

## **Interspecific competition among macroparasites in a density-dependent host population**

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**Abstract.** We analyze the dynamics of a community of macroparasite species that share the same host. Our work extends an earlier framework for a host species that would grow exponentially in the absence of parasitism, to one where an uninfected host population is regulated by factors other than parasites. The model consists of one differential equation for each parasite species and a single density-dependent nonlinear equation for the host. We assume that each parasite species has a negative binomial distribution within the host and there is zero covariance between the species (exploitation competition). New threshold conditions on model parameters for the coexistence and competitive exclusion of parasite species are derived via invadability and stability analysis of corresponding equilibria. The main finding is that the community of parasite species coexisting at the stable equilibrium is obtained by ranking the species according to the minimum host density  $H^*$  above which a parasite species can grow when rare: the lower  $H^*$ , the higher the competitive ability. We also show that ranking according to the basic reproduction number  $Q_0$  does not in general coincide with ranking according to  $H^*$ . The second result is that the type of interaction between host and parasites is crucial in determining the competitive success of a parasite species, because frequency-dependent transmission of free-living stages enhances the invading ability of a parasite species while density-dependent transmission makes a parasite very sensitive to other competing species. Finally, we show that density dependence in the host population entails a simplification of the portrait of possible outcomes with respect to previous studies, because all the cases resulting in the exponential growth of host and parasite populations are eliminated.

**Key words:** Host-parasite dynamics – Density dependence – Parasite community – Interspecific competition

## 1 Introduction

The majority of cross-sectional surveys of parasites in host populations shows that in general more than one parasite species is present (Dobson and Keymer, 1990; Bush and Holmes, 1986; Goater and Bush, 1988; Goater et al., 1987). It is therefore important to assess which demographic parameters of each parasite species determine the co-existence with, or the exclusion of, other parasite species competing for the same host. While the analysis of the interactions between a single parasite species and its host has received a lot of attention since the pioneering work by Anderson and May (1978), the study of the forces which shape parasitic communities is still in its infancy. An important step toward the identification of the relationships among the demographic parameters which determine the ability of a parasite species to invade a parasitic community has been accomplished by Dobson (1985). By using a two-species version of the Anderson and May model, he derived a number of conditions that determine when a parasite species can invade a community and when a species is likely to be squeezed out. More recently, Dobson and Roberts (1994) and Roberts and Dobson (1995) have extended the earlier framework for two parasite species and one host, to one for an arbitrary number of parasite species. The resulting diagram in parameter space which describes the different functioning modes of the model is rather complex. When two species of parasites are considered, there are twelve different modes in which the two species may be both excluded, exclude one another or coexist and regulate or not their host's growth. A limitation of these models of parasitic community is that the host species is capable of indefinite Malthusian growth when parasite-free. The argument behind this assumption is that wild animals are often not in equilibrium, for instance when they are colonizing new territory. However, this is not always the case and, as a matter of fact, any population, even if unregulated by parasites, will eventually find a bound to its growth as a consequence of the reduction of either life expectancy or reproduction, or both, due to competition for food and resources. The hypothesis of density dependence in the host rate of increase is therefore more general and flexible, as it accommodates both the exponential increase phase at low population densities and the slowdown due to intraspecific competition at high densities. Nothing is lost if a density dependent model for the host is employed, whereas much can be gained in terms of simplicity and novelty of the results. In particular, the Malthusian assumption has been shown to unnecessarily complicate the dynamics of the host-parasite interaction even when only one parasite species is present (e.g., Diekmann and Kretzschmar, 1991). In

fact, it results in two phenomena that are not possible if density dependence is assumed: (1) the hosts and the parasites grow without bound, but the mean number of parasites per host tends to zero (the so-called “washout” effect); (2) both hosts and parasites grow exponentially with the mean parasite burden per host tending to a positive finite limit (Anderson and May, 1978). If several parasite species are considered this complication is compounded. A first goal of our paper is to show that the introduction of host density dependence in models of interspecific competition between macroparasites leads to a simplification of the possible results, because these phenomena of unbounded growth are no longer possible. A second goal is to demonstrate that the competitive ability of a parasite is not linked uniquely to the basic reproduction number  $Q_0$  (expected number of adult parasites produced, in the absence of density-dependent constraints acting on the parasite, by a typical adult during its entire period of reproductive maturity, Smith and Scott, 1994). In fact, Roberts and Dobson (1995) showed that a stable community of parasites can be built by first ranking the parasite species according to their  $Q_0$ 's and then eliminating species with lowest  $Q_0$  by a conditional branching algorithm. Here, we show that the ranking should be done according to  $H^*$ , the host density above which each parasite species can grow when rare. This ranking can be quite different to that based on  $Q_0$  to the point that species with the highest  $Q_0$  can be excluded from competition. A third goal is a detailed analysis, for the case of two parasite species, of how the size and shape of the region of coexistence of parasites 1 and 2 in parameter space is influenced not only by  $Q_0$ , but also by the degree of aggregation of parasites within the host, their mortality, the contact rate and the longevity and fecundity of their host.

## 2 The host-parasite model with density dependence in the host

Parasite distributions in host populations may be highly heterogeneous, with most animals harboring few or no parasites and only a few being infected by a large number of parasites. In the last twenty years, many different models have been proposed to reflect the clumpy distribution of parasites inside their hosts (Anderson and May, 1978; Kretzschmar, 1993; Barbour and Kafetzaki, 1991; Grafen and Woolhouse, 1993). Frequently a negative binomial distribution is assumed, which is characterized by two parameters: the average number  $M$  of parasites per host and a clumping parameter  $k$  which is related to the variance  $\sigma^2$  of the parasite burden by  $\sigma^2 = M + M^2/k$ .

The general macroparasite model consists of an infinite system of differential equations for the variables  $p_i(t)$ , the numbers of hosts at time  $t$  harboring  $i$  parasites. The system can be derived by using assumptions typical for a birth-immigration-death process (see Diekmann and Kretzschmar, 1991). A simple approximation of the infinite system is obtained by considering only the host and parasite densities,  $H$  and  $P$ , respectively. Under the assumption that the additional mortality rate caused to one host by  $i$  parasites is proportional to  $i$ , while the host reproductive success decreases exponentially with  $i$ , one can easily obtain (see, e.g., Pugliese and Rosà, 1995) that the dynamics of

$$H(t) = \sum_{i=0}^{\infty} p_i(t) \quad P(t) = \sum_{i=0}^{\infty} i p_i(t)$$

are governed by the equations

$$dH/dt = a \sum_{i=0}^{\infty} p_i \zeta^i - bH - \alpha P \quad (1.1)$$

$$dP/dt = \phi H - (\mu + b)P - \alpha \sum_{i=0}^{\infty} i^2 p_i \quad (1.2)$$

where  $a$  is the per capita birth rate of parasite-free hosts,  $\zeta$  a parameter describing the reduction of birth rate due to the presence of parasites ( $0 < \zeta \leq 1$ ),  $b$  the rate of host mortality in the absence of parasites,  $\alpha$  the increase in host mortality rate due to a single parasite,  $\phi$  the infection rate,  $\mu$  the rate of mortality of adult parasites. This system has been analyzed by several authors under many different assumptions: density independence of host demography ( $a$  and  $b$  are constant), no influence of parasites on host birth rate ( $\zeta = 1$ ), frequency or density dependent infection rate ( $\phi$  is proportional to  $P/H$  or to  $P$ ). Although early work by Tallis and Layton (1966, 1969) considered different possible distributions for parasites inside the host, the most frequent assumption, as stated above, is that the distribution is negative binomial with a constant clumping parameter. In this way the moment Eqs. (1) can be closed and used as a brute-force approximation of the infinite system. Haderler and Dietz (1984) showed that there is broad agreement between this approximation and a more complex partial differential model of parasite-host systems. More recently, the negative binomial assumption has been relaxed by Kretzschmar (1993), Kretzschmar and Adler (1993), Pugliese et al. (1998) under further simplifying hypotheses.

