

Biased sex ratios and parasite mating probabilities

R. M. MAY and M. E. J. WOOLHOUSE

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS

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SUMMARY

An earlier paper (May, 1977) developed a theoretical framework for exploring the consequences of dioecy for the population dynamics of schistosomes, assuming an unbiased sex ratio. This paper extends the analysis to biased sex ratios, as have been reported in practice. We consider the relationships of the mean number and distribution of worms among hosts, the sex ratio, and the mating system (monogamous or polygamous) to: (i) the female mating probability, Φ ; (ii) the prevalence of mated female worms, Ω ; and (iii) the mean number of mated female worms per host, ξ . Among other results, we show how high values of Φ are associated with male-biased sex ratios and polygamous mating; that Ω is independent of the mating system and is relatively unaffected by the sex ratio; and that ξ is maximal for unbiased sex ratios given monogamous mating, and for female-biased sex ratios if mating is polygamous. These results, together with the confounding effects of the mean number and distribution of worms, are described in detail in the main body of the paper.

Key words: dioecy, helminths, mating probability, negative binomial distribution, prevalence.

INTRODUCTION

Schistosomes and many other species of parasitic helminth are dioecious. This means, amongst other things, that the female schistosomes in a given host are not necessarily all fertilized, which leads to some interesting complications for the dynamics of infection, recognized in the earliest mathematical models of schistosome transmission (Macdonald, 1965). In an earlier paper (May, 1977) a theoretical framework was developed for exploring the consequences of dioecy. This analysis focused on the probability that a given female worm was mated (as a function of the abundance and distribution of worms among hosts), and on the consequences for the prevalence of worms, the prevalence of mated female worms, and the egg output per host. The analysis assumed a 1:1 male:female sex ratio among worms.

In the current paper we extend this earlier work to consider the more general and more difficult case of biased sex ratios. Several studies have reported biased sex ratios for schistosomes and other parasitic helminths (Table 1). We also make a number of explicit comparisons between monogamous and polygamous mating systems (which received limited attention in the earlier paper). Schistosomes are generally considered to be monogamous, but polygamous mating may occur among other parasitic helminths.

DISTRIBUTION AND ABUNDANCE OF WORMS

The distribution of parasitic helminths among hosts is typically aggregated (see Anderson & May, 1991).

It has become usual in theoretical studies to represent this aggregated distribution using a negative binomial function. This allows the distribution of worms to be fully described by two parameters, the mean number of worms per host, m , and the parameter, k , where k is an inverse index of aggregation (with the limit $k \rightarrow \infty$ recovering a Poisson distribution, worms randomly distributed among hosts). The negative binomial distribution does have some empirical support, but its ubiquity is more a reflection of its convenience than of any fundamental biological validity. Both for reasons of analytical convenience and of continuity we assume here a negative binomial distribution of worms among hosts.

The fraction of all worms that are female is represented by q and the fraction of male worms by $p = 1 - q$. The male:female sex ratio (often simply called the 'sex ratio') is therefore $p/q:1$, and the mean number of female worms per host is mq . Results described in the earlier paper (May, 1977) correspond to the special case $p = q = 0.5$.

We examine the relationships to m , k and q of three quantities: (i) the mating probability, Φ , the probability that a given female worm will be mated; (ii) the prevalence of mated female worms, Ω , the expected fraction of hosts supporting one or more mated female worms; and (iii) the mean number of mated female worms per host, ξ .

We compare these quantities for two possible mating systems. In the case of monogamous mating a male worm can fertilize a maximum of one female worm in the same host. In the case of polygamous mating it is conventionally assumed that a male worm can fertilize all female worms in the same host.

Table 1. Examples of sex ratios reported from natural and experimental helminth infections

Parasite species	Host	Sex ratio (males/ females)	
<i>Schistosoma mansoni</i>	Mouse	1.8	Liberatos (1987)
<i>S. mansoni</i>	Mouse	1.1–5.7	Mitchell <i>et al.</i> (1990)
<i>S. mansoni</i>	Rat	1.5	Theron <i>et al.</i> (1992)
<i>S. mansoni</i>	Baboon	1.3–2.3	Sturrock <i>et al.</i> (1984)
<i>S. mansoni</i>	Baboon	1.5–1.6	Boulanger <i>et al.</i> (1991)
<i>S. haematobium</i>	Baboon	1.2	Damian & Chapman (1983)
<i>Ascaris lumbricoides</i>	Man	0.8	Croll <i>et al.</i> (1982)
<i>Necator americanus</i>	Man	1.0	Pritchard <i>et al.</i> (1990)
<i>Heligmosomoides polygyrus</i>	Mouse	1.1	Gregory <i>et al.</i> (1990)
<i>H. polygyrus</i>	Mouse	0.8	Quinnell (1992)

We use Φ , Ω and ξ when referring to the case of monogamous mating and replace these with Φ' , Ω' and ξ' when referring to polygamous mating.

The analysis makes several underlying assumptions. We assume that all possible pairings between male and female worms actually occur. Autopsy studies and studies of experimentally infected animals suggest that this is a reasonable approximation (see Cohen, 1977; Manning & Woolhouse, unpublished data). We confine attention to a static model, ignoring complications due to the immigration and death of worms, which have been considered elsewhere (Dietz, 1975). We assume that male and female worms are distributed together as a single negative binomial distribution with mean m and parameter k . This corresponds to 'Case I' in the earlier paper (May, 1977). For schistosomes this is expected to be a reasonable approximation when hosts are typically exposed to cercariae (free-swimming infective larvae) from several different snails (the intermediate hosts) or from snails supporting mixed-sex multiple infections (Bradley & May, 1978; Woolhouse, Chandiwana & Bradley, 1990), and is most consistent with field data.

