$  we obtain a first order linear differential equation for G that we can solve explicitly:

$$0 = -\nu \sum_{j=1}^{\infty} p_j z^j + \nu \sum_{j=1}^{\infty} p_{j-1} z^j + \sigma \sum_{j=1}^{\infty} (j+1) p_{j+1} z^j - \sigma \sum_{j=1}^{\infty} j p_j z^j$$
  
=  $\nu (G(z) - p_0) + \nu z G(z) + \sigma (G'(z) - p_1) - \sigma z G'(z)$   
=  $G(z)\nu(z-1) - G'(z)\sigma(z-1) + \nu p_0 - \sigma p_1.$ 

In the second equality we have used that  $G'(z) = \sum_{j=1}^{\infty} jp_j z^{j-1}$ . Finally by using the relation between  $p_0$  and  $p_1$ , we get that G must satisfy the differential equation

$$G'(z) = \frac{\nu}{\sigma}G(z).$$

Together with the boundary condition  $G(0) = p_0$  we see that

$$G(z) = p_0 \exp\left(\frac{\nu}{\sigma}z\right) = p_0 \sum_{j=0}^{\infty} \frac{(\nu/\sigma)^j}{j!} z^j.$$

Since by definition of G we also have  $G(z) = \sum_{j=0}^{\infty} p_j z^j$ , we see that

$$p_j = p_0 \frac{(\nu/\sigma)^j}{j!}.$$

We are left with solving the unknown  $p_0$ . For this we will use that  $\sum_{j=0}^{\infty} p_j = \frac{1}{2}$ :

$$\frac{1}{2} = \sum_{j=0}^{\infty} p_j = p_0 \sum_{j=0}^{\infty} \frac{(\nu/\sigma)^j}{j!} = p_0 e^{\nu/\sigma}$$

Hence

$$p_0^* = \frac{1}{2}e^{-\nu/\sigma}.$$

Finally, we use the explicit expression for  $\nu$ , the steady state of the system is given by  $(x^*, p^*)$ , where

$$x^{*} = \frac{\sigma}{\rho N + 2\sigma},$$

$$p_{j}^{*} = \frac{1}{2} \frac{\left(\frac{\rho N}{\sigma} x^{*}\right)^{j}}{j!} \exp\left(-\frac{\rho N}{\sigma} x^{*}\right)$$

$$= \frac{1}{2} \frac{\left(\frac{\rho N}{\rho N + 2\sigma}\right)^{j}}{j!} \exp\left(-\frac{\rho N}{\rho N + 2\sigma}\right), \qquad j = 0, 1, \dots$$
(2.28)

We see that  $x^* \ge 0$  and  $p_j^* \ge 0$ , j = 0, 1, ..., for all  $\rho, \sigma, N \ge 0$  so we do not have to put any restrictions on the parameters based on the steady state of the system. If we consider the distribution of the number of wives a man has, i.e.

 $\mathbb{P}(\text{man has } j \text{ wives}) = 2p_j^*, \quad j = 0, 1, \dots,$ 

then we recognize that this random variable is Poisson distributed with parameter

$$\frac{\rho N}{\rho N + 2\sigma}.$$

As the main motivation for this project arises from the virus HIV, we will not focus on a closed population. Indeed, the time-scale of HIV makes us wanting to consider a population *with* demographic turnover.

*Remark* 2.5. Note that, technically, we should also check that the special cases boil down to systems for which unique solutions exist given an initial condition. Otherwise, it is not worth knowing the steady states. We can do this by checking that the assumptions 1, 4, and 6 of [16] still hold. However, we will omit these tasks from this thesis as we will not consider the extreme cases further along. Intuitively, there should not be any reason to expect existence and uniqueness not to hold anymore, and the proof of this should really just be checking the assumptions.

Moreover, for these extreme situations, we would also like the steady states to be globally asymptotically stable (except for the situation that  $\rho = 0$ ). We will again omit this from this thesis for the extreme cases and only show that this is true for the situation that all parameters B,  $\mu$ ,  $\rho$ , and  $\sigma$  are strictly larger than zero in Section 2.5 below.

## 2.5 Stability of the steady state

In this section we will focus on proving that the steady state  $(x^*, p^*)$  is globally asymptotically stable on the state space C defined by (2.13). As in Section 2.2 we will use results from [16]. In Theorem 2.3, we have seen that if the initial condition  $(x(0), p(0)) = (\tilde{x}, \tilde{p})$  belongs to C, then the solution (x(t), p(t)) is also in C.

The proof will consist of two parts. First we will prove the existence of a compact attractor. Therefore we introduce its definition. Recall the notation for the semiflow of the system introduced in (2.14). A nonempty compact invariant subset A of C is called a compact attractor of  $B \subset C$  if for all open sets U with  $A \subset U \subset C$  there is an r > 0 such that

 $\Phi_t(B) \subset U$ , for all  $t \ge r$ .

Equivalently,

$$d(\Phi_t(B), A) = \sup_{(x, p \in B)} d(\Phi_t(x, p), A) \to 0, \quad \text{as } t \to \infty,$$

where  $d(\Phi_t(x,p), A) = \inf_{(\tilde{x},\tilde{p})\in A} \|\Phi_t(x,p) - (\tilde{x},\tilde{p})\|$  denotes the distance of  $\Phi_t(x,p)$  to the set A. A nonempty compact invariant subset  $A \subset C$  is called a compact attractor of bounded subsets of C if A is a compact attractor of every bounded subset B of C.

Remark 2.6. If a compact attractor of all bounded subsets of C exists, it is uniquely determined. Indeed, suppose we would have a compact attractor A, this attractor is invariant. Then necessarily it must contain all bounded invariant subsets of C. Suppose  $B \subset C$  is a bounded invariant subset of C with  $B \nsubseteq A$ . Then there is a point  $(x, p) \in B$ ,  $(x, p) \notin A$ . Since A is compact it is closed and therefore we find that

$$d((x,p),A) = \inf_{(\tilde{x},\tilde{p})\in A} \|(x,p) - (\tilde{x},\tilde{p})\| = \varepsilon > 0.$$

Then, as B is invariant we have  $\Phi_t(B) = B, t \ge 0$ , and

$$d(\Phi_t(B), A) = d(B, A) \ge \varepsilon > 0$$
, for all  $t \ge 0$ .

This contradicts A being a compact attractor of all bounded subsets. Hence, the compact attractor of all bounded subsets is unique.

After proving the first part, we will continue our proof of stability by proving the compact attractor consists of the steady state  $(x^*, p^*)$  only. This then allows us to conclude that  $(x^*, p^*)$  is globally asymptotically stable in C.

Before we start with either, we will formulate some approximations and estimates for solutions of (2.10), which will be useful in estimates we will make.

The following lemma has been mentioned already in the proof of Theorem 2.2. We are able to approximate solutions (x(t), p(t)) of system (2.10). In turn, this allows for useful estimates of (x(t), p(t)), which we will need in proving the stability of  $(x^*, p^*)$ .

**Lemma 1.** On every bounded interval of  $\mathbb{R}_+$ , the solution (x, p) of Theorem 2.2 is the uniform limit of solutions  $(x^{[n]}, p^{[n]})$  on  $\mathbb{R}_+$  with values in  $\mathbb{R}_+ \times \ell_+^{11}$  which solves the system

$$\frac{d}{dt}x^{[n]}(t) = -rx^{[n]}(t)\sum_{j=0}^{\infty} p_j^{[n]}(t) + (\sigma + 2\mu)\sum_{j=1}^{\infty} jp_j^{[n]}(t),$$

$$\frac{d}{dt}p_j^{[n]}(t) - x^{[n]}(t)\sum_{k=0}^{\infty} \gamma_{jk}p_k^{[n]}(t) = \begin{cases}\sum_{k=0}^{n} \alpha_{jk}p_k^{[n]}(t), & j = 0, \dots, n, \\ \alpha_{jj}p_j^{[n]}(t), & j > n. \end{cases}$$

$$(2.29)$$

$$(x^{[n]}(0), p^{[n]}(0)) = (\tilde{x}, \tilde{p}).$$

*Proof.* See [16, Remark 3, p. 64] which makes exactly this statement.  $\Box$ 

We will formulate two lemma's concerning the approximating solutions of Lemma 1. These lemma's will also be used in the proof of the stability of the steady state. In the first lemma, we show that we can estimate the norm of the approximating solutions (in  $\mathbb{R} \times \ell^{11}$ ) using the norm of the initial condition  $(\hat{x}, \hat{p})$ .

**Lemma 2.** Let  $(x^{[n]}(0), p^{[n]}(0)) = (\hat{x}, \hat{p})$  be the initial condition of system (2.29). The approximating solutions  $(x^{[n]}, p^{[n]})$  satisfy

$$x^{[n]}(t) + \sum_{j=1}^{\infty} j x_j^{[n]}(t) \le \hat{x} + \sum_{j=1}^{\infty} j \hat{p}_j,$$

and

$$\sum_{j=0}^{\infty} p_j^{[n]}(t) \le \sum_{j=0}^{\infty} \hat{p}_j.$$

*Proof.* The following estimates hold for the approximating solution:

$$\begin{split} \sum_{j=0}^{\infty} p_j^{[n]}(t) &\leq \sum_{j=0}^{\infty} \tilde{p}_j + \int_0^t \sum_{j=0}^{\infty} x^{[n]}(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k^{[n]}(s) ds, \\ \sum_{j=0}^{\infty} j p_j^{[n]}(t) &\leq \sum_{j=0}^{\infty} j \tilde{p}_j + \sum_{k=0}^{\infty} \sum_{j=0}^{\infty} j \alpha_{jk} \int_0^t p_k^{[n]}(s) ds \\ &+ \int_0^t \sum_{j=0}^{\infty} j x^{[n]}(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k^{[n]}(s) ds. \end{split}$$

See the proof of [16, Theorem 7] for the details of the derivation of the above estimates and note that  $\sum_{k=0}^{\infty} \sum_{j=0}^{\infty} \alpha_{jk} \int_{0}^{t} p_{k}^{[n]}(s) ds = 0$  by Proposition 1(b). Therefore,

$$\begin{aligned} x^{[n]}(t) &+ \sum_{j=1}^{\infty} jp_j^{[n]}(t) \\ &\leq \hat{x} + \sum_{j=1}^{\infty} j\hat{p}_j + \int_0^t \left( -rx^{[n]}(s) \sum_{j=0}^{\infty} p_j^{[n]}(s) + (\sigma + 2\mu) \sum_{j=1}^{\infty} jp_j^{[n]}(s) \right) ds \\ &+ \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk} \int_0^t p_k^{[n]}(s) ds + \int_0^t \sum_{j=1}^{\infty} jx^{[n]}(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k^{[n]}(s) ds \\ &= \hat{x} + \sum_{j=1}^{\infty} j\hat{p}_j. \end{aligned}$$

Here we have used that the double series  $\sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j\alpha_{jk} p_k^{[n]}$  exists absolutely; see Remark 2.1. Since the  $p_k^{[n]}$  are nonnegative, we may interchange summation and integration in the fourth summand. Proposition 4 then gives the equality. Furthermore, the calculations in the proof of Proposition 3(a) show that

$$\sum_{j=0}^{\infty} \hat{p}_j + \int_0^t \sum_{j=0}^{\infty} x^{[n]}(s) \sum_{k=0}^{\infty} \gamma_{jk} p_k^{[n]}(s) ds = \sum_{j=0}^{\infty} \hat{p}_j,$$

and this concludes the proof.

The following lemma shows convergence of approximating solutions.

**Lemma 3.** If we have two different initial conditions  $(\hat{x}, \hat{p})$  and  $(\check{x}, \check{p})$ , then the approximating solutions  $p^{[n]}$  and  $\tilde{p}^{[n]}$ , respectively, satisfy

$$\sum_{j=1}^{n} j |p_j^{[n]}(t) - \tilde{p}_j^{[n]}(t)| \to \sum_{j=1}^{\infty} j |p_j(t) - \tilde{p}_j(t)|, \quad \text{as } n \to \infty,$$

for all  $t \in \mathbb{R}_+$ .

*Proof.* Since  $p^{[n]}$  converges uniformly to p we find that

$$\left|\sum_{j=1}^{\infty} jp_j(t) - \sum_{j=1}^{n} jp_j^{[n]}(t)\right| = \left|\sum_{j=1}^{\infty} j(p_j(t) - p_j^{[n]}(t)) - \sum_{j=n+1}^{\infty} jp_j^{[n]}(t)\right|$$
$$\leq \sum_{j=1}^{\infty} j\left|p_j(t) - p_j^{[n]}(t)\right| + \sum_{j=n+1}^{\infty} jp_j^{[n]}(t).$$

And this converges to 0 as  $n \to \infty$ . Hence

$$\begin{split} \Big| \sum_{j=1}^{\infty} j \big| p_j(t) - \tilde{p}_j(t) \big| &- \sum_{j=1}^{n} j \big| p_j^{[n]}(t) - \tilde{p}_j^{[n]}(t) \big| \Big| \\ &\leq \Big| \sum_{j=1}^{\infty} j p_j(t) - \sum_{j=1}^{\infty} j \tilde{p}_j(t) - \sum_{j=1}^{n} j p_j^{[n]}(t) + \sum_{j=1}^{n} j \tilde{p}_j^{[n]}(t) \Big| \\ &\leq \Big| \sum_{j=1}^{\infty} j p_j(t) - \sum_{j=1}^{n} j p_j^{[n]}(t) \Big| + \Big| \sum_{j=1}^{n} j \tilde{p}_j^{[n]}(t) - \sum_{j=1}^{\infty} j \tilde{p}_j(t) \Big| \end{split}$$

converges to 0 as  $n \to \infty$ .

Before we start with proving the existence of a compact attractor note the following. The set C is a bounded subset of  $\mathbb{R} \times \ell^{11}$  and by Theorem 2.3 for the semiflow  $\Phi_t$  it holds that

$$\Phi_t(C) \subset C \quad \text{for all } t \ge 0. \tag{2.30}$$

Hence, if we want to show that a compact attractor of all subsets of C exists, it is enough to show that C has a compact attractor. We are now almost ready to start the actual proof.

Next we note that it is sufficient to show that

$$\alpha_s(\Phi_t(C)) \to 0 \quad \text{as } t \to \infty,$$
(2.31)

where  $\alpha_s$  is the separation measure of non-compactness. The compact attractor is then given by

$$\omega(C) = \bigcap_{t \ge 0} \overline{\bigcup_{s \ge t} \Phi_s(C)},\tag{2.32}$$

see [16, Lemma 5].<sup>5</sup>

If (X, d) is a metric space and  $Y \subset X$ , then  $\alpha_s(Y)$  is characterized as follows:

$$\alpha_s(Y) = \inf\{c \ge 0 : \text{ each sequence } (x_n)_n \text{ in } Y \text{ has a subsequence} (x_{n_k})_k \text{ with } \limsup_{j,k \to \infty} d(x_{n_j}, x_{n_k}) \le c\}.$$
(2.33)

The next theorem, which is concerned with proving the existence of a compact attractor, will work towards showing (2.31). The proof follows the structure of the proof of [16, Theorem 21]. The desired estimates follow from the fact that C is bounded and (2.30).

<sup>&</sup>lt;sup>5</sup>Recall that  $\omega(B)$  denotes the set of omega limit points of the set  $B \subset C$  under  $\Phi$ .

