Modeling of egg production and mating probability for helminth parasites

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Abstract

In the modeling of the transmission dynamics of helminthic parasites, the study of the reproductive characteristics of these parasites is essential.

The reproductive habits of macroparasite are important for the study of the dynamics of their transmission. For populations of parasites distributed by Poisson or negative binomial models, these habits have already been studied. However, other statistical models describe these populations, such as zero-inflated models, but where reproductive characteristics were not analyzed. Using an ar- bitrary model for the parasite population, we model the distribution of females and males per host, and from these we model the different reproductive variables such as the mean number of fertile females, the mean egg production, the mating probability, and mean fertilized egg production. We show that these variables change due to the effects of negative density-dependence fecundity, a characteristic of helminth parasites. We present the results obtained for particular models.

Keywords: Compound random variable; Macroparasites; Mating probability; Negative binomial distribution; Probability Model; Zero-inflated Model

Contents

1 Introduction

One of the most important factors in understanding the transmission dynamics of soil-transmitted helminths are reproductive behaviors.

Most helminths that infect humans are dioecious (separate sexes) and many are assumed to be polygamous (the presence of at least one male guarantee the fertility of all females present), but quantitative data are not available[3].

The production of offspring of these parasites is, in general, a function of their population size, the proportion of females, and their reproductive behavior and therefore developing mathematical models that allow understanding the distribution by sex (female and male) and the reproductive behavior of these parasites is important.

In a population where the distribution of parasites per host is described by a Poisson or a negative binomial statistical model, the distribution by sex was studied for the case of a sex ratio 1:1 in [17] and for a variable sex ratio in [16]. Also a dynamic model for the number of fertilized females is presented in [15].

In this work we present a generalization of what was developed by these previous works. To model the distribution by sex, we will assume an arbitrary model for the distribution of parasites per host and variable sex ratios. First we consider the case were the distribution of the total population is known, and therefore female and male host burden are not independent random variables. Later we will consider the case were these variables are independent.

We then calculated different reproductive variables such as mean number of fertile females, mean egg production, mating probability, and mean fertile egg production.

2 Distribution and abundance of parasites

- discutir la distribución de los parásitos que que presenta sobre-dispersión. binomial negativa como modelo estándar y mencionar los modelos inflados en cero

- discutir y dejar claro el sex ratio que usamos

The fractions of female and male parasites in a host are represented by α and β, respectively, where $\alpha + \beta = 1$. Then the ratio of males to females is given by $\beta/\alpha : 1$. Also if m is the mean burden of parasites, the mean number of female and male parasites are given by αm and βm respectively.

3 Parasite infection by egg ingestion

In this section, we consider that the infection by parasites occurs when a host ingests fertilized eggs of these parasites. This type of infection can occur when the host's contaminated hands are placed in the mouth or by consuming fruit and vegetables that have not been carefully cooked, washed, or peeled. The parasites responsible for this type of infection are the helminths, such as *Ascaris lumbricoides*, *Trichuris trichiura*, among others.

Since in this type of infection, the host can ingest one or more fertilized eggs. Then, the host can acquire one or more parasites, which can be male or female, depending on the sex ratio of the parasite. Therefore, when we analyze the variables "the number of male parasites per host" and "the number of female parasites per host", these variables cannot be independent.

In what follows, we develop the study some variables that intervene in the transmission dynamics of these parasitic infections, such as the mean number of fertile females per host, the mean number egg production per host, the mating probability, among others.

3.1 Distribution of parasites by sex

Let W be a random variable, the number of parasites per host, and F the number of female parasites per host. We propose that the distribution of female parasites per host is modeled by a compound random variable ([13]) and its probability generating function (pgf) is the function $G_W \circ G_B$, where G_B is the pgf of the Bernoulli distribution given by $G_B(s) = \beta + \alpha s$. Therefore F is given by $F = \sum_{i=1}^{W} Y_i$ where $Y_i \sim \mathrm{Ber}(\alpha)$, and its pgf is of the form

$$\begin{aligned} G_F(s) =& G_W(\beta + \alpha s) \\ =& \sum_{n \geq 0} \sum_{j=0}^{n} \Pr(W = n) \binom{n}{j} \alpha^j \beta^{n-j} s^j \end{aligned} \tag{1}$$

The first moments of F are

$$\mu_F = \alpha \mu_W \qquad \sigma_F^2 = \alpha^2 \sigma_W^2 + \alpha\beta\mu_W \tag{2}$$

The coefficient of dispersion, $D = \frac{\sigma_F^2}{\mu_F}$, is given by

$$D = \alpha \frac{\sigma_W^2}{\mu_W} + \beta$$

where $\frac{\sigma_W^2}{\mu_W}$ is the coefficient of dispersion of W. Therefore, if W is over-dispersed, so will F.

Similarly, if M is the number of male parasites per host, $M = W - F$ and therefore its mean and variance are $\mu_M = \beta\mu_W$ and $\sigma_M^2 = \beta^2\sigma_W^2 + \alpha\beta\mu_W$, respectively. By the definition F and M are dependent random variables.

falta decir algo de las distribuciones por sexo

We denoted by G to the pgf of the distribution of parasites per host G_W. Also, we denoted by $G(s;\theta)$ to $\sum_{n\geq 0} p(n;\theta)s^n$ where p is the probability mass function of the distribution of parasites per host and θ is a parameters vector. For example, θ may include the mean, m, of the distribution of parasites per host.

