General model of sex distribution, egg production and mating probability for macroparasites with a polygamous mating system

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SUMMARY: The reproductive habits of parasite 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, there are other statistical models that describe these populations, such as zero-inflated models, but where reproductive characteristics were not analyzed. Using an arbitrary 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, the mean fertilized egg production. We show that these variables change due to the effects of a negative density-dependence fecundity, a characteristic of helminth parasites. We present the results obtained for some particular models.

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1. Introduction

One of the most important factors in understanding the transmission dynamics of helminth parasites 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 Anderson and May (1992).

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 May (1977) and for a variable sex ratio in May and Woolhouse (1993). Also a dynamic model for the number of fertilized females is presented in Leyton (1968).

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 of parasites by sex

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 parasite burden, the mean number of female and male parasites are given by αm and βm respectively.

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 females parasites per host is modeled by a stopped sums distribution (Johnson et al. (2005)) and its probability generating function (pgf) is the function $G_W \circ G_B$, where G_B is the pgf of the Bernoulli distribution ($G_B(s) = \beta + \alpha s$)Johnson et al. (2005). Therefore the variable F is given by $F = \sum_{i=1}^{W} Y_i$ where $Y_i \sim \mathrm{Ber}(\alpha)$, and its pgf is

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

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, or variance-to-mean ratio $D = \frac{\sigma_F^2}{\mu_F}$, is given by

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

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

Similarly, if M is the number of male parasites, $M = W - F$ and therefore its mean is $\mu_M = \beta\mu_W$. By the definition of F and M these are dependent variables.

3. Mating probability

3.1 *Mean number of fertilized female parasites and mating probability (density-independent)*

The parasites treated in this work present a polygamous mating system, and therefore the presence of at least one male parasite in the host ensures the fertility of all females. Then, from the distribution of parasites by sex of the expression (1), the mean number of fertilized female parasites per host is given by

$$\sum_{n\geqslant 1}\sum_{j=0}^{n-1} jp_n \binom{n}{j}\alpha^j\beta^{n-j} = \alpha m - \alpha G'(\alpha) \tag{3}$$

where the term $\sum_{j=0}^{n-1} jp_n\binom{n}{j}\alpha^j\beta^{n-j}$ is the probability of having at least one male in a burden of n parasites. For more details of (3) see Appendix (A.1). We will denote by G to the pgf of the distribution of parasites per host G_W and $G'(x) = \frac{\partial G}{\partial s}\big|_x$.

We obtain that the mating probability of a female, as the ratio between the mean number of fertilized females and the mean number of females in a host,

$$\frac{\sum_{n\geqslant 1}\sum_{j=0}^{n-1} jp_n\binom{n}{j}\alpha^j\beta^{n-j}}{\sum_{n\geqslant 0}\sum_{j=0}^{n} jp_n\binom{n}{j}\alpha^j\beta^{n-j}} = \frac{\alpha m - \alpha G'(\alpha)}{\alpha m}$$

Therefore the probability of mating of a female that we will denote by ϕ is given by

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

3.2 *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 Churcher et al. (2006); Walker et al. (2009).

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 Hall and Holland (2000).

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

3.3 *Mean egg production per host*

Due to the effects of density-dependent fecundity, the total egg production per female decreases as the parasite burden in host increases. Therefore, from the distribution of parasites per host, the mean egg production per host is given by the expression

$$\sum_{n\geqslant 0}\sum_{j=0}^{n} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j} = \lambda_0\alpha G'(z) \tag{6}$$

where $j\lambda(n)$ is the egg production of j females and $p_n\binom{n}{j}\alpha^j\beta^{n-j}$ is the probability of having j females, both cases within a host with n parasites. For more details of (6) see Appendix (A.2).