**Theorem 2.7.** The semiflow  $\Phi$  on C induced by the solutions of (2.10) has a compact attractor of C.

*Proof.* Let  $y, \tilde{y} \in \mathbb{R}$ . For sufficiently small |h|,

$$|y + h\tilde{y}| - |y| = \begin{cases} h\tilde{y}, & y > 0, \\ |h||\tilde{y}|, & y = 0, \\ -h\tilde{y}, & y < 0. \end{cases}$$

We divide by h and take the limit  $h \to 0$  from the left,

$$D_{-}|y|\tilde{y} \coloneqq \lim_{h \to -0} \frac{|y + h\tilde{y}| - |y|}{h} = \begin{cases} \tilde{y}, & y > 0, \\ -|\tilde{y}|, & y = 0, \\ -\tilde{y}, & y < 0. \end{cases}$$

Therefore, the following estimate holds:

$$D_{-}|y|\tilde{y} \leq \tilde{y} \operatorname{sign}_{0}(y), \quad \text{where } \operatorname{sign}_{0}(y) = \begin{cases} 1, & y > 0, \\ 0, & y = 0, \\ -1, & y < 0. \end{cases}$$

Let  $(\hat{x}, \hat{p}), (\check{x}, \check{p}) \in C$ , and  $(x^{[n]}(t), p^{[n]}(t)), (\check{x}^{[n]}(t), \tilde{p}^{[n]}(t))$  be approximating solutions (as in Lemma 1) of  $\Phi_t(\hat{x}, \hat{p})$  and  $\Phi_t(\check{x}, \check{p})$ , respectively. If we let  $\frac{d_-}{dt}$  denote the left derivative, then (see [20, VI.4 Lemma 4.1]) we obtain

$$\begin{aligned} \frac{d_{-}}{dt} \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| &= D_{-} \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| \left( \frac{d}{dt} p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right) \\ &\leq \left( \frac{d}{dt} p_{j}^{[n]}(t) - \frac{d}{dt} \tilde{p}_{j}^{[n]}(t) \right) \operatorname{sign}_{0} \left( p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right) \\ &\leq \left| \frac{d}{dt} p_{j}^{[n]}(t) - \frac{d}{dt} \tilde{p}_{j}^{[n]}(t) \right|. \end{aligned}$$

Using (2.29), this yields

$$\begin{aligned} \frac{d_{-}}{dt} \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| &\leq \sum_{k=0}^{n} \alpha_{jk} \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ x^{[n]}(t) \sum_{k=0}^{\infty} \gamma_{jk} \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ \left| x^{[n]}(t) - \tilde{x}^{[n]}(t) \right| \sum_{k=0}^{\infty} \left| \gamma_{jk} \right| \cdot \left| \tilde{p}_{k}^{[n]}(t) \right| \end{aligned}$$

We multiply this inequality by j, sum with respect to j = 1, ..., n, change the

order of summation, and use that  $\alpha_{jk} \ge 0$  for  $j \ne k$ :

$$\begin{aligned} \frac{d_{-}}{dt} \sum_{j=1}^{n} j \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| &\leq \sum_{k=0}^{n} \sum_{j=1}^{\infty} \alpha_{jk} \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ x^{[n]}(t) \sum_{k=0}^{\infty} \sum_{j=1}^{n} j \gamma_{jk} \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ \left| x^{[n]}(t) - \tilde{x}^{[n]}(t) \right| \sum_{k=0}^{\infty} \sum_{j=1}^{\infty} j |\gamma_{jk}| \tilde{p}_{k}^{[n]}(t) \end{aligned}$$

Notice that

$$\sum_{j=1}^{\infty} j |\gamma_{jk}| = r(1+k) \le 2r(1+k) \text{ and } \sum_{j=1}^{\infty} j \alpha_{jk} = -(\sigma + 2\mu)k,$$

for  $k = 0, 1, \ldots$  Hence

$$\begin{aligned} \frac{d_{-}}{dt} \sum_{j=1}^{n} j \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| &\leq -(\sigma + 2\mu) \sum_{k=0}^{n} k \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ x^{[n]}(t) \sum_{k=0}^{\infty} \sum_{j=1}^{n} j \gamma_{jk} \left| p_{k}^{[n]}(t) - \tilde{p}_{k}^{[n]}(t) \right| \\ &+ 2r \left| x^{[n]}(t) - \tilde{x}^{[n]}(t) \right| \cdot \| \tilde{p}_{k}^{[n]}(t) \|_{1}. \end{aligned}$$

In the last summand we have used that  $||x||_1 = \sum_{k=0}^{\infty} (1+k)|x|$  for  $x \in \ell^{11}$ . We integrate the above differential equation and obtain

$$\begin{split} \sum_{j=1}^{n} j \left| p_{j}^{[n]}(t) - \tilde{p}_{j}^{[n]}(t) \right| \\ &\leq e^{-(\sigma+2\mu)t} \sum_{j=1}^{n} j \left| p_{j}^{[n]}(0) - \tilde{p}_{j}^{[n]}(0) \right| \\ &+ \int_{0}^{t} e^{-(\sigma+2\mu)(t-s)} x^{[n]}(s) \sum_{k=0}^{\infty} \sum_{j=1}^{n} j \gamma_{jk} \left| p_{k}^{[n]}(s) - \tilde{p}_{k}^{[n]}(s) \right| ds \\ &+ 2r \int_{0}^{t} e^{-(\sigma+2\mu)(t-s)} \left| x^{[n]}(s) - \tilde{x}^{[n]}(s) \right| \cdot \| \tilde{p}^{[n]}(s) \|_{1} ds. \end{split}$$

Next, Lemma 3 shows us that  $\sum_{j=1}^{n} j |p_j^{[n]}(t) - \tilde{p}_j^{[n]}(t)| \rightarrow \sum_{j=1}^{\infty} j |p_j(t) - \tilde{p}_j(t)|$  as  $n \to \infty$ . We apply Lebesgue dominated convergence and interchange integration and summation with the limit of  $n \to \infty$  in the above inequality. Let's show explicitly that we may apply this to the summands.

We have the estimate

$$\sum_{k=0}^{\infty} \left| \sum_{j=1}^{n} j \gamma_{jk} x^{[n]}(s) \left| p_k^{[n]}(s) - \tilde{p}_k^{[n]}(s) \right| \right| \le r \sum_{k=0}^{\infty} k x^{[n]}(s) \left| p_k^{[n]}(s) - \tilde{p}_k^{[n]}(s) \right|$$
$$\le r x^{[n]}(s) \| p^{[n]}(s) - \tilde{p}^{[n]}(s) \|_1$$
$$\le r,$$

where we have used

$$\sum_{j=1}^{n} j\gamma_{jk} = \begin{cases} r, & n \ge k+1, \\ -rk, & n = k, \\ 0, & n < k, \end{cases}$$

in the first inequality and Lemma 2 and  $(\hat{x}, \hat{p}), (\check{x}, \check{p}) \in C$  in the final estimate. Therefore we may interchange the limit of  $n \to \infty$  with first the integral and second the infinite sum of k = 0 to  $\infty$  and we obtain

$$\lim_{n \to \infty} \int_0^t e^{-(\sigma + 2\mu)(t-s)} x^{[n]}(s) \sum_{k=0}^\infty \sum_{j=1}^n j\gamma_{jk} |p_k^{[n]}(s) - \tilde{p}_k^{[n]}(s)| ds$$
$$= \int_0^t e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=0}^\infty \sum_{j=1}^\infty j\gamma_{jk} |p_k(s) - \tilde{p}_k(s)| ds$$
$$= r \int_0^t e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=0}^\infty |p_k(s) - \tilde{p}_k(s)| ds,$$

where the last inequality holds since  $\sum_{j=1}^{\infty} j\gamma_{jk} = r$  for all  $k \in \mathbb{N}$ . Since  $e^{-(\sigma+2\mu)(t-s)}|x^{[n]}(s) - \tilde{x}^{[n]}(s)| \cdot \|\tilde{p}^{[n]}(s)\|_1 \leq 1$  for all  $s \in (0,t)$  we may also use Lebesgue dominated convergence in the following:

$$\lim_{n \to \infty} 2r \int_0^t e^{-(\sigma + 2\mu)(t-s)} |x^{[n]}(s) - \tilde{x}^{[n]}(s)| \cdot \|\tilde{p}^{[n]}(s)\|_1 ds$$
$$= 2r \int_0^t e^{-(\sigma + 2\mu)(t-s)} |x(s) - \tilde{x}^{(s)}| \cdot \|\tilde{p}(s)\|_1 ds.$$

Therefore

$$\begin{split} \sum_{j=1}^{\infty} j \left| p_j(t) - \tilde{p}_j(t) \right| &\leq e^{-(\sigma + 2\mu)t} \sum_{j=1}^{\infty} j \left| p_j(0) - \tilde{p}_j(0) \right| \\ &+ r \int_0^t e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=0}^{\infty} |p_k(s) - \tilde{p}_k(s)| ds \\ &+ 2r \int_0^t e^{-(\sigma + 2\mu)(t-s)} |x(s) - \tilde{x}(s)| \cdot \|\tilde{p}(s)\|_1 ds. \end{split}$$

We split up the second sum of the right-hand side in the above inequality at k=i where  $i\in\mathbb{N}$  is arbitrary. Then

$$\begin{split} \sum_{j=1}^{\infty} j \left| p_j(t) - \tilde{p}_j(t) \right| &\leq e^{-(\sigma + 2\mu)t} \sum_{j=1}^{\infty} j \left| p_j(0) - \tilde{p}_j(0) \right| \\ &+ r \int_0^t e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=0}^i \left| p_k(s) - \tilde{p}_k(s) \right| ds \\ &+ r \int_0^t e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=i+1}^{\infty} \left| p_k(s) - \tilde{p}_k(s) \right| ds \\ &+ 2r \int_0^t e^{-(\sigma + 2\mu)(t-s)} \left| x(s) - \tilde{x}(s) \right| \cdot \| \tilde{p}(s) \|_1 ds. \end{split}$$

Note the inequality

$$\sum_{k=i+1}^{\infty} |p_k(s) - \tilde{p}_k(s)| \le \frac{1}{i} \sum_{k=i+1}^{\infty} k |p_k(s) - \tilde{p}_k(s)| \\ \le \frac{1}{i} ||p(s) - \tilde{p}(s)||_1.$$

Hence,

$$\begin{split} \sum_{j=1}^{\infty} j \left| p_{j}(t) - \tilde{p}_{j}(t) \right| \\ &\leq e^{-(\sigma + 2\mu)t} \sum_{j=1}^{\infty} j \left| p_{j}(0) - \tilde{p}_{j}(0) \right| \\ &+ r \int_{0}^{t} e^{-(\sigma + 2\mu)(t-s)} x(s) \sum_{k=0}^{i} \left| p_{k}(s) - \tilde{p}_{k}(s) \right| ds \\ &+ \frac{r}{i} \int_{0}^{t} e^{-(\sigma + 2\mu)(t-s)} x(s) \| p(s) - \tilde{p}(s) \|_{1} ds \\ &+ 2r \int_{0}^{t} e^{-(\sigma + 2\mu)(t-s)} |x(s) - \tilde{x}(s)| \cdot \| \tilde{p}(s) \|_{1} ds. \end{split}$$
(2.34)

Let  $((\hat{x}^{\{n\}}, \hat{p}^{\{n\}}))_n$  be a sequence in C and  $(x^{\{n\}}, p^{\{n\}}) = \Phi_t(\hat{x}^{\{n\}}, \hat{p}^{\{n\}})$ . We will show that  $(x^{\{n_k\}})_k$ , and for each j,  $(p_j^{\{n_k\}})_k$  are Cauchy sequences on every finite interval in  $\mathbb{R}_+$ . We are then able to show that (2.31) holds, allowing us to conclude that a compact attractor exists.

Since C is bounded by 1 in the space  $\mathbb{R} \times \ell^{11}$  with respect to the norm given by (2.9), the sequence  $(x^{\{n\}})_n$  and, for each  $j \geq 0$ ,  $(p_j^{\{n\}})_n$  are equi-bounded with respect to n. We will show that they are also equi-continuous with respect to n on every finite interval in  $\mathbb{R}_+$ .

Let  $n \in \mathbb{N}$  be arbitrary. Then writing

$$x^{\{n\}}(t) = \hat{x}^{\{n\}} + (\sigma + 2\mu) \int_0^t \sum_{k=1}^\infty k p_k^{\{n\}}(u) du + r \int_0^t x^{\{n\}}(u) \sum_{k=0}^\infty p_k^{\{n\}}(u) du,$$

shows  $(x^{\{n\}})_n$  is equi-continuous:

$$\begin{aligned} \left| x^{\{n\}}(t) - x^{\{n\}}(s) \right| &\leq (\sigma + 2\mu) \left| \int_{t}^{s} \sum_{k=1}^{\infty} k p_{k}^{\{n\}}(u) du \right| \\ &+ r \left| \int_{t}^{s} x^{\{n\}}(u) \sum_{k=0}^{\infty} p_{k}^{\{n\}}(u) du \right| \\ &\leq (\sigma + 2\mu + r) |t - s|, \end{aligned}$$

Similarly, by using the expression for  $p_j$  given in (2.10), we can make the following estimates for  $p_j^{\{n\}}$ . Let  $t \leq s$ , then

$$\begin{aligned} \left| p_{j}^{\{n\}}(t) - p_{j}^{\{n\}}(s) \right| \\ &\leq \sum_{k=0}^{\infty} |\alpha_{jk}| \int_{t}^{s} p_{k}^{\{n\}}(u) du + \sum_{k=0}^{\infty} |\gamma_{jk}| \int_{t}^{s} x^{\{n\}}(u) p_{k}^{\{n\}}(u) du \end{aligned}$$

Note that  $\sum_{k=0}^{\infty} |\gamma_{jk}| \le 2r, j = 0, 1, \ldots,$ 

$$\sum_{k=0}^{\infty} |\alpha_{0k}| \int_{t}^{s} p_{k}^{\{n\}}(u) du = \int_{t}^{s} \sum_{k=0}^{\infty} |\alpha_{0k}| p_{k}^{\{n\}}(u) du = \frac{1}{2} \mu |t-s|.$$

and

$$\begin{split} \sum_{k=0}^{\infty} |\alpha_{jk}| \int_{t}^{s} p_{k}^{\{n\}}(u) du &= \int_{t}^{s} \sum_{k=0}^{\infty} |\alpha_{jk}| p_{k}^{\{n\}}(u) du \\ &= \int_{t}^{s} \left( |\alpha_{jj}| x_{j}^{\{n\}}(u) + |\alpha_{j,j+1}| x_{j+1}^{\{n\}}(u) \right) du \\ &\leq (\sigma + 2\mu) |t - s|, \end{split}$$

for  $j \ge 1$ . Hence  $|p_j^{\{n\}}(t) - p_j^{\{n\}}(s)| \le K|t-s|, j = 0, 1, \ldots$ , for some finite constant K > 0. These estimates show that  $(p_j^{\{n\}})_n$  is equi-continuous for each  $j = 0, 1, \ldots$ 