If it is assumed that all mated female worms produce eggs, then Ω and ξ can be interpreted as follows: Ω , the prevalence of mated female worms, corresponds to the fraction of hosts releasing fertilized eggs; ξ , the mean number of mated female worms per host, is related to the mean egg output per host. These are commonly used indices of the prevalence and intensity of infection with schistosomes or other parasitic helminths.

MATING PROBABILITY

If worms are distributed among hosts according to a negative binomial, with mean m and aggregation

parameter k , the probability to find exactly n worms in a given host is given by:

$$(1-\alpha)^k \frac{\Gamma(k+n)}{\Gamma(k)n!} \alpha^n. \quad (1)$$

Here Γ is the standard gamma function: $\Gamma(k+n) = (k+n-1)!$ if k is an integer, and more generally $\Gamma(k+n) = (k+n-1)(k+n-2)\dots(k+1)k\Gamma(k)$. For notational convenience we have defined α as

$$\alpha \equiv \frac{m}{(m+k)}. \quad (2)$$

Each of these n worms is female with probability q and male with probability $p = 1-q$. The probability that n worms comprise exactly i females and j males (where $i+j = n$) is therefore

$$\frac{(i+j)!}{i!j!} q^i p^j. \quad (3)$$

Putting equations (1) and (3) together, we find that the probability for a host to have exactly i female and j male worms is

$$P(i, j; q, m, k) = (1-\alpha)^k \frac{\Gamma(i+j+k)}{\Gamma(k)} \frac{(\alpha q)^i (\alpha p)^j}{i! j!}. \quad (4)$$

It is easy to show that the mean number of female worms per host (obtained by summing $iP(i, j)$ over all i and j) is mq , and that the corresponding number of males is mp , as intuition suggests. We now use equation (4) to derive expressions for the mating probability, Φ , defined above, first for the case of monogamous mating systems and second for polygamous mating.

Monogamous mating

We begin by noting that, for a strictly monogamous mating system, the total number of mated female worms must equal the total number of mated male

worms. We defined $\Phi(q; m, k)$ as the probability that a female worm is mated, so the average number of mated females per host is $\xi(q) = m\Phi(q)$. As females and males are treated symmetrically in the basic expression, equation (4), for their probability distribution, it follows that the probability for a male worm to be mated (given proportions q female and $p = 1 - q$ male) is obtained by interchanging q and p in calculations (such as those below) based on equation (4); that is, the probability for a male worm to be mated is given by $\Phi(p)$, with Φ , as always, defined to be the female mating probability. The average total number of mated male worms per host is thus $mp\Phi(p)$. We therefore have the identity

$$mq\Phi(q; m, k) = m(1 - q)\Phi(1 - q; m, k). \quad (5)$$

This will be useful in what follows. In particular, it means we need calculate only $\Phi(q)$ for $q \leq \frac{1}{2}$; $\Phi(q)$ for $q > \frac{1}{2}$ can then be obtained from equation (5).

The presentation is rather simpler if we calculate the fraction of female worms that are not mated, Ψ (i.e. $\Psi = 1 - \Phi$). If there are at least as many males as females, $i \leq j$, no females are unmated. But if there are more females than males, $i > j$, then $i - j$ of these females are unmated. It follows that, of the average number mq of females per host, the fraction remaining unmated, Ψ , is given by

$$mq\Psi(q) = \sum_{j=0}^{\infty} \sum_{i=j}^{\infty} (i - j) P(i, j; q). \quad (6)$$

Here $P(i, j; q)$ is given by equation (4), for worms distributed negatively binomially.

Substituting from equation (4) into equation (6), and writing $i = j + l$, we can obtain an explicit expression for the female mating probability, $\Phi = 1 - \Psi$, involving a double summation:

$$\Phi(q; m, k) = 1 - \frac{(1 - \alpha)^{k-1}}{\alpha k q} \sum_{l=0}^{\infty} l(\alpha q)^l \sum_{j=0}^{\infty} \frac{\Gamma(2j + l + k)}{\Gamma(k)} \cdot \frac{(\alpha^2 q p)^j}{j!(j + l)!}. \quad (7)$$

Here we have used the identity $m = \alpha k / (1 - \alpha)$, from the definition in equation (2), to write the right-hand side of equation (7) in terms of the two parameters α and k only.

Equation (7) can now be used to compute Φ , for specified values of q , k and m (i.e. q , k and α). The summation converges reasonably fast if $q \leq \frac{1}{2}$, and $\Phi(q > \frac{1}{2})$ can then be obtained directly from equation (5).

In the Appendix we derive a more compact expression for $\Phi(q)$:

$$\Phi(q; m, k) = \mathcal{J}(q) - 2(1 - q) I(k, \alpha, \gamma). \quad (8)$$

Here \mathcal{J} is defined as

$$\mathcal{J}(q) = 1, \quad \text{for } q \leq \frac{1}{2} \quad (9a)$$

$$\mathcal{J}(q) = (1 - q)/q, \quad \text{for } q > \frac{1}{2} \quad (9b)$$

and I is the integral

$$I(k, \alpha, \gamma) = \frac{(1 - \alpha)^{k+1}}{\pi} \int_0^{\pi} \frac{[\sin^2 \theta] d\theta}{[1 + \alpha\gamma \cos \theta]^{k+1} [1 + \gamma \cos \theta]}. \quad (10)$$

The parameter α is defined in terms of m and k by equation (2), and γ has been defined, again for notational convenience, as

$$\gamma \equiv 2(pq)^{\frac{1}{2}}. \quad (11)$$

This expression, equations (8)–(10), for $\Phi(q)$ is the basis for most of the useful limiting cases given immediately below, most of which cannot easily be derived directly from equation (7). If the sex ratio is 1:1, so that $q = \frac{1}{2}$ (and $\gamma = 1$), equation (10) immediately reduces to the expression given by May (1977, equation (2.15)) for this special case.

