

# Modeling macroparasite diseases dynamics

## Modelado de la dinámica de enfermedades por macroparásitos

Gonzalo Maximiliano Lopez<sup>1,2</sup> and Juan Pablo Aparicio<sup>1,3</sup>

<sup>1</sup> Instituto de Investigaciones en Energía no Convencional, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Salta, Av. Bolivia 5150, 4400 Salta, Argentina

<sup>2</sup> Departamento de Matemática, Facultad de Ciencias Exactas, Universidad Nacional de Salta, Av. Bolivia 5150, 4400 Salta, Argentina

<sup>3</sup> Simon A. Levin Mathematical, Computational and Modeling Sciences Center, Arizona State University, PO Box 871904 Tempe, AZ 85287-1904, USA

Reception date of the manuscript: dd/mm/aaaa

Acceptance date of the manuscript: dd/mm/aaaa

Publication date: dd/mm/aaaa

---

**Abstract**— In this work we present a general framework for the modeling of the transmission dynamics of macroparasites which do not reproduce within the host like *Ascaris lumbricoides*, *Trichuris trichiura*, *Necator americanus* y *Ancylostoma duodenale*. The basic models are derived from general probabilistic models for the parasite density-dependent mating probability. Here we considered the particular, and common case, of a negative binomial distribution for the number of parasites in hosts. We find the basic reproductive number and we show that the system exhibit a saddle-node bifurcation at some value of the basic reproduction number. We also found the equilibria and basic reproduction number of a model for the more general case of heterogeneous host populations.

**Keywords**—Basic reproductive number; Macroparasite; Mathematical modeling; Negative binomial distribution; Saddle-node bifurcation

---

**Resumen**— En este trabajo presentamos un marco general para el modelado de la dinámica de transmisión de macroparásitos que no se reproducen dentro del hospedador como *Ascaris lumbricoides*, *Trichuris trichiura*, *Necator americanus* y *Ancylostoma duodenale*. Los modelos básicos se derivan de modelos probabilísticos generales para la probabilidad de apareamiento denso-dependiente del parásito. Aquí consideramos el caso particular y común de una distribución binomial negativa para el número de parásitos en hospedadores. Encontramos el número reproductivo básico y mostramos que el sistema presenta una bifurcación nodo silla en algún valor del número reproductivo básico. También encontramos los equilibrios y el número básico de reproducción de un modelo para el caso más general de poblaciones heterogéneas de hospedadores.

**Palabras clave**—Bifurcación nodo silla; Distribución binomial negativa; Macroparásito; Modelo matemático; Número reproductivo básico

---

### INTRODUCTION

Mathematical models play an important role in understanding the transmission and impact of macroparasite diseases control measures (Anderson and May, 1992; Anderson et al., 2014; Truscott et al., 2016).

The first works on the theory of helminth infection was published in the 1960s by Tallis and Leyton by developing stochastic models of nematode parasite transmission in sheep and cattle (Leyton, 1968; Tallis and Leyton, 1966, 1969).

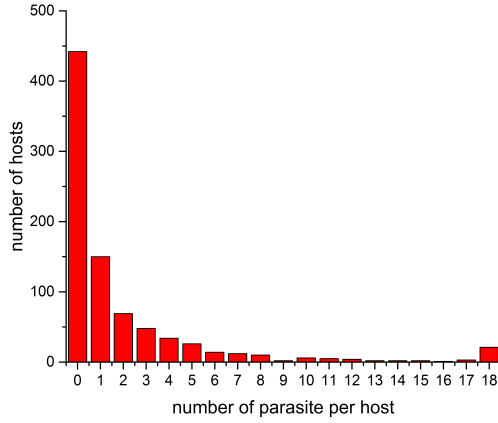
Simultaneously Macdonald show that a consequence of sexual reproduction of distributed parasites within individual hosts was the inability to generate fertile infectious material when prevalence is low (Macdonald et al., 1965).

Anderson and May then introduced much more general

descriptions of helminth population dynamics. They developed descriptions for a model based on host age, distribution of parasite numbers per host, density dependence of egg production, and sexual mating functions that depend on parasite distribution and reproductive habits (Anderson and May, 1982, 1992).