We conclude that  $(x^{\{n\}})_n$  and for each  $j \ge 0$ ,  $(p_j^{\{n\}})_n$  are equi-bounded and equi-continuous with respect to n on every finite interval in  $\mathbb{R}_+$ . By the Arzela-Ascoli theorem and a diagonalization procedure, after choosing appropriate subsequences,  $(x^{\{n\}})_n$  and for each  $j \ge 0$ ,  $(p_j^{\{n\}})_n$  are Cauchy sequences on every finite interval in  $\mathbb{R}_+$ . Let  $m, n \in \mathbb{N}$ . By setting  $(x, p) = (x^{\{m\}}, p^{\{m\}})$ and  $(\tilde{x}, \tilde{p}) = (x^{\{n\}}, p^{\{n\}})$  in inequality (2.34), we find the following estimate:

$$\begin{split} \limsup_{m,n\to\infty} \sum_{j=1}^{\infty} j \left| p_{j}^{\{m\}}(t) - p_{j}^{\{n\}}(t) \right| \\ &\leq e^{-(\sigma+2\mu)t} \limsup_{m,n\to\infty} \| p_{j}^{\{m\}}(0) - p_{j}^{\{n\}}(0) \|_{1} \\ &\qquad + \frac{r}{i} \int_{0}^{t} e^{-(\sigma+2\mu)(t-s)} x^{\{m\}}(s) \| p_{j}^{\{m\}}(s) - p_{j}^{\{n\}}(s) \| ds. \end{split}$$

$$(2.35)$$

Here we have used that

$$\begin{split} \limsup_{m,n\to\infty} r \int_0^t e^{-(\sigma+2\mu)(t-s)} x^{\{m\}}(s) \sum_{k=0}^i \left| p_k^{\{m\}}(s) - p_k^{\{n\}}(s) \right| ds \\ &\leq r \int_0^t e^{-(\sigma+2\mu)(t-s)} \limsup_{m,n\to\infty} x^{\{m\}}(s) \sum_{k=0}^i \left| p_k^{\{m\}}(s) - p_k^{\{n\}}(s) \right| ds \\ &= 0, \end{split}$$

where the inequality follows from Fatou's lemma (we are integrating a continuous function over a finite interval), and the equality follows from  $(p_k^{\{n\}})_n$  being a Cauchy sequence on the finite interval (0, t). Similar reasoning gives

$$\limsup_{m,n\to\infty} \int_0^t e^{-(\sigma+2\mu)(t-s)} |x^{\{m\}}(s) - x^{\{n\}}(s)| ||p^{\{m\}}(s)||_1 ds = 0.$$

Note that we also used  $\|p^{\{m\}}(s)\|_1 \leq 1 < \infty$  for all  $s \in (0, t)$ . We can estimate  $x^{\{k\}}(s) \leq \frac{1}{2}$  and  $\|p^{\{k\}}(s)\|_1 \leq 1$  for all  $k = 0, 1, \ldots$  and  $s \in (0, t)$ . Therefore

$$\limsup_{m,n\to\infty} \int_0^t e^{-(\sigma+2\mu)(t-s)} x^{\{m\}}(s) \|p_j^{\{m\}}(s) - p_j^{\{n\}}(s)\| ds < \infty.$$

This shows us we can take the limit of  $i \to \infty$  in (2.35), and we obtain

$$\limsup_{m,n\to\infty}\sum_{j=1}^{\infty}j\left|p_{j}^{\{m\}}(t)-p_{j}^{\{n\}}(t)\right| \leq e^{-(\sigma+2\mu)t}\limsup_{m,n\to\infty}\|p_{j}^{\{m\}}(0)-p_{j}^{\{n\}}(0)\|_{1}.$$

We can estimate  $||p||_1 \leq |p_0| + 2\sum_{j=1}^{\infty} j|p_j|$  for all  $p \in \ell^{11}$ . Note that

$$\begin{split} \left\| \Phi_t \big( \tilde{x}^{\{m\}}, \tilde{p}^{\{m\}} \big) - \Phi_t \big( \tilde{x}^{\{n\}}, \tilde{p}^{\{n\}} \big) \right\| \\ &= \left| x^{\{m\}}(t) - x^{\{n\}}(t) \right| + \| p^{\{m\}}(t) - p^{\{n\}}(t) \|_1 \\ &\leq |x^{\{m\}}(t) - x^{\{n\}}(t)| + |p_0^{\{m\}}(t) - p_0^{\{n\}}(t)| + 2\sum_{j=1}^{\infty} j |p_j^{\{m\}}(t) - p_j^{\{n\}}(t)|. \end{split}$$

Therefore, since both  $(x^{\{n\}})_n$  and  $(p_0^{\{n\}})_n$  are Cauchy sequences,

$$\begin{split} & \limsup_{m,n\to\infty} \left\| \Phi_t \left( \tilde{x}^{\{m\}}, \tilde{p}^{\{m\}} \right) - \Phi_t \left( \tilde{x}^{\{n\}}, \tilde{p}^{\{n\}} \right) \right\| \\ & \leq 2e^{-(\sigma+2\mu)t} \limsup_{m,n\to\infty} \| p^{\{m\}}(0) - p^{\{n\}}(0) \|_1. \end{split}$$

If we let  $||C||_1 := \sup_{(\tilde{x}, \tilde{p}) \in C} ||\tilde{p}||_1 \le 1 < \infty$ , then we see that

$$\begin{split} \limsup_{m,n\to\infty} \left\| \Phi_t \big( \tilde{x}^{\{m\}}, \tilde{p}^{\{m\}} \big) - \Phi_t \big( \tilde{x}^{\{n\}}, \tilde{p}^{\{n\}} \big) \right\| &\leq 2e^{-(\sigma+\mu)t} 2 \|C\|_1 \\ &\leq 4e^{-(\sigma+2\mu)t}. \end{split}$$

Now use characterization (2.33), we see that

$$\alpha_x(\Phi_t(C)) \le 4e^{-(\sigma+2\mu)t} \to 0 \quad \text{as } t \to \infty.$$

By [16, Lemma 5], this implies C has a compact attractor

$$A \coloneqq \omega(C) = \bigcap_{t \ge 0} \overline{\bigcup_{s \ge t} \Phi_s(C)}, \tag{2.36}$$

and this concludes our proof (recall (2.32)).

We are now ready to prove the result that we are actually interested in, namely that  $(x^*, p^*)$  is globally asymptotically stable in C. We will prove this by showing that the compact attractor A in the previous theorem is equal to this steady state, i.e.  $(x^*, p^*)$  is the compact attractor of C.

**Theorem 2.8.** The steady state  $(x^*, p^*)$  is globally asymptotically stable in C.

*Proof.* Let A denote the compact attractor of Theorem 2.7. A first observation is that  $(x^*, p^*) \in A$ .

Let  $(\tilde{x}, \tilde{p}) \in A$ . By definition, A is an invariant subset of C. Therefore  $\Phi_t(\tilde{x}, \tilde{p})$  is defined for all  $t \in \mathbb{R}$  (rather than only  $t \in \mathbb{R}_+$ ) and takes its values in A. Since  $\Phi_t(C) \subset C$ , we have the relations  $x = \frac{1}{2} - \sum_{j=1}^{\infty} jp_j$  and  $\sum_{j=0}^{\infty} p_j = \frac{1}{2}$  and we can reduce the differential equation for x to a first order linear inhomogeneous differential equation:

$$x' = -\frac{1}{2}rx + (\sigma + 2\mu)(\frac{1}{2} - x).$$

With initial data  $x(0) = \tilde{x}$ , we obtain an explicit expression for x:

$$x(t) = x^* - e^{-\frac{1}{2}(r+2(\sigma+2\mu))t}(x^* - \tilde{x}).$$

Since C is bounded, also x(t) must be bounded for all  $t \in \mathbb{R}$ . This holds only if  $\tilde{x} = x^*$ , and we see that  $x(t) = x^*$  for all  $t \in \mathbb{R}$ . Since  $(\tilde{x}, \tilde{p})$  is an arbitrary element of A we conclude that A is contained in the set  $\{(x^*, p) \in C\}$ .

For all  $(x^*, \tilde{p}) \in C$  we can show convergence of  $\Phi_t(x^*, \tilde{p}) \to (x^*, p^*)$  as  $t \to \infty$ . Obviously, with  $x(t) = x^*$  in its steady state, we get a set of linear differential equations for p. Let  $\nu$  be given by (2.17). Then

$$\begin{split} p_0' &= \mu \sum_{n=1}^{\infty} p_n - \nu p_0 + (\sigma + \mu) p_1 \\ p_j' &= \nu p_{j-1} - \left( \nu - (\sigma + \mu) j \right) p_j + (\sigma + \mu) (j+1) p_{j+1} - \mu p_j, \quad j \geq 1. \end{split}$$

We can rewrite this in the more condensed form

$$p'_j = \sum_{k=0}^{\infty} \beta_{jk} p_k, \quad j = 0, 1, \dots$$

This system is known as Kolmogorov's differential equations; see [22, p. 57] and references therein for more on Kolmogorov's differential equations. In a Markov chain describing population growth,  $\beta_{jk}$  can be interpreted as the transition rate of the population of size j changing to a population size of k. The vector  $p = (p_j)_k$  can be interpreted as the probability distribution of the population size, i.e.  $p_j(t)$  is the probability that the population has size j at time t. The coefficients  $\beta_{jk}$  are defined as follows

$$\begin{cases} \beta_{00} = -\nu, \\ \beta_{01} = \sigma + 2\mu, \\ \beta_{0n} = \mu, & n \ge 2, \\ \beta_{n,n-1} = \nu, & n \ge 1, \\ \beta_{n,n} = -(\nu + (\sigma + \mu)n + \mu), & n \ge 1, \\ \beta_{n,n+1} = (\sigma + \mu)(n+1), & n \ge 1, \\ \beta_{nk} = 0, & \text{otherwise} \end{cases}$$

In the Markov chain description we may also interpret this as a continuoustime birth and death process with immigration and catastrophes, and births and immigrations do not stop however large the population is. This Markov chain has a unique stationary probability distribution  $p_*$  such that  $p(t) \rightarrow p_*$ as  $t \rightarrow \infty$  for all probability distributions p, with convergence in the  $\ell^{11}$ -norm. One may check that the  $(\beta_{jk})_{j,k}$  satisfy the assumptions of [22, Theorem 11] which states the existence of the unique stationary probability distribution  $p_*$ with convergence of all probability distributions to  $p_*$  in the  $\ell^{11}$ -norm. By renormalising we see the relation with our  $p^*$ , i.e.  $p^* = \frac{1}{2}p_*$ .

Therefore,

$$\Phi_t(x^*, \tilde{p}) \to (x^*, p^*) \text{ as } t \to \infty.$$

In particular,  $\omega(x^*, \tilde{p}) = \{(x^*, p^*)\}$  for all  $(x^*, \tilde{p}) \in C$ . Hence  $\omega(A) = \{(x^*, p^*)\}$ .

Next, from  $\omega(C) = A$  (recall (2.36)) it follows that

$$\omega(C) = \omega\left(\omega(C)\right) = \omega(A) = \{(x^*, p^*)\}.$$

Hence

$$A = \omega(C) = \{(x^*, p^*)\}.$$

By definition of a compact attractor

$$\|\Phi_t(\tilde{x}, \tilde{p}) - (x^*, p^*)\| \to 0 \text{ as } t \to \infty$$

for all  $(\tilde{x}, \tilde{p}) \in C$  showing us the steady state  $(x^*, p^*)$  is globally asymptotically stable on C.

The steady state of the pair-formation process allows us to simplify the statistical description of the dynamic sexual network. In the next chapter, when studying the spread of an infection along the network, we will assume the sexual network to be in equilibrium. The reasoning behind this is that we assume the pair-formation process to have stabilized long before the infection is introduced in the population.

An interesting aspect to consider, that we have not done here, and which we will not do, is to consider the time it takes to reach the equilibrium value when starting with any initial condition for the pair-formation process. If it would take millions and millions of years before the steady state is reached, then the assumption of the dynamic sexual network to be in equilibrium may be quite unreasonable. In order to gain some information about the rate of convergence we would need to study the spectral bound of the linearization of (2.6). The closer this value is to 0, the longer it takes for the solutions of (2.6) to converge to  $(x^*, p^*)$ .

What we are really after is to understand how an infectious disease spreads along the dynamic sexual network that we have studied here. In a sense, this chapter has been the preparatory work for our main investigation. Therefore, we now leave the analysis of the pair-formation process and continue this text by studying an infection model in the next chapter. This will be constructed by superimposing an STI on the dynamic sexual network that we have discussed and analysed in this chapter.

## Chapter 3

# Infectious disease

In this chapter we will introduce the infectious-disease model, discuss some of the assumptions we make, and describe the model with an infinite-dimensional system of ODEs. We will discuss some problems that we do not try to solve in this research but which are interesting for future research. The focus will be on deriving an epidemic threshold for the system: when does the infection-free equilibrium switch from being (globally) asymptotically stable to unstable? Finally, we compare the basic reproduction number  $R_0$  of our polygynous population with the basic reproduction number of a monogamous population.

## 3.1 Infectious-disease model

As mentioned in the introduction, the pair-formation model is inspired by polygyny and HIV in sub-Saharan Africa. In this section we will therefore consider an infectious disease without recovery. Let's superimpose an STI and make a few assumptions on this infectious disease and its effect on the individuals in the population.

Individuals all enter the population as susceptible singles. There is only one disease stage. An individual is either susceptible or infectious. We define a contact as a sexual act between two individuals.<sup>1</sup> A susceptible individual can become infectious through sexual contact with an infectious individual. Since we are considering a heterosexual population, transmission of the infection can only occur through sexual contact between man and woman. We will assume that an infectious individual remains so until (s)he dies.

We assume individuals to be unaffected by their infection status, i.e. there is no disease-induced death rate and the pair-formation process is not influenced by the infection. We may think of individuals being unaware or indifferent of their partner's and their own infection status for motivating the latter assumption.

We let h denote the transmission rate. This can be viewed as the product of the number of sexual acts per unit of time c and the probability of transmission in one sexual contact p. As we have assumed with the parameters involved in the pair-formation process in Chapter 2, h is independent of sex, marital status,

<sup>&</sup>lt;sup>1</sup>Unlike some other infectious diseases such as airborne diseases, it is clearly defined what a contact is for STI: sexual acts generate the possibility of transmitting an STI.

etc. In particular we assume the infectivity to be the same for each infectious individual.

In our model, it may happen that a partnership dissolves before any sexual contact has taken place between the individuals. So the start of a partnership is not initiated with sexual contact. Of course, these partnerships are not of any interest from the point of view of the infectious disease as they do not allow for the transmission of the infection.

An important assumption we will make regarding the sexual acts is that each woman with a husband will have the same number of sexual contacts c per unit of time with her husband. This is regardless of the marital status of her husband. Put differently, the average number of sexual contacts per unit of time in a partnership is equal to c. For a man with n wives, this means he will have  $c \cdot n$  number of sexual contacts per unit of time,  $n \geq 1$ . This is not necessarily a very realistic assumption, especially if you take into account the assumptions for the pair-formation model. Indeed, there is no upper bound on the number of wives one man may have. At some point a man can have 1000 partners at the time and he will have to have sex all day long to 'satisfy' the  $1000 \cdot c$  sexual contacts.<sup>2</sup> However, for now, in order not to complicate the analysis, we will not modify this assumption.

As is true for the pair-formation model, we can extend this model in the future by making some different or additional assumptions.

Another assumption we will make regarding the transmission rate is that each sex act will generate a fixed probability p of transmitting the disease. Implicitly we assume that each sex act has the same risk behaviour, e.g. condomuse is the same with each contact and each wife. This also means a man does not distinguish between his wives. This is probably not usually the case. A man may distinguish between his first wife and junior wives and consequently his condom-use may be different for each wife [23].