A variety of particular cases and limiting results are worth noting.

For $k = 1$, equation (8) reduces to (see Appendix):

$$\Phi(q; m, 1) = \frac{1}{2q} \left\{ 1 - \frac{1 - 4\alpha pq}{(1 - 4\alpha^2 pq)^{\frac{1}{2}}} \right\}. \quad (12)$$

Here, of course, $\alpha = m/(1 + m)$.

In the limit $k \rightarrow 0$ (i.e. $k \ll 1$), we find (see Appendix)

$$\Phi(q; m, k \ll 1) = \frac{1}{2\alpha q} [1 - (1 - 4\alpha^2 pq)^{\frac{1}{2}}]. \quad (13)$$

The correction terms for this approximation are of relative magnitude k . As always, α is defined by equation (2), $\alpha = m/(m + k)$. If $k \ll m$, then $\alpha \rightarrow 1$ and $\Phi \rightarrow \mathcal{J}(q)$, with \mathcal{J} defined by equation (9). Conversely, if $1 \gg k \gg m$, then $\alpha \ll 1$ and $\Phi \rightarrow \alpha(1 - q)$. Fig. 1C for $k = 0.1$ illustrates this behaviour, with Φ depending essentially linearly on q for values of m significantly less than k ($m = 0.01$ in Fig. 1C).

No particular simplification occurs in the opposite limit, $k \rightarrow \infty$ (Poisson distribution); we can, however, write $(1 - \alpha)^{k+1} \rightarrow e^{-m}$ and $\Gamma(2j + l + k)/[k\Gamma(k)] \rightarrow (2j + l - 1)!$ in equation (7), thus simplifying its computation somewhat.

In the limit when either q or $p = 1 - q$ tend to zero, so that $\gamma \rightarrow 0$ in equation (11), we find $I \rightarrow \frac{1}{2}(1 - \alpha)^{k+1}$ in equation (10). Substituting this into equation (8), we have for $q \rightarrow 0$:

$$\Phi(q \rightarrow 0; m, k) = 1 - (1 + m/k)^{-k-1} + \mathcal{J}(q). \quad (14)$$

Here and elsewhere, the symbol \mathcal{J} means 'of the order of'.

For $q \rightarrow 1$ ($p \rightarrow 0$), we get:

$$\Phi(q \rightarrow 1; m, k) = (1 - q) [1 - (1 + m/k)^{-k-1} + \mathcal{J}(1 - q)]. \quad (15)$$

For small average worm burdens, $m \ll k$, it can be seen (see Appendix) that

$$\Phi(q; m \ll k, k) = m(1 - q)(1 + 1/k) [1 - m(k + 2)/(2k) + \mathcal{J}(m^2)]. \quad (16)$$

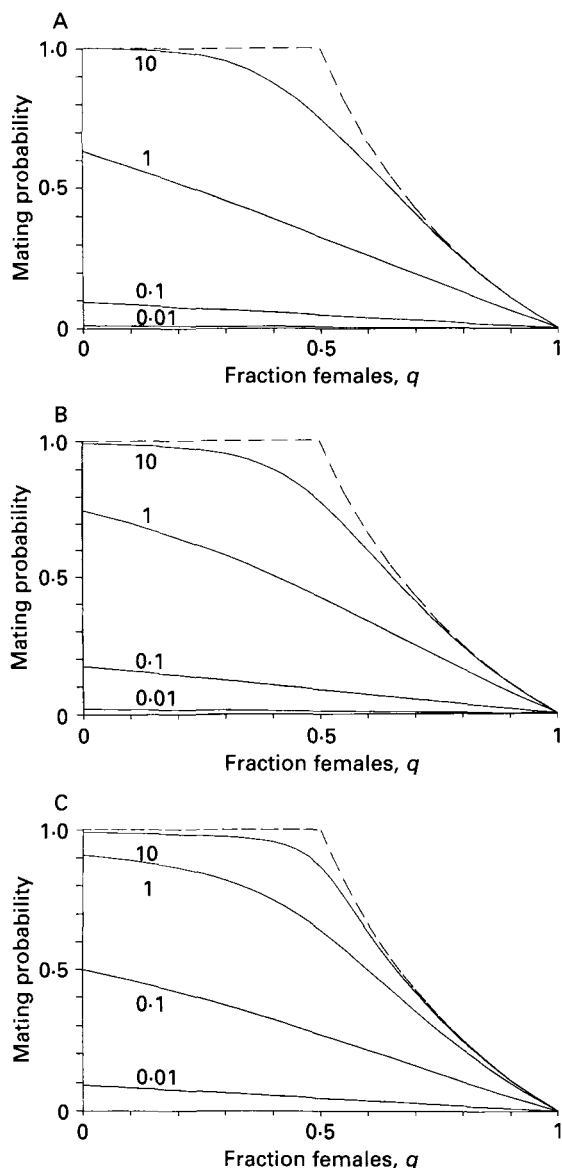


Fig. 1. The mating probability, Φ , as a function of the fraction of female worms in the population, q . The relationship is compared for different values of the mean number of worms per host (—) with $m = 0.01$ to $m = 10$ as indicated. The relationship for the limit $m \rightarrow \infty$ is also shown (---). Graphs (A)–(C) compare these relationships for distributions of worms among hosts given by a negative binomial function with different values for the aggregation parameter k : (A) $k = \infty$ (a Poisson distribution); (B) $k = 1$; (C) $k = 0.1$. All these graphs assume a monogamous mating system.