3.2 Fertilized female parasites

The parasites treated in this work present a polygamous mating system, it is conventionally assumed that a male parasite can fertilize all female parasites in the same host [16]. Since the term $\sum_{j=0}^{n-1} p_n \binom{n}{j} \alpha^j \beta^{n-j}$ is the probability of having at least one male parasite in a burden parasite of size n, we obtained the following result

Proposition 3.2.1. *The mean number of fertilized female parasites is given by*

$$\alpha m - \alpha G'(\alpha) \tag{3}$$

Proof. The presence of at least one male parasite in the host ensures the fertility of all females, so

$$\begin{aligned}\sum_{n\geq 1}\sum_{j=0}^{n-1} j p_n \binom{n}{j} \alpha^j \beta^{n-j} &= \sum_{n\geq 1} p_n \sum_{j=0}^{n-1} j \binom{n}{j} \alpha^j \beta^{n-j} \\ &= \sum_{n\geq 1} p_n (n\alpha - n\alpha^n)\end{aligned}$$

where the last line is obtained from the expression of the mean of $\mathrm{B}(n,\alpha)$,

$n\alpha = \sum_{j=0}^{n} j\binom{n}{j}\alpha^j\beta^{n-j}$. Therefore

$$\begin{aligned}\sum_{n\geq 1}\sum_{j=0}^{n-1} jp_n\binom{n}{j}\alpha^j\beta^{n-j} &= \alpha\sum_{n\geq 1} np_n(1-\alpha^{n-1}) \\ &= \alpha\left[\sum_{n\geq 1} np_n - \sum_{n\geq 1} n\alpha^{n-1}p_n\right] \\ &= \alpha m - \alpha G'(\alpha)\end{aligned}$$

□

On the other hand, if we consider the quotien between the mean number of fertilized female parasites per host, $\alpha m - \alpha G'(\alpha)$, and the mean number of female parasites per host, αm. We can obtain a simple expression for the mating probability of a female parasite as a function of the mean parasite burden m. Therefore, the mating probability of a female parasite that we denoted by ϕ is given by

$$\phi(m) = 1 - \frac{G'(\alpha; m)}{m} \tag{4}$$

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3.3 Density-dependent fecundity

In population ecology, density-dependent processes occur when population growth rates are regulated by population density.

In macroparasites life-cycles, density-dependent processes can influence parasite fecundity, establishment and survival within the host . In the case of soil-transmitted helminths, there is a density-dependent fecundity in which the weight of females and their egg production rates decrease as the parasite burden on the host increases [8, 21].

This negative density-dependence can be described mathematically by the negative exponential function

$$\lambda(n) = \lambda_0 \exp[-\gamma(n-1)] \tag{5}$$

where $\lambda(n)$ is the per capita female fecundity within a host with a parasite burden of size n, λ_0 is the intrinsic fecundity in absence of density-dependence effects and γ is the density-dependence intensity. A study of density-dependent effects for Ascaris *lumbricoides* is presented in [11].

To simplify notation in rest of the text we will express the female fecundity by $\lambda(n) = \lambda_0 z^{n-1}$ where $z = e^{-\gamma}$.

3.4 Egg production and mating probability

Due to the effects of density-dependent fecundity, the egg production per female decreases as the parasite burden in host increases. Therefore, if $j\lambda(n)$ is the egg production of j female parasites within a host with n parasites and $p_n\binom{n}{j}\alpha^j\beta^{n-j}$ is the probability of a host with n parasites having j female parasites. Then, we obtain the following result for the mean egg production per host

Proposition 3.4.1. *The mean egg production per host is given by*

$$\lambda_0\alpha G'(z) \tag{6}$$

Proof. We consider that all females present in the host can produce eggs according to their per-capita fecundity

$$\begin{aligned}
\sum_{n\geq 0}\sum_{j=0}^{n} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j} &= \lambda_0\sum_{n\geq 0}\sum_{j=0}^{n} jz^{n-1}p_n\binom{n}{j}\alpha^j\beta^{n-j} \\
&= \lambda_0\sum_{n\geq 0} z^{n-1}p_n\sum_{j=0}^{n} j\binom{n}{j}\alpha^j\beta^{n-j} \\
&= \lambda_0\sum_{n\geq 0} z^{n-1}p_n n\alpha \\
&= \lambda_0\alpha\sum_{n\geq 0} nz^{n-1}p_n \\
&= \lambda_0\alpha G'(z)
\end{aligned}$$

□

For the case of the mean fertilized egg production per host, we use the previous proof, but considering only the egg production by fertilized female parasites. Therefore, an expression for the mean fertilized egg production is given by

Proposition 3.4.2. *The mean fertilized egg production per host is given by*

$$\lambda_0\alpha G'(z)\left[1-\frac{G'(\alpha z)}{G'(z)}\right]$$

Proof.

$$
\begin{aligned}
\sum_{n\geq 0}\sum_{j=1}^{n-1} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j} &= \lambda_0\sum_{n\geq 0}\sum_{j=1}^{n-1} jz^{n-1}p_n\binom{n}{j}\alpha^j\beta^{n-j}\\
&= \lambda_0\sum_{n\geq 0} z^{n-1}p_n\sum_{j=1}^{n-1} j\binom{n}{j}\alpha^j\beta^{n-j}\\
&= \lambda_0\sum_{n\geq 0} z^{n-1}p_n(n\alpha - n\alpha^n)\\
&= \lambda_0\alpha\sum_{n\geq 0} nz^{n-1}p_n(1-\alpha^{n-1})\\
&= \lambda_0\alpha\left[\sum_{n\geq 0} nz^{n-1}p_n - \sum_{n\geq 0} n(\alpha z)^{n-1}p_n\right]\\
&= \lambda_0\alpha G'(z)\left[1-\frac{G'(\alpha z)}{G'(z)}\right]
\end{aligned}
$$

□

According to the results previously obtained, if we consider the quotien between the mean fertilized egg production and the mean egg production, we can obtain the probability of fecundity of the eggs or mating probability of female parasites, under the density-dependence effects. Therefore, we obtain the mating probability of a female parasite as a function of the mean parasite burden m by

Theorem 3.4.3. *The mating probabillity of a female parasite is given by*

$$\phi(m) = 1 - \frac{G'(\alpha z; m)}{G'(z; m)} \tag{7}$$

From this expression (7) we notice that for the case where there is no density-dependence ($z \approx 1$) this expression is equivalent to expression (4), therefore, this is a generalization of the mating probability obtained above.