In this paper we assume a general kind of density dependence in the host with birth and death rate being a decreasing and increasing

function of density, respectively. The infection rate takes on a form (Anderson and May, 1978) which encompasses both frequency and density dependence transmission:

$$\phi = \lambda P / (H_0 + H) .$$

This expression is derived (see Diekmann and Kretzschmar, 1991) from a submodel that considers transmission of parasites through free-living stages: via a time-scale argument it can be shown that  $H_0$  is a semisaturation constant that equals  $\gamma/\beta$  with  $\gamma$  being the rate of mortality of parasite larvae and  $\beta$  the contact rate, while  $\lambda$  is the rate of production of transmission stages per adult parasite. We will assume no influence of parasites on host birth rate ( $\xi = 1$ ), as it is well-known that  $\xi < 1$  may destabilize the host-parasite interaction with considerable complications for the dynamics (May and Anderson, 1978; Roberts et al., 1995; Pugliese and Rosà, 1995) which would tremendously increase when more than one parasite species are considered. Finally, we assume a negative binomial distribution of parasites inside the host with constant clumping parameter, because the relaxation of this hypothesis would further complicate the model of interspecific competition.

To sum up, the model we consider is as follows:

$$dH/dt = R(H)H - \alpha P \quad (2.1)$$

$$dP/dt = \lambda PH / (H_0 + H) - (\mu + \alpha + b(H))P - \alpha(P^2/H)(k + 1)/k \quad (2.2)$$

where  $R(H)$  is the per capita rate of increase of the host population and  $k$  the clumping parameter.  $R(H) = a(H) - b(H)$  is a decreasing function that equals zero at  $H = K$ , the carrying capacity,  $a(H)$  is a non-negative decreasing function of host density and  $b(H)$  is a nonnegative increasing function of  $H$ . All the other parameters are assumed to be strictly positive and constant.

To analyze the behavior of model (2) it is convenient to introduce  $M = P/H$ , the mean parasite load per host, as a state variable. Equations (2) can then be restated as follows

$$dH/dt = [R(H) - \alpha M]H \quad (3.1)$$

$$dM/dt = [\lambda H / (H_0 + H) - (\mu + \alpha + a(H)) - \alpha M/k]M . \quad (3.2)$$

Although we consider a general kind of density dependence, the dynamics of model (3) in the positive quadrant are basically well known (Anderson, 1980; Pugliese and Rosà, 1995) and are briefly reviewed here. There are three possible equilibria: (i)  $H = 0, M = 0$ ; (ii)  $H = K, M = 0$ ; (iii)  $H = \bar{H}, M = \bar{M}$ , where  $\bar{M} = R(\bar{H})/\alpha$  and  $\bar{H}$  is the

positive solution of

$$\lambda H / (H_0 + H) - (\mu + \alpha + a(H)) - R(H) / k = 0 . \tag{4}$$

It is easy to check that  $\bar{H}$  exists and is unique, because the left-hand side of (4) is an increasing function of  $H$ , which is negative for  $H = 0$  and goes to infinity for  $H \rightarrow \infty$ . Note that the third equilibrium is biologically feasible and distinct from the second (i.e.,  $\bar{M} > 0$ ) only if  $\bar{H} < K$ , i.e., only if  $\lambda K / (H_0 + K) - (\mu + \alpha + b(K))$  is positive, as one can easily check from Eq. (4).

The stability properties of the three equilibria are easily assessed by linearization. The  $(0, 0)$  equilibrium is a saddle for any value of the parameters. The  $(K, 0)$  equilibrium eigenvalues are  $K(dR(K)/dH)$  and  $\lambda K / (H_0 + K) - (\mu + \alpha + a(K))$ . Therefore this equilibrium is a stable node if  $\lambda K / (H_0 + K) - (\mu + \alpha + a(K))$  is negative (which occurs if the third equilibrium is nonpositive), otherwise it is a saddle. Biologically, one can say that, following the introduction of a single parasite into a population of  $K$  hosts, the parasite population can spread if the intrinsic rate of increase  $\lambda K / (H_0 + K) - (\mu + \alpha + a(K))$  is positive, or (remember that  $a(K) = b(K)$ ) if

$$Q_0 = \frac{\lambda K}{(H_0 + K)(\mu + \alpha + b(K))} > 1 .$$

$Q_0$  (the basic reproduction number) is usually interpreted as the expected number of adult parasites produced, in the absence of density dependent constraints, by a typical parasite during its entire period of reproductive maturity. Under this condition the hosts will eventually settle to a coexistence equilibrium with their parasites. In fact it is easy to prove that the third equilibrium, when positive, is also stable, because

$$\begin{aligned} \text{tr } \mathbf{L} &= \bar{H} \frac{dR(\bar{H})}{dH} - \alpha \bar{M} / k < 0 \\ \det \mathbf{L} &= -\frac{\alpha}{k} \frac{dR(\bar{H})}{dH} \bar{H} \bar{M} + \alpha \left[ \frac{\lambda H_0}{(H_0 + \bar{H})^2} - \frac{da(\bar{H})}{dH} \right] \bar{H} \bar{M} > 0 , \end{aligned}$$

where  $\mathbf{L}$  is the Jacobian matrix and  $\text{tr } \mathbf{L}$  and  $\det \mathbf{L}$  are the trace and the determinant of  $\mathbf{L}$ , respectively.

### 3 More than one parasite species competing for the same host

Let us now consider the case of many parasite species harbored in the same host. Equations (2) can be extended to the case of one host and

many parasites (as shown by Roberts and Dobson, 1995, for the case when the host growth rate is density independent). Using assumptions typical for a birth-immigration-death process, one can again derive an infinite system of differential equations for the variables  $p_{i_1 i_2 \dots i_n}(t)$ , the numbers of hosts at time  $t$  harboring  $i_1$  parasites of species 1,  $i_2$  parasites of species 2,  $\dots$ ,  $i_n$  parasites of species  $n$ . Under the assumption that the additional mortality rate caused to one host by the parasitic loads of the different species is a linear combination of  $i_1, i_2, \dots, i_n$ , while the host reproductive success decreases exponentially with a linear combination of  $i_1, i_2, \dots, i_n$ , one can obtain the dynamics of the host density  $H$  and the parasite densities  $P_j, j = 1, 2, \dots, n$  and thus generalize Eqs. (1) to the case of many parasite species. The model is given by

$$dH/dt = a(H) \sum_{i_1 \geq 0, i_2 \geq 0, \dots, i_n \geq 0} p_{i_1, i_2, \dots, i_n} \zeta_1^{i_1} \zeta_2^{i_2} \dots \zeta_n^{i_n} - b(H)H - \sum_{m=0}^{\infty} \alpha_m P_m \tag{5.1}$$

$$dP_j/dt = -(\mu_j + b(H))P_j + \phi_j H - H \sum_{m=0}^{\infty} \alpha_m E[i_m i_j] \tag{5.2}$$

where  $E[ ]$  indicates expectation with respect to the joint frequency distribution of parasitic loads in the host population and the various symbols are obviously extended to the case of many parasite species. System (5) will be simplified and closed under some further assumptions. First, we suppose there is no influence of parasites on the host reproductive success:  $\zeta_1 = \zeta_2 = \dots = \zeta_n = 1$ . Second, we assume no cross correlation in the process of the host getting infected through free-living stages. This implies that the infection rates  $\phi_j$  are simply given by