Conversely, for $m \gg 1$, we have the result that intuition would suggest:

$$\Phi(q; m \rightarrow \infty, k) \rightarrow \mathcal{J}(q), \quad (17)$$

with $\mathcal{J}(q)$ given by equation (9).

Numerical results for the relations between mating probability, Φ , and proportion of female worms, q , are shown in Fig. 1A–C for a range of values of m , for three representative values of k ($k = \infty$, 1, and 0.1). These figures illustrate the various trends and limits shown by the limiting cases discussed above.

Polygamous mating

In this case the mating probability is equivalent to the fraction of female worms found in hosts supporting one or more male worms. From equation (4), the mean number of female worms found in hosts with no male worms ($j = 0$) can be calculated simply as:

$$\sum_{i=0}^{\infty} iP(i, 0; q, m, k) = mq(1 + mp/k)^{-k-1}. \quad (18)$$

The mean number of female worms per host is mq . Therefore the fraction of female worms in hosts with no male worms is $(1 + mp/k)^{-k-1}$, and

$$\Phi'(q; m, k) = 1 - (1 + mp/k)^{-k-1}. \quad (19)$$

For the limit $k \rightarrow 0$ (or, more generally, $k \ll mp$) we obtain

$$\Phi'(q; m, k \rightarrow 0) \rightarrow 1 - (k/mp) + \dots \quad (20)$$

for $1 > q \geq 0$, and $\Phi' = 0$ for $q = 1$. For the opposite limit $k \rightarrow \infty$ (Poisson distribution), we obtain

$$\Phi'(q; m, k \rightarrow \infty) = 1 - e^{-mp} + \dots \quad (21)$$

For the limit $q \rightarrow 0$, equation (19) again converges to

$$\Phi'(q \rightarrow 0; m, k) = 1 - (1 + m/k)^{-k-1} + \mathcal{O}(q). \quad (22)$$

This is the same as equation (14) for monogamous mating, because in the limit $q \rightarrow 0$ essentially all hosts have 0 female worms, while a few have 1, and thus the differences between monogamy and polygamy do not show up. In the opposite limit $q \rightarrow 1$ ($p \rightarrow 0$), the polygamous mating probability is different from the monogamous one of equation (15):

$$\Phi'(q \rightarrow 1; m, k) = m(1 - q)(1 + 1/k)[1 - \mathcal{J}(1 - q)], \quad (23)$$

although both are zero for $q = 1$.

For small average worm burdens, $m \ll 1$, equation (19) for Φ' reduces to an expression very similar to that given above for the monogamous mating probability in this limit, equation (16):

$$\Phi'(q; m \ll 1, k) = m(1 - q)(1 + 1/k)[1 - m(1 - q)(k + 2)/(2k) + \mathcal{O}(m^2)]. \quad (24)$$

The similarity between equations (24) and (16) arises for the same reason as the similarity between equations (22) and (14): when the average number of female worms per host is low, the differences between monogamous and polygamous mating systems are, to first order, unimportant. When m is large, $m \gg 1$, $\Phi' \rightarrow 1$ for $1 > q \geq 0$ (and $\Phi' = 0$ for $q = 1$); this differs from the monogamous mating system result, equation (17), for this limit where $\Phi \rightarrow 1$ for $q \leq \frac{1}{2}$, but $\Phi \rightarrow (1 - q)/q$ for $q > \frac{1}{2}$.

The relations between $\Phi'(q)$ and q for a range of values of m are shown, for three representative values

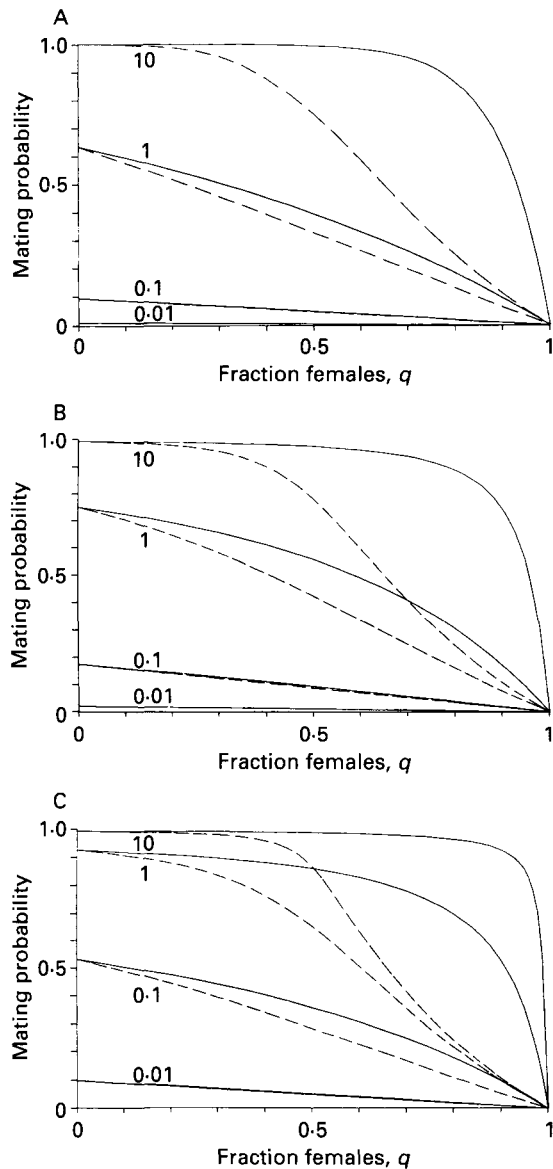


Fig. 2. As for Fig. 1A–C but comparing the mating probabilities, Φ or Φ' , as functions of the fraction of female worms in the population, q , for polygamous (Φ' , —) and monogamous (Φ , ---) mating systems. (A) $k = \infty$ (a Poisson distribution); (B) $k = 1$; (C) $k = 0.1$.