In this article we develop an analytical framework to describe the transmission dynamics of most macroparasite infections. We first describe the dynamics of infection transmission by macroparasites. We then present two deterministic models for these transmission dynamics, the first for a homogeneous host community and the second for a heterogeneous host community.

In both models, reproductive characteristics of the parasite are considered, such as egg production and mating probabi-



**Figure 1:** Distribution of *Ascaris lumbricoides* parasite numbers per host in a study in rural populations in Korea (Seo et al., 1979).

Most hosts are uninfected or infected with a low burden of parasites while few are infected by large numbers of parasites.

lity, both modeled by the density-dependent fecundity of the parasite and the distribution of parasites per host, which we assume to be negative binomial.

For both models we present the calculations of the equilibrium values and the basic reproduction number  $R_0$  defined for the case of macroparasites as the average number of new parasite offspring caused by a typical parasite, from one generation to the next. Finally for the homogeneous model we show that it has a saddle-node bifurcation.

## GENERAL FRAMEWORK

Microparasite diseases are usually modeled using compartmental models. After infection, microparasite population may rapidly grow into the host. This intra-host parasite dynamics determines the level of infectiousness of the individual. In a simple compartmental model like the *SIR*-model all the susceptible individuals are grouped in one class of size  $S$ , all the infected and infectious individuals in a class of size  $I$  and all the recovered individuals in a class of size  $R$ . Many refinements are possible, but the evolution of the parasite population within the host it is not considered or very simplified (for models including intra-host population dynamics see for example Gandolfi et al. (2015)). The most common refinement consists in dividing infected individuals in two classes, exposed (those infected but not infectious yet) and infectious which leads to the well known *SEIR* type models.

For most macroparasites the situation is completely different as these type of parasites do not reproduce within the host. Most infected individuals have few macroparasites with a non-bell shaped distribution (see Figure 1) where few individuals concentrate most of the parasites in the host population (Seo et al., 1979; Lopez and Aparicio, 2022b). Negative binomial distributions usually provide a good description of the data. On the other hand, there is no host-to-host transmission of macroparasites as life cycle completes in the environment (from where host get infected).

Therefore the number of infected hosts it is not a representative variable of the parasite burden. Simple models for macroparasites consider the evolution of the mean burden of

parasite within the population as well as the environmental parasite reservoir (which is composed by eggs or larvae). From the mean burden, the total parasite population is easily estimated.

## A BASIC MODEL

### Model structure

The model presented in this paper is based on a model developed by Anderson and May (Anderson and May, 1992, 1985). The conceptual framework of parasite transmission dynamics is conceptualized as a population of mature parasites within human hosts and a population of infective stages (eggs or larvae) found in the environment (reservoir). Hosts can become infected by contact with the infective stages and can contaminate the environment with infective stages.

In a simple model for transmission dynamics of macroparasites in a population (where host demography is ignored) of size  $N$  of hosts the dynamic variables are the mean parasite burden of the population,  $m$ , and the infective stages in the environment formed by eggs or larvae,  $\ell$ .

In the following we will sketch the procedure to find parasite-related parameters from a statistical-probabilistic model for the parasite population.

The environmental parasite reservoir, composed by eggs or larvae, increases due to the contribution of adult parasites within the hosts. As most host harbor only few parasites, only hosts with at least one female and one male parasites will contribute with fertilized eggs to the reservoir. We will consider that the random variable  $W$ , the number of parasites in a host follow a negative binomial distribution. Therefore, the probability of observing  $n$  parasites in a host is

$$P(W = n) = \frac{\Gamma(k+n)}{\Gamma(n+1)\Gamma(k)} \left(\frac{k}{m+k}\right)^k \left(\frac{m}{m+k}\right)^n \quad (1)$$

where  $\Gamma$  is the gamma function,  $m$  is the mean value (the mean population parasite burden) and  $k$  the shape parameter, where the variance increases with the reciprocal of  $k$  as  $\sigma^2 = m + m^2/k$ . The term  $\frac{k}{m+k}$  is the probability of success and  $\frac{m}{m+k}$  is the probability of failure.