$$\phi_j = \lambda_j P_j / (H_{0j} + H)$$

with  $\lambda_j$  and  $H_{0j}$  being positive constants depending only on species  $j$ . Third, we hypothesize the usual negative binomial distribution which establishes a relationship between the variance of the parasite burden of each species and the mean burden, namely

$$E[i_j^2] = P_j/H + P_j^2/k_j H^2 + P_j^2/H^2$$

where  $k_j$  is the clumping parameter for each species. The fourth assumption regards the covariance between the loads of parasite species  $m$  and  $j$ , with  $m \neq j$ . Dobson (1985) classified the interaction between two parasite species that utilize the same host as exploitation

or interference competition. In the former case the parasite species utilize the resources coming from the same host independently, and hence the covariance is zero. In the latter the presence of one species directly influences the probability of the presence of the other, and hence there is a positive (synergistic) or negative (antagonistic) covariance between their distribution. Synergism or antagonism are, respectively, in favor or against coexistence of parasite species. Therefore, we confine our analysis to exploitation competition, because this a sort of “neutral hypothesis” for exploring the structure of a community of parasite species. Exploitation competition implies that

$$E[i_m i_j] = E[i_m]E[i_j] = P_m P_j / H^2, \quad m \neq j.$$

Therefore, we finally obtain

$$dH/dt = R(H)H - \sum_m \alpha_m P_m \tag{6.1}$$

$$dP_j/dt = P_j \{ \lambda_j H / (H_{0j} + H) - (\mu_j + \alpha_j + b(H)) - \sum_m \alpha_m P_m / H - \alpha_j P_j / k_j H \}, \quad j = 1, \dots, n \tag{6.2}$$

Note that compared with the model of exploitation competition considered by Roberts and Dobson (1995) this one is more general in two respects: (i) instead of Malthusian growth a general kind of density dependence in the parasite-free host population is considered and (ii) the semisaturation constants  $H_{0j}$  are different for different species. However, Roberts and Dobson (1995) included interference competition which is neglected here. As in the previous section, it is more convenient to use the mean parasite loads  $M_j = P_j/H, j = 1, 2, \dots, n$ , instead of the parasite densities. The corresponding system of equations is given by

$$dH/dt = [R(H) - \sum_i \alpha_i M_i] H$$

$$dM_j/dt = \{ \lambda_j H / (H_{0j} + H) - (\mu_j + \alpha_j + a(H)) - (\alpha_j / k_j) M_j \} M_j, \quad j = 1, 2, \dots, n$$

By letting

$$\Gamma_j(H) = \lambda_j H / (H_{0j} + H) - (\mu_j + \alpha_j + a(H))$$

one obtains

$$dH/dt = [R(H) - \sum_i \alpha_i M_i] H \tag{7.1}$$

$$dM_j/dt = \{ \Gamma_j(H) - (\alpha_j / k_j) M_j \} M_j, \quad j = 1, 2, \dots, n \tag{7.2}$$

$\Gamma_j(H)$  can be interpreted as the rate of invasion of parasite species  $j$ , namely the rate of increase of  $j$  in a population of  $H$  hosts when the species is initially rare ( $M_j \approx 0$ ). The  $\Gamma_j(H)$  are increasing functions of  $H$  such that  $\Gamma_j(0) < 0$ . To study the possible coexistence of some of the  $n$  parasite species, from now on we will assume that each of the  $n$  parasite species can spread in a parasite-free host population. This implies that  $\Gamma_j(K) > 0, j = 1, 2, \dots, n$ , and from what we have seen in the previous section this entails that, for each pair host-parasite  $j$ , there exists a corresponding strictly positive equilibrium which is stable. Our goal is now to find a community of parasite species that enjoys the property of possessing a biologically meaningful (nonnegative, because some species might be competitively excluded) equilibrium that is stable. More precisely, we define a feasible assemblage of parasite species in the following way.

**Definition 1.** *A nonempty set of parasite species  $S \subseteq \{1, 2, \dots, n\}$  is feasible if Eqs. (7) possess an equilibrium  $H$  such that  $0 < H < K, M_j > 0$  for  $j \in S, M_j = 0$  for  $j \notin S$ .  $\square$*

It is easy to derive that  $S$  is feasible if and only if there exists a value  $H_S$  of host density such that

$$\sum_{i \in S} k_i \Gamma_i(H_S) = R(H_S) \quad (8.1)$$

$$\Gamma_j(H_S) > 0 \quad \text{for } j \in S \quad (8.2)$$

Note that, even if  $S$  is nonfeasible, provided it is not empty, Eq. (8.1) has a unique solution  $H_S$  such that  $0 < H_S < K$ . This easily follows from the properties of  $R$  and the  $\Gamma_j$ . We recall that from these same properties (specifically from  $\Gamma_j(K) > 0$ ) follows that all the singletons  $\{1\}, \{2\}, \dots, \{n\}$  are feasible. The feature we now define is invadability of a community of species.

**Definition 2.** *We say that a feasible set  $S'$  (i.e.,  $\Gamma_j(H_S) > 0$  for  $j \in S'$ ) can invade a feasible set  $S$  if*

$$\Gamma_j(H_S) > 0 \quad \text{for all } j \in S'$$

In other words, a parasite community  $S'$  can invade another community  $S$  if each parasite species of  $S'$  can invade  $S$ . We can now establish the main properties of communities of parasite species in terms of feasibility, invadability and, finally, stability.

**Lemma 1.** *If  $S$  is a feasible set and  $S' \subset S$  and nonempty, then  $S'$  is feasible and  $H_S < H_{S'}$ .*

*Proof.* Since  $S$  is feasible, the equation

$$\sum_{i \in S} k_i \Gamma_i(H) - R(H) = 0$$

has a solution  $H_S$  such that  $\Gamma_i(H_S) > 0, \forall i \in S$ . Consider the corresponding equation for  $S' \subset S$

$$\sum_{i \in S'} k_i \Gamma_i(H) - R(H) = 0$$

which has the solution  $H_{S'}$ .

At  $H = H_S$  we have

$$\sum_{i \in S'} k_i \Gamma_i(H_S) - R(H_S) < \sum_{i \in S} k_i \Gamma_i(H_S) - R(H_S) = 0 .$$

Therefore  $H_{S'} > H_S$  and, as the  $\Gamma_i$  are increasing functions of  $H$ ,  $\Gamma_i(H_{S'}) > \Gamma_i(H_S) > 0 \forall i \in S'$ . This proves that  $S'$  is feasible.  $\square$

**Lemma 2.** *If  $S$  and  $S'$  are feasible sets of parasites and  $H_{S'} < H_S$ , then  $S'$  can invade  $S$ , namely  $\Gamma_i(H_S) > 0 \forall i \in S'$ .*

*Proof.* As  $H_{S'} < H_S$ , we have

$$\Gamma_i(H_S) > \Gamma_i(H_{S'}) \quad \forall i \in S'.$$

$S'$  being feasible entails  $\Gamma_i(H_{S'}) > 0$ , whence follows the assertion.  $\square$

**Lemma 3.** *If  $S$  and  $S'$  are feasible sets of parasites and  $S'$  can invade  $S$ , then  $S'$  can invade any proper subset  $S'' \subset S$ .*

*Proof.* By Lemma 1,  $S'' \subset S$  is feasible and  $H_{S''} > H_S$ . As  $\Gamma_i(H_S) > 0 \forall i \in S'$ , it follows that

$$\Gamma_i(H_{S''}) > \Gamma_i(H_S) > 0 \quad \forall i \in S',$$

namely  $S'$  can invade  $S''$ .  $\square$

**Lemma 4.** Consider a feasible set  $S$  of parasites and any two proper subsets  $S' \subset S$  and  $S'' \subset S$ . Then  $S'$  can invade  $S''$  and vice versa.