Furthermore, we assume that the transmission rate h does not change over time. Individuals are equally infectious in their entire infectious life. This is a major simplification if we consider a disease such as HIV, where there are significant differences in infectivity in the course of the infectious life of an individual [24, 25]. Following the initial infection, there is a period of relatively high infectivity in the so-called acute phase. The infectivity then decreases and more or less stabilizes in the chronic phase, which are the years after the acute phase and before the development of AIDS. In this phase, the infectivity increases again, although, due to factors connected with AIDS, most individuals will leave the sexually active population by then. This last observation is like a disease-induced death, something we have not incorporated in our model (recall we assume there to be no disease-induced death rate). In our model, we assume the expected life length of infectious individuals not to decrease due to their infection status. For future work, it would be interesting to explore the effect of an additional death rate of infectious individuals on the transmission of the infection through the population.

The significant difference in infectivity over the course of the infectious life of an infective is an important point as it may be the cause that concurrency yields higher prevalence than serial monogamy. Simulations done in e.g. [14] show

 $<sup>^2 \</sup>mathrm{On}$  the other hand, we may expect a man with three wives to be more sexually active than a man with 'only' one wife.

significant differences in the prevalence when taking the variable infectivity into account. We will not incorporate this variable infectivity in our current model. However, it is certainly worth investigating in future extensions of this model.

Now, let us describe the model using a system of ODEs. The following variables are of interest to us:

 $X_0$ : the number of single and susceptible women,

 $X_1$ : the number of single and infectious women,

 $P_{n,k}$ : the number of susceptible men with

n-k susceptible and k infectious partners,

 $Q_{n,k}$ : the number of infectious men with

n-k susceptible and k infectious partners,

 $n, k \geq 0, k \leq n$ . Note that  $P_{0,0}$  and  $Q_{0,0}$  denote the number of single susceptible and single infectious men, respectively.

The model is described by

$$\begin{aligned} \frac{dX_0}{dt} &= B - \rho X_0 \sum_{n=0}^{\infty} \sum_{k=0}^n (P_{n,k} + Q_{n,k}) \\ &+ (\sigma + \mu) \sum_{n=1}^{\infty} \sum_{k=0}^{n-1} (n-k)(P_{n,k} + Q_{n,k}) - \mu X_0, \\ \frac{dX_1}{dt} &= -\rho X_1 \sum_{n=0}^{\infty} \sum_{k=0}^n (P_{n,k} + Q_{n,k}) \\ &+ (\sigma + \mu) \sum_{n=1}^{\infty} \sum_{k=1}^n k(P_{n,k} + Q_{n,k}) - \mu X_1, \\ \frac{dP_{0,0}}{dt} &= B - \rho (X_0 + X_1) P_{0,0} + (\sigma + \mu)(P_{1,0} + P_{1,1}) - \mu P_{0,0}, \\ \frac{dQ_{0,0}}{dt} &= -\rho (X_0 + X_1) Q_{0,0} + (\sigma + \mu)(Q_{1,0} + Q_{1,1}) - \mu Q_{0,0}. \end{aligned}$$

For  $n \ge 1$ ,

$$\begin{split} \frac{dP_{n,0}}{dt} &= \rho X_0 P_{n-1,0} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) P_{n,0} \\ &+ (\sigma + \mu) \left((n+1)P_{n+1,0} + P_{n+1,1}\right) - \mu P_{n,0}, \\ \frac{dQ_{n,0}}{dt} &= \rho X_0 Q_{n-1,0} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) Q_{n,0} \\ &+ (\sigma + \mu) \left((n+1)Q_{n+1,0} + Q_{n+1,1}\right) - \mu Q_{n,0} \\ &- hnQ_{n,0}, \\ \frac{dP_{n,n}}{dt} &= \rho X_1 P_{n-1,n-1} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) P_{n,n} \\ &+ (\sigma + \mu) \left((n+1)P_{n+1,n+1} + P_{n+1,n}\right) - \mu P_{n,n} \\ &- hnP_{n,n}, \\ \frac{dQ_{n,n}}{dt} &= \rho X_1 Q_{n-1,n-1} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) Q_{n,n} \\ &+ (\sigma + \mu) \left((n+1)Q_{n+1,n+1} + Q_{n+1,n}\right) - \mu Q_{n,n} \\ &+ h(Q_{n,n-1} + nP_{n,n}). \end{split}$$

For  $n \ge 1, k \ge 1, k < n$ ,

$$\begin{aligned} \frac{dP_{n,k}}{dt} &= \rho X_0 P_{n-1,k} + \rho X_1 P_{n-1,k-1} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) P_{n,k} \\ &+ (\sigma + \mu) \left((n+1-k)P_{n+1,k} + (k+1)P_{n+1,k+1}\right) - \mu P_{n,k} \\ &- hk P_{n,k}, \end{aligned}$$
$$\begin{aligned} \frac{dQ_{n,k}}{dt} &= \rho X_0 Q_{n-1,k} + \rho X_1 Q_{n-1,k-1} - \left(\rho(X_0 + X_1) + (\sigma + \mu)n\right) Q_{n,k} \\ &+ (\sigma + \mu) \left((n+1-k)Q_{n+1,k} + (k+1)Q_{n+1,k+1}\right) - \mu Q_{n,k} \\ &+ h \left((n-k+1)Q_{n,k-1} + kP_{n,k} - (n-k)Q_{n,k}\right). \end{aligned}$$

One can check (which I have done only for the first equality) that we have

$$\frac{dN}{dt} = 2B - \mu N,$$
$$\frac{dN_f}{dt} = B - \mu N_f,$$
$$\frac{dN_m}{dt} = B - \mu N_m,$$

where

$$N = X_0 + X_1 + \sum_{n=0}^{\infty} \sum_{k=0}^{n} (1+n) (P_{n,k} + Q_{n,k}),$$
$$N_f = X_0 + X_1 + \sum_{n=0}^{\infty} \sum_{k=0}^{n} n (P_{n,k} + Q_{n,k}),$$
$$N_m = \sum_{n=0}^{\infty} \sum_{k=0}^{n} (P_{n,k} + Q_{n,k}),$$

denote the total population size, the total number of women, and the total number of men, respectively. We assume the population to be in equilibrium, hence  $N = N^* = 2B/\mu$ ,  $N_f = N^*_f = B/\mu$ , and  $N_m = N^*_m = B/\mu$ .

We also assume the pair-formation process to be in equilibrium. The following relations are therefore satisfied:

$$X^* = X_0 + X_1$$
: the total number of single women,  
 $P_n^* = \sum_{k=0}^n (P_{n,k} + Q_{n,k})$ : the total number of men with *n* partners,  $n \ge 0$ ,

where  $(X^*, P^*) = N^*(x^*, p^*)$  is the steady state of the pair-formation process (2.1) for which we found an explicit expression (2.23). The reasoning behind this assumption is that we are considering a population and its corresponding dynamic sexual network that have existed long before the infection is introduced in the population. In fact, we assume that the population has existed for such a long time that the pair-formation process has already converged to its steady state  $(X^*, P^*)$ , which we know to happen for time  $t \to \infty$ ; see Section 2.5.

We are interested in the total number of infectious individuals in the population. This is given by the total number of infectious women

$$X_1 + \sum_{n=1}^{\infty} \sum_{k=1}^{n} k(P_{n,k} + Q_{n,k}),$$

plus the total number of infectious men

$$\sum_{n=0}^{\infty} \sum_{k=0}^{n} Q_{n,k}.$$

As in the case for the system (2.2) describing the pair-formation model

we may consider fractions rather than numbers. Let the small letters  $x_0$ ,  $x_1$ ,  $p_{n,k}$ , and  $q_{n,k}$  denote the fractions corresponding to the quantities represented by the capital letters  $X_0$ ,  $X_1$ ,  $P_{n,k}$ , and  $Q_{n,k}$ , respectively. Compared to the above system, we need to make the following changes. Replace the capital letters with the small letters, replace B with  $\frac{\mu}{2}$  and  $\rho$  with  $\frac{2B\rho}{\mu}$ .

The sex ratio 1:1 needs to be maintained. Therefore

$$\frac{1}{2} = x_0 + x_1 + \sum_{n=0}^{\infty} \sum_{k=0}^{n} n(p_{n,k} + q_{n,k}) = \sum_{n=0}^{\infty} \sum_{k=0}^{n} (p_{n,k} + q_{n,k}).$$

Assuming the pair-formation process to be in equilibrium allows us to eliminate all susceptible components from the system, i.e. the susceptible singles and all star-shaped components where each individual involved is susceptible. These components consist of  $x_0$ ,  $p_0$ , and  $p_{n,0}$ , n = 1, 2, ... Indeed we have

$$x_0 = x^* - x_1,$$
  

$$p_{0,0} = p_0^* - q_{0,0},$$
  

$$p_{n,0} = p_n^* - \sum_{k=1}^n (p_{n,k} + q_{n,k}) - q_{n,0}, \quad n = 1, 2, \dots$$

Note however that this does not allow for a great reduction of the number of differential equations. If we consider all stars consisting of n + 1 individuals,  $n = 0, 1, \ldots$ , then there are 2(n+1) different stars of that size. Different should be interpreted in the labels susceptible and infectious assigned to the members of the star. Of the 2(n+1) different stars, we are only able to eliminate the fully susceptible star. For example, if we consider all stars of one man with two wives, then we have the following different stars, in the usual notation,  $p_{2,0}$ ,  $p_{2,1}$ ,  $p_{2,2}$ ,  $q_{2,0}$ ,  $q_{2,1}$ , and  $q_{2,2}$ . Assuming the pair-formation process to be in equilibrium we are able to eliminate the variable  $p_{2,0}$  only.

Let us denote the fraction of infectious men and infectious women with  $i_m$ and  $i_f$ , respectively. Then

$$i_m = \sum_{n=0}^{\infty} \sum_{k=0}^{n} q_{n,k},$$

and

$$i_f = x_1 + \sum_{n=1}^{\infty} \sum_{k=1}^{n} k(p_{n,k} + q_{n,k}).$$

Hence the total fraction of infectives in the population i is

$$i = i_f + i_m = x_1 + \sum_{n=1}^{\infty} \sum_{k=1}^n k(p_{n,k} + q_{n,k}) + \sum_{n=0}^{\infty} \sum_{k=0}^n q_{n,k}.$$

Remark 3.1. We have paid attention to the existence and uniqueness of solutions of the system (2.10) in the previous chapter. Indeed we have proven that, given some initial condition, the system describing the pair-formation process has unique solutions, and this comprised a large part of the analysis in the previous chapter. In this chapter, we have again described a model with a system of

ODEs on page 56. Formally, we would need to check existence and uniqueness of solutions of this system. However, time constraints oblige us to make decisions. We focus instead on understanding the initial growth of an epidemic process in this chapter. In the rest of this chapter we will mainly be dealing with determining a threshold value for the model.

## 3.2 Steady states

By definition, our infectious-disease model has at least one steady state, namely the infection free state  $(x^0, p^0, q^0)$  with

$$x_0^0 = x^*, \quad p_{j,0}^0 = p_j^*, \ j = 0, 1, \dots$$

and  $x_{1}^{0} = p_{ik}^{0} = q_{ik}^{0} = 0$  otherwise.

Intuitively, we would expect there to exist a unique endemic equilibrium tot the system, which, under the right conditions, is asymptotically stable. At least there does not seem to be a reason to suspect otherwise. This is no convincing argument for anything. We need to formally prove the existence of an endemic equilibrium. In case of the pair-formation process we could prove the existence of a unique steady state by explicitly calculating it. For the infectious-disease model the approach we have taken there seems to be too complicated.

As we are quite confident that there must exist a unique endemic equilibrium, we will leave it as an open problem for now. Let's find the condition for the infection-free equilibrium to be globally asymptotically stable in the rest of this chapter.

## **3.3** Determining $R_0$

To determine  $R_0$  for our model we will use the next-generation matrix (NGM) as defined in Diekmann et al. [26, Ch. 7: *The basic reproduction ratio*]. We consider the states-at-infection, i.e. states that individuals can be in immediately after infection. These individuals-at-infection are nonsingle by construction of the model. Indeed, contacts are not instantaneous, they occur within partnerships. Immediately after infection, an individual will be in a partnership with its epidemiological parent.

An individual-at-infection may be female-at-infection or a male-at-infection with n wives, n = 1, 2, ... We need to distinguish between a male-at-infection with  $n_1$  wives or a male-at-infection with  $n_2$  wives,  $n_1, n_2 = 1, 2, ..., n_1 \neq n_2$ . Therefore, we have countably many states-at-infection. The exact number of wives a man has at the start of his infectious life matters for the expected number of secondary cases he produces. We shall see this in Section 3.3.2. However, as the pair-formation process is in steady state, we know the distribution  $(2p_j^*)_j$  of wives per man. This allows us to reduce the infinitely many males-at-infection to one 'typical' male-at-infection. This newly infected male is typical in the sense that we average over all men with n = 1, 2, ... partners weighted with some appropriate probability distribution  $(\lambda_n)_n$  (which will be given by (3.4)). If the expected number of secondary cases of a man with n wives, n = 1, 2, ..., is given by  $R_m(n)$ , then we find  $R_m$ , the expected number of secondary cases one typical newly infected male can make in the beginning of an epidemic, to be

$$R_m = \sum_{n=1}^{\infty} \lambda_n R_m(n).$$

Our NGM K is then a  $2 \times 2$ -matrix

$$K = \left(\begin{array}{cc} 0 & R_f \\ R_m & 0 \end{array}\right).$$

Here, the quantity  $R_f$  denotes the expected number of secondary cases one newly infected female can make in the beginning of an epidemic. Since we assume a heterosexual population, a secondary case is necessarily from the opposite sex. This is reflected in the zero-diagonal of K. The basic reproduction number  $R_0$ is defined as the dominant eigenvalue of K. For this  $2 \times 2$  matrix, we can easily determine the dominant eigenvalue to be equal to

$$R_0 = \sqrt{R_f R_m}.\tag{3.1}$$

In a sense we have reduced an infinite dimensional situation to a two-dimensional problem, which is easier to work with.

As we will also explain in Section 3.3.1, a female-at-infection is simply a nonsingle infectious female, i.e. it will not matter how many co-wives this woman has for the calculation of  $R_f$ , contrary to the situation of a male-at-infection. This should coincide with the intuition one has for the model. In a heterosexual population, a woman has at most one partner at the time who she may potentially infect, while this is not the case for a man with more sexual partnerships at once.

We are left to calculate the two unknowns  $R_f$  and  $R_m$ . Before determining  $R_m$ , let us start with the relatively simple case of determining  $R_f$ .

### **3.3.1** The basic reproduction number $R_f$

If we take the point of view of an infectious woman in an otherwise susceptible population, then the number of men she will infect will not depend on the partnership status of the men she will acquire (or the partnership status of the man at the beginning of her infectious lifetime). Note that this is based on the assumption that each man will have the same number of sex acts per unit of time with each of his partners, regardless of his number of partners. The same is true for the rate of separation and death of her husband; both do also not depend on the partnership status of her husband. Also, we have assumed that women do not have a preference for the marital status of a future husband. At the start of her infectious life, the woman is in a partnership with her epidemiological parent. Before she can infect anyone, she needs to separate from her current husband and find new husbands.

We assume that each man acquired by this infectious woman is susceptible and she has susceptible co-wives only. She either infects an acquired husband or their partnership dissolves before this happens. In particular, there is no possibility of him to become infectious through infection from one of his other (future) wives. This is reasonable to assume as we are considering a large population at the beginning of an epidemic. There are only very few infectious individuals, and she will not encounter any infectious men or women, except for the infectious individuals of the star she is part of at the start of her infectious life or the men that she will infect herself.