Mean egg production depends of the number of parasites within the host, it is a density-dependent process. A simple model for the average female fecundity of a female parasite in competition with  $n - 1$  parasites is given by

$$\lambda(n) = \lambda_0 z^{n-1}$$

where  $z = e^{-\gamma}$ , and  $\gamma$  is a parameter quantifying the intensity of the competition (Hall and Holland, 2000).

Using the parasite host distribution (1) we may compute the mean egg production per host as (Lopez and Aparicio, 2022a)  $\lambda_0 \alpha m \psi(m, k, z)$  where  $\alpha$  is the fraction of female parasites in a host and  $\psi$  is given by

$$\psi(m, k, z) = \left[1 + (1 - z) \frac{m}{k}\right]^{-(k+1)} \quad (2)$$

is known as the effective contribution of the female population to the parasite reservoir (in the form of eggs or larvae) (Churcher et al., 2006).

However only hosts with at least one female and one male parasites will effectively contribute to the parasite's reservoir

by laying fertilized eggs. Therefore the mean fertilized egg production per host is

$$\lambda_0 \alpha m \psi(m, k, z) \phi(m, k, z) \quad (3)$$

where  $\phi(m, k, z)$  is the mating probability for the negative binomial distribution computed in Lopez and Aparicio (2022a)

$$\phi(m, k, z) = 1 - \left[ \frac{1 + (1 - \alpha z) \frac{m}{k}}{1 + (1 - z) \frac{m}{k}} \right]^{-(k+1)} \quad (4)$$

Therefore the mean fertilized egg contribution to the environmental reservoir per host and per unit of time is  $\rho \lambda_0 \alpha m \psi(m, k, z) \phi(m, k, z)$  where  $\rho$  is the host's own contribution rate and the total contribution of eggs to the reservoir per unit of time of a host population  $N$  is  $\rho \lambda_0 \alpha m \psi(m, k, z) \phi(m, k, z) N$ . The population of eggs or larvae in the environment ( $\ell$ ) also decreases due to egg/larval mortality ( $\mu_\ell$ ) or due to host infection at the rate  $\beta \ell$  per host. Therefore the dynamics of the reservoir is given by

$$\frac{d\ell}{dt} = \rho \lambda_0 \alpha m \psi(m, k, z) \phi(m, k, z) N - \mu_\ell \ell - \beta N \ell \quad (5)$$

Finally, the dynamics for the mean burden  $m$  is obtained as follow. Parasites are taken from the environment at the rate  $\beta N \ell$  and therefore the mean burden increases at the rate  $\beta N \ell / N = \beta \ell$ . Parasites within the host die at the rate  $\mu_p$  and hosts at the rate  $\mu_h$  (killing all their parasites). Thus, the dynamics of  $m$  is

$$\frac{dm}{dt} = \beta \ell - (\mu_h + \mu_p) m \quad (6)$$

The system (5)-(6) is the basic model of the transmission dynamics of macroparasites in a population of hosts.

### Equilibria and basic reproduction number

From the equation (5) we obtain that in equilibrium

$$\ell^* = \frac{\rho N \lambda_0 \alpha}{(\mu_\ell + \beta N)} m \psi(m) \phi(m) \quad (7)$$

and substituting (7) in the equation (6) we get the following equation for the dynamics of  $m$

$$\frac{dm}{dt} = (\mu_h + \mu_p) [R_0 \psi(m) \phi(m) - 1] m \quad (8)$$

where the parameter  $R_0$  is the basic reproductive number which, by definition, is independent of the effects of density-dependence and mating probability

$$R_0 = \frac{N \lambda_0 \alpha \rho \beta}{(\mu_\ell + \beta N)(\mu_h + \mu_p)} \quad (9)$$

where for a large  $N$  value  $R_0 \approx \frac{\lambda_0 \alpha \rho}{(\mu_h + \mu_p)}$ .