*Proof.* By Lemma 1 both  $S'$  and  $S''$  are feasible and  $H_{S'} > H_S, H_{S''} > H_S$ . It follows that, by Lemma 2, any species of  $S$ , hence of  $S'$ , can invade  $S''$  and any species of  $S$ , hence of  $S''$ , can invade  $S'$ .  $\square$

As all the  $\Gamma_j(H)$  are increasing functions of  $H$  such that  $\Gamma_j(0) < 0$  and  $\Gamma_j(K) > 0$ , there exists a unique  $H_j^*$ , with  $0 < H_j^* < K$ , which is a root of  $\Gamma_j(H)$ .  $H_j^*$  is the host density above which parasite species  $j$  can increase when rare. Consider the minimum  $H_{\min}$  of the  $H_j^*$ . Then  $\Gamma_j(H_{\min}) \leq 0 \forall j$ , which implies that for any set of species  $S \neq \emptyset$  one has

$$\sum_{i \in S} k_i \Gamma_i(H_{\min}) \leq 0.$$

Therefore the density  $H_S$  at equilibrium corresponding to a feasible set  $S$  of parasites must be greater than  $H_{\min}$ . We can now outline the structure of a stable community of parasites, namely a community that is feasible, can invade and cannot be invaded by any other feasible community. This goal is achieved by the following procedure, which is similar to that of Roberts and Dobson (1995):

### Procedure

1. Order the  $n$  parasite species according to  $H_j^*$ :  $H_1^* \leq H_2^* \leq \dots \leq H_n^*$ .
2. Set  $m = n$
3. Find  $H^{(m)}$  that is a solution to the following equation

$$\sum_{i=1}^m k_i \Gamma_i(H) = R(H)$$

4. If  $H_m^* < H^{(m)}$  then
5.  $\{1, 2, \dots, m\}$  is the stable community
6. Else
7.  $m \leftarrow m - 1$
8. Go to step 3
9. End

The procedure defines the stable community of parasite species as detailed in the following theorem.

**Theorem 1.** *Under the assumption that each parasite can spread in a parasite-free host, namely  $\Gamma_j(K) > 0$ , the community  $\{1, 2, \dots, m\}$  obtained with the above procedure*

- (i) *is nonempty ( $m \geq 1$ ),*
- (ii) *is feasible,*
- (iii) *cannot be invaded by species  $m + 1, \dots, n$  not belonging to it,*
- (iv) *can invade any other feasible community,*
- (v) *is such that any nonempty subset of its species is feasible and any two subsets can invade each other.*

*Proof.* (i) As  $H_S > H_{\min} = H_1^*$  for any  $S \neq \emptyset$ , and  $\{1\}$  is feasible because  $\Gamma_1(K) > 0$ , we have that  $H_1 = H^{(1)} > H_1^*$ . Therefore in the worst case the procedure will end with  $m = 1$ .

(ii) As the procedure stops as soon as  $H_m^* < H^{(m)}$ , it follows that

$$\Gamma_j(H^{(m)}) > \Gamma_j(H_m^*) \geq 0 \quad \text{for } j = 1, \dots, m.$$

(iii) For  $m + 1 \leq i \leq n$ , we have  $H_1^* \geq H^{(i)}$ , which implies  $\Gamma_i(H^{(i)}) \leq 0$ . As  $H^{(i)}$  satisfies, by definition, the equation

$$\sum_{j=1}^i k_j \Gamma_j(H^{(i)}) - R(H^{(i)}) = 0$$

it follows that

$$\sum_{j=1}^{i-1} k_j \Gamma_j(H^{(i)}) - R(H^{(i)}) \geq 0.$$

This in turn implies that  $H^{(i-1)} \leq H^{(i)}$ . In other words we have  $H^{(m)} \leq H^{(m+1)} \leq \dots \leq H^{(n)}$ . As  $H_{m+1}^* \geq H^{(m+1)}$  one can conclude that

$$\Gamma_j(H^{(m)}) \leq \Gamma_j(H^{(m+1)}) \leq \Gamma_j(H_{m+1}^*) \leq 0 \quad \text{for } m + 1 \leq j \leq n.$$

(iv) Consider a feasible community  $S$ . If  $S \subset \{1, 2, \dots, m\}$ , then  $H_S > H^{(m)}$  by Lemma 1 and  $\{1, 2, \dots, m\}$  invades  $S$  by Lemma 2. Otherwise  $S$  contains at least one species  $j$  with  $m + 1 \leq j \leq n$ . As  $S$  is feasible, it follows that  $H_S > H_j^*$ , because we must have  $\Gamma_j(H_S) > 0$ . Since  $H_1^* \leq H_2^* \leq \dots \leq H_m^* \leq H_j^*$ , it turns out that  $\Gamma_i(H_S) > 0$  for  $i = 1, \dots, m$ .

(v) the assertion follows from point (ii) above, Lemma 1 and Lemma 4 □

The stable community of parasites is also stable in terms of its equilibrium as shown in the following theorem.

**Theorem 2.** *The equilibrium*

$$H = H^{(m)}$$

$$M_j = \frac{k_j}{\alpha_j \Gamma_j}(H^{(m)}) \equiv M_j^{(m)} \quad 1, 2, \dots, m$$

$$M_j = 0 \quad j = m + 1, m + 2, \dots, n$$

corresponding to the community obtained with the above Procedure is asymptotically stable.

*Proof.* Because of Theorem 1, one can state that  $0 < H^{(m)} < K$ ,  $M_j^{(m)} > 0$ ,  $j = 1, 2, \dots, m$ . The Jacobian matrix  $J$  evaluated at the



**Theorem 3.** Consider a feasible set  $S$  of parasites and the corresponding value  $H_S$  of the hosts at equilibrium. Let  $H^{(m)}$  be the host density at equilibrium for the stable community of parasites. Then we have  $H^{(m)} \leq H_S$  for any feasible  $S$ .

*Proof.* If  $S$  is contained in  $\{1, 2, \dots, m\}$  the assertion follows trivially from Lemma 1. Suppose then that  $S$  is not contained in  $\{1, 2, \dots, m\}$  and  $H^{(m)} > H_S$ . Then, by Lemma 2,  $S$  would invade  $\{1, 2, \dots, m\}$ , namely one of the species  $m + 1, m + 2, \dots, n$  would invade  $\{1, 2, \dots, m\}$ , which contradicts Theorem 1.  $\square$

According to Theorem 3 one could find the stable parasite community by considering all the feasible sets of parasites and finding out the one characterized by the minimum  $H_S$ . Clearly, the procedure based on the ranking of the  $H^*$  is much more simple and efficient. However, Theorem 3 has an obvious conceptual importance as it points out an optimization principle: the stable community of parasite species is the one that minimizes the host density.

