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"The Population Dynamics of Parasitic Helminth Communities"

Andrew P. Dobson
Department of Ecology and Evolutionary Biology
Princeton University
Princeton, NJ 08544-1003
U.S.A.

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The population dynamics of parasitic helminth communities

A. DOBSON[1] *and* M. ROBERTS[2]

[1] *Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA*
[2] *AgResearch, Wallaceville Animal Research Centre, P.O. Box 40063, Upper Hutt, New Zealand*

SUMMARY

This paper describes a mathematical model which allows us to compare the data collected from short-term cross-sectional surveys with the population dynamics of host and parasite populations over longer periods of time. The model extends an earlier framework for two parasite species in one host, to one for an arbitrary number of species. We show that the conditions necessary for the coexistence of two parasite species extend to expressions for the coexistence of three or more parasite species. Furthermore, the model suggests that those species which form the 'core' of the parasite community are those whose high fecundity and transmission efficiency permit them to readily colonize hosts. In contrast, those species which are classified as 'satellite' species of the community are either species with low fecundity, or low transmission efficiencies. This work confirms earlier studies that suggest that increasing degrees of aggregation are crucial in allowing several species of parasites to coexist in the same species of hosts.

The properties of the model are compared with patterns observed in data collected for helminth parasites of anolis lizards and wood mice. This combined theoretical and empirical approach confirms the importance of the life history strategies of the parasite in determining the abundance of each species in the community. It suggests that studies of parasite community structure have to pay more attention to the strategies pursued by each individual species before interactions between species are considered.

Key words: Helminth community, competition, mathematical model, transmission, life history, interspecific interactions.

INTRODUCTION

Ecological communities are composed of populations of different species. Populations are in turn composed of individuals each of which is the result of selection to maximize R_0, the basic reproduction number of the species. The derivation of expressions for R_0 has proved a fundamental unifying concept in the study of interactions between parasites and their hosts (May & Anderson, 1990*a*). Models for single parasite–single host systems consistently show that the long term dynamics of the interactions between and the abundances of the parasite and host populations are crucially dependent upon key life history attributes of the parasite and host (Anderson & May, 1982; Dobson, 1988; May & Anderson, 1990*b*; Mollison, 1991). R_0 is usually defined as the product of the birth, survival, and transmission terms in the parasite's life-cycle in the absence of density-dependent constraints. Changes in the behaviour of the parasite or changes it produces in the behaviour of the host are both likely to affect either parasite transmission rates or host and parasite survival, and are thus important in determining R_0. Understanding how changes in behaviour affect R_0 is fundamental to understanding the evolution of parasite behaviour and parasite induced changes in host behaviour (Dobson 1988).

The study of parasite communities presents a number of opportunities which are not usually present for ecologists studying the structure of free-living animal and plant communities (Holmes, 1973; Holmes & Price, 1986). The primary advantage is that hosts may be considered as individual patches of habitat for the parasite species of the community (Dobson & Keymer, 1990). The ability of any parasite species to colonize a host is dependent upon its value of R_0. Now that models for single parasite species in host populations have been successfully developed, their assumptions tested and their properties understood, it is possible to begin constructing models for more complex parasite and host communities (Dobson 1990; Roberts & Dobson 1994). In this paper we use a recently published model (Roberts & Dobson, 1994) to examine the long-term dynamics of parasite communities through time. The framework is used to ask the following questions about the structure of the parasite community: (1) What determines the abundance of a parasite species in the community? Obviously, birth, death and transmission rates but how do interactions between species affect these processes? (2) When can a parasite species invade a community and when is a species likely to be squeezed out? (3) Are life history and behavioural constraints on parameter values important in determining the ability of a parasite

Parasitology (1994) **S109**, 000–000

species to invade a community, or in allowing it to exclude other species? (4) Is there a limit to the diversity of parasite communities, and which features of parasite host ecology determine observed levels of diversity? (5) Do parasite induced modifications of host behaviour change the structure of parasite communities and alter levels of diversity?