of k ($k = \infty, 1$, and 0.1) in Fig. 2A–C. Again these numerical results bear out the analytical insights set out above. Explicit comparisons between the mating probabilities for a polygamous mating system, Φ' , and those for monogamous mating, Φ , are given in Fig. 2 by showing the former as solid curves and the latter as dashed curves.

PREVALENCE OF MATED FEMALE WORMS

The prevalence of mated female worms, Ω , is simply given by the fraction of hosts supporting one or more female worms and one or more male worms. As such, Ω does not depend on whether the mating system is

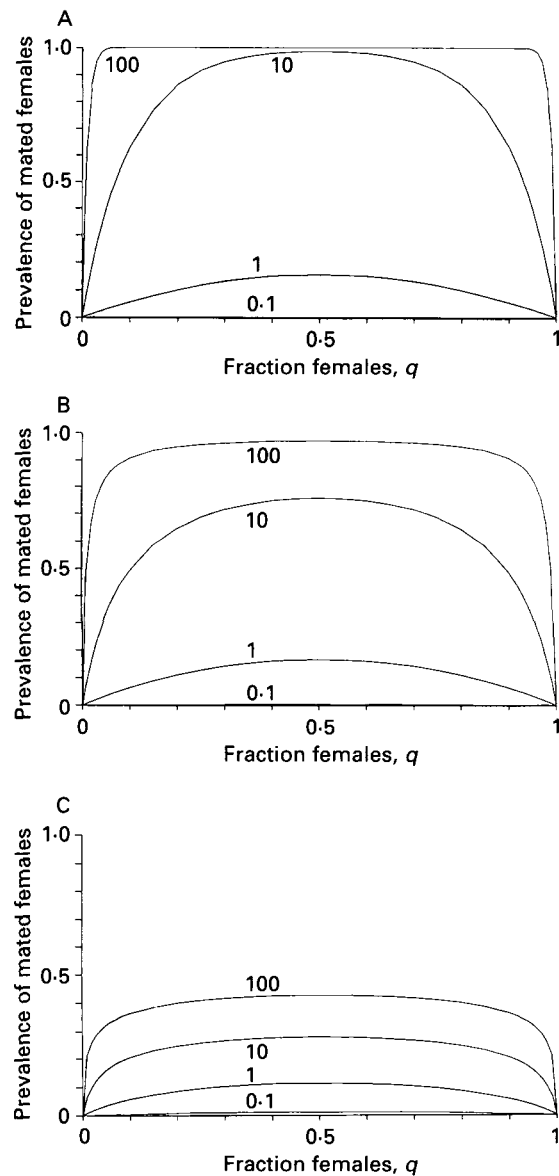


Fig. 3. The prevalence of mated female worms, Ω or Ω' , as functions of the fraction of female worms in the population, q . The relationship is compared for different values of the mean number of worms per host (—) with $m = 0.1$ to $m = 100$ as indicated. Graphs (A)–(C) compare these relationships for distributions of worms among hosts given by a negative binomial function with different values for the aggregation parameter k : (A) $k = \infty$ (a Poisson distribution); (B) $k = 1$; (C) $k = 0.1$. All these graphs apply to both a monogamous (Ω) and a polygamous (Ω') mating system.

monogamous or polygamous; it is the same for both, that is $\Omega = \Omega'$.

To calculate Ω , we first observe that the proportion of hosts supporting no worms is

$$P(0, 0; m, k, q) = (1 + m/k)^{-k}. \quad (25)$$

The proportion of hosts supporting no female worms is

$$\sum_{j=0}^{\infty} P(0, j; q, m, k) = (1 + mq/k)^{-k}. \quad (26)$$

Similarly, the proportion of hosts supporting no male worms is

$$\sum_{i=0}^{\infty} P(i, 0; q, m, k) = (1 + m(1-q).k)^{-k}. \quad (27)$$

Therefore the prevalence of mated females is given by

$$\Omega(m, k, q) = 1 - (1 + mp/k)^{-k} - (1 + mp/k)^{-k} + (1 + m/k)^{-k}. \quad (28)$$

The last of the four terms in the right-hand side of equation (28) allows for the double counting of the '0, 0' term in the second plus third terms.

For the limit $k \rightarrow \infty$ we obtain

$$\Omega(m, k \rightarrow \infty, q) = (1 - e^{-mq})(1 - e^{-mp}). \quad (29)$$

The relationships between Ω and q for a range of values of m are shown in Fig. 3A–C, for representative values of k . The value of q when Ω is a maximum, q^* , is always $q^* = 0.5$. The function is symmetrical about this value. The reason is simple. As noted above, Ω (or Ω') is the fraction of hosts harbouring one or more female worms and one or more male worms. That is, females and males enter into the calculation of Ω in a completely symmetrical way, so that Ω will be the same for proportions q females and p males or for p females and q males. Thus $\Omega(q, m, k) = \Omega(1-q, m, k)$, and hence the symmetry about $q = 0.5$.