*Remark 1.* Note that the converse of Lemma 3 is not true in general. For instance, if we have three feasible species (i.e.,  $Q_{0j} > 1$ ,  $j = 1, 2, 3$ ), and species 2 and 3 can constitute a feasible community, the fact that species 1 can separately invade both 2 and 3 does not imply that it can invade the set  $\{2, 3\}$ . In fact, consider a host species with rate of increase  $R(H) = r(1 - H/K)$ ,  $r = 0.1$ ,  $K = 1$ , and death rate  $b(H) = 0.1 + 0.05H$ , and three parasite species with  $\lambda_1 = 2.5$ ,  $\mu_1 = 0.5$ ,  $\alpha_1 = 0.01$ ,  $H_{01} = 0.8$ ,  $k_1 = 0.05$ ,  $\lambda_2 = 2.8$ ,  $\mu_2 = 1$ ,  $\alpha_2 = 0.01$ ,  $H_{02} = 0.2$ ,  $k_2 = 0.08$ ,  $\lambda_3 = 4.5$ ,  $\mu_3 = 2$ ,  $\alpha_3 = 0.08$ ,  $H_{03} = 0.1$ ,  $k_3 = 0.03$ . Species 1 can invade species 2, because  $H_1^* = 0.308 < H_2 = 0.426$ ; species 1 can invade species 3, because  $H_1^* = 0.308 < H_3 = 0.536$ . However, species 1 cannot invade the set  $\{2, 3\}$ , because  $H_1^* = 0.308 > H_{2,3} = 0.292$ . Therefore the establishment of a parasite species in a host population depends on the particular assemblage of species already present there.  $\square$

*Remark 2.* Suppose that  $S$  is feasible and  $S = S' \cup S''$  with  $S'' \neq \emptyset$ ,  $S' \neq \emptyset$ ,  $S' \cap S'' = \emptyset$ . Lemma 4 implies that  $S'$  can invade  $S''$  and vice versa. Conversely, if  $S'$  and  $S''$  are feasible and  $S'$  can invade  $S''$  and  $S''$  can invade  $S'$ ,  $S' \cup S''$  may not be feasible in general. One should not be deceived by the fact that this property is instead true if we consider just two parasite species, as shown in the subsequent section. In practice, when  $n \geq 3$  reciprocal invadability of assemblages of parasite species

does not imply that all these species can coexist at equilibrium. For instance, with the same parameter values reported in Remark 1, the assemblage of species 1 and 2 is feasible because  $H_{12} = 0.395$  is larger than both  $H_1^* = 0.308$  and  $H_2^* = 0.151$ . Species 3 can invade the subset  $\{1, 2\}$  ( $H_3^* = 0.102 < H_{12}$ ), the subset  $\{1, 2\}$  can invade species 3 ( $H_1^* < H_3 = 0.536$  and  $H_2^* < H_3$ ), but the assemblage  $\{1, 2, 3\}$  is not feasible, as shown in remark 1.  $\square$

*Remark 3.* Note that Roberts and Dobson (1995) construct the stable community by ranking species according to their basic reproduction numbers  $Q_{0j} = \lambda_j/(\mu_j + \alpha_j + a)$ . Obviously their procedure can be obtained from ours by letting the carrying capacity go to  $\infty$  and setting  $H_{0j} = H_0$ . In fact, in this special case

$$H_j^* = H_0/(Q_{0j} - 1)$$

and the two kinds of ranking coincide. But whenever the host carrying capacity is finite or larval mortalities and contact rates differ among parasite species, ranking according to  $H_j^*$  can be quite different than ranking according to  $Q_{0j}$  even if the Malthusian  $Q_{0j} = \lambda_j/(\mu_j + \alpha_j + a)$  are replaced by their density-dependent counterparts  $\lambda_j K/(H_{0j} + K)$  ( $\mu_j + \alpha_j + a(K)$ ). As a result the stable community of parasite species can be totally different and, in particular, the core species may not be those with high reproduction number. For instance, with the parameter values given in Remark 1, species 1 attains the highest reproduction number ( $Q_{01} = 2.104$ ,  $Q_{02} = 2.011$ ,  $Q_{03} = 1.834$ ) and yet we showed that it is outcompeted by the community of species 2 and 3. In fact, core species are characterized by low  $H_j^*$  ( $H_2^* = 0.151$ ,  $H_3^* = 0.102$  vs.  $H_1^* = 0.308$ ).  $\square$

#### 4 The case of two parasite species

We now consider in greater detail the case of two parasite species with logistic growth in the host, because this allows deeper insight in the influence of various characteristics of both the host and the parasite species on the possible coexistence between parasites. However, the case of two parasite species is in a way special, because reciprocal invadability implies coexistence, which is not true in general, as pointed out in Remark 2. We have the following

**Theorem 4.** *Let  $n = 2$  and assume that both parasite species 1 and 2 can invade a parasite-free host. If species 1 can invade species 2 and vice versa, the two species coexist at a stable equilibrium.*

*Proof.* Rank the species according to the procedure of Theorem 1:  $H_1^* \leq H_2^*$ . As both species can establish in a parasite-free host,  $H_1^* < H_1$  and  $H_2^* < H_2$ , where  $H_1$  and  $H_2$  are the host densities at the stable equilibrium when only species 1 or species 2 are present. On the other hand, the reciprocal invadibility implies that  $H_1^* < H_2$  and  $H_2^* < H_1$ . In practice both  $H_1$  and  $H_2$  are bigger than  $H_2^*$ . Consider now the equation

$$\sum_{j=1}^2 k_j \Gamma_j(H) - R(H) = 0$$

whose solution is  $H^{(2)}$ . We have

$$\sum_{j=1}^2 k_j \Gamma_j(H_2^*) - R(H_2^*) = k_1 \Gamma_1(H_2^*) - R(H_2^*) < 0$$

which implies  $H_2^* < H^{(2)}$ . Therefore, according to Theorems 1 and 2 the community of species  $\{1, 2\}$  is feasible and the corresponding equilibrium is stable.  $\square$

The region of parameters in which coexistence is possible can be calculated by assuming that the host population grows according to a logistic equation. If one assumes that  $R(H) = r(1 - H/K)$  and the host mortality is density independent, one gets:

$$dH/dt = [r(1 - H/K) - \alpha_1 M_1 - \alpha_2 M_2]H \tag{10.1}$$

$$dM_1/dt = \{ \lambda_1 H / (H_{01} + H) - (\mu_1 + \alpha_1 + b) - (\alpha_1 / k_1) M_1 - r(1 - H/K) \} M_1 \tag{10.2}$$

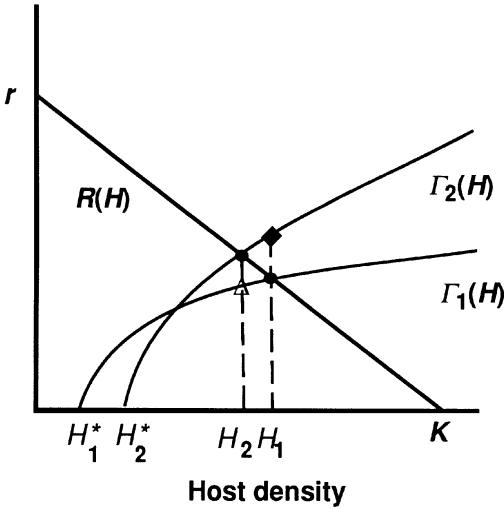
$$dM_2/dt = \{ \lambda_2 H / (H_{02} + H) - (\mu_2 + \alpha_2 + b) - (\alpha_2 / k_2) M_2 - r(1 - H/K) \} M_2, \tag{10.3}$$

where  $r$  and  $b$  are positive constants. The determination of the possible equilibria and the characterization of invadibility is graphically represented in Fig. 1.