Empirical studies of parasite communities consist of a large number of cross-sectional surveys of parasites in a host population at any time, and a few studies which follow the community through time. The majority of the former studies are descriptions of the relative abundance of parasite species in the community, with the (somewhat arbitrary) division of the parasite community into core and satellite species depending on their relative prevalence (Dobson & Keymer, 1990; Bush & Holmes, 1986*a*, *b*; Goater & Bush, 1988; Goater, Esch & Bush, 1987). Some recent review articles have collated data from a number of these surveys (Esch *et al.* 1988; Kennedy, Bush & Aho, 1986; Sousa, 1994). These provide an empirical comparison of the levels of diversity observed in helminth communities and suggest that there are significant differences in this respect between the parasite communities of birds, fish and mammals. However, studies based on surveys at one point in time do not permit quantification of the mechanisms that determine the relative abundance of parasite species (Dobson, 1990; Sousa, 1994). Further progress in understanding the structure of parasite communities will require the development of models that include details of the life history of each parasite species, and details of the interactions between species.

The influence of parasite induced changes in host behaviour on the basic reproduction number (R_0) of helminth parasites with life cycles of varying complexity were discussed in Dobson (1988). For a helminth species, R_0 can be considered to be the number of reproductively mature daughters that would be produced by a female worm in the course of her lifetime, in the absence of (parasite) density dependent constraints on the host and parasite populations. Behavioural modifications that increase transmission rates will increase R_0 unless they have any major detrimental effect on the survival of the worm during any stage of its life cycle. In this paper, we show how an understanding of the values of R_0 for the different parasite species in a community is fundamental in determining the relative abundances of the species in that community.

Finally we note that Heesterbeek & Roberts (1994; see also Roberts & Heesterbeek in prep.) have argued that a more formal definition of a quantity analogous to R_0 is required for the study of helminth population dynamics, and have derived such a quantity which they designated Q_0. The change in notation was to forestall fruitless speculation on whether this quantity was equal to the more familiar R_0, whereas what is important is that it has the correct threshold behaviour. For the models considered in the present paper the two quantities (R_0 and Q_0) are equal, and we have used the more familiar symbol R_0.

DESCRIPTION OF THE MODEL

As with the work of Anderson & May (1978), we assume that the statistical distribution of the parasites within the host population is a negative binomial and invariant with time. The basic model for macroparasites consists of an equation for the size of the host population (H), (we assume a fixed area, and an increase in size therefore equates to an increase in density):

$$\frac{dH}{dt} = rH - \alpha P \tag{1}$$

and one for the total size of the parasite population (P)

$$\frac{dP}{dt} = \frac{\lambda P H}{H_0 + H} - (s-r)\,P - \frac{\alpha(1+k)}{k}\frac{P^2}{H} \tag{2}$$

Here the birth and death rates of the host are a and b respectively, in the absence of parasites the host population grows at a rate $r = a-b$; the death rate of the adult parasites is μ (their life expectancy is thus $1/\mu$), λ is the rate of production of transmission stages per parasite. The increase in the rate of mortality of the host due to a single parasite is α, this assumes host mortality rates increase linearly with increasing parasite burden. The parameters $s = a+\mu+\alpha$, and the net rate of mortality of the host population is $s-r = b+\mu+\alpha$.

The proportion of transmission stages that become adult parasites is $H(t)/(H(t)+H_0)$; note that H_0 incorporates all parts of the parasite life cycle external to the definitive host, for example the dynamics of the free-living or intermediate stages. In the case of a simple direct life cycle helminth we can split H_0 into two parameters: the transmission rate β, and the mortality rate of free-living infective stages γ, with $H_0 = \gamma/\beta$ (May & Anderson 1978). Modifications of parasite or host behaviour that lead to changes in transmission rate will thus enter the model in the term H_0. If the behavioural modifications increase transmission efficiency, H_0 is reduced, if they reduce transmission efficiency, H_0 increases (Dobson, 1988).