From the point of view of the infectious woman, we may as well have a completely monogamous population and she can be in three states only: single, paired with a susceptible man, and paired with an infectious man.



Figure 3.1: Flowchart of the different states the infectious woman can be in.

We can use a Markov-chain description to determine an expression for  $R_f$ , the expected number of men a newly infected woman infects in her lifetime in a fully susceptible population. The women is in state 0 if she is single, in state (1,0) if paired with a susceptible man, and in state (1,1) if paired with an infectious man.<sup>3</sup> Let  $P_{i,j}$  denote the transition probability from *i* to *j*,  $i, j \in \{0, (1, 0), (1, 1)\}$ . The following transition probabilities describe the entire process:

$$P_{0,(1,0)} = \frac{\rho N_m^*}{\rho N_m^* + \mu},$$
  

$$P_{(1,0),0} = \frac{\sigma + \mu}{h + \sigma + 2\mu},$$
  

$$P_{(1,0),(1,1)} = \frac{h}{h + \sigma + 2\mu},$$
  

$$P_{(1,1),0} = \frac{\sigma + \mu}{\sigma + 2\mu}.$$

All other transition probabilities are equal to zero. Note that 'death' is a hypothetical fourth state of the Markov chain.

We determine  $R_f$ , the expected number of men one newly infected woman infects in her lifetime in a fully susceptible population, using first step analysis of the Markov chain. In order to find  $R_f$  we want to know the expected number of times the infectious woman visits state (1, 1) (not including the first time she is in state (1, 1), which is when she is newly infected). After all, each time she enters state (1, 1), she will have infected one man.

If we let  $\pi_{i,j}$ ,  $i, j \in \{0, (1, 0), (1, 1)\}$  denote the probability to ever arrive in state j when starting from state i, then we find

$$R_f = \pi_{(1,1),(1,1)}(1+R_f).$$

<sup>&</sup>lt;sup>3</sup>This process is exactly the one described in [26, Sec. 7.8: *Pair Formation models*]. The states 1, 2, and 3 in this book correspond to state 0, (1,0), and (1,1), respectively. The notation for the parameters used in the book correspond to the parameters in our model. In the book, two different methods are presented to derive  $R_f$  (plus another threshold value). We will explain the second method to derive  $R_f$  here.

Indeed, the woman's infectious life starts in state (1,1), with probability  $\pi_{(1,1),(1,1)}$  she will have infected one man and she is again in state (1,1). By the memoryless property of the Markov chain it is as if she is in this state for the first time. The expected number of additional infectees is therefore also equal to  $R_f$ .

To determine  $\pi_{(1,1),(1,1)}$ , we will first find an expression for  $\pi_{0,(1,1)}$ . In order to arrive at state (1,1) from state 0, one must first pass state (1,0). To enter state (1,1) from this state, the woman may either jump to (1,1) directly or she separates from her partner and enters the single state again. The probability that she arrives at state (1,1) is again equal to  $\pi_{0,(1,1)}$  in the latter case. To summarise,  $\pi_{0,(1,1)}$  satisfies the relation

$$\pi_{0,(1,1)} = \frac{\rho N_m^*}{\rho N_m^* + \mu} \left( \frac{h}{h + \sigma + 2\mu} + \frac{\sigma + \mu}{h + \sigma + 2\mu} \pi_{0,(1,1)} \right).$$

Now we observe that  $\pi_{(1,1),(1,1)}$  is equal to the probability to enter state 0 from state (1,1) times the probability that we ever arrive at state (1,1) from state 0, i.e.

$$\pi_{(1,1),(1,1)} = \frac{\sigma + \mu}{\sigma + 2\mu} \pi_{0,(1,1)}$$

Solving the above equations for  $R_f$ ,  $\pi_{0,(1,1)}$ , and  $\pi_{(1,1),(1,1)}$  we find

$$R_{f} = \frac{\rho N_{m}^{*} h(\sigma + \mu)}{\mu (\rho N_{m}^{*} + \sigma + 2\mu)(h + \sigma + 2\mu)}.$$
(3.2)

#### **3.3.2** The basic reproduction number $R_m$

To determine  $R_m$ , the expected number of secondary cases a typical newly infected man can make in his lifetime in the beginning of the epidemic, we make a few assumptions first. We assume that every partner this infectious man acquires is susceptible. Beside his epidemiological parent, all current wives are also susceptible and might get infected by their infectious husband. Each event occurring in the life of the infectious man (acquiring a partner, separation, infection, death) only depends on the last event, independent of any previous events, and the waiting times are exponentially distributed.

We can subdivide the wives of an infectious man into two categories.

- The wives at the start of the infectious life. Let's call these current partners.
- The wives he acquires during his infectious life. Let's call these new partners.

By assumption, each wife is independent of the other wives. The dependence is created by the death of the man: if the husband dies, all wives become single.

We will derive an explicit expression for  $R_m$  in two ways. First, we will give an intuitive argument. After this, we will derive it in a more exact way, and we will verify that the two arguments lead to the same expression for  $R_m$ . Intuitively, we can reason as follows. The probability a wife gets infected is the probability that infection takes place before separation or death of either the husband or the wife. Hence this probability is

$$\frac{h}{h+\sigma+2\mu}.$$

Suppose the man has n susceptible current partners. Since we assume all wives behave independently of each other (as long as the husband is alive) we get that the expected number of infected current wives equals

$$\frac{hn}{h+\sigma+2\mu},\tag{3.3}$$

see also Remark 3.2. The probability the husband has n susceptible current partners,  $n = 0, 1, \ldots$ , given that he has at least one, infectious, partner, is equal to

 $\mathbb{P}(\text{man has } n+1 \text{ partners} \mid \text{man is not single})$ 

$$= \frac{\mathbb{P}(\text{man has } n+1 \text{ partners})}{\mathbb{P}(\text{man is not single})}$$
$$= \frac{2p_{n+1}^*}{1-2p_0^*},$$
(3.4)

 $n = 0, 1, 2, \ldots$  Note that the pair-formation process does not depend on the infection status of the individuals involved. Therefore, this also does not play a role in the above probability. Since we are considering a male-at-infection, we consider only men with 1 partner or more. A man at the start of his infectious career with n susceptible partners has n + 1 partners in total. The expected number of infected current wives of a typical newly infected man is therefore given by

$$\sum_{n=1}^{\infty} \frac{2p_{n+1}^*}{1 - 2p_0^*} \frac{hn}{h + \sigma + 2\mu}.$$

New wives arrive according to a Poisson stream with rate  $\rho X^*$ . Note that, while (single) women can choose to form a partnership with any man in the population, men are restricted in their choice of women since they can only choose from the pool of single women. The expected life length of the infectious husband is equal to  $\frac{1}{\mu}$ . Therefore, the expected number of new wives is  $\frac{\rho X^*}{\mu}$ . This is independent of initial star-size. The expected number of infected new wives of any infectious man is equal to

$$\frac{\rho X^*}{\mu} \frac{h}{h + \sigma + 2\mu}$$

In particular, it is the expected number of infected new wives of a typical newly infected man.

The sum of the expected number of infected current wives and the expected number of infected new wives then gives us  $R_m$ , the total expected number of secondary cases of one typical newly infected man at the beginning of an epidemic. Remark 3.2 (The pitfall of overlooking dependence). One should note that (3.3) is an expected value (and for its derivation one should read on until equation (3.5)). We have not made any statements about the probability distribution of infected current wives. One might be tempted to say that this distribution is the binomial distribution

$$P(i) = \binom{n}{i} \left(\frac{h}{h+\sigma+2\mu}\right)^{i} \left(\frac{\sigma+2\mu}{h+\sigma+2\mu}\right)^{n-i}$$

However, this is not true. This is the pitfall of overlooking dependence. The current wives are correlated with each other: if the husband dies, then they all become single. For a slightly different example and an elaborate explanation see[26, Sec. 2.3 *The pitfall of overlooking dependence*].

Let us now derive  $R_m$  more carefully. Let L denote the life length of the infectious husband. By assumption, L is exponentially distributed with mean  $\frac{1}{\mu}$ . Let's consider one current partner. We introduce three more random variables. Let  $X_1 \sim \exp(h)$ ,  $X_2 \sim \exp(\sigma)$  and  $X_3 \sim \exp(\mu)$  denote the time of infection, separation, and death of the current partner, respectively. These three random variables can be viewed as being independent from each other and of L. We just assume that infection, separation, and death can occur in any order for this wife. However, for an infection to actually count as a secondary case, the infection must take place before separation, death of husband, and death of herself.

Assume  $L = \tau$ , with  $\tau \in [0, \infty)$ . The wife gets infected if both  $\{X_1 = \min\{X_1, X_2, X_3\}\}$  and  $\{X_1 < \tau\}$ . The probability this happens is

$$\int_{t=0}^{\tau} \mathbb{P}(X_2 > t) \mathbb{P}(X_3 > t) h e^{-ht} dt = \int_{t=0}^{x} h e^{-(h+\sigma+\mu)t} dt$$
$$= \frac{h}{h+\sigma+\mu} \left(1 - e^{-(h+\sigma+\mu)\tau}\right)$$

The wife does *not* get infected if either  $\{X_1 \neq \min\{X_1, X_2, X_3\}\}$  or  $\{X_1 = \min\{X_1, X_2, X_3\}, X_1 > \tau\}$ . This probability is given by

$$\mathbb{P}(X_1 \neq \min\{X_1, X_2, X_3\}) + \mathbb{P}(X_1 = \min\{X_1, X_2, X_3\}, X_1 > \tau)$$
$$= 1 - \frac{h}{h + \sigma + \mu} + \int_{t=\tau}^{\infty} h e^{-(h + \sigma + \mu)t} dt$$
$$= \frac{\sigma + \mu}{h + \sigma + \mu} + \frac{h}{h + \sigma + \mu} e^{-(h + \sigma + \mu)\tau}.$$

Suppose we know the husband starts his infectious life with n + 1 wives,  $n \ge 1$ . Then we know that n of these wives are susceptible and therefore they may become infected by their husband. The probability that k out of n wives get infected, given  $L = \tau$ , is given by

$$\xi_{n,k}(\tau) \coloneqq \binom{n}{k} \left( \frac{h\left(1 - e^{-(h+\sigma+\mu)\tau}\right)}{h+\sigma+\mu} \right)^k \left( \frac{\sigma+\mu}{h+\sigma+\mu} + \frac{he^{-(h+\sigma+\mu)\tau}}{h+\sigma+\mu} \right)^{n-k}.$$

The expected number of infected current partners, given L = x and n current

partners, is given by

$$\sum_{k=1}^{n} k\xi_{n,k}(\tau) = n \frac{h}{h+\sigma+\mu} (1 - e^{-(h+\sigma+\mu)\tau}) \sum_{k=0}^{n-1} \xi_{n-1,k}(\tau)$$
$$= n \frac{h}{h+\sigma+\mu} (1 - e^{-(h+\sigma+\mu)\tau}) \left(\frac{h}{h+\sigma+\mu} + \frac{\sigma+\mu}{h+\sigma+\mu}\right)$$
$$= n \frac{h}{h+\sigma+\mu} (1 - e^{-(h+\sigma+\mu)\tau}).$$

Hence, the expected number of infected current partners, given n susceptible current partners at the start of the infectious life of the man, is

$$\int_{\tau=0}^{\infty} \frac{hn}{h+\sigma+\mu} (1 - e^{-(h+\sigma+\mu)\tau}) \mu e^{-\mu\tau} d\tau$$
$$= \frac{hn}{h+\sigma+\mu} \left( 1 - \frac{\mu}{h+\sigma+2\mu} \right)$$
$$= \frac{hn}{h+\sigma+2\mu}.$$
(3.5)

Again, keep in mind Remark 3.2.

The probability that a man has n+1 partners, n = 1, 2, ..., given that he has at least one partner, is given by  $\frac{2p_{n+1}^*}{1-2p_0^*}$ ; see also (3.4). Therefore, the expected number of current partners a man infects equals

$$\begin{split} \sum_{n=1}^{\infty} \frac{2p_{n+1}^*}{1-2p_0^*} \frac{hn}{h+\sigma+2\mu} &= \frac{h}{h+\sigma+2\mu} \frac{1}{1-2p_0^*} \left( \sum_{n=2}^{\infty} 2np_n^* - \sum_{n=2}^{\infty} 2p_n^* \right) \\ &= \frac{h\big( \left(1-2x^*-2p_1^*\right) - \left(1-2p_0^*-2p_1^*\right) \right)}{(h+\sigma+2\mu)(1-2p_0^*)} \\ &= \frac{h}{h+\sigma+2\mu} \frac{2p_0^*-2x^*}{1-2p_0^*}. \end{split}$$

This expected number is always strictly larger than zero.

Now, we have to calculate the expected number of infectees among the new partners, i.e. the partners arriving after the start of the man's infectious period. Again assume  $L = \tau$ , with  $\tau \in [0, \infty)$ . Women arrive according to a Poisson stream with rate  $\rho X^*$ . In order for an arriving woman to become a partner, her arrival time T must be  $t < \tau$ , with  $t \in (0, \tau)$ . Given that a woman arrives before the death of the husband, the arrival point will be a random point within his life, i.e. the arrival time T is uniformly distributed with the life length interval  $(0, \tau)$ :

$$\mathbb{P}(t \le T \le t + dt | L = \tau) = \frac{dt}{\tau}, \quad t \le \tau,$$

and the conditional probability is zero if  $t > \tau$ . Suppose a new partner arrives at time t and  $L = \tau$ . The probability the partner gets infected is given by

$$\mathbb{P}(X_1 = \min\{X_1, X_2, X_3\}, X_1 < \tau - t) = \frac{h}{h + \sigma + \mu} \left(1 - e^{-(h + \sigma + \mu)(\tau - t)}\right).$$

The probability the partner gets infected, given L = x, is then

$$\int_{t=0}^{\tau} \frac{1}{x} \frac{h}{h+\sigma+\mu} (1 - e^{-(h+\sigma+\mu)(\tau-t)}) dt$$
  
=  $\frac{h}{h+\sigma+\mu} - \frac{h}{\tau(h+\sigma+\mu)^2} (1 - e^{-(h+\sigma+\mu)\tau}) =: \eta(\tau).$ 

Since new partners arrive according to a Poisson process with rate  $\rho X^*$ , the probability that *n* partners,  $n = 1, 2, \ldots$ , arrive in the time interval  $(0, \tau)$  is given by

$$\frac{(\rho X^*\tau)^n}{n!}e^{-\rho X^*\tau},$$

and each of these n partners has probability  $\eta(\tau)$  of acquiring the infectious disease. Therefore, the expected number of secondary cases among the new partners is equal to

$$\begin{split} &\int_{\tau=0}^{\infty} \sum_{n=1}^{\infty} n \frac{(\rho X^* \tau)^n}{n!} e^{-\rho X^* \tau} \eta(\tau) \mu e^{-\mu \tau} d\tau \\ &= \int_{\tau=0}^{\infty} \rho X^* \tau \eta(\tau) \mu e^{-\mu \tau} d\tau \\ &= \frac{\rho X^* h}{\mu (h + \sigma + \mu)} - \frac{\rho h}{(h + \sigma + \mu)^2} - \frac{\rho h \mu}{(h + \sigma + \mu)^2 (h + \sigma + 2\mu)} \\ &= \frac{\rho X^* h}{\mu (h + \sigma + 2\mu)}. \end{split}$$

As in the intuitive approach, we see that this expected number of secondary cases among the new partners is independent of the number of current wives. Based on our modelling assumptions, this independence is exactly what we would like.