3.5 An application for mean burden-based models for helminth infections

In deterministic population models based on the mean parasite burden for transmission dynamics of helminth infections such as [2, 3, 20], it is necessary to know the effective transmission contribution of the female population to the parasite reservoir (in form of eggs or larvae) [7, 8]. The effective transmission contribution is denoted by ψ and we can calculate it as follows [7, 8],

$$\psi = \frac{\sum_{n\geq 0}\sum_{j=1}^{n} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j}}{\sum_{n\geq 0}\sum_{j=0}^{n} jp_n\binom{n}{j}\alpha^j\beta^{n-j}} \tag{8}$$

where the negative density-dependence function $\lambda(n)$ is redefined as $\lambda(n)/\lambda_0$. This allows the function $\lambda(n)$ to have a maximum value of 1 and separate the density-independent term λ_0, from the density-dependent processes (n-dependent).

Using the results obtained in this work we can calculate this term ψ as a function of mean parasite burden m by

$$\psi(m) = \frac{G'(z;m)}{m} \tag{9}$$

Therefore, if we know distribution of parasites in hosts, we can calculate the mean egg production per host as

$$\lambda_0\alpha m\psi(m) = \lambda_0\alpha G'(z;m) \tag{10}$$

However, only hosts with at least one female parasite and one male parasite will effectively contribute to the parasite reservoir by producing fertilized (or infective) eggs. Then, the mean fertilized eggs production per host is (see, for example, [3])

$$\lambda_0\alpha m\psi(m)\phi(m) = \lambda_0\alpha G'(z;m)\left[1 - \frac{G'(\alpha z;m)}{G'(z;m)}\right] \tag{11}$$

where we assume that ψ and ϕ are functions of the mean parasite burden m.

3.6 Some examples

In this section we will consider the most common statistical models used to describe the distribution of parasites among hosts.

3.6.1 Poisson

A simple model for the distribution of parasites per host is the Poisson distribution [14],

$$\Pr(X = x) = \frac{m^x e^{-m}}{x!}, \tag{12}$$

where m is the mean parasite burden and its pgf is given by

$$G(s) = e^{m(s-1)} \tag{13}$$

For this parasite distribution the effective contribution of female parasites to the transmission cycle is given by (see eq (9))

$$\psi(m) = e^{m(z-1)} \tag{14}$$

Another important factor in parasite dynamics is the mating probability ϕ which is given by (see eq 7)

$$\phi(m) = 1 - e^{-mz\beta} \tag{15}$$

This expression of ϕ is a generalization for the mating probability obtained in the works [3, 16, 17].

3.6.2 Negative binomial

In most cases, soil-transmitted helminths, present a distribution of parasites per host that can be well described by a negative binomial distribution [5, 12, 18],

$$P(X = x) = \frac{\Gamma(k + x)}{\Gamma(x + 1)\Gamma(k)} \left(\frac{k}{k + m}\right)^k \left(\frac{m}{k + m}\right)^x \tag{16}$$

where m is the mean parasite burden and k is the inverse dispersion parameter of the parasites. The corresponding pgf is given by

$$G(s) = \left[1 - \frac{m}{k}(s - 1)\right]^{-k} \tag{17}$$

Therefore, the expression for ψ, the effective contribution, which is given by (see eq. (9))

$$\psi(m) = \left[1 - \frac{m}{k}(z - 1)\right]^{-(k+1)} \tag{18}$$

Finally the mating probability, ϕ, is given by (see eq. (7))

$$\phi(m) = 1 - \left[\frac{1 - \frac{m}{k}(\alpha z - 1)}{1 - \frac{m}{k}(z - 1)}\right]^{-(k+1)} \tag{19}$$

This expression of ϕ results in a generalization for the mating probability obtained in works [3, 16, 17].

3.6.3 Zero-inflated and hurdle Models

Other frequently used models are the zero-inflated and hurdle models (see for example [1, 9, 10, 22]). For a zero-inflated model, its probability mass function is

$$P(Y = y) = \begin{cases} \pi + (1-\pi)p_0 & y = 0 \\ \\ (1-\pi)p_y & y \neq 0 \end{cases}$$

where p is the probability mass function of a distribution with no excess of zero counts and G_X the corresponding pgf. Then the pgf of the zero-inflated distribution is

$$G_Y(s) = \pi + (1-\pi)G_X(s)$$

and the mean burden is

$$m_Y = (1-\pi)m_X$$

For this model the expression for ψ, the mean contribution per female parasite, which is given by

$$\psi = \frac{G_Y'(z)}{m_Y} = \frac{(1-\pi)G_X'(z; m_X)}{m_Y} = \frac{G_X'\left(z; \frac{m_Y}{1-\pi}\right)}{\frac{m_Y}{1-\pi}} \tag{20}$$