MEAN NUMBER OF MATED FEMALE WORMS PER HOST

Monogamous mating

In this case the mean number of mated female worms per host is given by

$$\xi(q, m, k) = mq\Phi(q, m, k), \quad (30)$$

where the mating probability $\Phi(q, m, k)$ is given by equations (7) or (8).

For the limit $k \rightarrow 0$ (or, more generally, $k \ll m$) we obtain from equations (8) and (30)

$$\xi(q; m, k \ll m) = mq, \quad \text{for } q \leq \frac{1}{2} \text{ and} \quad (31a)$$

$$= m(1-q), \quad \text{for } q > \frac{1}{2}. \quad (31b)$$

The correction terms are of relative order k/m . That is to say, for small k or large m the mean number of mated females per host, $\xi(q)$, has a 'triangular' or 'tent-shaped' dependence on q .

Conversely, for small m ($m \ll 1$), we can combine equation (30) with the limiting expression, equation (16), for Φ we get

$$\xi(q; m \ll 1, k) = m^2 q(1-q)(1 + 1/k). \quad (32)$$

Here the correction terms are of relative order $m(k+2)/(2k)$. The dependence of ξ on q is thus parabolic in the limit of small m .

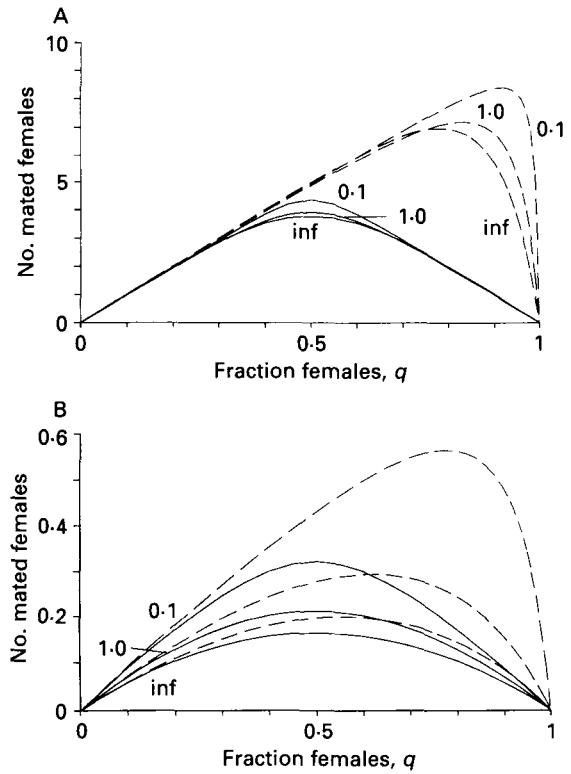


Fig. 4. The mean number of mated female worms per host, ξ or ξ' , as functions of the fraction of female worms in the population, q . The relationship is compared for monogamous (ξ , —) and polygamous (ξ' , ---) mating systems and for different values of the aggregation parameter k (lines with $k = 0.1$ to $k = \infty$ as indicated). Graphs (A) and (B) compare these relationships for different total mean worm burdens per host: (A) $m = 10$; (B) $m = 1$.

Fig. 4A and B shows numerical results for the dependence of $\xi(q)$ on q , for a range of values of k and two representative values of m ($m = 10$ and 1). These curves further illustrate the analytical results just discussed for limiting cases.

Notice that $\xi(q)$ for monogamous mating is always symmetrical, about its maximum value, which is at $q^* = 0.5$. As observed at the beginning of our discussion of mating probabilities, for a monogamous mating system the number of mated females is necessarily equal to the number of mated males. It follows that $\xi(q, m, k) = \xi(1-q, m, k)$ for all m and k ; hence the symmetry about $q^* = 0.5$. To establish that ξ always has its maximum at $q^* = 0.5$ for monogamous mating, we need only add the observation that ξ is a monotonically increasing function of q for $q < \frac{1}{2}$.

Polygamous mating

In this case the mean number of mated female worms per host is given by

$$\xi'(q; m, k) = mq\Phi'(q; m, k), \quad (33)$$

where the mating probability $\Phi'(m, k, q)$ is given by equation (19).

For the limit $k \rightarrow 0$ (or, more generally, $k \ll m$), equation (20) for Φ' can be substituted into equation (33) to give

$$\xi'(q; m, k \rightarrow 0) = mq, \quad (34)$$

for all $1 > q \geq 0$. For $q = 1$, $\xi' = 0$.

The relations between $\xi'(q)$ and q are also shown in Fig. 4A and B, for a range of values of k and for representative values of m ($m = 10$ and 1).

The function $\xi'(q)$ is asymmetric, with its maximum value attained for a value of q^* in the range $1 > q^* > \frac{1}{2}$. More explicitly, the value of q^* which maximizes ξ' is found in the usual way by differentiating ξ' and seeking solutions of $d\xi'/dq = 0$. After some rearrangement, this leads to an implicit relation for q^* :

$$(1 + m(1 - q^*)/k)^{k+2} = 1 + m(q^* + 1/k). \quad (35)$$

The value of q^* depends on both m and k . As can be seen from Fig. 4, the value of q^* increases as m increases (tending asymptotically to unity as $m \rightarrow \infty$). Likewise it can be seen that q^* decreases with increasing k ; that is, q^* increases as aggregation becomes more pronounced (in the limit $k \rightarrow 0$, $q^* \rightarrow 1 - (k/m)^{\frac{1}{2}}$).

DISCUSSION

Several interesting points emerge from this analysis.