Therefore from the equation (8) we can obtain the equilibrium condition for the mean parasite burden

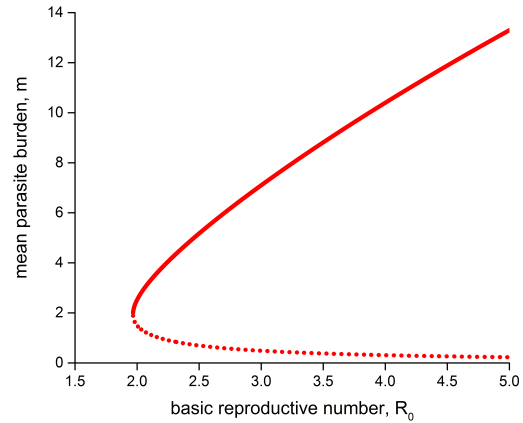
$$\psi(m^*, k, z) \phi(m^*, k, z) = 1/R_0 \quad (10)$$

By bifurcation analysis we obtain that the system of the equations (5)-(6) present a saddle-node bifurcation. The bifurcation point is  $(\tilde{m}, \tilde{R}_0)$  where

$$\tilde{m} = \frac{k \left( \frac{1-\alpha z}{1-z} \right)^{\frac{1}{k+2}} - k}{(z-1) \left( \frac{1-\alpha z}{1-z} \right)^{\frac{1}{k+2}} + (1-\alpha z)} \quad (11)$$

$$\tilde{R}_0 = [\psi(\tilde{m}; k, z) \phi(\tilde{m}; k, z)]^{-1}$$

As shown in the next section, the system undergoes a saddle-node bifurcation and therefore, for  $R_0 > \tilde{R}_0$  there are three equilibria (see Figure 2). One of the solutions is the **stable** endemic equilibrium which is an attractor for a range of values of  $R_0 > \tilde{R}_0$ . The other solution is an **unstable** equilibrium and corresponds to a repulsor in the phase plane, that is, a barrier where values of  $m(t)$  above the unstable equilibrium are attracted towards the stable equilibrium and values of  $m(t)$  below the unstable equilibrium are attracted to the **extinction** equilibrium  $m^* = 0$ , which is the trivial solution of the equation (8).



**Figure 2:** Bifurcation diagram generated by eq. (10), parameter values  $\alpha = 0,5$ ,  $k = 0,7$  and  $z = 0,93$ . The solid line and dotted line correspond to the stable and unstable branch, respectively, of the saddle-node bifurcation.

To develop better control measures for macroparasitic diseases, it is necessary to know the relative importance of the different factors responsible for transmission.

The transmission of macroparasitic diseases is related to the value of  $R_0$ . To predict which parameters have a higher impact on  $R_0$ , we must perform a sensitivity analysis on  $R_0$ .

The elasticity index or normalized sensitivity index measures the relative change of  $R_0$  with respect to a parameter  $x$ , denoted by  $\Gamma_x^{R_0}$ , and defined as

$$\Gamma_x^{R_0} = \frac{\partial R_0}{\partial x} \frac{x}{R_0} \quad (12)$$

The sign of  $\Gamma_x^{R_0}$  tells whether  $R_0$  correlates positively or negatively with the parameter  $x$ ; whereas its magnitude determines the relative importance of the parameter.

For this model, the calculation of the elasticity indices are given by

$$\Gamma_{\lambda_0}^{R_0} = \Gamma_{\alpha}^{R_0} = \Gamma_{\rho}^{R_0} = 1, \quad \Gamma_{\mu_h}^{R_0} = -\frac{\mu_h}{\mu_h + \mu_p}, \quad \Gamma_{\mu_p}^{R_0} = -\frac{\mu_p}{\mu_h + \mu_p} \quad (13)$$

if  $\frac{1}{\mu_h} \gg \frac{1}{\mu_p}$ , then  $\Gamma_{\mu_p}^{R_0} \approx -1$  and  $\Gamma_{\mu_h}^{R_0} \approx 0$ .

Therefore the more sensitive parameters for  $R_0$  are  $\lambda_0$ ,  $\alpha$ ,  $\rho$  and  $\mu_p$ . However,  $\lambda_0$  and  $\alpha$  correspond to parameters related to the life-cycle of the parasite which are quite difficult to modify, so a control measure for macroparasitic diseases should target to the reduction of  $\rho$  and/or the increase of  $\mu_p$ .

Therefore, we can conclude from this analysis that the reduction of  $R_0$  is possible by reducing the egg contribution from the hosts to the reservoir, for example, by building latrines in the host community or by increasing parasite mortality, for example, through the application of periodic and specific antiparasitic treatments.