An expression for the basic reproduction number of the parasite, R_0, can readily be derived from the equations by first considering the rate of growth of the parasite population when a single female worm is introduced into a population of hosts. Then recall that R_0 is defined in the absence of density-dependent constraints. For the model defined by equations (1 & 2) this means letting the host population grow to infinity.

$$R_0 = \lim_{H\to\infty} \frac{\lambda H}{(H_0+H)(s-r)} = \frac{\lambda}{s-r} = \frac{\lambda}{b+\mu+\alpha} \tag{3}$$

When similar models are developed for helminths with more complex life cycles the expressions for R_0 always consist of the product of the transmission rates at each stage of the life cycle, divided by the product of the net mortality rates at each stage of the life cycle (Dobson, 1988, 1990; Anderson & May, 1982, 1991; Heesterbeek & Roberts, 1994).

The parameter λ is the rate of transmission from the definitive stage of the life cycle to the next, i.e. the birth rate of the parasite. The behaviour of the model is highly dependent upon λ. The long-term behaviour of solutions of (1, 2) may be summarised as a sequence of behaviours for increasing values of λ, and is determined by the relation of λ to three thresholds. If $0 \leqslant \lambda < s-r (R_0 < 1)$, the parasite population becomes extinct and the host population grows without bound. If $s-r < \lambda < s$, both host and parasite populations grow without bound, but the mean number of parasites per host tends to zero. This is known as 'washout'. Although $R_0 > 1$ the host population grows much faster than the parasite population. If $s < \lambda < s+r/k$, both host and parasite populations grow without bound, and the mean number of parasites per host tends to a positive finite limit. If $\lambda > s+r/k$, both host and parasite populations tend to a bounded steady state.

In reality, of course, neither population will grow without bound, but will grow until density-dependent factors not included in the model become important and limit the population size. The stability properties of the model are described in Anderson & May (1978) and May & Anderson (1978); here we merely remind the reader that once parasite fecundity is sufficient to regulate the host population, the model will exhibit either damped cycles or stable constant host and parasite numbers. Increasingly stable dynamics are produced by parasites that are more aggregated in their distribution in the host population.

MORE THAN TWO PARASITE SPECIES IN THE SAME HOST POPULATION

We have recently extended this framework to examine the dynamics of multiple parasite host communities (Roberts & Dobson, 1994). The model is based on a two parasite species version of the above, which was developed by Dobson (1985). The interactions between the parasite species are classified as either exploitation or interference competition. In the simpler case of exploitation competition, the parasite species are independent of each other in their use of the host species; hence the covariance between their distributions in the host population is zero. This assumes that exploitation competition does not lead to the exclusion from a host of one parasite species due to the presence of another. In contrast, in the case of interference competition, interactions between the two parasite species may be antagonistic or synergistic. These interactions cause the presence of one species to influence the probability that the other is present; there is thus a non-zero covariance term which alters the statistical distribution of each parasite species. Where interactions between the parasite species are antagonistic, the covariance term is negative; where interactions are synergistic, the covariance is positive.

In order to develop models for parasite communities utilizing a single host population it is necessary to specify the generating function for a mixture of negative binomial distributions. We choose:

$$\Pi_{i=1,n} F(m_i, k_i, z_i) + \frac{\Sigma_{i,j=1,n,i\neq j} [1-F(m_i, k_i, z_i)][1-F(m_j, k_j, z_j)]}{l_{ij}} \tag{4}$$

for suitable parameters m_i, k_i and l_{ij}. Here the n individual parasite species are distributed with mean m_i and variance $m_i(1+m_i/k_i)$ respectively, the covariance between species i and species j is $m_i m_j / l_{ij}$ (Roberts & Dobson, 1994).

The equations for the dynamics of the n parasite species are easier to analyse following the transformations $X = H/(H+H_0)$, $Y_i = m_i = P_i/H$ to obtain

$$\frac{dX}{dt} = H_0 X(1-X)[r - \Sigma_{i=1,n} \alpha_i Y_i] \tag{5}$$

$$\frac{dY_j}{dt} = Y_j\left[\lambda_j X - s_j - \Sigma_{i=1,n} \frac{\alpha_i}{l_{ij}} Y_i\right] \tag{6}$$

where $s_i = a + \mu_i + \alpha_i$, and $l_{ii} = k_i$. From equation (6) the steady state values of the Y_i satisfy

$$Y_j = 0 \quad \text{or} \quad \Sigma_{i=1,n} \frac{\alpha_i}{l_{ij}} Y_i = \lambda_j X - s_j \tag{7}$$