The mating probability, Φ or Φ' , is a decreasing function of the fraction of all worms that are female, q . Mating probabilities approach unity if the mean number of worms per host is high, $m \geq 10$ say, and/or if the distribution of worms is highly aggregated, $k < 1$, and/or if the sex ratio of worms is male biased, q significantly less than one half. These conditions are probably typical of human (but not necessarily non-human – see Theron *et al.* 1992) schistosome infection in the field.

The mating probability also depends upon the mating system. Polygamous mating obviously results in higher mating probabilities, but the effect is not marked for low worm burden (low m), and/or a highly aggregated distribution of worms (low k), and/or male-biased sex ratios (low q). Conversely, the effect of polygamous mating on the mating probability may be substantial for combinations of high worm burdens and female biased sex ratios, $q > \frac{1}{2}$ (cf. May, 1977).

The prevalence of mated female worms is relatively insensitive to the fraction of all worms that are female, q , especially if the mean number of worms per host is very high or very low, $m \gg 1$ or $m \ll 1$, and/or the worm distribution is highly aggregated, $k < 1$. This holds unless the sex ratio is highly male or female biased, $q \rightarrow 0$ or $q \rightarrow 1$. The prevalence of mated female worms is independent of the mating system, because the presence of both male and female worms in the same host ensures that at least one female worm is mated.

The mean number of mated female worms per host is, in the case of monogamous mating, at a maximum when the sex ratio is unity, $q = \frac{1}{2}$. In contrast, for the case of polygamous mating the maximum occurs for a female biased sex ratio, $q > \frac{1}{2}$, and is dependent on the abundance and distribution of worms among hosts, i.e. on m and k . These results imply that the male biased sex ratios reported for schistosomes result in a sub-maximal abundance of mated female schistosomes. More generally, the results also suggest that abundance and distribution of worms among hosts may influence the selective pressures favouring the evolution of monogamous or polygamous mating systems in parasitic helminths, or any other dioecious organism distributed in a patchy environment.

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APPENDIX

In this Appendix, we first show how the compact and relatively illuminating equation (8) for the monogamous mating probability, $\Phi(q; m, k)$, is obtained from the straightforward but untidy equation (7), which gives Φ in terms of a double summation. We then indicate how the various limiting cases given in the main text are derived.

We begin by observing that $\Gamma(2j + l + k)$ in equation (7) can, by definition, be rewritten as

$$\Gamma(2j + l + k) = \int_0^\infty x^{2j+l+k-1} e^{-x} dx. \quad (A1)$$

The second term on the right-hand side of equation (7), which is the probability to be unmated, Ψ , can now be rewritten as

$$\Psi = \frac{(1-\alpha)^{k+1}}{\alpha q k \Gamma(k)} \int_0^\infty e^{-x} x^{k-1} dx \sum_{l=0}^\infty l(\alpha q x)^l \sum_{j=0}^\infty \frac{(\alpha^2 x^2 q p)^j}{j!(j+l)!}. \quad (A2)$$

The sum over j can be rewritten in terms of the modified Bessel function of order l :

$$I_l(z) = (z/2)^l \sum_{j=0}^\infty \frac{(z/2)^{2j}}{j!(j+l)!}. \quad (A3)$$

Putting $z = 2\alpha x(qp)^{\frac{1}{2}}$, this gives

$$\Psi = \frac{(1-\alpha)^{k+1}}{\alpha q k \Gamma(k)} \int_0^\infty e^{-x} x^{k-1} dx \sum_{l=0}^\infty l(q/p)^{l/2} I_l(2\alpha x \sqrt{[qp]}). \quad (A4)$$

The modified Bessel function can alternatively be expressed as

$$I_l(z) = \frac{(-1)^l}{\pi} \int_0^\pi e^{-z \cos \theta} \cos(l\theta) d\theta. \quad (A5)$$

Substituting this expression into equation (A4), with

$z = 2\alpha x(pq)^{\frac{1}{2}}$, and performing the integral over x , we arrive at

$$\Psi = \frac{(1-\alpha)^{k+1}}{\alpha q k \pi} \sum_{l=0}^{\infty} \int_0^{\pi} \frac{\cos(l\theta) d\theta}{(1+\alpha\gamma \cos \theta)^k} l(-1)^l (q/p)^{l/2}. \quad (\text{A6})$$

Here α is, as always, defined by equation (2), and $\gamma = 2(qp)^{\frac{1}{2}}$ is the parameter defined in equation (11).

The subsequent analysis is simpler if, before summing over l , we note that $l \cos(l\theta) = d(\sin(l\theta))/d\theta$ and thence perform a partial integration in equation (A6):

$$\Psi = -\frac{\gamma(1-\alpha)^{k+1}}{q\pi} \int_0^{\pi} \frac{(\sin \theta) d\theta}{(1+\alpha\gamma \cos \theta)^{k+1}} \sum_{l=0}^{\infty} (-1)^l \sin(l\theta) (q/p)^{l/2}. \quad (\text{A7})$$

If $q < \frac{1}{2}$, then $q/p < 1$, and the sum over l is well-behaved. Things are more complicated if $q > \frac{1}{2}$ and $q/p > 1$ (we need to deal with Cauchy principal values), but these difficulties can be avoided by calculating $\Phi(q) = 1 - \Psi(q)$ for $q < \frac{1}{2}$, and then using the identity given in equation (5) to derive $\Phi(q > \frac{1}{2}) = [(1-q/q) \Phi(1-q)]$, with $(1-q) < \frac{1}{2}$. So, writing $\sin(l\theta) = \text{Im}(e^{il\theta})$, we can easily perform the summation over l when $q < \frac{1}{2}$, to get

$$\Psi = -\frac{\gamma(1-\alpha)^{k+1}}{q\pi} \int_0^{\pi} \frac{(\sin \theta) d\theta}{(1+\alpha\gamma \cos \theta)^{k+1}} \text{Im} \left\{ \frac{1}{1+(q/p)^{\frac{1}{2}} e^{i\theta}} \right\}. \quad (\text{A8})$$