### Saddle-node bifurcation

We will show that the basic model developed in the section presents a saddle-node bifurcation. Assuming the parasite reservoir at equilibrium (7) the system reduces to the one-dimensional system

$$\frac{dm}{dt} = (\mu_h + \mu_p) [R_0 \psi(m) \phi(m) - 1] m$$

which we compactly denote by  $\frac{dm}{dt} = f(m, R_0)$ . A necessary condition for the existence of a saddle-node bifurcation at  $(\tilde{m}, \tilde{R}_0)$  is

$$\begin{aligned} f(\tilde{m}, \tilde{R}_0) &= 0 \\ \frac{\partial f}{\partial m}(\tilde{m}, \tilde{R}_0) &= 0 \end{aligned} \quad (14)$$

where the first of these conditions is the equilibrium condition (10) of the system

$$\psi(\tilde{m}; k, z) \phi(\tilde{m}; k, z) = 1/\tilde{R}_0,$$

and so we get the following equilibrium condition for  $\tilde{m}$

$$\frac{\partial}{\partial m} \psi(\tilde{m}; k, z) \phi(\tilde{m}; k, z) = 0 \quad (15)$$

The value of  $m$  corresponding to this last condition is

$$\tilde{m} = \frac{k \left( \frac{1-\alpha z}{1-z} \right)^{\frac{1}{k+2}} - k}{-(1-z) \left( \frac{1-\alpha z}{1-z} \right)^{\frac{1}{k+2}} + (1-\alpha z)} \quad (16)$$

and its corresponding basic reproductive number is

$$\tilde{R}_0 = [\psi(\tilde{m}; z, k) \phi(\tilde{m}; z, k)]^{-1} \quad (17)$$

A sufficient condition for the existence of a saddle-node bifurcation at  $(\tilde{m}, \tilde{R}_0)$  is

$$\begin{aligned} \frac{\partial f}{\partial R_0}(\tilde{m}, \tilde{R}_0) &\neq 0 \\ \frac{\partial^2 f}{\partial m^2}(\tilde{m}, \tilde{R}_0) &\neq 0 \end{aligned} \quad (18)$$

By a Taylor series expansion of the function  $f$  in a neighborhood of  $(\tilde{m}, \tilde{R}_0)$ , the equation (8) is left

$$\begin{aligned} \frac{dm}{dt} &= f(\tilde{m}, \tilde{R}_0) + (m - \tilde{m}) \frac{\partial f}{\partial m} \Big|_{(\tilde{m}, \tilde{R}_0)} + (R_0 - \tilde{R}_0) \frac{\partial f}{\partial R_0} \Big|_{(\tilde{m}, \tilde{R}_0)} \\ &\quad + \frac{1}{2} (m - \tilde{m})^2 \frac{\partial^2 f}{\partial m^2} \Big|_{(\tilde{m}, \tilde{R}_0)} + \dots \end{aligned} \quad (19)$$

Therefore locally at the point  $(\tilde{m}, \tilde{R}_0)$  the equation is of the form

$$\frac{dm}{dt} = A(R_0 - \tilde{R}_0) + B(m - \tilde{m})^2, \quad (20)$$

where the values  $A$  and  $B$  are

$$A = (\mu_h + \mu_p) \frac{\tilde{m}}{\tilde{R}_0}, \quad B = (\mu_h + \mu_p) R_0 \tilde{m} \frac{\partial^2 F}{\partial m^2}(\tilde{m}), \quad (21)$$

with  $F(m) = \psi(m, z, k) \phi(m, z, k)$  which is the normal form of a saddle-node bifurcation.

## A HETEROGENEOUS MODEL

In this section we will consider the more general and realistic case for a host population  $H$ . Unlike the homogeneous model presented in the previous section, here we present a model that accounts for host population heterogeneity, where subpopulations  $H_i$  (e.g., age groups, risk groups, Anderson and May (1992); Anderson et al. (2014); Truscott et al. (2014)) have different infection risks. The dynamics of infection for the case of a heterogeneous population is described as follows

$$\begin{aligned} \frac{dm_i}{dt} &= \beta_i \ell - (\mu_h + \mu_p) m_i \\ \frac{d\ell}{dt} &= \lambda_0 \alpha \sum_i N_i \rho_i m_i F(m_i) - (\mu_\ell + \sum_i \beta_i N_i) \ell \end{aligned} \quad (22)$$

where the parameters that detail correspond to each subgroup  $H_i$

- $m_i$  is mean parasite burden,
- $\beta_i$  and  $\rho_i$  are the rate of contact (or exposure) and the rate contribution of a host to the reservoir  $L$ , respectively,
- $N_i$  is the number of host,

the rest of the parameters are defined as in the previous section.