for $j = 1, n$. The solutions of equation (7) fall into two categories. The first category is where $X = 1$, which corresponds to $H(t)$ tending to infinity with time; i.e. the host population is unregulated. The second category is where $X = X^* < 1$, and the host population is unregulated. For the former category any combination of Y_i may have limit zero, and hence there are $n!$ steady states. The same applies for the second category, except that all Y_i may not simultaneously be zero, and hence there are $n!$-1 steady states. The Y_i for this category are found from (7) as functions of X^*, which is in turn determined from the equation

$$\Sigma_{i=1,n} \alpha_i Y_i = r \tag{8}$$

The trivial steady-state (no hosts or parasites) always exists, but is of no interest here. All the other steady-states except $X = 1$, $Y_j = 0$ for all j exist for a limited range of parameter values, and each steady-state is stable only for a further restricted range of parameter values.

In the absence of any antagonistic or synergistic interactions between the parasite species (zero co-variance), the steady-state values of the Y_j satisfy $Y_j = 0$ or

$$\frac{\alpha_j}{k_j} Y_j = \lambda_j X - s_j \qquad (9)$$

which can be easily explicitly solved. When the host population is regulated X^* can then be calculated directly from equations (8 & 9). Assume that $Y_j \neq 0$ for $j = 1, m, m \leqslant n$, and $Y_j = 0$ for $j = m+1, n$, then

$$X^* = \frac{r + \Sigma_{i=1,m} k_i s_i}{\Sigma_{i=1,m} k_i \lambda_i} \qquad (10)$$

The population dynamics of the parasite community

The properties of the model for two parasite species can be illustrated graphically for both exploitation and interference competition. As with the model for one parasite and one host, the dynamics of models for more complex parasite communities are dependent upon the magnitude of the fecundity, transmission and mortality rates of each parasite species (Fig. 1). When λ is small the parasites cannot establish and the host population grows (to a carrying capacity determined by factors other than the parasite and not included in the model). As λ is increased the parasites first become able to establish in the host population and then able to regulate it. There are seven different non-trivial steady-state solutions to equations (5 & 6). Note that a steady-state solution of the equations corresponds to a long-term outcome of the population dynamics, as $X \rightarrow 1$ corresponds to $H \rightarrow \infty$. Increases in the fecundity of either parasite species always increases its chances of establishing and potentially regulating the host population.

The relative magnitude of the areas of parameter space that lead to different dynamics are dependent upon several key parameters of the model. In particular, reducing the degree of aggregation of either parasite species, k_i, considerably reduces the region in Fig. 1 where both species can coexist, S7. Similarly, increasing the mortality rate or decreasing the fecundity rate of the host (reducing r) leads to a decrease in the size of S7, but increases in S5 and S6. Hence short-lived host species harbour less diverse parasite communities than longer lived species, and are more likely to be regulated by their parasites.

The conditions for invasion of a single parasite-host system by a second species of parasite are illustrated in Fig. 2. The invasion criteria for a parasite to enter an already established parasite host community are again highly dependent upon the fecundity of the invading species. In Fig. 2A parasite species 1 regulates the host to a constant level of abundance, and when the fecundity of the invading parasite species (λ_2) is small, it is unable to establish. Once λ_2 is sufficient for parasite species 2 to establish, the host population declines to lower levels than when parasite species 1 alone was present. Further increases in λ_2 finally lead to parasite species 1 being driven to extinction; parasite species 2 and the host then settle at a new steady-state. A similar pattern is shown in Fig. 2B, but here the host population is initially growing with only one species present. As λ_2 passes successive thresholds species 2 is able to