Finally the mating probability ϕ can be calculated by

$$\phi = 1 - \frac{G_Y'(\alpha z)}{G_Y'(z)} = 1 - \frac{G_X'\left(\alpha z; \frac{m_Y}{1-\pi}\right)}{G_X'\left(z; \frac{m_Y}{1-\pi}\right)} \tag{21}$$

A hurdle model is a two-part model, the first part, π, which is the probability of observing the zero value, and the second part which gives the probability of observing non-zero values. The use of hurdle models is often motivated by an excess of zeros in the data, which is not sufficiently accounted for in more standard statistical models [13]. For this model its probability mass function is given by

$$P(Y = y) = \begin{cases} \pi & y = 0 \\ \\ (1-\pi)\frac{p(y)}{1-p_0} & y \neq 0 \end{cases}$$

Its pgf G_Y and its mean are of the form

$$G_Y(s) = \pi + (1-\pi)\frac{G_X(s) - p_0}{1-p_0}$$
$$m_Y = (1-\pi)\frac{m_X}{1-p_0}$$

Therefore, the expresions for ψ and ϕ are given by

$$\begin{aligned}\psi &= \frac{G'_Y(z)}{m_Y} = \frac{\rho G'_X(z; m_X)}{m_Y} = \frac{G'_X\left(z; \frac{m_Y}{\rho}\right)}{\frac{m_Y}{\rho}} \\ \phi &= 1 - \frac{G'_Y(\alpha z)}{G'_Y(z)} = 1 - \frac{G'_X\left(\alpha z; \frac{m_Y}{\rho}\right)}{G'_X\left(z; \frac{m_Y}{\rho}\right)}\end{aligned} \tag{22}$$

where $\rho = \frac{1-\pi}{1-p_0}$.

3.6.4 Zero-inflated Poisson and zero-inflated negative binomial models

The negative binomial distribution is widely used to describe the distribution of parasites in hosts [9, 18]. However in many cases the negative binomial distribution (or other similar distributions) cannot account for the excess of zeros observed [9]. A solution to this problem are zero-inflated models which have been widely used in the last decade for parasite counting [1, 10, 22].

In Table 1 we present the expressions for the effective contribution and mating probability for the zero-inflated Poisson and zero-inflated negative binomial models.

Table 1: The Effective contribution ψ and the mating probability ϕ for zero-inflated Poisson (ZIPo) and zero-inflated negative binomial (ZINB) models.

Statistical model	effective contribution	mating probability
ZIPo	$\psi = \exp\left(\frac{m}{1-\pi}(z-1)\right)$	$\phi = 1 - \exp\left(-\frac{mz\beta}{1-\pi}\right)$
ZINB	$\psi = \left[1 - \frac{m}{k(1-\pi)}(z-1)\right]^{-(k+1)}$	$\phi = 1 - \left[\frac{1 - \frac{m}{k(1-\pi)}(\alpha z - 1)}{1 - \frac{m}{k(1-\pi)}(z-1)}\right]^{-(k+1)}$

In Figure 1 we show plots of the effective mean contribution (ψ) and the mating probability (ϕ) for all the distributions discussed above. We consider the parameters z =0.93, k =0.7, π =0.3, $\alpha = 0.574$ ([19]).

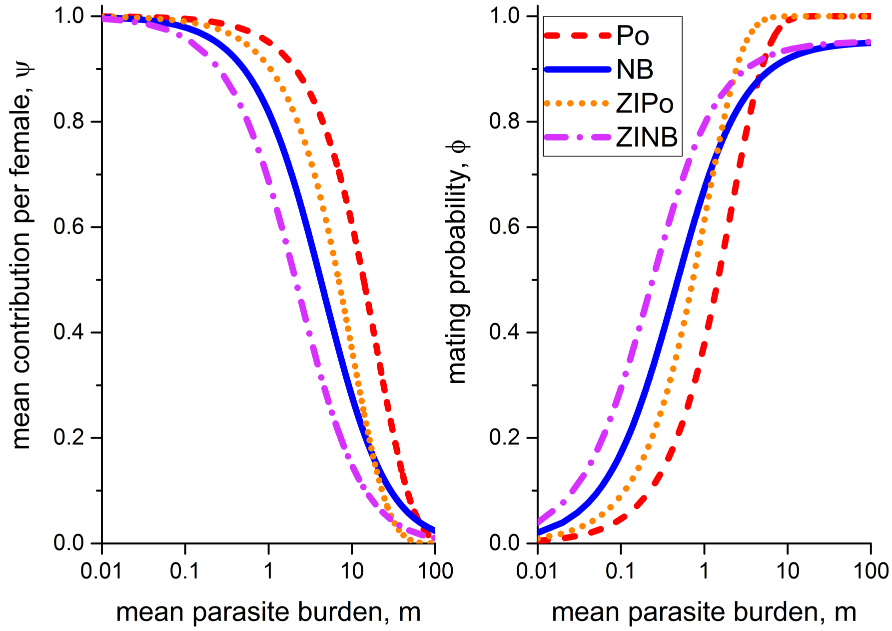

Figure 1: The mean effective contribution per female parasite, ψ (left) and the mating probability, ϕ (right) corresponding to Poisson (dash curve), negative binomial (solid curve), zero-inflated Poisson (dot curve) and zero-inflated negative binomial (dash dot curve) distributions. All as a function of the mean parasite burden m.

4 Parasite infection by skin-penetrating

Unlike in section 3, we consider that the transmission of parasites occurs through the skin penetration. This type of transmission occurs in parasites such as Ancylostoma duodenale, Necator americanus, among others [4, 6].