The total number of secondary cases one typical newly infected man can make at the beginning of the epidemic is therefore

$$R_m = \frac{h}{h+\sigma+2\mu} \frac{2p_0^* - 2x^*}{1-2p_0^*} + \frac{\rho X^* h}{\mu(h+\sigma+2\mu)}.$$
(3.6)

We see that this expression is the same as what we derived earlier with the intuitive approach. We see that  $R_m$  only depends on the fraction of single men and women in the population. Indirectly, we also see the mean star size  $\mathbb{E}(S)$  to play a role in this expression as we have found  $\mathbb{E}(S) = 1 - 2x^*$  in (2.24).

Recall the expression for  $x^*$  and  $R_f$  (see (2.16) and (3.2)). We see that

$$\frac{\rho X^*}{\mu} = \frac{\rho N_m^*(\sigma + \mu)}{\mu(\rho N_m^* + \sigma + 2\mu)} = R_f.$$

Hence the expected number of new wives an infectious man infects is the same as the expected number of men an infectious woman infects (at the beginning of an epidemic)  $R_f$ .

## **3.3.3** $R_0$ revisited

The expression for  $R_0$  is now found by combining the pieces of Subsections 3.3.2 and 3.3.1. Consider expressions (3.2) and (3.6). We find that

$$R_{0} = \sqrt{R_{f}R_{m}}$$

$$= \frac{h}{h+\sigma+2\mu}\sqrt{\left(\frac{2p_{0}^{*}-2x^{*}}{1-2p_{0}^{*}}+\frac{\rho X^{*}}{\mu}\right)\frac{\rho N_{m}^{*}(\sigma+\mu)}{\mu(\rho N_{m}^{*}+\sigma+2\mu)}} \qquad (3.7)$$

$$= \frac{h}{h+\sigma+2\mu}\sqrt{\left(\frac{2p_{0}^{*}-2x^{*}}{1-2p_{0}^{*}}+\frac{\rho N_{m}^{*}(\sigma+\mu)}{\mu(\rho N_{m}^{*}+\sigma+2\mu)}\right)\frac{\rho N_{m}^{*}(\sigma+\mu)}{\mu(\rho N_{m}^{*}+\sigma+2\mu)}}.$$

We now have to show that this is indeed the threshold value, i.e. we have to show that  $R_0 < 1$  if and only if the infection-free state is asymptotically stable and  $R_0 > 1$  if and only if the infection-free state is unstable. However, we do not manage to provide this proof in this thesis and therefore leave it as an open problem.

Before we will concern ourselves with describing our thoughts on this problem in Section 3.5, we will derive a different threshold quantity for the infection model, denoted  $\tilde{R}_0$ . The derivation of this quantity is simpler than is the case for  $R_0$  in the sense that we need less steps to arrive at it. It also allows us to get rid of square root in the expression. But really, it is just another way to of bookkeeping. In Section 3.5 we will show a simple relation between the two threshold parameters  $R_0$  and  $\tilde{R}_0$ .

## 3.4 Another threshold

In this section we will derive a threshold quantity different from  $R_0$ , and we will denote this with  $\tilde{R}_0$ . We will be able to find that  $\tilde{R}_0$  satisfies the equivalence  $R_0 = 1$  if and only if  $\tilde{R}_0 = 1$ , and  $R_0 > 1$  if and only if  $\tilde{R}_0 > 1$ . This at least does not discard  $R_0$  or  $\tilde{R}_0$  as a threshold quantity.

We make the standard assumptions concerning the pair-formation process and the infection process at the beginning of an epidemic, which we have written down explicitly in Sections 3.3.1 and 3.3.2. Infectious men and women do not encounter any other infectious individuals except for their epidemiological parents or children. In case of infectious women, they may also see other epidemiological siblings if she is still in the star with her epidemiological parent. But, as the transmission can occur only by heterosexual contact, this does not influence the expected number of secondary cases an infectious woman at the beginning of an epidemic can create. There is an infinite supply of susceptibles for these infectious individuals at the beginning of the epidemic.

Start with one newly infected single woman. We count the number of infectious single women caused by this woman. These secondary cases of infectious single women can be considered as 'indirect' epidemiological children of the initial infectious woman as we are considering a heterosexual population. The initial infectious single woman may infect her husbands she acquires from the susceptible population. In turn, these men may infect a certain number of women. We count these infectious women that also become single. Let's denote this quantity with  $\widetilde{R}_0$ .

We determine  $\tilde{R}_0$  in the following way. If the woman acquires a man, then this man has probability

$$\frac{h}{h+\sigma+2\mu}$$

of becoming infected by this infectious woman. The probability that this newly infected man has n wives is given by (3.4), n = 1, 2, ... Indeed, this probability does not depend on the man being infected. Therefore it is equal to the probability a man has n wives given that he has at least one wife, namely his epidemiological parent. Note that the number of wives the man has is always larger than zero as he has been infected by his partner and he is at the start of his infectious life. If the man has n wives, then one of them is infectious, namely his epidemiological parent, while the other n-1 are susceptible. Hence he can potentially infect n-1 of them, n = 1, 2, ... The expected number of wives he will infect in his life time is

$$\frac{h(n-1)}{h+\sigma+2\mu} + \frac{\rho X^* h}{\mu(h+\sigma+2\mu)}$$

where the first term is the expected number of current wives and the second term is the expected number of new wives he will infect; see also (3.5) for the derivation. The probability that one of his infectious wives becomes single again, and who may cause new infections in the population, is given by the probability that either the husband and wife separate or that the husband dies. Hence this is

$$\frac{\sigma + \mu}{\sigma + 2\mu}.$$

So the expected number of single infectious women that arise from the initial infective woman, given that the man she acquires has n partners at moment of infection, n = 1, 2, ... is

$$\frac{h}{h+\sigma+2\mu} \left(\frac{h(n-1)}{h+\sigma+2\mu} + \frac{\rho X^* h}{\mu(h+\sigma+2\mu)}\right) \frac{\sigma+\mu}{\sigma+2\mu}$$
$$= \left(\frac{h}{h+\sigma+2\mu}\right)^2 \left(n-1 + \frac{\rho X^*}{\mu}\right) \frac{\sigma+\mu}{\sigma+2\mu}.$$

By summing over all possibilities n = 1, 2, ..., weighted with the right probability (3.4), we obtain the expected number of single infectious woman that are caused by this initial infectious woman, given that she infects one man

$$\sum_{n=1}^{\infty} \frac{2p_n^*}{1 - 2p_0^*} \left(\frac{h}{h + \sigma + 2\mu}\right)^2 \left(n - 1 + \frac{\rho X^*}{\mu}\right) \frac{\sigma + \mu}{\sigma + 2\mu} = \left(\frac{h}{h + \sigma + 2\mu}\right)^2 \left(\frac{2p_0^* - 2x^*}{1 - 2p_0^*} + \frac{\rho X^*}{\mu}\right) \frac{\sigma + \mu}{\sigma + 2\mu}.$$
(3.8)

Here we have used  $\sum_{n=1}^{\infty} p_n^* = \frac{1}{2} - p_0^*$  and  $\sum_{n=1}^{\infty} np_n^* = \frac{1}{2} - x^*$ . A single infectious woman has an expected number of partners equal to

$$H = \frac{\rho N_m^*(\sigma + 2\mu)}{\mu(\rho N_m^* + \sigma + 2\mu)},$$
as we have seen in (2.26). Therefore, in order to obtain  $\tilde{R}_0$ , we need to multiply (3.8) with this factor H:

$$\widetilde{R}_{0} = \frac{\rho N_{m}^{*}(\sigma + \mu)}{\mu(\rho N_{m}^{*} + \sigma + 2\mu)} \left(\frac{h}{h + \sigma + 2\mu}\right)^{2} \left(\frac{2p_{0}^{*} - 2x^{*}}{1 - 2p_{0}^{*}} + \frac{\rho X^{*}}{\mu}\right).$$
(3.9)

We find that the following reasoning yields the same expression for  $\widetilde{R}_0$ . A woman infects a man with probability  $\frac{h}{h+\sigma+2\mu}$ . This typical man produces an expected number of  $R_m$  infectious women, with  $R_m$  given by (3.6). Each of these women separates him with probability  $\frac{\sigma+\mu}{\sigma+2\mu}$ . Taking into account the expected number of partners a woman acquires in her infectious life time, we find

$$\frac{\rho N_m^*(\sigma+\mu)}{\mu(\rho N_m^*+\sigma+2\mu)}\frac{h}{h+\sigma+2\mu}R_m\frac{\sigma+\mu}{\sigma+2\mu},$$

and this is the same expression that we found in (3.9).

Since we claim that this  $\tilde{R}_0$  is a threshold value, we need to prove that this is indeed the case, i.e.  $\tilde{R}_0 < 1$  if and only if the infection-free state is asymptotically stable and  $\tilde{R}_0 > 1$  if and only if the infection-free state is unstable.

By comparing  $R_0$ , the threshold quantity that we found in Section 3.3, with this new threshold quantity  $\tilde{R}_0$ , we find that we only need to prove the stability switch of the infection-free state for either of the two threshold quantities. In the next section we will compare  $R_0$  with  $\tilde{R}_0$ . Furthermore, we will describe our current thoughts on the problem of proving the stability switch. This problem remains an open problem in this thesis as we have not managed to provide a proof within the time available.

### **3.5** $R_0$ and $\widetilde{R}_0$ : threshold parameters

If we compare expression (3.7) for  $R_0$  and expression (3.9) for  $\widetilde{R}_0$ , then we immediately see that

$$R_0^2 = R_f R_m = \left(\frac{h}{h+\sigma+2\mu}\right)^2 \left(\frac{2p_0^* - 2x^*}{1-2p_0^*} + \frac{\rho X^*}{\mu}\right) \frac{\rho N_m^*(\sigma+\mu)}{\mu(\rho N_m^* + \sigma + 2\mu)} = \widetilde{R}_0.$$

In particular,  $R_0 = 1$  if and only if  $\tilde{R}_0 = 1$ . For any of the two expressions  $R_0$  and  $\tilde{R}_0$  we need to show the threshold behaviour, i.e. the stability of the infection-free state switches from asymptotically stable to unstable at  $R_0 = \tilde{R}_0 = 1$ .

Although this relation does not help us in proving that either of the two, and therefore both, is actually a threshold quantity, we do have consistency. If the two quantities do not satisfy the equivalence  $R_0 = 1$  if and only if  $\tilde{R}_0 = 1$ , then we would already have that one or both of the quantities can not be a threshold quantity.

Proving the threshold behaviour of (3.7) or (3.9) is a gap in the research that has yet to be filled. Due to lack of time it remains an open problem. In the rest of this section we will describe our thoughts and ideas on this problem.

Suppose we would have a finite-dimensional set of nonlinear ODEs describing an infection model. Then, in order to determine the threshold  $R_0$  of the system, we can do the following. Consider the infection subsystem and linearise around the infection-free steady state, which, as a rule, exists. This linearised system can be written in matrix notation

$$\frac{dx}{dt} = Ax.$$

We can write the matrix A as the sum of two matrices T and  $\Sigma$ , where T corresponds to transmissions and  $\Sigma$  to transitions. These matrices can then be used to determine  $R_0$ . Indeed, we have  $R_0 = \rho(-T\Sigma^{-1})$ ; see [27] for a proof of this relation.

This does not immediately generalise to our system of ODEs. First of all, we are now dealing with an infinite-dimensional system. Luckily, this is not necessarily a big problem, as we find a generalization of the above method in [28]. One will need to make sure that the linear operators A, T, and  $\Sigma$  satisfy certain assumptions, but then we still have that the infection-free state to be locally asymptotically stable if s(A) < 0 and equivalently  $\rho(-T\Sigma^{-1}) < 1$  [28, Theorem 3.16].

In case of a pair-formation process, in which we do not have instantaneous contacts, it is not clear how to choose which events correspond to transmissions and which to transitions. In principle, this does not matter in order to determine a threshold quantity. However, an interpretation for the spectral radius we find may be lacking. In particular, it may not necessarily be what we call  $R_0$ .

If we are able to find a threshold quantity using this method, and if we are able to connect its behaviour with that of the  $R_0$  or  $\tilde{R}_0$  that we have found before, then we are done. The problem is how to choose T and  $\Sigma$  in such a way that we can

- 1. invert the operator  $\Sigma$ ,
- 2. determine the spectral radius of  $-T\Sigma^{-1}$ ,

if any of that is at all possible.

We would like to reduce the system of differential equations as given on page 56. We can discard the infection-free stars  $x_0$  and  $p_n, 0, n = 0, 1, 2, ...$ , since we have assumed the pair-formation process to be in equilibrium. Can we further reduce the system?

Suppose we want to determine  $\hat{R}_0$  by means of the 'next-generation-matrixmethod'. Suppose we would start with an infectious single woman at the beginning of an epidemic. As unlikely it is for a susceptible man to acquire an infectious woman, it is even more unlikely that he acquires two or more infectious women. This reasoning has been used when deriving  $R_0$  and  $\tilde{R}_0$  from the interpretation. We would also like to see this reflected in the variables  $p_{n,k}$ ,  $n,k \geq 2, k \leq n$ , not to play a role in the linearized system. In other words, we would like to see that we only need the differential equations for  $x_1, p_{n,1},$  $n = 1, 2, \ldots$ , and  $q_{n,k}, k \leq n, k, n = 0, 1, \ldots$  in the linearization.

Linearisation of the differential equations of  $x_1$ ,  $p_{n,1}$ , n = 1, 2, ..., and  $q_{n,k}$ ,

 $k \leq n$  yields the following system (if we keep the same notation):

$$\begin{aligned} \frac{dx_1}{dt} &= -\left(\frac{1}{2}r + \mu\right)x_1 \\ &+ (\sigma + \mu)\left(\sum_{n=1}^{\infty}\sum_{k=1}^n kq_{n,k} + \sum_{n=1}^{\infty}p_{n,1} + \sum_{n=1}^{\infty}\sum_{k=2}^n kp_{n,k}\right), \\ \frac{dp_{1,1}}{dt} &= rx_1p_0^* - (rx^* + \sigma + 2\mu + h)p_{1,1} + (\sigma + \mu)(p_{2,1} + 2p_{2,2}), \\ \frac{dp_{n,1}}{dt} &= rx^*p_{n-1,1} + rx_1p_{n-1}^* - (rx^* + (\sigma + \mu)n + \mu + h)p_{n,1} \\ &+ (\sigma + \mu)(np_{n+1,1} + 2p_{n+1,2}), \end{aligned}$$

for n = 2, 3, ...

$$\begin{aligned} \frac{dq_{0,0}}{dt} &= -(rx^* + \mu)q_{0,0} + (\sigma + \mu)(q_{1,0} + q_{1,1}),\\ \frac{dq_{n,0}}{dt} &= rx^*q_{n-1,0} - (rx^* + (\sigma + \mu)n + \mu + hn)q_{n,0} \\ &+ (\sigma + \mu)((n+1)q_{n+1,0} + q_{n+1,1}), \end{aligned}$$

for n = 1, 2, ...

$$\frac{dq_{n,n}}{dt} = -(rx^* + (\sigma + \mu)n + \mu)q_{n,n} + (\sigma + \mu)((n+1)q_{n+1,n+1} + q_{n+1,n}) + h(q_{n,n-1} + np_{n,n}),$$

for n = 1, 2, ...

$$\begin{aligned} \frac{dq_{n,k}}{dt} &= rx^* q_{n-1,k} - (rx^* + (\sigma + \mu)n + \mu + h(n-k))q_{n,k} \\ &+ (\sigma + \mu)((n+1-k)q_{n+1,k} + (k+1)q_{n+1,k+1}) \\ &+ h((n-k+1)q_{n,k-1} + k\boldsymbol{p_{n,k}}), \end{aligned}$$

with k < n, n, k = 1, 2, ... We see the  $p_{n,k}$  to still be present in the above linearization. So is there a reasoning that makes the  $p_{n,k}$  disappear? Perhaps we need a more refined argument to eliminate the  $p_{n,k}$ , k > 1.