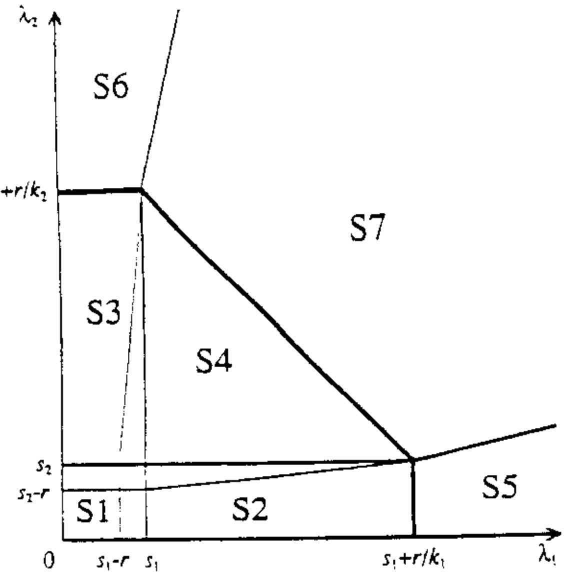

Fig. 1. The relationship between the fecundity, λ, for each of two parasite species and the dynamic behaviour of the parasite host community. When two species of parasite are present the parameter space can be divided into a number of different regions each determined by the magnitude of λ for each parasite. The figure illustrates all of the possibilities for two species in one host. The seven different regions of parameter space are numbered S1 through to S7. In S1, the host population grows exponentially and neither parasite species can establish. In regions S2 and S3, the host population still grows exponentially, but in the former case parasite species 1 may establish whereas parasite species 2 goes extinct, in region S3 the alternative happens, parasite species 2 may establish whereas parasite species 1 goes extinct. In region S4, both parasite species can persist although the host population continues to grow exponentially. In region S5, parasite species 1 can exist and regulate the host population to a steady density, parasite 2 is unable to establish. In region S6 we get the alternative, parasite species 2 establishes and regulates the host to a constant population density while parasite species 1 is unable to establish. Finally, in region S7, both parasite species can establish and co-exist, and the host population is regulated (after Roberts & Dobson, 1994).

invade, the two parasite species regulate the host population, and finally species 2 is driven to extinction.

The effect of non-zero covariance

We can caricature direct competition between parasite species by a non-zero (positive or negative) covariance term in the statistical distribution of each parasite species. For biological reasons we assume that the covariance between the distributions of the two species is small compared to their individual variances. Modifications to the previous (zero covariance) steady-state conditions for the mean burden of each parasite species and equilibrium host density are then found as small amplitude linear combinations of the previous solutions. Full details may be found in Roberts & Dobson (1994). Interactions between parasite size thus produce changes in the size of regions of parameter space for which each of the steady-states is locally stable. Essentially, synergistic interactions between the parasites tend to reduce the areas of co-existence of the two parasite species, while antagonistic competitive interactions between the species increase the range of parameter values for which it is likely that two parasite species coexist within the community (Roberts & Dobson, 1994). Here it is important to notice that antagonistic interactions between parasite species lead to increases in the total levels of parasite species diversity, but reductions in the abundance of each individual parasite species. As in the case for simple exploitation competition, the more aggregated the distribution of each individual parasite species, the greater the possibilities for co-existence and the less chance that interactions between different species are likely to occur.

A COMMUNITY WITH ONE HOST AND FIVE PARASITE SPECIES

In Roberts & Dobson (1994), the regions in parameter space corresponding to the different dynamics of a community with an arbitrary number of parasite species are derived, but when more than three species are present these become difficult to display graphically. In this section we use numerical simulations to examine the relative abundance of 5 species of parasite which utilize one species of host (Fig. 3). In order to prevent the host population from growing unrealistically, we have modified the equivalent of equation (1) by replacing the term rH with $r(1-H/K)H$. This models a density-depen-