3.4 *Mean fertilized egg production*

For the fertilized egg production, we must consider only the fertilized females. Therefore the expression for the mean fertilized egg production is given by

$$\sum_{n\geqslant 1}\sum_{j=0}^{n-1} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j} = \lambda_0\alpha G'(z)\left[1 - \frac{G'(\alpha z)}{G'(z)}\right] \tag{7}$$

where $j\lambda(n)$ is the egg production of j females and $\sum_{j=0}^{n-1} p_n\binom{n}{j}\alpha^j\beta^{n-j}$ is the probability of having at least one male in a burden of n parasites. For more details of (7) see Appendix (A.3).

3.5 *Mating probability and density-dependence effects*

If we consider the ratio between the mean fertilized egg production and the mean egg production, we obtain the fraction of the eggs that are fertilized by the male parasites, and therefore we obtain the probability of fecundity of the eggs or mating probability of female parasites, under the density-dependence effects, as

$$\phi = 1 - \frac{G'(\alpha z)}{G'(z)} \tag{8}$$

From this expression (8) 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.

3.6 *Mean effective transmission contribution per female parasite*

In deterministic population models for the mean parasite burden such as Anderson and May (1985, 1992); Truscott et al. (2014), it is necessary to know the effective transmission contribution of the female population to the parasite reservoir (in form of eggs or larvae) Churcher et al. (2005, 2006). Using the results obtained in this work we can calculate this term denoted by ψ as

$$\psi = \frac{\sum_{n\geqslant 0}\sum_{j=1}^{n} j\lambda(n)p_n\binom{n}{j}\alpha^j\beta^{n-j}}{\sum_{n\geqslant 0}\sum_{j=0}^{n} jp_n\binom{n}{j}\alpha^j\beta^{n-j}} = \frac{G'(z)}{m} \tag{9}$$

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).

In this class of models it also necessary to obtain that the contribution of fertilized egg production by mean parasite burden which is modeled in terms of functions ψ and ϕ by (see, for example, Anderson and May (1992))

$$\lambda_0\alpha m\psi(m)\phi(m) = \lambda_0\alpha G'(z)\left[1 - \frac{G'(\alpha z)}{G'(z)}\right] \tag{10}$$

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

4. Some examples

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

4.1 *Poisson*

A simple model for the distribution of parasites per host Lahmar et al. (2001) is the Poisson distribution,

$$\Pr(X = x) = \frac{\lambda^x e^{-\lambda}}{x!}, \tag{11}$$

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

$$G(s) = e^{m(s-1)} \tag{12}$$

For this parasite distribution the mean number of fertilized female parasites per host is given by $\alpha\lambda\left[1 - e^{-m\beta}\right]$. On the other hand, the effective contribution of parasites to the transmission cycle is given by (see eq (9))

$$\psi = e^{-m(1-z)} \tag{13}$$

Another important factor in parasite dynamics is the mating probability ϕ which is given by (see eq (8))

$$\phi = 1 - e^{-mz\beta} \tag{14}$$

This expression of ϕ is a generalization for the mating probability obtained in the works Anderson and May (1992); May and Woolhouse (1993); May (1977).

4.2 *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 Bundy et al. (1987); Hoagland and Schad (1978); Seo et al. (1979b),

$$P(X = x) = \frac{\Gamma(k + x)}{\Gamma(x + 1)\Gamma(k)} \left(\frac{k}{k + m}\right)^k \left(\frac{m}{k + m}\right)^x \tag{15}$$

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

$$G(s) = \left[1 - \frac{m}{k}(s - 1)\right]^{-k} \tag{16}$$

Therefore the mean number of fertilized female parasites per host is given by the fraction $1-\left[1-\frac{m}{k}(\alpha-1)\right]^{-(k+1)}$ of αm. Another important result is the expression for ψ, the effective contribution, which is given by (see eq. (9))

$$\psi = \left[1-\frac{m}{k}(z-1)\right]^{-(k+1)} \tag{17}$$

Finally the mating probability, ϕ, is given by (see eq. (8))

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

This expression of ϕ results in a generalization for the mating probability obtained in works Anderson and May (1992); May and Woolhouse (1993); May (1977).

4.3 *Zero-inflated and hurdle Models*

Other frequently used models are the zero-inflated and hurdle models (see for example Abdybekova and Torgerson (2012); Crofton (1971); Denwood et al. (2008); Ziadinov et al. (2010)).