Let's also consider the linearisation of the differential equations of  $p_{n,k}$ ,  $n, k > 1, k \le n$ .

$$\frac{dp_{n,n}}{dt} = -(\rho x^* + (\sigma + \mu)n + \mu + hn)p_{n,n} + (\sigma + \mu)((n+1)p_{n+1,n+1} + p_{n+1,n}),$$

for n = 2, 3, ..., and

$$\frac{dp_{n,k}}{dt} = \rho x^* p_{n-1,k} - (\rho x^* + (\sigma + \mu)n + \mu + hk)p_{n,k} + (\sigma + \mu)((n+1-k)p_{n+1,k} + (k+1)p_{n+1,k+1})$$

for k < n, n, k = 2, 3, ... We see that the above system is independent of  $x_1$ ,  $q_{n,k}$ , and  $p_{n,1}$  (we see that in the differential equation for  $p_{n,k}$ , k > 1,  $p_{m,l}$  does not play a role with l < k.)

We could call 'transmission events' to be the transitions from state  $p_{n,1}$  to  $q_{n,1}$  (susceptible man gets infected by his infectious wife) and the transitions from state  $q_{n,k}$  to  $x_1$  (infectious woman becomes single again after a marriage with either her epidemiological parent or child). All other transitions will then fall under the 'transition events'. The exact details on how we can determine  $R_0$  from this distinction between transmission and transition events is not entirely clear. In any case it does not seem to be straightforward.

These are our thoughts on the problem of proving the stability switch so far. Since the interpretation allowed us to derive an expression (3.7), we are quite convinced that the stability switch does occur at  $R_0 = 1$  with  $R_0$  given by (3.7).

### 3.6 Monogamy vs polygyny

We conclude this chapter by comparing the infection spread in a population with a pair-formation process as described in Chapter 2 to the infection spread in a population which is completely monogamous, i.e. the individuals in the population have sequential partnerships only.

This comparison can be done by comparing e.g. the endemic level in both populations, the time it takes to converge to the endemic equilibrium, the expected number of secondary cases one 'typical' infectious individual causes at the beginning of the epidemic, etc. We will do the latter, i.e. we will compare the basic reproduction numbers of the two populations with different sexual behaviour. Let's reserve  $R_0$  for expression (3.7), the basic reproduction number of the polygynous population, while we let  $R_0^M$  denote the basic reproduction number of the monogamous population.

First, let us consider the polygynous population. Consider expressions (3.2) and (3.6). They have the factor  $h/(h + \sigma + 2\mu)$  in common. Since  $(2p_0^* - 2x^*)/(1 - 2p_0^*)$  is always strictly larger than zero we see that  $R_m > R_f$ . This means that, at the beginning of an epidemic, an infectious man causes, on average, more secondary cases than an infectious woman.

Does this mean that there are more infectious women than infectious men in equilibrium? Not necessarily. We would need information about the endemic equilibrium to make a statement about this, something we do not have. However, we would expect there to be an asymmetry in the fraction of infectious men and infectious women in equilibrium due to the asymmetry of the pair-formation process.

Do we expect  $R_0$  of the polygynous population to be always greater than  $R_0^M$  in a monogamous population? One might be inclined to say this is indeed the case. Women have the same role if we compare the women in the monogamous population to the women in the polygynous population: both may only have one husband at a time. Therefore, one may be tempted to conclude that, at the beginning of an epidemic, an infectious woman in the polygynous population causes on average the same number of secondary cases as an infectious woman in the monogamous population. Since an infectious man in the polygynous population causes more secondary cases than an infectious woman, i.e.  $R_m > R_f$ , one would conclude that  $R_0 > R_0^M$ . However, this all depends on the assumptions we make. For example, although women are only allowed one husband at the time in both the polygynous and the monogamous population, there is a difference in the pair formation rate

since we derived the pair-formation function from the mass-action principle. Suppose that in both populations the per pair formation rate is given by  $\rho$ . In the polygynous population, women can choose a husband among all men, so single women acquire a partner at rate  $\rho N_m^*$ . In the monogamous population, women can only choose a husband from the pool of Ssingle men, which limits their choice, and single women acquire a partner at rate  $\rho N^* \bar{y}$ , where  $N^* \bar{y}$ denotes the number of single men in the monogamous population in steady state.

Now let's consider a heterosexual population that practises monogamy: men and women are both allowed at most one partner at the time. In contrast to the polygynous population, this means that men and women are equal (as far as their role in the pair-formation process is concerned).

We make assumptions similar to the assumptions in Chapter 2, and let m (of marriage),  $\sigma$ , B, and  $\mu$  denote the per pair formation rate, the separation rate, the population birth rate, and the death rate, respectively. Note that we have used the same notation as in Chapter 2 except for the per pair formation rate, which we have denoted with  $\rho$  in the polygynous population. Of course this has been done intentionally, to make life easier when gauging the two models.

Introduce the following variables for the model describing the pair-formation process in a monogamous population.

- x: the fraction of single women,
- y: the fraction of single men
- p: the fraction of pairs.

Consistency requires

$$x + y + 2p = 1,$$
  
$$x + p = y + p = \frac{1}{2}$$

We have the following set of ODEs describing the model.

$$\frac{dx}{dt} = \frac{\mu}{2} - mN^*xy + (\sigma + \mu)p - \mu x, 
\frac{dy}{dt} = \frac{\mu}{2} - mN^*xy + (\sigma + \mu)p - \mu y, 
\frac{dp}{dt} = mN^*xy - (\sigma + 2\mu)p,$$
(3.10)

with  $N^* = \frac{2B}{\mu}$  the equilibrium population size. Note that

$$\frac{d}{dt}(x+y+2p) = \mu - \mu(x+y+2p) = 0.$$

In order to find the steady state  $(\bar{x}, \bar{y}, \bar{p})$  of the system we note that  $x = y = \frac{1}{2} - p$ . In order to find  $(\bar{x}, \bar{y}, \bar{p})$  we set dp/dt = 0 and solve the quadratic equation

$$mN^* \left(\frac{1}{2} - p\right)^2 - (\sigma + 2\mu)p = 0 \tag{3.11}$$

in p. We find

$$\bar{x} = \bar{y} = \frac{\sqrt{\mu(\sigma + 2\mu)(4Bm + \mu(\sigma + 2\mu))} - \mu(\sigma + 2\mu)}{4Bm},$$
$$\bar{p} = \frac{2Bm + \mu(\sigma + 2\mu) - \sqrt{\mu(\sigma + 2\mu)(4Bm + \mu(\sigma + 2\mu))}}{4Bm}.$$

Note that  $\bar{x}, \bar{y}, \bar{p} \ge 0$  for all parameter values  $B, \mu, m, \sigma$ .

We will assume that the pair-formation process is in steady state when introducing an infection in the population (as we have done for the polygynous population).

Consider two heterosexual populations of equal size  $N^*$  and an equal number of men and women  $\frac{1}{2}N^*$ . Suppose one of these populations practises monogamy, i.e. individuals have sequential partnerships only. We describe this sexual behaviour with the set of ODEs as given in (3.10). The other population is asymmetric in its sexual behaviour if we consider men and women: this population has a sexual network with star-shaped components as described in Chapter 2. We want to compare the two epidemic models by comparing the basic reproduction numbers. In order to do so we need to gauge the models.

Suppose we would gauge the two models by equating the total number of sexual partnerships in the two populations. In the monogamous population, the total number of sexual partnerships is given by  $\bar{p}N^*$ , i.e. the total number of pairs. In the polygynous population we find the total number of sexual partnerships (in steady state) to be

$$\left(\frac{1}{2} - x^*\right)N^* = \frac{B\rho}{2(B\rho + \mu(\sigma + 2\mu))}N^*$$

Indeed, the number of sexual partnerships is equal to the number of women in a sexual partnership, i.e. the number of non-single women (recall Section 2.4.2).

We may equate the total number of sexual partnerships by assuming the separation and death rate to be the same in the two populations, and choose the per pair formation rate m in the monogamous population in the right way. Hence we solve

$$\bar{p} = \frac{1}{2} - x^*$$

for m. This yields

$$m = \frac{\rho(B\rho + \mu(\sigma + 2\mu))}{\mu(\sigma + 2\mu)} = \frac{\rho}{2x^*},$$

if we simply use the expressions for  $x^*$  (see (2.16)) and  $\bar{p}$  that we have calculated before. We can also find the appropriate m as follows. We have  $\bar{p}$  such that it satisfies (3.11), i.e.  $mN^*(1/2-\bar{p})^2 - (\sigma+2\mu)\bar{p} = 0$ . Since we equate the total number of partnerships in both populations, we want m such that

$$mN^*(x^*)^2 - (\sigma + 2\mu)\left(\frac{1}{2} - x^*\right) = 0.$$

If we let  $m = \rho/(2x^*)$ , then we find

$$\frac{\rho}{2}N^*x^* - (\sigma + 2\mu)\left(\frac{1}{2} - x^*\right),\,$$

and this is always equal to zero since  $x^*$  solves (2.15), which is the equation we find above except for a minus sign (recall that we have defined r as  $\rho N^*$ in (2.15)).

Now that we have found the expression for m that makes sure that the number of sexual partnerships in the monogamous and polygynous population is the same, we can consider the expected number of partners a single individual in the monogamous population has in its lifetime. This expected number is given by

$$Q^M = \frac{mN^*\bar{x}(\sigma+2\mu)}{\mu(mN^*+\sigma+2\mu)}.$$

This expression is the same as (2.26), except for the fact that single women (men) in the monogamous population may only choose a partner from the population of single men (women), hence the factor  $N^*\bar{x}$  (=  $N^*\bar{y}$ ) rather than  $N_m^* = \frac{1}{2}N^*$ in the polygynous population. If we use  $\bar{x} = \frac{1}{2} - \bar{p} = x^*$ , then we can simplify  $Q^M$  to be

$$Q^{M} = \frac{\frac{1}{2}\rho N^{*}(\sigma + 2\mu)}{\mu(\frac{1}{2}\rho N^{*} + \sigma + 2\mu)} = H = W,$$

i.e. the expected number of partners of a single individual in the monogamous population equals the expected number of partners of a single individual in the polygynous population.

Note that the expected duration of one partnership and the expected life length are given by  $1/(\sigma + 2\mu)$  and  $1/\mu$ , respectively, so these quantities are the same in both populations.

We introduce the infection in the monogamous population using the same assumptions as in Chapter 3. We again let h denote the transmission rate. In case of a monogamous population we do not have an asymmetry between men and women. Therefore  $R_m^M = R_f^M$ , where  $R_m^M (R_f^M)$  denotes the expected number of secondary cases one infectious man (woman) creates at the beginning of the epidemic in a monogamous population, with

$$R_m^M = R_f^M = \frac{mN^*\bar{x}h(\sigma+\mu)}{\mu(mN^*\bar{x}+\sigma+2\mu)(h+\sigma+2\mu)}$$

This expression is derived in the same way we derived the expression for  $R_f$  in Section 3.3.1, only now the rate at which an infectious single man acquires a partner is  $mN^*\bar{x}(=mN^*\bar{y})$ .

The basic reproduction number  $R_0^M$  is given by

$$R_0^M = R_f^M$$

If we now use  $m = \rho/(2x^*)$  and  $\bar{x} = x^*$ , then we see that

$$R_0^M = R_f,$$

with  $R_f$  the basic reproduction number for an infectious woman in the polygynous population (see (3.2) for its expression). We have already observed that  $R_m > R_f$ . Therefore

$$R_0 = \sqrt{R_m R_f} > R_f = R_0^M,$$

i.e. the basic reproduction number is always larger in the polygynous population than in the monogamous population.

We have decided to adjust the per pair formation rate m in the monogamous population to match the total number of sexual partnerships with that of the monogamous population. This is not the only choice we could have made, i.e. there is no canonical choice to solve  $1/2 - x^* = \bar{p}$ . Note that equating the total number of sexual partnerships means that there are as many single women in the monogamous population as there are in the polygynous population. However, there are more single men in the polygynous population than there are in the monogamous population  $(p_0N^* \text{ and } \bar{y}N^*, \text{ respectively}).$ 

Our decision of adjusting m changed the per pair formation rate in the monogamous model such that the total pair formation rate equals the pair formation rate for women in the polygynous model, i.e. the rate a single individual acquires a new partner. Since we let the expected duration of a partnership and the expected life length to be the same in both models, the expected number of partners of a single individual is also the same in both models. As the infectivity is chosen to be h in both models, the probability of infection in a partnership with one susceptible and one infectious partner is  $h/(h + \sigma + 2\mu)$  in both populations.



**Figure 3.2:** Comparing  $R_0$  (purple dashed line) and  $R_0^M$  (orange solid line) as functions of the infectivity h. The remaining parameters are chosen as  $\rho = 1/3000000$ ,  $\sigma = 1/1000$ ,  $\mu = 1/9120$ ,  $B = \frac{1}{2}\mu N_0$  with  $N_0 = 10000$ . This means that the average life length is  $1/\mu \approx 25$  years, the average duration of a partnership is  $1/(\sigma + 2\mu) \approx 2.25$  years, and the average number of partners of a single individual is  $Q^M = H = W \approx 1.35$ . The number of sexual partnerships is given by  $\bar{p}N^* \approx 602.2$  (so the majority of the population is single in both populations with a larger number of single men in the polygynous population). We see that  $R_0$  and  $R_0^M$  are increasing functions of h (as to be expected),  $R_0 > R_0^M$ , and  $R_0 > 1$  for  $h \gtrsim 0.0038$ ,  $R_0^M > 1$  for  $h \gtrsim 0.0053$ .

We have that infectious individuals in the monogamous model cause, on average, the same number of secondary cases as the infectious women in the polygynous model (at the beginning of an epidemic). At the same time, infectious men in the polygynous population produce, on average, a larger number of secondary cases. In the situation we investigated, the star-shaped components do not provide a protective effect compared to the sequential partnerships. Indeed, we always have  $R_0 > R_0^M$  and it is possible that an infection becomes endemic in the polygynous population  $(R_0 > 1)$ , while that same infectious disease dies out in the monogamous population  $(R_0^M < 1)$ ; see Figure 3.2 for an example. Based on our assumptions and models, we conclude that, from the viewpoint of the virus at the beginning of the epidemic, the practice of polygyny is beneficial compared to the practice of monogamy.

We have compared the basic reproduction numbers of two populations with a different sexual network. One should keep in mind that the basic reproduction number gives us information about the growth of an epidemic at the beginning of the epidemic (when almost all individuals are susceptible) on a generation basis. We can not use  $R_0$  and  $R_0^M$  to make statements about the initial growth in real time. For this we would need the exponential growth rate or Malthusian parameter (which is denoted with r in [26]). We can also not use  $R_0$  and  $R_0^M$  to gain information about the endemic levels. Suppose  $R_0$  and  $R_0^M$  are both larger than 1, so the infectious disease can become endemic in both the polygynous and monogamous population. Even though  $R_0 > R_0^M$ , this does not imply that the endemic level in the polygynous population is larger than that in the monogamous population.