That is (using the definition $\gamma = 2(qp)^{\frac{1}{2}}$),

$$\Psi = \frac{2p(1-\alpha)^{k+1}}{\pi} \int_0^{\pi} \frac{(\sin \theta)^2 d\theta}{(1+\alpha\gamma \cos \theta)^{k+1} (1+\gamma \cos \theta)}. \quad (\text{A9})$$

Equation (A9) for $\Psi(q)$ is simply $2pI(k, \alpha, \gamma)$, with I defined by equation (10). We therefore have derived the expression of equation (8) for $\Phi(q)$ when $q < \frac{1}{2}$ (in which case $\mathcal{J} \equiv 1$). As mentioned above, for $q > \frac{1}{2}$ we find, from equation (5), that $\Phi(q > \frac{1}{2}) = [(1-q)/q] \Phi(1-q)$. That is, to get an expression for $\Phi(q > \frac{1}{2})$ we interchange p and q in our expression for $\Phi(q < \frac{1}{2})$, and then multiply the result by p/q . In equation (A9) for $\Psi(q < \frac{1}{2})$, q and p enter symmetrically into $\gamma \equiv 2(qp)^{\frac{1}{2}}$, and so the only change resulting from the interchange of q and p is that the 'p' outside the integral in equation (A9) becomes 'q'. When we then multiply $\Phi(1-q) = 1 - \Psi(1-q)$ by p/q , the first term on the right-hand side becomes $(1-q)/q$, while the second reverts identically to the expression given by equation (A9); hence we arrive at equation (8) of the main text, for $q > \frac{1}{2}$.

Limiting cases

For $k = 1$, the integral $I(k, \alpha, \gamma)$ takes the particular form

$$\Psi = \frac{1}{\pi(m+1)^2} \int_0^{\pi} \frac{(\sin \theta)^2 d\theta}{(1+\alpha\gamma \cos \theta)^2 (1+\gamma \cos \theta)}. \quad (\text{A10})$$

Here $\alpha = m/(m+1)$. Evaluation of this trigonometric integral is routine, if tedious. One direct method is to write $z = e^{i\theta}$, so that we are integrating a function of the complex variable z , around the unit circle in the complex plane. The integral can then be expressed in terms of the residues at the poles of the integrand (details available on request). The result, for $q < \frac{1}{2}$, is given by equation (12) in the main text. If we now interchange q and p in equation (12), and multiply the result by p/q to get $\Phi(q > \frac{1}{2})$, we obviously get identically the same expression. Thus equation (12) gives $\Phi(q; m, 1)$ for all $1 \geq q \geq 0$.

For $k \leq 1$, the factors $(1-\alpha)^{k+1}$ and $(1+\alpha\gamma \cos \theta)^{-k-1}$ in equation (10) for $I(k, \alpha, \gamma)$ can be approximated by $(1-\alpha)$ and $(1+\alpha\gamma \cos \theta)^{-1}$, respectively; the correction terms are clearly of relative magnitude k . The integral I thus reduces to

$$I(k \leq 1, \alpha, \gamma) \simeq \frac{(1-\alpha)}{\pi} \int_0^{\pi} \frac{(\sin \theta)^2 d\theta}{(1+\alpha\gamma \cos \theta)(1+\gamma \cos \theta)}. \quad (\text{A11})$$

This integral can be evaluated by the techniques used to derive equation (12) from equation (A10) above, or alternatively it can be evaluated directly by using relationships between equations (A10) and (A11). The result is

$$I(k \leq 1, \alpha, \gamma) = \frac{[(1-\alpha^2\gamma^2)^{\frac{1}{2}} - \alpha(1-\gamma^2)^{\frac{1}{2}} - (1-\alpha)]}{(\alpha\gamma^2)}. \quad (\text{A12})$$

Substituting this into equation (8) for $\Phi(k \leq 1)$, and noticing that $(1-\gamma^2)^{\frac{1}{2}} = |p-q|$, we arrive at equation (13) in the main text.

Notice that this derivation makes no assumption about whether k (itself small) is larger or smaller than m ; that is, about whether α is small or close to unity. For very small m , such that $\alpha \ll 1$, routine expansion of the right-hand side of equation (13) gives $\Phi \rightarrow \alpha p(1+\alpha^2 pq + \dots)$. The opposite limit of $k \ll m$ (that is, $\alpha \rightarrow 1$) is trickier: we find $\Phi \rightarrow \mathcal{J}(q)$, with correction terms of relative order k/m if $|p-q|$ is larger than $(k/m)^{\frac{1}{2}}$, and of relative order $(k/m)^{\frac{1}{2}}$ otherwise.

If either $q \rightarrow 0$ or $p \rightarrow 0$ ($q \rightarrow 1$), it follows that $\gamma \rightarrow 0$. The denominator in equation (10) can then be expanded as a power series in γ , and the integrals easily evaluated. In this way, simple expressions are obtained for Φ when $q \rightarrow 0$ or $q \rightarrow 1$: equations (14) and (15).

The limit $m \ll k$ (which usually means small m) can most easily be studied via equation (7) for $\Phi(q)$; in this limit, $\alpha \approx m/k \ll 1$, and so only the first few terms in the summations in equation (7) are needed. Hence equation (16) is easily derived.

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