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 mean number of fertilized female parasites per host is given by

$$\alpha G_Y'(1)\left[1-\frac{G_Y'(\alpha)}{G_Y'(1)}\right] = \alpha(1-\pi)G_X'(1)\left[1-\frac{G_X'(\alpha)}{G_X'(1)}\right]$$

Another important result is the expression for ψ, the mean contribution per female parasite, which is given by

$$\psi = \frac{G'_Y(z)}{m_Y} = \frac{(1-\pi)G'_X(z;m_X)}{m_Y} = \frac{G'_X\left(z;\frac{m_Y}{1-\pi}\right)}{\frac{m_Y}{1-\pi}} \tag{19}$$

Finally the mating probability ϕ can be calculated by

$$\phi = 1 - \frac{G'_Y(\alpha z)}{G'_Y(z)} = 1 - \frac{G'_X\left(\alpha z;\frac{m_Y}{1-\pi}\right)}{G'_X\left(z;\frac{m_Y}{1-\pi}\right)} \tag{20}$$

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 Johnson et al. (2005). 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

$$\begin{aligned} \psi &= \frac{G'_Y(z)}{m_Y} = \frac{\rho G'_X(z;m_X)}{m_Y} = \frac{G'_X\left(z;\frac{m_Y}{\rho}\right)}{\frac{m_Y}{\rho}} \\ \phi &= 1 - \frac{G'_Y(\alpha z)}{G'_Y(z)} = 1 - \frac{G'_X\left(\alpha z;\frac{m_Y}{\rho}\right)}{G'_X\left(z;\frac{m_Y}{\rho}\right)} \end{aligned} \tag{21}$$

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

4.3.1 *Zero-inflated Poisson and zero-inflated negative binomial models.* The negative binomial distribution is widely used to describe the distribution of parasites in hosts Crofton (1971); Seo et al. (1979b). However in many cases the negative binomial distribution (or other similar distributions) cannot account for the excess of zeros observed Crofton (1971). A solution to this problem are zero-inflated models which have been widely used in the last decade for parasite counting Abdybekova and Torgerson (2012); Denwood et al. (2008); Ziadinov et al. (2010).

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 about here.]

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, $\alpha = 0.574$ (Seo et al. (1979a)).

[Figure 1 about here.]

5. Independence in the variables F and M

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 section 2 we assumed that we know the parasite distribution in host, $W = F + M$, and therefore the variables F and M are not independent. In this section we study the case in which these variables are independent, that is, W, F and M verify the following properties

$$\begin{aligned} W &= F + M \\ G_W(s) &= G_F(s)G_M(s) \end{aligned} \tag{22}$$

The independence of the variables F and M can occur when the parasites are acquired individually, as in case of hookworm parasites that can penetrate the skin of host Bethony et al. (2006); Hotez et al. (2004).

We present all the expressions developed in the sections 2 and 3, proofs are in the Appendix

- Mean number of fertilized female parasites

$$\alpha m \left[1 - p_M(0)\right] \tag{23}$$

- Mating probability

$$1 - p_M(0) \tag{24}$$

- Mean egg production per host

$$\lambda_0 G_M(z) G_F'(z) \tag{25}$$

- Mean fertilized egg production

$$\lambda_0 G_M(z) G_F'(z) \left[1 - \frac{p_M(0)}{G_M(z)}\right] \tag{26}$$

- Mean effective transmission contribution by female parasite

$$\psi = \frac{G_M(z) G_F'(z)}{\alpha m} \tag{27}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} \tag{28}$$

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

$$\lambda_0 \alpha m \psi(m) \phi(m) \tag{29}$$

5.1 *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 (22), 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.

5.1.1 *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 2, which shows the independence of these variables in that section. We show some of the expressions obtained in the previous section 2 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 4.