### Equilibria and basic reproduction number

From the system (22) we obtain that in equilibrium

$$\ell^* = \frac{\lambda_0 \alpha}{(\mu_\ell + \sum_i N_i \beta_i)} \sum_i \rho_i N_i m_i F(m_i) \quad (23)$$

and substituting this in the rest of the equations of the initial system we obtain the following equation for the dynamics of the mean burden  $m_i$  of the subpopulation  $H_i$  of hosts

$$\frac{dm_i}{dt} = \beta_i \frac{\lambda_0 \alpha}{(\mu_\ell + \sum_j N_j \beta_j)} \sum_j N_j \rho_j m_j F(m_j) - (\mu_h + \mu_p) m_i \quad (24)$$

The mean burden  $m$  of the total host population  $H = \bigcup_i H_i$  is given by

$$m = \sum_i \pi_i m_i \quad (25)$$

where  $\pi_i$  is the portion of the population  $H$  corresponding to the subpopulation  $H_i$ , and which is described by

$$\frac{dm}{dt} = \sum_i N_i \beta_i \frac{\lambda_0 \alpha}{(\mu_\ell + \sum_j N_j \beta_j)} \sum_j \rho_j \pi_j m_j F(m_j) - (\mu_h + \mu_p) m \quad (26)$$

From this equation, the equilibrium mean parasite burden,  $m^*$ , for the total population is given by

$$\sum_i \pi_i \frac{\lambda_0 \alpha \rho_i}{(\mu_\ell + \sum_j N_j \beta_j)(\mu_h + \mu_p)} \left( \sum_j N_j \beta_j \right) F(m_i^*) m_i^* - m^* = 0 \quad (27)$$

This is not an explicit expression of the equilibria  $m_i^*$ . Therefore, the equilibrium value can only be solved numerically. An equilibrium condition for the mean burdens of each subpopulation  $H_i$  is given by

$$F(m_i^*) = \frac{1}{R_0^i}, \quad (28)$$

where we define the basic reproductive number of each subpopulation  $H_i$  by

$$R_0^i = \frac{\lambda_0 \alpha \rho_i}{(\mu_\ell + \sum_j N_j \beta_j)(\mu_h + \mu_p)} \left( \sum_j N_j \beta_j \right), \quad (29)$$

which is the number of adult females that are born of a adult female from a host in subpopulation  $H_i$  in the absence the effects of density-dependence and the mating probability. Note what for a large  $N$  value the reproductive number for each  $H_i$  is given by

$$R_0^i \approx \frac{\lambda_0 \alpha \rho_i}{(\mu_h + \mu_p)}, \quad (30)$$

where

Also for this equilibrium situation, we obtain that the mean parasite burden of each subpopulation  $H_i$  is given by

$$m_i^* = \frac{\beta_i}{\sum_j \pi_j \beta_j} m^*, \quad (31)$$

where

The general basic reproductive number  $R_0$  for the total population is given by

$$R_0 = \frac{\lambda_0 \alpha}{(\mu_\ell + \sum_j N_j \beta_j)(\mu_h + \mu_p)} \sum_i N_i \rho_i \beta_i \quad (32)$$

where we assume the absence the effects of density-dependence and the mating probability (Anderson and May, 1992), that is, we assume in the system (22) the function  $F$  equal to unity. A relationship between  $R_0$  and  $R_0^i$  is given by

$$R_0 = \frac{\sum_i N_i \beta_i R_0^i}{\sum_j N_j \beta_j} \quad (33)$$

therefore we get that  $\min R_0^i \leq R_0 \leq \max R_0^i$ , then we can interpret to  $R_0$  as an average value of the  $R_0^i$ .

## DISCUSSION AND CONCLUSIONS

In this work, we developed deterministic mathematical models for the transmission dynamics of macroparasite infections.