One should be careful when making a statement such as 'polygyny has a protective effect'. First of all, compared to what kind of population? Is it a monogamous population with the same kind of sexual behaviour (i.e. the same expected number of partners, expected life length, etc.) and an equal number of sexual partnerships in total, like we have done in this section? Or is it because populations that practice polygyny are different from a cultural and a social point of view? Secondly, is polygyny protective because of the the initial growth of an epidemic on a generation basis or in real time, or is it protective on the endemic level? For example, if one studies the correlation between HIV prevalence and polygyny in 34 sub-Saharan African countries [13], then are the areas one compares in the same stage of the epidemic? In some areas, HIV may already be endemic, while the epidemic is still growing in other areas. We do not find any assumptions about this in [13].

We have shown in this section that, given our models and assumptions, we find  $R_0 > R_0^M$ . To conclude, there is no simple yes or no answer to the question: 'Does polygyny have a protective effect?' One should always be careful to consider the (implicit) assumptions that one makes.

## Chapter 4

## Discussion

There are quite a few extensions or adjustments we can make to the dynamic sexual network or the infectious-diseases model that we presented in Chapters 2 and 3. Some have already been discussed briefly in the main text. We mention the most interesting extensions for future work.

#### Simplifying reality with a mathematical model

We are able to describe a dynamic sexual network with a system of ODEs that we can analyse mathematically. Assumptions that we have made about this network corresponds to a greatly simplified picture of reality.

The simplification has both advantages and disadvantages. The disadvantage is of course that we do not include a very detailed description of reality, even in cases we know it could be important. The advantage of the relatively simple models we have developed is that they are analytically tractable. Furthermore, there are only few parameters included in the models. It is probably possible to estimate the pair-formation parameters from data obtained on sexual behaviour, e.g.  $1/\mu$ , the mean number of years an individual is sexually active. Medical investigators have investigated the probability of transmitting HIV in one sexual act, and such numbers can be found in literature, e.g. [24].

A more practically inclined researcher will probably wonder about this lack of data in this research. We could have used data in e.g. our investigation of the steady states of the pair-formation model by estimating the model parameters  $\rho$ ,  $\sigma$ ,  $\mu$ , and B from data on sexual behaviour in different populations. This would have allowed us to see to what extent the model agrees with reality; see also Section 2.4.3 for discussion of estimating the parameters of the model. However, one needs to keep in mind that data on this topic is often flawed. For example, individuals may be under- or over reporting the number of sexual partners they have (had).

As we have also noted in Section 2.4.3, the numerical investigation that we have performed on the sexual network is quite limited (and the numerical values assigned to the parameters have been chosen quite arbitrarily). It would be interesting to extend this investigation and better understand e.g. the distribution  $(2p_j^*)_j$ . Among others we may estimate the parameters  $B, \mu, \rho, \sigma$  from actual data. Will we then still find a reasonable distribution  $(2p_j^*)_j$ ?

The disadvantage of simplifying reality we have mentioned is not entirely a

disadvantage. The simplification of reality that we have made can still result in a model that is able to describe the most important features that we also observe from reality. The limited numerical exploration of the steady state of the pair-formation model in Section 2.4.3 shows us results for the sexual network that are not in total disagreement with reality, e.g.  $(2p_j^*)_j$ , the distribution of the number of wives a man has.

#### **Open problems**

In the text we have pointed out some issues that we still need to deal with. In this chapter we recall the most important ones.

In Section 3.2 we have briefly discussed the existence and uniqueness of an endemic steady state of the system describing the infectious-disease model. We have not given a proof of this.

Having more information about the endemic steady state is also of interest to us. We would like to know how the infectives are distributed among the two sexes. We have seen in Section 3.6 that  $R_m \ge R_f$ . Does this also result in a higher endemic level for women than for men? Also, it would be interesting to compare the endemic level in a polygynous population with that in a monogamous population. This would allow us to understand the effect of the polygynous structure on the infectious disease compared to a monogamous population.

In Chapter 3 we have derived explicit expressions for  $R_0$  and  $R_0$  using the interpretation for the model. A problem that still needs to be solved is to prove that the thresholds  $R_0$  and  $\tilde{R}_0$  are indeed threshold values, i.e. do we indeed have a stability switch of the disease-free equilibrium at  $R_0 = \tilde{R}_0 = 1$ ? Intuitively, this should be true. However, the main text lacks a mathematical proof for it. We have described our thoughts on this problem in Section 3.5, in the future we hope that these will lead to an actual proof.

Concerning the  $R_0$  there is more work that we can do. Something we have not done yet is seeing how  $R_0$  behaves as a function of the different parameters, e.g. how does  $R_0$  change if we change the duration of one partnership?

We have not used the description of the infection model as given on page 56 and only given this description. Concerning our analysis of the infection model in Chapter 3 we may as well have omitted this description. However, it will be useful when proving  $R_0$  is a threshold, which is still one of the goals. We could also use it to do simulations and gain insights on the endemic state. Often it is not straightforward how to translate a model to a simulation program. There is a risk of (accidentally) creating dependencies where one does not want them. In that case, it will not be clear how to interpret simulation results and how general the conclusions are that are obtained for a particular choice of parameter values. The fact that we are able to describe the infection model as a set of ODEs probably allows us to do simulations in a more straightforward way.

#### Maximum number of wives

One of the assumptions we have made on the pair-formation process is that there is no limit on the number of wives a man may have. How does the system change if we put a bound on the number of wives one man may have? Suppose we would put a restriction on the maximum number of wives per man; a restriction we find in real life imposed by e.g. the law. We also see this reflected in survey data about marriages. In this case the model description is then no longer infinite dimensional, but this does not necessarily make it easier to analyse.

The number of differential equations needed to describe the models when assuming a maximum star size grows quite fast. If we would have a maximum star size of two, then we have four equations describing the pair formation process (using the variables  $x, p_0, p_1$ , and  $p_2$ ). We already need fourteen equations for the description of the infection model (equations for  $x_0, x_1, p_{0.0}, q_{0.0}, p_{1.0},$  $q_{1,0}, p_{1,1}, q_{1,1}, p_{2,0}, q_{2,0}, p_{2,1}, q_{2,1}, p_{2,2}$ , and  $q_{2,2}$ ), which we are able to reduce to at least ten by eliminating the equations for  $x_0$ ,  $p_{0,0}$ ,  $p_{1,0}$ , and  $p_{2,0}$ . For a maximum star size of three we need five equations to describe the pair-formation process and 22 equations to describe the infection model, which we can again reduce, this time to a maximum of seventeen equations. It is not necessarily easier to analyse such a large finite-dimensional system compared to the infinitedimensional system introduced in this text. Our life does become easier if we consider the existence and uniqueness of solutions to the finite-dimensional system of ODEs describing the model. However, a bound on the star size creates all kinds of dependencies between wives of one husband. We will not be able to derive an explicit expression for  $R_0$  using the interpretation when such dependencies exist, as we did in Chapter 3. There may be other difficulties involved.

#### Variable infectivity

A different extension we should explore is the following. In the model for the infectious disease we have assumed an infectious individual to be equally infectious in his entire infectious life. What changes if we would assume this infectivity to be variable? The infectiousness of HIV in one infectious individual is known to change over time [24, 25], as we have discussed in Section 3.1.

Roughly, we can subdivide it in the acute primary phase in the first few weeks following the initial infection, the chronic phase that can last for years, and the AIDS phase as the last disease stage. The infectivity is relatively high in the acute phase and low in chronic phase before the infectivity increases again when one develops AIDS. Researchers hypothesize that this variable infectivity in combination with concurrent partnerships, i.e. partnerships that overlap in time, allow for HIV prevalence to be higher in populations that are monogamous [11, 12, 29]. In this short window of the acute phase, infectious individuals are exposed to more potential infectees than is the case without concurrency. In this case, there is less time between an individual becoming infected and transmitting it to another partner. This compared to individuals who are monogamous, in which case an infected individual must first separate from its epidemiological parent before it can transmit the infection to a new partner. Often, new transmissions will then occur in the chronic phase rather than the acute phase.

Some believe that concurrency is a major contributor to the spread of HIV in sub-Saharan Africa. Typically, individuals in this region report a number of sexual partners in their life time similar to heterosexual individuals in western countries. However, many individuals in sub-Saharan Africa seem to have these sexual partnerships overlapping in time, contrary to the western population [11]. In order to see the effect of this variable infectivity on a polygamous population we should incorporate this in our model. We have compared the basic reproduction number of an infection model in a monogamous population with our polygynous population in Section 3.6. We did this by taking two populations of equal size and an equal number of sexual partnerships (by choosing the per pair formation rate of the monogamous population, and keeping all other parameters the same as in the polygynous population). This resulted in a larger basic reproduction number in the polygynous population than in the monogamous population. If we would include the variable infectivity in both populations rather than a constant infectivity, then we would expect this difference in the basic reproduction numbers to grow. Indeed, infectious men in the acute phase of the infection in the polygynous population would in general have more susceptible wives than do infectious men in the monogamous population. Then what about the endemic levels? How will they change when incorporating variable infectivity?

#### Polygyny vs monogamy

To end this thesis, we want to mention the discussion at the end of Section 3.6. Based on the assumptions we have made about the infection model for the monogamous and polygynous population we have found  $R_0 > R_0^M$ . Therefore, we see that the star-shaped components of our sexual network do not provide any protection to the infectious disease in the initial phase of an epidemic on a generation basis compared to a strictly monogamous population. In future work, we could extent the comparison between the two populations and also consider e.g. the endemic levels and see whether polygyny does or does not provide a protective effect in this stage of the epidemic. Either way, one should always keep in mind that any conclusions drawn in this text are based on the models we have considered. One should always be careful to consider the (implicit) assumptions.

# Bibliography

- R. Anderson and R. May, Population biology of infectious diseases. Springer-Verlag, 1982.
- [2] F. Brauer, "Mathematical epidemiology is not an oxymoron," BMC Public Health, vol. 9, p. Suppl 1, 2009.
- [3] R. Ross, The prevention of malaria. London: Murray, 2nd ed., 1911.
- [4] N. Bacaër, A short history of mathematical population dynamics. Springer, 2011.
- [5] C. Fraser, S. Riley, R. M. Anderson, and N. M. Ferguson, "Factors that make an infectious disease outbreak controllable," *PNAS*, vol. 101, pp. 6146–6151, 20 April 2004.
- [6] N. M. Ferguson, D. A. T. Cummings, C. Fraser, J. C. Cajka, P. C. Cooley, and D. S. Burke, "Strategies for mitigating an influenza pandemic," *Nature*, vol. 442, pp. 448–452, 27 July 2006.
- [7] P. S. Bearman, J. Moody, and K. Stovel, "Chains of affection: the structure of adolescent romantic and sexual networks," AJS, vol. 110, pp. 44–91, July 2004.
- [8] N. T. J. Bailey, The mathematical theory of infectious diseases. New York: Hafner, 1957.
- [9] S. Helleringer and H. Kohler, "Sexual network structure and the spread of HIV in Africa: evidence from Likoma Island, Malawi," *AIDS*, vol. 21, no. 17, pp. 2323–2332, 2007.
- [10] Joint United Nations Programme on HIV/AIDS (UNAIDS), "Data and analysis." Available at: http://www.unaids.org/en/dataanalysis/. [Accessed March 2011].
- [11] D. T. Halperin and H. Epstein, "Concurrent sexual partnerships help to explain Africa's high HIV prevalence: implications for prevention," *Lancet*, vol. 364, pp. 4–6, 3 July 2004.
- [12] T. Mah and D. Halperin, "Concurrent sexual partnerships and the HIV epidemics in Africa: evidence to move forward," *AIDS Behav*, vol. 14, pp. 11–16, 2010.
- [13] G. Reniers and S. Watkins, "Polygyny and the spread of hiv in sub-saharan africa: a case of benign concurrency," *AIDS*, vol. 24, no. 2, pp. 299–307, 2010.
- [14] M. Kretzschmar and K. Dietz, "The effect of pair formation and variable infectivity on the spread of an infection without recovery," *Math Biosci*, vol. 148, pp. 83–113, 1998.

- [15] H. R. Thieme, "Global stability of the endemic equilibrium in infinite dimension: Lyapunov functions and positive operators," J Differ Equations, vol. 250, pp. 3772–3801, 2011.
- [16] M. Martcheva and H. Thieme, Structured population models in biology and epidemiology, ch. Infinite ODE System Modeling Size-Structured Metapopulations, Macroparasitic Diseases, and Prion Proliferation, pp. 51–113. No. 1936 in Lecture notes in mathematics. Mathematical Biosciences subseries, Springer-Verlag, 2008.
- [17] G. Sell and Y. You, Dynamics of Evolutionary Equations. No. 143 in Applied Mathematical Sciences, Springer, 2002.
- [18] A. Pazy, Semigroups of linear operator and applications to partial differential equations, vol. 44 of Applied mathematical sciences. New York: Springer, 1983.
- [19] K. Engel and R. Nagel, One-parameter semigroups for linear evolution equations. New York: Springer, 2000.
- [20] R. H. Martin, Nonlinear operators and differential equations in Banach spaces. New York: John Wiley & Sons, 1976. VI.4 one-sided estimates: Lemma 4.1 (ii).
- [21] NIST Handbook of mathematical functions, ch. 8 Incomplete gamma and related functions. NIST and Cambridge University Press, 2009.
- [22] M. Martcheva, H. Thieme, and T. Dhirasakdanon, "Kolmogorov's differential equations and positive semigroups on first moment sequence spaces," *J Math Biol*, vol. 53, pp. 642–671, 2006.
- [23] T. Mitsunaga, A. Powell, N. Heard, and U. Larsen, "Extramarital sex among Nigerian men. Polygyny and other risk factors.," J Acquir Immune Defic Syndr, vol. 39, pp. 478 – 488, August 2005.
- [24] S. Pinkerton, "Probability of HIV transmission during acute infection in Rakai, Uganda," AIDS Behav, vol. 12, pp. 677–684, 2008.
- [25] M. J. Wawer, R. H. Gray, N. K. Sewankambo, D. Serwadda, X. Li, O. Laeyendecker, N. Kiwanuka, G. Kigozi, M. Kiddugavu, T. Lutalo, F. Nalugoda, F. Wabwire-Mangen, M. P. Meehan, and T. C. Quinn, "Rates of hiv-1 transmission per coital act, by stage of hiv-1 infection, in rakai, uganda," *J Infect Dis*, vol. 191, pp. 1403–1409, 2005.
- [26] O. Diekmann, J. A. P. Heesterbeek, and T. Britton, "Mathematical epidemiology of infectious diseases. model building, analysis and interpretation." Unpublished, 2010.
- [27] O. Diekmann, J. A. P. Heesterbeek, and M. G. Roberts, "The construction of next-generation matrices for compartmental epidemic models," J R Soc Interface, vol. 7, pp. 873–885, 2010. online first (5 Nov 2009).
- [28] H. R. Thieme, "Spectral bound and reproduction number for infinitedimensional population structure and time heterogeneity," SIAM J Appl Math, vol. 70, no. 1, pp. 188–211, 2009.
- [29] J. Eaton, T. Hallett, and G. Garnett, "Concurrent sexual partnerships and primary hiv infection: a critical interaction," *AIDS Behav*, vol. 15, pp. 687–692, 2010.