5.1.2 *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 (22) 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 2, since it was shown that the variables were not independent. We show some of the expressions obtained in the previous section 2 for case of independence between variables

- Mean effective transmission contribution by female parasite

$$\psi = \frac{G_M(z)G'_F(z)}{\alpha m} = \left[1 - \frac{m}{k}(z-1)\right]^{-(k+1)} \tag{30}$$

- Mating probability and density-dependence effects

$$\phi = 1 - \frac{p_M(0)}{G_M(z)} = 1 - \left[\frac{1+\frac{m}{k}}{1-\frac{m}{k}(z-1)}\right]^{-\beta k} \tag{31}$$

Note that the expression ψ is the same one obtained in the section 4.

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 about here.]

6. Discussion and Conclusions

In most cases total macroparasites 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.

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 Leyton (1968); May (1977); May and Woolhouse (1993).

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 and 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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Appendix

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

Mean number of fertilized female parasites

The mean number of fertilized female parasites is given by

$$\alpha m - \alpha G'(\alpha) \tag{A.1}$$

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

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

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

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

Mean egg production per host

The mean egg production per host is given by

$$\lambda_0\alpha G'(z) \tag{A.2}$$

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

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

Mean fertilized egg production per host

The mean fertilized egg production per host is given by

$$\lambda_0\alpha G'(z)\left[1-\frac{G'(\alpha z)}{G'(z)}\right] \tag{A.3}$$

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

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

Independence in the variables F and M

- Mean number of fertilized female parasites

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

- Mating probability

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

- Mean egg production per host

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

- Mean fertilized egg production per host

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

- Mean effective transmission contribution by female parasite

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

- Mating probability and density-dependence effects

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

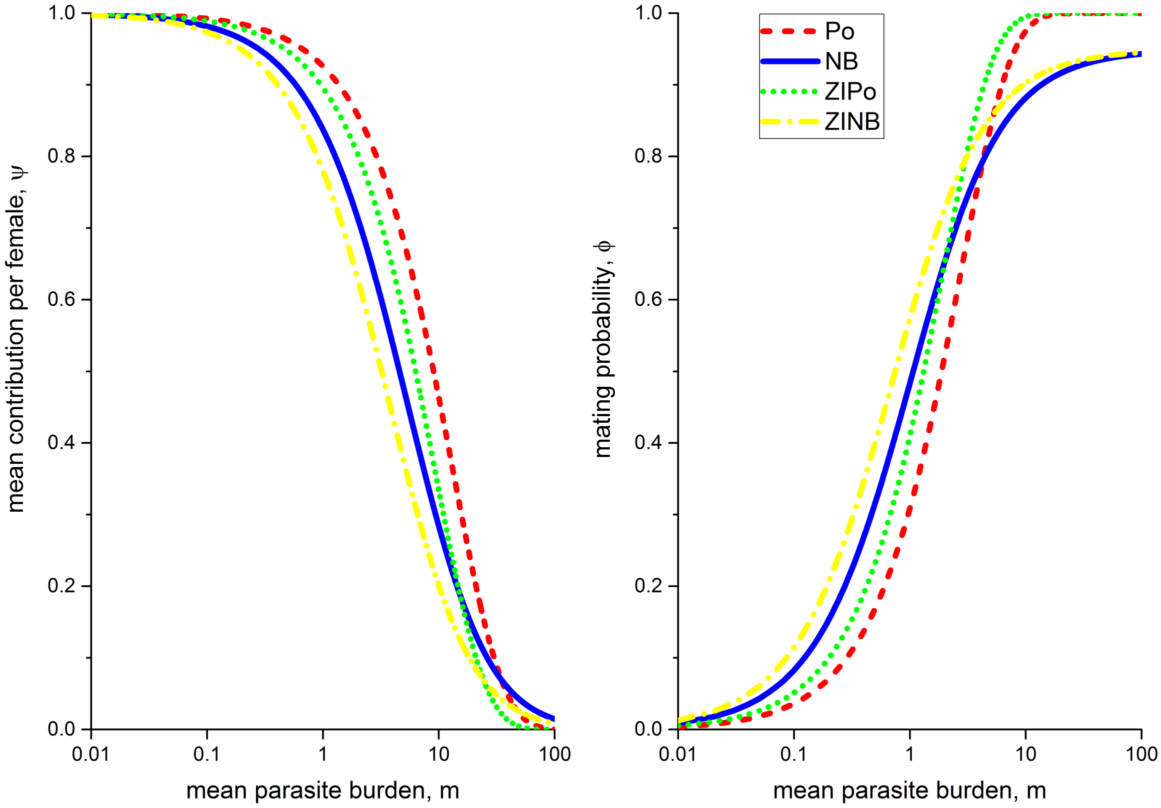

Figure 1. The mean effective contribution per female parasite, ψ (left) and the mating probability, ϕ (right) corresponding to Poisson (dash curve), negative binomial (solid curve), zero-inflated Poisson (dot curve) and zero-inflated negative binomial (dash dot curve) distributions. All as a function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

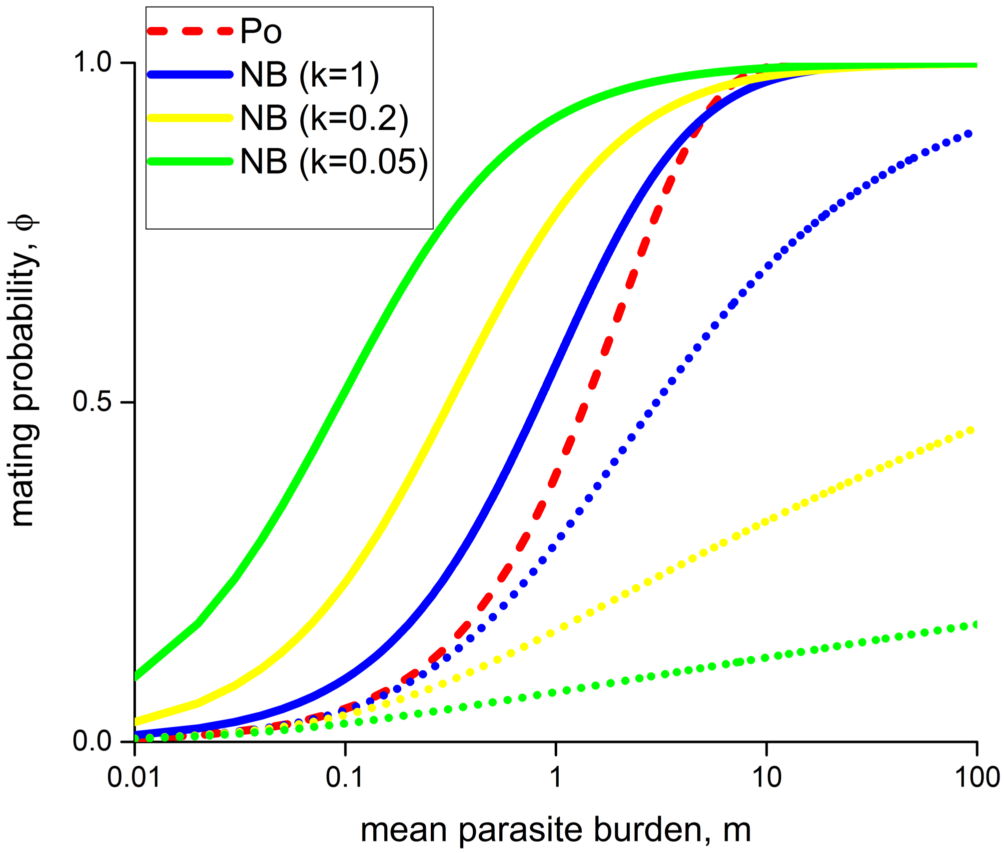

Figure 2. Mating probability as a function of mean parasite burden m. The dashed curve (red) corresponds to a Poisson distribution ($k \to \infty$). The solid and dotted curves correspond to a negative binomial distribution with joint or independent distribution by sex, respectively, where $k = 1$ (blue),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

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