The results following from combinations of different demographic parameters of host and parasite species are shown in Fig. 2. It displays the regions in the  $Q_{01} - Q_{02}$  plane where different equilibrium solutions are realized. In this case the reproduction numbers are given by

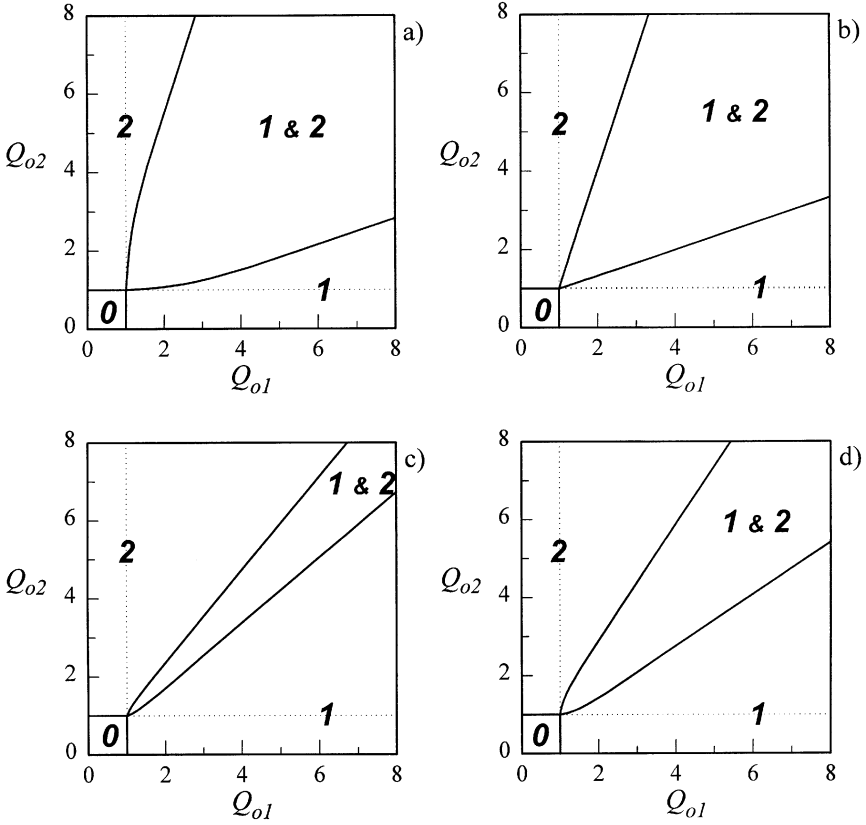
$$Q_{0j} = \frac{\lambda_j K}{(H_{0j} + K)(\mu_j + \alpha_j + b)}.$$

If both  $Q_0$ 's are  $< 1$  the unique stable equilibrium is characterized by zero parasite densities and the host at its carrying capacity. If  $Q_{01} > 1$



**Fig. 1.** Graphical determination of the result of competition between parasite species 1 and 2 for the same host.  $R(H) = r(1 - H/K)$  is the per capita growth of the hosts when disease-free.  $\Gamma_1(H) = \lambda_1 H / (H_{01} + H) - (\mu_1 + \alpha_1 + b) - r(1 - H/K)$  and  $\Gamma_2(H) = \lambda_2 H / (H_{02} + H) - (\mu_2 + \alpha_2 + b) - r(1 - H/K)$  are the invasion rates of each parasite species. The roots  $H_1^*$  and  $H_2^*$  of  $\Gamma_1(H)$  and  $\Gamma_2(H)$  determine the values of host density above which each parasite species can increase when initially rare. The intersection (●) between  $\Gamma_1(H)$  and  $R(H)$  determines the density  $H_1$  of hosts when they harbor only parasite 1 and have reached a coexistence equilibrium with it. The intersection between  $\Gamma_2(H)$  and  $R(H)$  determines the density  $H_2$  of hosts when they harbor only parasite 2 and have reached a coexistence equilibrium with it. If  $\Gamma_1(H_2)$  is positive (cf.  $\Delta$  in the figure and note that  $H_2 > H_1^*$ ) parasite 1 can invade the complex host-parasite 2, namely it can increase when rare inside a host which is already harboring parasite 2. If  $\Gamma_2(H_1)$  is positive (cf.  $\blacklozenge$  in the figure and note that  $H_1 > H_2^*$ ) parasite 2 can invade the complex host-parasite 1, namely it can increase when rare inside a host which is already harboring parasite 1. Note that one can infer that parasite 1 can invade parasite 2 directly, because  $H_1^* < H_2^*$ . When there is reciprocal invadability (as it occurs in the figure), parasite 1 and 2 will coexist inside the same host population

and  $Q_{02} < 1$ , the unique stable equilibrium is characterized by zero density of parasite 2 and positive densities of the host and parasite 1. We have similar results when  $Q_{01} < 1$  and  $Q_{02} > 1$ . If both  $Q_{01} > 1$  and  $Q_{02} > 1$ , the parasites can coexist or exclude each other depending on the values not only of  $Q_{01}$  and  $Q_{02}$ , but of the other parameters too. More precisely, given the values of the parameters that do not determine  $Q_{01}$  and  $Q_{02}$ , the boundaries of the coexistence region (indicated as 1 and 2 in Fig. 2) can be easily found via the invadability conditions. In fact, within this region parasite species 1 must invade parasite species 2 and vice versa according to Theorem 4. Therefore, the curve separating the region of coexistence 1 and 2 from the region 1, where



**Fig. 2a-f.** Region in the plane  $Q_{o1} - Q_{o2}$  for which different steady states of model (10) are possible. In region 0, both  $Q_{o1}$  and  $Q_{o2}$  are smaller than 1, thus neither parasite can establish in the host population. In region 1, parasite 2 is excluded and parasite 1 is at a positive and stable equilibrium with its host. In region 2, parasite 1 is excluded. In region 1 and 2 parasites 1 and 2 coexist at a positive and stable equilibrium with their host. **a** Parameters set to:  $k_1 = k_2 = 0.01$ ,  $\rho_1 = \rho_2 = 0.02$ ,  $\eta_1 = \eta_2 = 0.1$ ; these values may refer to a medium size herbivore ( $\sim 50-100$  kg), whose carrying capacity is about 5 individuals/km<sup>2</sup>, life expectancy ca. 10 y and fertility rate equal to  $0.3 \text{ y}^{-1}$  (according to Peters, 1983) with both parasites having frequency dependent transmission of the infective stage, high level of aggregation, life expectancy ca. 1 month and inducing a mortality of  $0.01 \text{ HP}^{-1} \text{ y}^{-1}$ . **b** Density-dependent transmission of the infective stage:  $k_1 = k_2 = 0.01$ ,  $\rho_1 = \rho_2 = 0.02$ ,  $\eta_1 = \eta_2 = 10$ ; **c** Low parasite aggregation:  $k_1 = k_2 = 0.1$ ,  $\rho_1 = \rho_2 = 0.02$ ,  $\eta_1 = \eta_2 = 0.1$ . **d** Low host reproductive rate:  $k_1 = k_2 = 0.01$ ,  $\rho_1 = \rho_2 = 0.005$ ,  $\eta_1 = \eta_2 = 0.1$ . **e** Parasite 1 has shorter life expectancy which is compensated by higher fertility when  $Q_{o1} = Q_{o2}$ :  $k_1 = k_2 = 0.01$ ,  $\rho_1 = 0.02$ ,  $\rho_2 = 0.2$ ,  $\eta_1 = \eta_2 = 0.1$ . **f** Frequency-dependent transmission of parasite 1 and density dependent transmission of parasite 2:  $k_1 = k_2 = 0.01$ ,  $\rho_1 = \rho_2 = 0.02$ ,  $\eta_1 = 0.1$ ,  $\eta_2 = 10$