We show how fundamental parameters related to production of fertilized parasites eggs are estimated from statistical models for the distribution of parasites within hosts.

We considered both homogeneous and heterogeneous host communities. The analyzed models show that the basic reproduction number  $R_0$  strongly depends on the host egg contributions to the reservoir (which depend of the parameters

$\rho$ ,  $\alpha$ , and the parasite fecundity at low densities  $\lambda_0$ ), and on the parasite mortality ( $\mu_p$ ). Therefore, to achieve a reduction in  $R_0$  we must, for example, build latrines in the host community or implement regular and specific antiparasitic treatments.

For the homogeneous model we present a bifurcation analysis and show that this model exhibits a saddle-node bifurcation. The bifurcation parameter depends on the functions  $\psi$  and  $\phi$  which in turn depend on the assumed distribution of parasites (see Lopez and Aparicio (2022a)).

More refined models may be developed from the simple models presented here which may be useful in the design and evaluation of different control strategies.

## ACKNOWLEDGMENTS

This work was partially supported by grant CIUNSA 2018-2467. JPA is a member of the CONICET. GML is a doctoral fellow of CONICET.

## REFERENCES

- [1] Anderson, R. and May, R. (1982). "Population dynamics of human helminth infections: control by chemotherapy". *Nature*, 297(5867):557–563.
- [2] Anderson, R. and May, R. (1992). *Infectious diseases of humans: dynamics and control*. Oxford university press.
- [3] Anderson, R., Truscott, J., and Hollingsworth, T. (2014). "The coverage and frequency of mass drug administration required to eliminate persistent transmission of soil-transmitted helminths". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1645):20130435.
- [4] Anderson, R. M. and May, R. M. (1985). "Helminth infections of humans: mathematical models, population dynamics, and control". In: *Advances in parasitology*, volume 24, pages 1–101. Elsevier.
- [5] Churcher, T. S., Filipe, J. A., and Basáñez, M. G. (2006). "Density dependence and the control of helminth parasites". *Journal of animal ecology*, 75(6):1313–1320.
- [6] Gandolfi, A., Pugliese, A., and Sinisgalli, C. (2015). "Epidemic dynamics and host immune response: a nested approach". *Journal of mathematical biology*, 70(3):399–435.
- [7] Hall, A. and Holland, C. (2000). "Geographical variation in ascaris lumbricoides fecundity and its implications for helminth control". *Parasitology Today*, 16(12):540–544.
- [8] Leyton, M. (1968). "Stochastic models in populations of helminthic parasites in the definitive host, ii: sexual mating functions". *Mathematical Biosciences*, 3:413–419.
- [9] Lopez, G. M. and Aparicio, J. P. (2022a). "General model of sex distribution, mating probability and egg production for macroparasites with polygamous mating system". *arXiv preprint arXiv:2202.11552*.
- [10] Lopez, G. M. and Aparicio, J. P. (2022b). "Simple models for macroparasite distributions in hosts". *arXiv preprint arXiv:2202.11282*.
- [11] Macdonald, G. et al. (1965). "The dynamics of helminth infections, with special reference to schistosomes." *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 59(5):489–506.
- [12] Seo, B. S., Cho, S. Y., and Chai, J. Y. (1979). "Frequency distribution of ascaris lumbricoides in rural koreans with special reference on the effect of changing endemicity". *Korean J Parasitol*, 17(2):105–113.
- [13] Tallis, G. and Leyton, M. (1966). "A stochastic approach to the study of parasite populations". *Journal of Theoretical Biology*, 13:251–260.
- [14] Tallis, G. and Leyton, M. (1969). "Stochastic models of populations of helminthic parasites in the definitive host. i". *Mathematical Biosciences*, 4(1-2):39–48.
- [15] Truscott, J., Hollingsworth, T. D., and Anderson, R. (2014). "Modelling the interruption of the transmission of soil-transmitted helminths by repeated mass chemotherapy of school-age children". *PLoS neglected tropical diseases*, 8(12):e3323.
- [16] Truscott, J., Turner, H., Farrell, S., and Anderson, R. (2016). "Soil-transmitted helminths: mathematical models of transmission, the impact of mass drug administration and transmission elimination criteria". *Advances in parasitology*, 94:133–198.