In this type of transmission, the host can acquire a single parasite per infection event. Thus, the host can be infected with only one male or female parasite at a time. Therefore, when analyzing the number of male or female parasites per host, these variables must be independent. Here we will present an analysis of these variables.

4.1 Distribution of parasites by sex

As in the previous section, let W be the random variable count of the number of parasites in a host and F, M are the number of female and male parasites, respectively. In this section we analyze the case in which these variables are independent and therefore verify the following properties

$$\begin{aligned} W &= F + M \\ G_W(s) &= G_F(s) G_M(s) \end{aligned} \tag{23}$$

where G_W, G_F and G_M are probability generating function of the variables W, F and M, respectively.

We present an expression for all the variables developed in section 3, proofs are in the Appendix A.4

- Mean number of fertilized female parasites

$$\alpha m \left[1 - p_M(0)\right] \tag{24}$$

- Mating probability

$$1 - p_M(0) \tag{25}$$

- Mean egg production per host

$$\lambda_0 G_M(z) G_F'(z) \tag{26}$$

- Mean fertilized egg production

$$\lambda_0 G_M(z) G_F'(z) \left[1 - \frac{p_M(0)}{G_M(z)}\right] \tag{27}$$

- Mean effective transmission contribution by female parasite

$$\psi = \frac{G_M(z) G_F'(z)}{\alpha m} \tag{28}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} \tag{29}$$

- Contribution of mean fertilized egg production for mean-based deterministic model of parasite burden

$$\lambda_0 \alpha m \psi(m) \phi(m) \tag{30}$$

4.2 Some examples

Distributions for the variables F and M are expected to be the same, but with different parameter values if the sex ratio it is not 1:1. However the total parasite burden distribution (M), obtained from the conditions (23), may have a different distribution.

In the examples presented here we show some cases where the variables W , F and M have all the same statistical model. We work with some of the most popular distributions used to model parasites and in all cases and arbitrary sex ratio $\alpha : \beta$, where $\alpha + \beta = 1$, it is assumed.

4.2.1 Poisson

For the case where the distribution of parasites per host is Poisson with mean λ, that is, $W \sim \mathrm{Po}(\lambda)$. A solution for the independence of variables F and M are the following distributions

$$F \sim \mathrm{Po}(\alpha\lambda) \qquad M \sim \mathrm{Po}(\beta\lambda)$$

$$\begin{aligned} G_F(s)G_M(s) &= e^{\alpha\lambda(s-1)}e^{\beta\lambda(s-1)} \\ &= e^{(\alpha+\beta)\lambda(s-1)} \\ &= e^{\lambda(s-1)} \\ &= G_{F+M}(s) \\ &= G_W(s) \end{aligned}$$

Note that the pgf of F and M coincide with what was obtained in section 3.1, which shows the independence of these variables in that section. We show some of the expressions obtained in the previous section 3.1 for this case:

- Mean effective transmission contribution by female parasite

$$\psi = \frac{G_M(z)G'_F(z)}{G'_F(1)} = e^{-m(1-z)}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} = 1 - e^{-mz\beta}$$

Note that the expression for ψ and ϕ are the same as those obtained in the section 3.6.

4.2.2 Negative binomial

If F and M are negative binomial distributed with parameters $m_F = \alpha m$, $k_F = \alpha k$, $m_M = \beta m$, $k_M = \beta k$,

$$F \sim \mathrm{NB}(\alpha m, \alpha k) \qquad M \sim \mathrm{NB}(\beta m, \beta k)$$

Then the distribution of $W = F+M$ is the negative binomial distribution with parameters m and k. In fact, a solution to problem (23) is given by

$$\begin{aligned} G_F(s)G_M(s) &= \left[1 - \frac{\alpha m}{\alpha k}(s-1)\right]^{-\alpha k}\left[1 - \frac{\beta m}{\beta k}(s-1)\right]^{-\beta k} \\ &= \left[1 - \frac{m}{k}(s-1)\right]^{-\alpha k - \beta k} \\ &= \left[1 - \frac{m}{k}(s-1)\right]^{-k} \\ &= G_{F+M}(s) \\ &= G_W(s) \end{aligned}$$

For this case, the pgf of F and M are not equal to those obtained in section 3.1, since it was shown that the variables were not independent. We show some of the expressions obtained in the previous section 3.1 for case of independence between variables

- Mean effective transmission contribution by female parasite

$$\psi = \frac{G_M(z)G'_F(z)}{\alpha m} = \left[1 - \frac{m}{k}(z-1)\right]^{-(k+1)} \tag{31}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} = 1 - \left[\frac{1 + \frac{m}{k}}{1 - \frac{m}{k}(z-1)}\right]^{-\beta k} \tag{32}$$

Note that the expression ψ is the same one obtained in the section 3.6.

In Figure 2 we show the behavior of the mating probability function for the cases in which the female and male parasites are distributed together or independently.