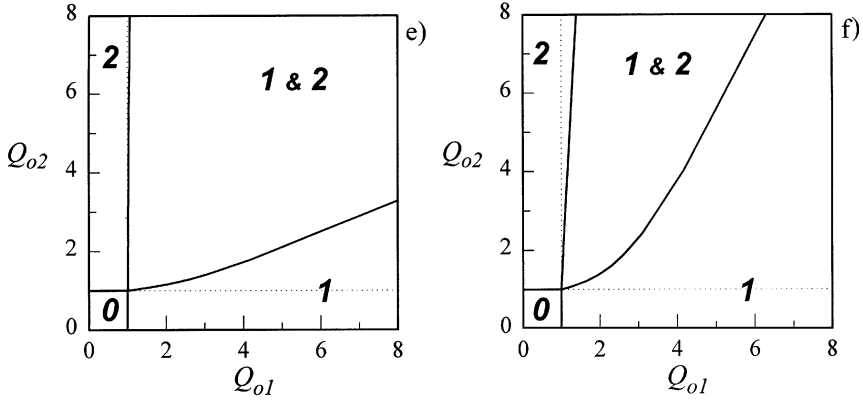


Fig. 2. (continued)

parasite 2 is unable to invade a parasite-free host or is competitively excluded by parasite 1, is defined by the equations

$$\lambda_1 H_1 / (H_{01} + H_1) - (\mu_1 + \alpha_1 + b) - (k_1 + 1)r(1 - H_1/K)/k_1 = 0 \tag{11.1}$$

$$\lambda_2 H_1 / (H_{02} + H_1) - (\mu_2 + \alpha_2 + b) - r(1 - H_1/K) = 0 . \tag{11.2}$$

The first equation simply defines the equilibrium density  $H_1$ , while the second states that parasite 2 can neither increase nor decrease when rare. Note that Eqs. (11) define a curve parametrically in  $H_1$ , with  $H_1$  varying between zero and the carrying capacity. Therefore, by introducing the following nondimensional parameters

$$x = H_1/K, \quad \rho_1 = r/(\mu_1 + \alpha_1 + b), \quad \rho_2 = r/(\mu_2 + \alpha_2 + b)$$

$$\eta_1 = H_{01}/K, \quad \eta_2 = H_{02}/K,$$

Eqs. (11) can be restated, after some cumbersome calculations, as

$$Q_{01} = \frac{\left[ 1 + \frac{k_1 + 1}{k_1} \rho_1(1 - x) \right] (x + \eta_1)}{(1 + \eta_1)x} \quad 0 < x \leq 1 .$$

$$Q_{02} = \frac{[1 + \rho_2(1 - x)](x + \eta_2)}{(1 + \eta_2)x}$$

Note that the parameter  $x$  is just the ratio between the population density of the host and its carrying capacity  $K$  at the parasite-free equilibrium; thus  $x$  is maximum and equals 1 at the invasion threshold (where the reproduction number is 1) and decreases for increasing values of  $Q_{01}$ . Similar equations define the curve that separates the region of coexistence 1 and 2 from the region 2 where parasite 1 is

excluded. The introduction of nondimensional parameters points out that the coexistence between species 1 and 2 depends upon 8 parameters:  $Q_{01}$ ,  $Q_{02}$ ,  $\rho_1$ ,  $\rho_2$ ,  $\eta_1$ ,  $\eta_2$ ,  $k_1$ ,  $k_2$ .

Figure 2 shows how the shape of the coexistence region in the  $Q_{01}$ – $Q_{02}$  plane is affected by the degree of clumping of the parasites, their mortalities in the different stages, the contact rate and the host fertility. In general, high values of  $H_0$ , i.e., high values of larval mortality and/or low values of the contact rate, tend to straighten up the boundaries of the coexistence region (Fig. 2b). On the other hand, high values of  $k$  (low clumping in the parasite distribution) do not favor coexistence, because region 1 and 2 is smaller (Fig. 2c). Note that the coexistence region vanishes as the clumping parameters  $k_1$  and  $k_2$  tend to infinity (random distribution of parasites inside their hosts). Also, low host fertility compared to parasite mortality favors competitive exclusion, because the region 1 and 2 is smaller (Fig. 2d). Moreover, parasites with short life expectancy but high fertility rate may exhibit a distinct competitive advantage with respect to parasites with low fertility rate and long generation time (Fig. 2e). Finally, parasites with frequency-dependent transmission of free living stages ( $H_0 \approx K$ ) are better off than parasites with similar  $Q_0$  but density-dependent transmission of infective larvae ( $H_0 \gg K$ , Fig. 2f). Figure 2f clearly shows that ranking parasite competitive ability according to  $Q_0$  is incorrect: for example, parasite species 2 with  $Q_{02} = 8$  is excluded by parasite species 1 with  $Q_{01} = 7$ .

## 5. Conclusions

This paper presents some innovative results with respect to previous studies on interspecific competition between macroparasites (Dobson and Roberts, 1994; Roberts and Dobson, 1995), which considered Malthusian growth for the parasite-free host and equal semisaturation constants for the infection rates of different parasite species. First, our results show that in species exploitatively competing for the same host, the community of parasite species coexisting at the stable equilibrium is obtained by ranking the species not according to  $Q_0$ , but according to the minimum host density  $H^*$  above which a parasite species can grow when rare. Therefore, the basic reproduction number  $Q_0$  may not be an effective way to determine competitive ability and species with higher  $Q_0$  can be outcompeted by species with lower  $Q_0$ .

In fact, the balance between parasite fertility, virulence and parasite mortality may be tricky and is not always reflected in the actual value of the reproduction number.  $Q_0$  is the overall number of secondary

infections produced by an adult parasite *over its entire reproductive life* in absence of density dependent constraints. This parameter is qualitatively similar to the reproductive number in Malthusian age-structured populations, and thus is not discounted by generation length. It is well known that, given the same life-time reproductive success, a population with short life expectancy but high fertility may actually have higher growth rate (Malthusian fitness) than a population with long generation time and low fertility. Demographers have long recognized that generation length and age at first reproduction have in general a greater impact than the reproductive number on the intrinsic growth rate of a population (Birch, 1948; Cole, 1954). In a similar way, the parasite population with the highest growth rate may not be the one with the highest  $Q_0$  (De Leo and Gatto, 1996; Frank, 1996). Moreover,  $Q_0$  is defined for the equilibrium of the uninfected population. As reported by Ebert and Herre (1996), once a parasite spreads, the host population is no longer at its disease free equilibrium and  $Q_0$  is not a good indicator for the final fate of the parasite species. As a consequence, selection in parasite communities may not operate to maximize  $Q_0$  (Ebert and Herre, 1996). On the other hand we have pointed out (Theorem 3) that the stable parasite community is the one that minimizes the corresponding host density at equilibrium. If host is considered as a resource for the parasites, this minimization principle is the same that holds for competition systems of one resource and several consumers (Tilman, 1982) or one prey and several predators (Matessi and Gatto, 1984). There is a difference, however, between predators, or consumers, and parasites competing for the same resource. Coexistence at equilibrium for predators is not possible (competitive exclusion principle), whereas it is possible for several parasite species. The key-factor in the competitive coexistence of several parasite species is their clumpy distribution inside the host population.

Second, frequency-dependent transmission of the free-living stages enhances the competing ability of a parasite species. When transmission is density-dependent ( $H_0 \gg K$ ), the transmission success of the infective stages is very sensitive to variations in host density due to other competing parasites. As a result, a parasite species might not be able to sustain itself in the population if another species substantially reduces the density of the host. On the contrary, when  $H_0 \ll K$  (frequency-dependent transmission) the rate of spread of the parasitic infection may not even depend upon the actual density of the host population. Whether transmission is actually frequency- or density-dependent is a matter of debate. Dobson and Roberts (1994) report values of  $H_0$  comparable to that of the host carrying capacity, thus suggesting that frequency-dependent transmission may actually be

more common in communities of some helminth parasites. As for intestinal nematodes, De Leo and Dobson (1999) argue that a combination of high parasite fertility, high mortality of free living stages and low contact rate may actually lead to values of  $H_0$  much greater than  $K$ . If this is the case, density-dependent transmission should be the norm in natural communities of intestinal nematodes.