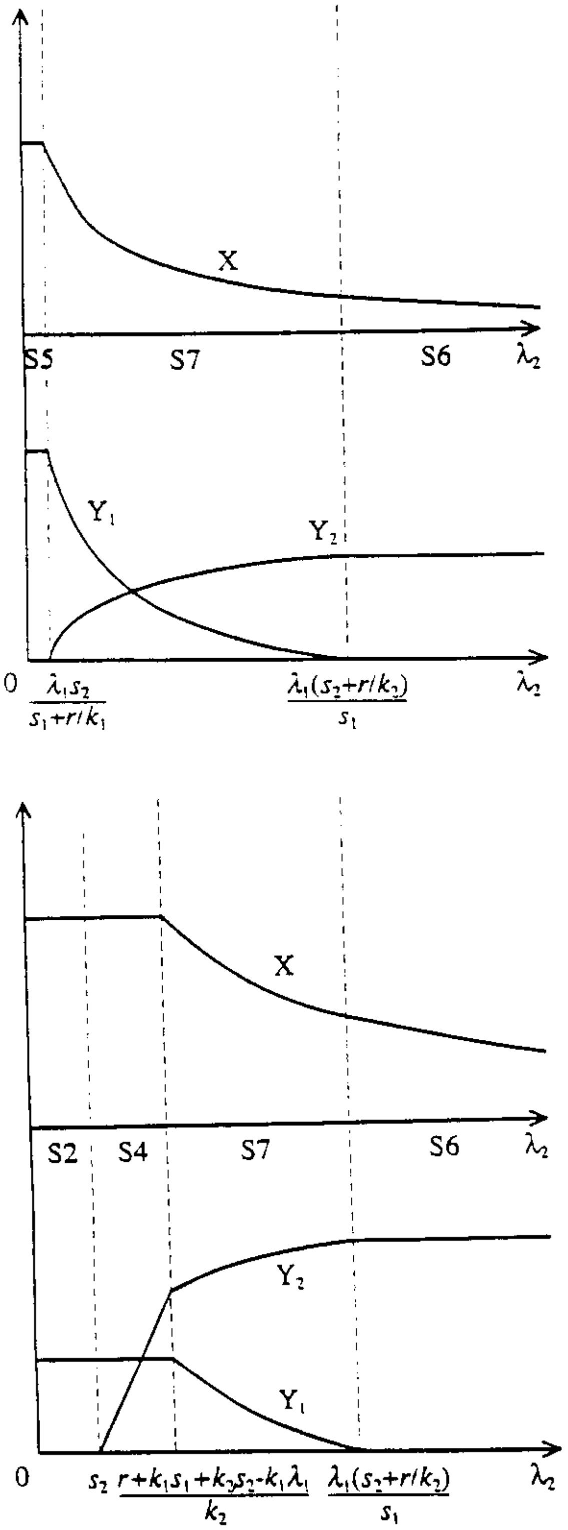

Fig. 2. The invasion criteria for a parasite introduced into an already established single parasite, one host community. Both figures illustrate the success of an invading parasite species with a range of fecundity from 0 to $\lambda_2 > s_2+r/k_2$. Fig. 2A illustrates the case where $\lambda_1 > s_1+r/k_1$; figure 2B $s_1 < \lambda_2 < s_2+r/k_2$. In both cases we show steady state values of the mean numbers of parasite per host, Y_i ($= P_i/H$) and the variable X ($= H/(H+H_0)$); so when $X = 1$, the parasites are unable to control the host and its population has either grown to infinity or it is regulated by factors not included in the model (after Roberts & Dobson, 1994).