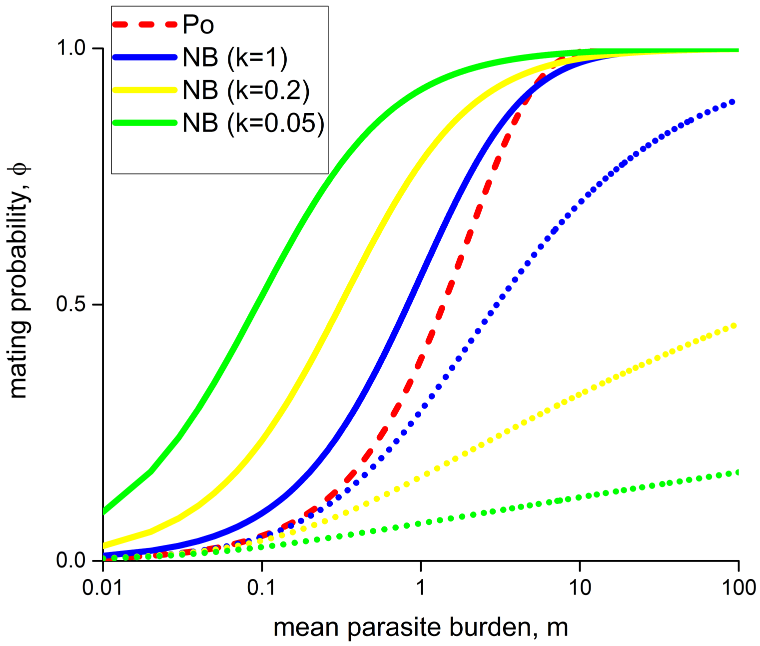

Figure 2: Mating probability as a function of mean parasite load. The dashed curve (red) corresponds to a Poisson distribution ($k \to \infty$). The solid and dotted curves correspond to a negative binomial distribution with joint or independent distribution by sex, respectively, where $k = 1$ (blue), $k = 0.2$ (yellow) and $k = 0.05$ (green).

4.2.3 Zero-inflated negative binomial

- Mean effective transmission contribution by female parasite

$$\begin{aligned}
\psi &= \frac{G_M(z)G'_F(z)}{\alpha m} \\
&= \pi \left[1 - \frac{m}{(1-\pi)k}(z-1)\right]^{-(\alpha k+1)} \\
&\quad + (1-\pi)\left[1 - \frac{m}{(1-\pi)k}(z-1)\right]^{-(k+1)}
\end{aligned} \tag{33}$$

- Mating probability and density-dependence effects

$$\begin{aligned}
\phi &= 1 - \frac{p_M(0)}{G_M(z)} \\
&= 1 - \frac{\pi + (1-\pi)\left[1 + \frac{m}{(1-\pi)k}\right]^{-\beta k}}{\pi + (1-\pi)\left[1 - \frac{m}{(1-\pi)k}(z-1)\right]^{-\beta k}}
\end{aligned} \tag{34}$$

5 Monte Carlo simulation

5.1 Parasite infection by egg ingestion

For this case we consider that the transmission of parasites is produced by the ingestion of fertilized eggs of these parasites. Here we can consider infection by *Ascaris lumbricoides* and *Trichuris trichiura*.

5.1.1 Model assumptions

Simulation algorithms presented in this section are based on the following assumptions and rules:

- We considered a host population of size N.
- The parasite burden of each host is a random variable W.
- In the ingestion of infectious eggs, a host may acquire one or more parasites per transmission event. Thus, a host may acquire female or male parasites in the same transmission event.

- The female and male parasite burden are dependent random variables F and M, respectively. The female parasite burden F is obtained by doing W Bernoulli trials with the parameter α, where α is the sex ratio of the female parasites. The male parasite burden is given by $M = W - F$.
- The egg production per host is given by Fz^{W-1}, where $z = \exp(\sigma)$ with σ (Falta)
- The infective egg production per host is given by $I_{M>0}(M)Fz^{W-1}$, where $I_{M>0}$ is the indicator function of the set $M > 0$.
- The mating probability is obtained by quotient between the mean infective egg production and the mean egg production.
- The mean effective contribution per female parasite is obtained by quotient between the mean egg production per host and the mean of female parasites per host.

All the simulations were carried out in RStudio (Version 1.0.136) .

5.2 Parasite infection by skin-penetrating

5.3 Some examples

5.3.1 Negative Binomial

$$\psi = \left[1 - \frac{m}{k}(z-1)\right]^{-(k+1)} \tag{35}$$

Finally the mating probability, ϕ, is given by (see eq. (7))

$$\phi = 1 - \left[\frac{1 - \frac{m}{k}(\alpha z - 1)}{1 - \frac{m}{k}(z-1)}\right]^{-(k+1)} \tag{36}$$

Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} = 1 - \left[\frac{1 + \frac{m}{k}}{1 - \frac{m}{k}(z-1)}\right]^{-\beta k} \tag{37}$$

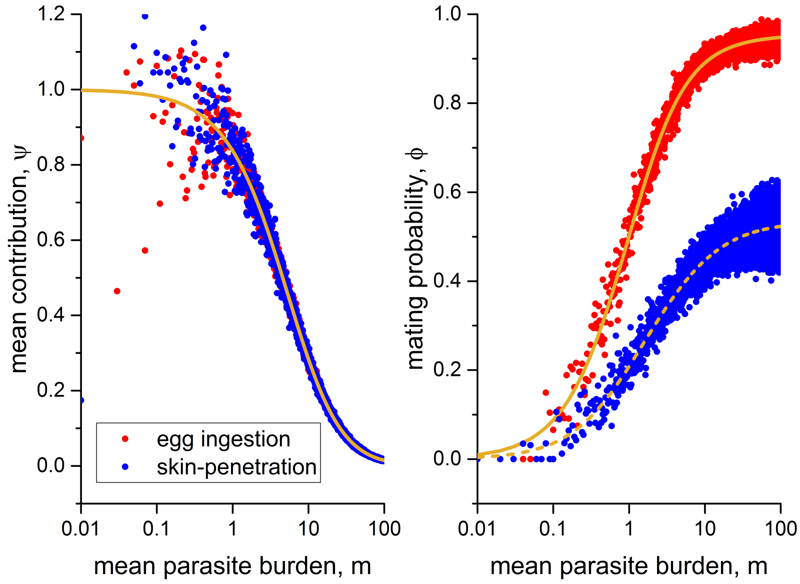

Figure 3: The mean contribution, ψ, and the mating probability, ϕ, as a function of the mean parasite burden, m, for a parasite population with a negative binomial distribution. The dots (red and blue) are the empirical values of ψ and ϕ, obtained for the host population simulated. of the simulations. The curves (continue and dash) correspond to the theorical models ψ and ϕ obtained in REF. The red dots and continue curves correspond to the infection by egg ingestion. The blue dots and dash curves correspond to the infection by skin-penetrating.