The final result of our paper is that the portrait of possible outcomes in the case of two parasite species competing for the same host is simplified with respect to the one derived by Dobson and Roberts (1994), because the introduction of host density dependence eliminates all those cases resulting in exponential growth of host and parasite populations. In fact, only four outcomes are possible: (i) the host is parasite free; (ii) parasite 1 and the host coexists at equilibrium, with parasite 2 not being able to invade the host or being competitively excluded by parasite 1; (iii) parasite 2 coexists at equilibrium with the host and parasite 1 is absent; (iv) parasite 1, parasite 2 and host coexist at equilibrium. These results may become considerably more complex if the host reproductive success is affected by the parasitic load ( $\xi_1$  and  $\xi_2$  smaller than unity), because oscillatory coexistence is then possible. Very preliminary results (De Leo et al., 1996) are available, but the bifurcation analysis is quite complicated.

The present study does not investigate the effect of interference competition, as defined by Dobson (1985). The possibility that interactive or non-interactive processes may shape community structure has been continually debated in ecology (Schoener, 1986). Empirical studies present evidence for both synergistic and antagonistic interactions among parasite species (Lotz and Font, 1991; Haukisalmi and Henttonen, 1993). Yet, a simulation study by Janovy et al. (1990) shows that positive and negative interactions may actually play little role in shaping a natural community of parasites. Roberts and Dobson (1995) suggest that interactions between parasites and their hosts are more important in determining community structure than direct interactions among parasite species: the coexistence region of a parasite community is only slightly modified by the positive or negative interactions between parasites. We thus think that our basic findings should not be greatly affected by the introduction of interference competition: the results presented in this paper are representative of a large class of parasitic species with direct transmission and demonstrate that the interaction of individual life histories of both host and parasites determine the actual structure of a parasite community.

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## References

- Anderson, R. M., Depression of host population abundance by direct life cycle macroparasites. *J. theor. Biol.*, **82**, 283–311 (1980)
- Anderson, R. M. and May, R. M., Regulation and stability of host-parasite population interactions – I Regulatory processes. *J. Anim. Ecol.*, **47**, 219–247 (1978)
- Barbour, A. D. and Kafetzaki, M., Modelling the overdispersion of parasite loads. *Math Biosci.*, **107**, 249–253 (1991)
- Birch, L. C., The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.*, **17**, 15–26 (1948)
- Bush, A. O. and Holmes, J. C., Intestinal helminths of lesser scaup duck: an interactive community. *Can. J. Zool.*, **64**, 142–152 (1986)
- Cole, L. C., The population consequences of life history phenomena. *Quart. Rev. Biol.*, **29**, 103–137 (1954)
- De Leo, G. A. and Dobson, A. P., Allometry and the population of parasitic nematodes and their hosts. In preparation (1999)
- De Leo, G. A. and Gatto, M., Models of optimal body size in parasites of wild animals, Proceedings of the 7th Congress of the Italian Society of Ecology, Naples, September 1996
- De Leo, G., Fava, M. and Gatto, M., Models of interspecific competition between macroparasites, Second International Symposium on Mathematics and Environment, Naples, September 1996
- Diekmann, O. and Kretzschmar, M., Patterns in the effects of infectious diseases on population growth. *J. Math. Biol.*, **29**, 539–570 (1991)
- Dobson, A., The population dynamics of competition between parasites. *Parasitology*, **91**, 317–347 (1985)
- Dobson, A. P. and Keymer, A. E., Population dynamics and community structure of parasitic helminths. In B. Shorrochs and I. R. Swingland (eds), *Living in a Patchy Environment*, pp. 107–126, Oxford: Oxford University Press, 1990
- Dobson, A. P. and Roberts M., The population dynamics of parasitic helminth communities. *Parasitology*, **109**, S97–S108 (1994)
- Ebert, D. and Herre, E. A., The evolution of parasitic diseases. *Parasitology Today*, **2**(3), 96–101 (1996)
- Frank, S. A., Models of parasite virulence. *Q. Rev. Biol.*, **71**, 37–78 (1996)
- Grafen, A. and Woolhouse, M. E. J., Quantification of parasite aggregation: a simulation study. *Acta Trop.*, **54**, 131–139 (1993)
- Goater, C. P. and Bush, A. O., Intestinal helminth communities in long-billed curlews: the importance of congeneric host-specialists. *Holar. Ecol.*, **11**, 140–145 (1988)
- Goater, C. P., Esch, G. W. and Bush, A. O., Helminth parasites of sympatric salamanders: ecological concepts at infracommunity, component and compound community levels. *Am. Mid. Nat.*, **118**, 289–300 (1987)
- Hadeler, K. P. and Dietz, K., Population dynamics of killing parasites which reproduce in the host. *J. Math. Biol.*, **21**, 45–65 (1984)

- Haukiskalmi, V. and Henttonen, H., Coexistence in helminths of the bank vole *Clethrionomys glareolus*, I. patterns of co-occurrence. *J. Anim. Ecol.*, **62**, 221–229 (1993)
- Janovy Jr, J., Ferding, M. T. and McDowell, M. A., A model of dynamic behavior of a parasite species assemblage. *J. Theor. Biol.*, **142**, 517–529 (1990)
- Kretzschmar, M., A renewal equation with a birth-death process as a model for parasite infections. *J. Math. Biol.*, **27**, 191–221 (1989)
- Kretzschmar, M., Comparison of an infinite dimensional model for parasitic diseases with a related 2-dimensional system. *J. Math. Anal. Appl.*, **176**, 235–260 (1993)
- Kretzschmar, M. and Adler, F., Aggregated distributions in models for patchy populations. *Theor. Pop. Biol.*, **43**, 1–30 (1993)
- Lotz, J. M. and Font W. F., The role of positive and negative interspecific associations in the organization of communities of intestinal helminths of bats. *Parasitology*, **103**, 127–138 (1991)
- Matessi, C. and Gatto, M., Does *K*-selection imply prudent predation? *Theor. Pop. Biol.*, **25**, 347–363 (1984)
- May, R. M., and Anderson, R. M., Regulation and stability of host-parasite population interactions – II. Destabilising processes. *J. Anim. Ecol.*, **47**, 249–267 (1978)
- Peters, R. H., *The Ecological Implications of Body Size*. Cambridge: Cambridge Univ. Press, 1983
- Pugliese A. and Rosà R., Epidemic 2-dimensional model with logistic growth for the host-macroparasite system. *J. Biol. Sys.*, **3**, 833–849 (1995)
- Pugliese A., Rosà R. and Damaggio, M. L., Analysis of a model for macroparasitic infection with variable aggregation and clumped infections. *J. Math. Biol.* **36**, 419–447 (1998)
- Roberts, M. G. and Dobson, A. P., The population dynamics of communities of parasitic Helminths. *Math. Biosci.*, **126**, 191–214 (1995)
- Roberts, M. G., Smith, G. and Grenfell, B. T., Mathematical models for macroparasites of wildlife. In P. Dobson and B. T. Grenfell (eds), *Ecology of Infectious Diseases in Natural Populations*, pp. 177–208, Cambridge: Cambridge University Press (1995)
- Schoener, T. W., Overview: Kinds of Ecological communities – Ecology becomes pluralistic. In J. M. Diamond and T. J. Case (eds), *Community Ecology*, New York: Harper and Row, 1986
- Smith, G. and Scott, M. E., Model behavior and the basic reproduction ratio. In M. E. Scott and G. Smith: *Parasitic and Infectious Diseases: Epidemiology and Ecology*, pp. 21–28, San Diego: Academic Press 1994
- Tallis, G. M. and Leyton, M., A stochastic approach to the study of parasite populations. *J. theor. Biol.*, **13**, 251–260 (1966)
- Tallis, G. M. and Leyton, M., Stochastic models of populations of helminthic parasites in the definitive host, I. *Math. Biosci.*, **4**, 39–48 (1969)
- Tilman, D., *Resource Competition and Community Structure*. Princeton: Princeton University Press, 1982