5.3.2 Zero-inflated negative binomial

$$\psi = \left\{ \pi + (1-\pi)\left[1 - \frac{m}{(1-\pi)k}(z-1)\right]^{-\beta k} \right\} \left[1 - \frac{m}{(1-\pi)k}(z-1)\right]^{-(1+\alpha k)} \tag{38}$$

6 Discussion and Conclusions

In most cases total macro-parasites distribution is determined by the infection process and therefore the variables F and M (number of female and male parasites within the host) are not independent variables. We presented a general form to obtain the parasite female burden distribution in hosts from the observed total parasite distribution.

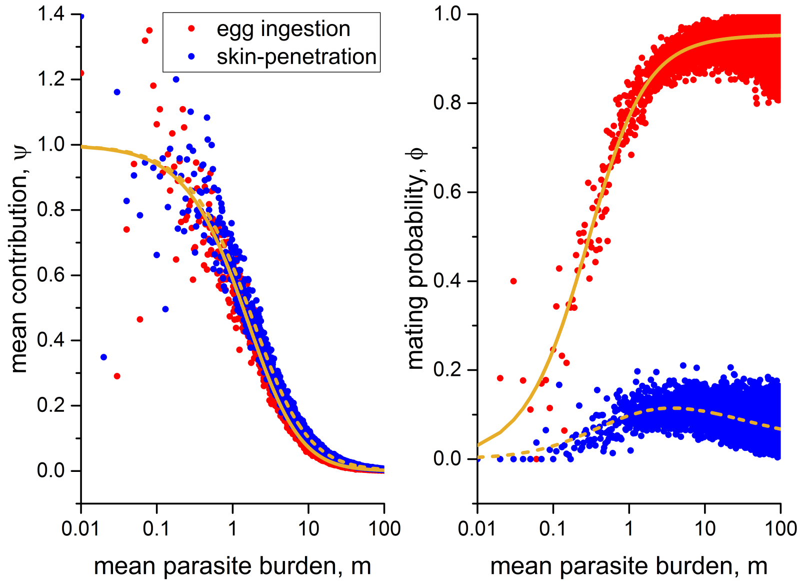

Figure 4: The mean egg contribution, ψ, and the mating probability, ϕ, as functions of the mean parasite burden, m, for a parasite population with a zero-inflated negative binomial distribution. The dots (red and blue) are the simulation values of ψ and ϕ. The curves (continue and dash) correspond to the theorical models ψ and ϕ obtained in REF. The red dots and continued curves correspond to the infection by egg ingestion (dependiented distributions by sex). The blue dots and dashed curves correspond to the infection by skin-penetrating.

Different reproductive variables of parasites of importance for population dynamics, such as the mean number of fertilized female parasites, mean egg production, mating probability, mean fertilized egg production and mating probability, were obtained.

The expressions obtained for these reproductive variables in the different examples are generalizations (for the case of density-dependent fertility on reproductive behavior of parasites) of those obtained in[15, 16, 17].

When parasites are acquired individually we expect the random variables F and M to be independent. We also expect that these variables have the same type of distribution.

But the total host parasite burden $W = F + M$ not necessarily will inherit the same distribution os F amd M. There are some obvious cases where it is known that the distribution of the sum of random variables have the same distribution of the the variables like in the case of independent Poisson distributed variables. However for the important case of negative binomial distributed variables this is not generally true. In this work we show that only if $F \sim \mathrm{NB}(\alpha m, \alpha k)$ and $M \sim \mathrm{NB}(\beta m, \beta k)$ then the total burden is negative binomial distributed with parameters m and k.

One of the main limitations of this work is that it only considers parasites with a polygamous mating system and we do not consider monogamous and hermaphroditic parasites.

In conclusion, in this work we obtained a general expression for egg production and the mating probability of the parasites. We show how these expressions depend on the sex distribution of the parasites and whether these distributions are considered joint or independent. We also show that these expressions vary due to the effects of the density-dependence of the parasites.

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Conflict of Interest

The authors have declared no conflict of interest.

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A Appendix

We will assume that p is the probability mass function of the distribution of parasites per host and G its probability generating function.

A.1 Mean number of fertilized female parasites

Proposition A.1.1. *The mean number of fertilized female parasites is given by*

$$\alpha m - \alpha G'(\alpha)$$

Proof. The presence of at least one male parasite in the host ensures the fertility of all females, so

$$\begin{aligned}\sum_{n\geq 0}\sum_{j=1}^{n-1} j p_n \binom{n}{j} \alpha^j \beta^{n-j} &= \sum_{n\geq 0} p_n \sum_{j=1}^{n-1} j \binom{n}{j} \alpha^j \beta^{n-j} \\ &= \sum_{n\geq 0} p_n (n\alpha - n\alpha^n)\end{aligned}$$

where the last line is obtained from the expression of the mean of $\mathrm{B}(n,\alpha)$, $n\alpha = \sum_{j=0}^{n} j \binom{n}{j} \alpha^j \beta^{n-j}$. Therefore

$$\begin{aligned}\sum_{n\geq 0}\sum_{j=1}^{n-1} j p_n \binom{n}{j} \alpha^j \beta^{n-j} &= \alpha \sum_{n\geq 0} n p_n (1-\alpha^{n-1}) \\ &= \alpha \left[\sum_{n\geq 0} n p_n - \sum_{n\geq 0} n \alpha^{n-1} p_n \right] \\ &= \alpha m - \alpha G'(\alpha)\end{aligned}$$

□

A.2 Mean egg production per host

Proposition A.2.1. *The mean egg production per host is given by*

$$\lambda_0 \alpha G'(z)$$

Proof. We consider that all females present in the host can produce eggs according to their per-capita fecundity

$$\begin{aligned}\sum_{n\geq 0}\sum_{j=0}^{n} j \lambda(n) p_n \binom{n}{j} \alpha^j \beta^{n-j} &= \lambda_0 \sum_{n\geq 0}\sum_{j=0}^{n} j z^{n-1} p_n \binom{n}{j} \alpha^j \beta^{n-j} \\ &= \lambda_0 \sum_{n\geq 0} z^{n-1} p_n \sum_{j=0}^{n} j \binom{n}{j} \alpha^j \beta^{n-j} \\ &= \lambda_0 \sum_{n\geq 0} z^{n-1} p_n n \alpha \\ &= \lambda_0 \alpha \sum_{n\geq 0} n z^{n-1} p_n \\ &= \lambda_0 \alpha G'(z)\end{aligned}$$

□

A.3 Mean fertilized egg production per host

Proposition A.3.1. *The mean fertilized egg production per host is given by*

$$\lambda_0 \alpha G'(z) \left[1 - \frac{G'(\alpha z)}{G'(z)}\right]$$

Proof. Identical to the previous demonstration but considering only fertilized females

$$\begin{aligned}
\sum_{n\geq 0}\sum_{j=1}^{n-1} j\lambda(n)p_n \binom{n}{j}\alpha^j\beta^{n-j} &= \lambda_0 \sum_{n\geq 0}\sum_{j=1}^{n-1} jz^{n-1}p_n \binom{n}{j}\alpha^j\beta^{n-j} \\
&= \lambda_0 \sum_{n\geq 0} z^{n-1}p_n \sum_{j=1}^{n-1} j\binom{n}{j}\alpha^j\beta^{n-j} \\
&= \lambda_0 \sum_{n\geq 0} z^{n-1}p_n(n\alpha - n\alpha^n) \\
&= \lambda_0 \alpha \sum_{n\geq 0} nz^{n-1}p_n(1-\alpha^{n-1}) \\
&= \lambda_0 \alpha \left[\sum_{n\geq 0} nz^{n-1}p_n - \sum_{n\geq 0} n(\alpha z)^{n-1}p_n\right] \\
&= \lambda_0 \alpha G'(z)\left[1 - \frac{G'(\alpha z)}{G'(z)}\right]
\end{aligned}$$

□

A.4 Independence in the variables F and M

- Mean number of fertilized female parasites

$$\begin{aligned}
\sum_{i\geq 1}\sum_{j\geq 0} jp_F(j)p_M(i) &= \sum_{i\geq 1} p_M(i) \sum_{j\geq 0} jp_F(j) \\
&= [1 - p_M(0)]\,\alpha m
\end{aligned}$$

- Mating probability

$$\begin{aligned}
\frac{\sum_{i\geq 1}\sum_{j\geq 0} jp_F(j)p_M(i)}{\sum_{j\geq 0} jp_F(j)} &= \frac{[1 - p_M(0)]\,\alpha m}{\alpha m} \\
&= 1 - p_M(0)
\end{aligned}$$

- Mean egg production per host

$$\begin{aligned}
\sum_{i\geq 0}\sum_{j\geq 1} j\lambda(i+j)p_F(j)p_M(i) &= \sum_{i\geq 0}\sum_{j\geq 1} j\lambda_0 z^{i+j-1}p_F(j)p_M(i)\\
&= \lambda_0 \sum_{i\geq 0} z^i p_M(i)\sum_{j\geq 1} jz^{j-1}p_F(j)\\
&= \lambda_0 G_M(z)G_F'(z)
\end{aligned}$$

- Mean fertilized egg production per host

$$\begin{aligned}
\sum_{i\geq 1}\sum_{j\geq 1} j\lambda(i+j)p_F(j)p_M(i) &= \sum_{i\geq 1}\sum_{j\geq 1} j\lambda_0 z^{i+j-1}p_F(j)p_M(i)\\
&= \lambda_0 \sum_{i\geq 1} z^i p_M(i)\sum_{j\geq 1} jz^{j-1}p_F(j)\\
&= \lambda_0 \left[G_M(z) - p_M(0)\right] G_F'(z)\\
&= \lambda_0 G_M(z)G_F'(z)\left[1 - \frac{p_M(0)}{G_M(z)}\right]
\end{aligned}$$

- Mean effective transmission contribution by female parasite

$$\psi = \frac{\sum_{i\geq 0}\sum_{j\geq 1} j\lambda(i+j)p_F(j)p_M(i)}{\sum_{j\geq 1} jp_F(j)} = \frac{G_M(z)G_F'(z)}{\alpha m}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)}$$