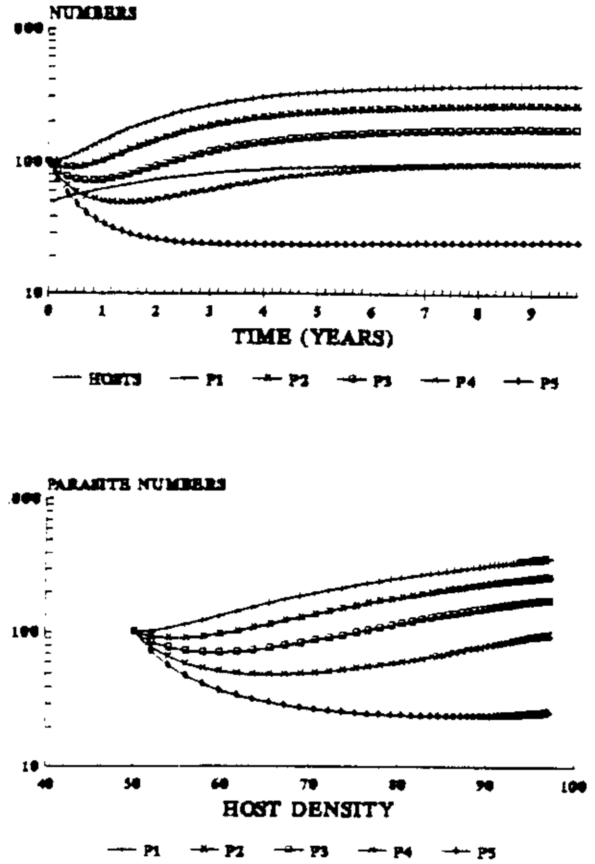

Fig. 3. The transient dynamics of the model for five parasite species utilizing a single host species. The upper figure illustrates changes in the size of the host and total parasite populations with time. The lower figure plots the mean parasite burden against host population size. The parameter values used for the host population in the simulation are $a = 0{\cdot}8$, $b = 0{\cdot}3$, and $K = 100$. The parameters used for parasite species 1 are $\alpha_1 = 0{\cdot}001$, $\lambda_1 = 20$ and $\mu_1 = 0{\cdot}5$. The vital rates of the other parasite species in the community are obtained by modifying the values for each species by a factor 1·2: thus $\alpha_{i+1} = 1{\cdot}2\alpha_i$ and $\mu_{i+1} = 1{\cdot}2\mu_i$; but $\lambda_{i+1} = \lambda_i/1{\cdot}2$. $H_0 = 240$ for all species.

dent birth rate, and in the absence of parasites the host population settles to a steady equilibrium at the carrying capacity K. The numerical solution of the model was initiated with a population of 50 host animals and 100 parasites of each species. After a time period of ten years the community settled to a steady-state of just under 100 hosts; all five parasite species remained in the community with mean burdens 5·00, 4·16, 3·47, 2·89 and 2·41. Their values of R_0 were 7·34, 5·44, 4·00, 2·92 and 2·12 respectively.

The parasite diversity supported by the host population is ultimately dependent upon the net impact of the parasites on the host. Different aspects of the host and parasite population biology enter into this relationship in subtle ways; Fig. 4 illustrates the effect of systematic changes in four key parameters on the five parasite single host community. The changes all lead to reductions in the diversity of the parasite community. In (a) changes in the life history characteristics of the host which increase its fecundity, but reduce its longevity, lead to the loss of two species from the community. The species lost are those with the smallest values of R_0. Because the growth rate of the host population ($r = a{-}b$) is maintained at the same level, this implies that long lived host species with low fecundity will tend to support more diverse parasite communities than short-lived hosts with higher fecundity.

In Fig. 4B the similarity in the life history attributes of the parasite is reduced. This produces the initially counter-intuitive effect that diversity decreases as the parasites using the host become more dissimilar in their life history attributes. Those species that are squeezed out of the community are again those with lower R_0 values. An intriguing complementary result to this is that the models suggest that hosts can support a greater diversity of parasite species that are similar in their use of the host population! This does not, of course, imply that the parasite species are identical in their use of host resources, but that similarity in life history attributes is an important condition for coexistence.

In Fig. 4C the importance of parasite aggregation (or overdispersion) is illustrated. This life history attribute is a joint feature of both the host and any particular parasite species. The degree of aggregation reflects physiological, immunological, behavioural and genetic differences in the susceptibility of individual hosts to infection; these effects may be further compounded by spatial and temporal heterogeneity in the habitat in which the parasite and host coexist. Reductions in the level of aggregation lead to reductions in the diversity of parasite species supported by the host population. The parasite species that are lost are those with low levels of aggregation. This result implies that large degrees of aggregation should be apparent in the distributions of parasites in highly diverse parasite communities. In contrast, the structure of parasite communities is likely to be less diverse in habitats that are uniform, or in host populations which show low levels of differences between hosts in their susceptibility to parasites.

Fig. 4D illustrates a feature of the model that is a curious consequence of host population density. When regulation of the host population is relaxed and it is allowed to increase in density, several of the parasite species exhibit large increases in density. This allows them to exclude other parasite species from the community by causing increased host mortality in concomitantly infected hosts. This phenomenon is in some ways analogous to the paradox of enrichment observed in many predator-prey models, where increased predator efficiency may lead to reduced predator density (Rosenzweig & MacArthur, 1967). It is likely to be an important effect in agricultural situations where artificially increasing the density of a host species may lead to

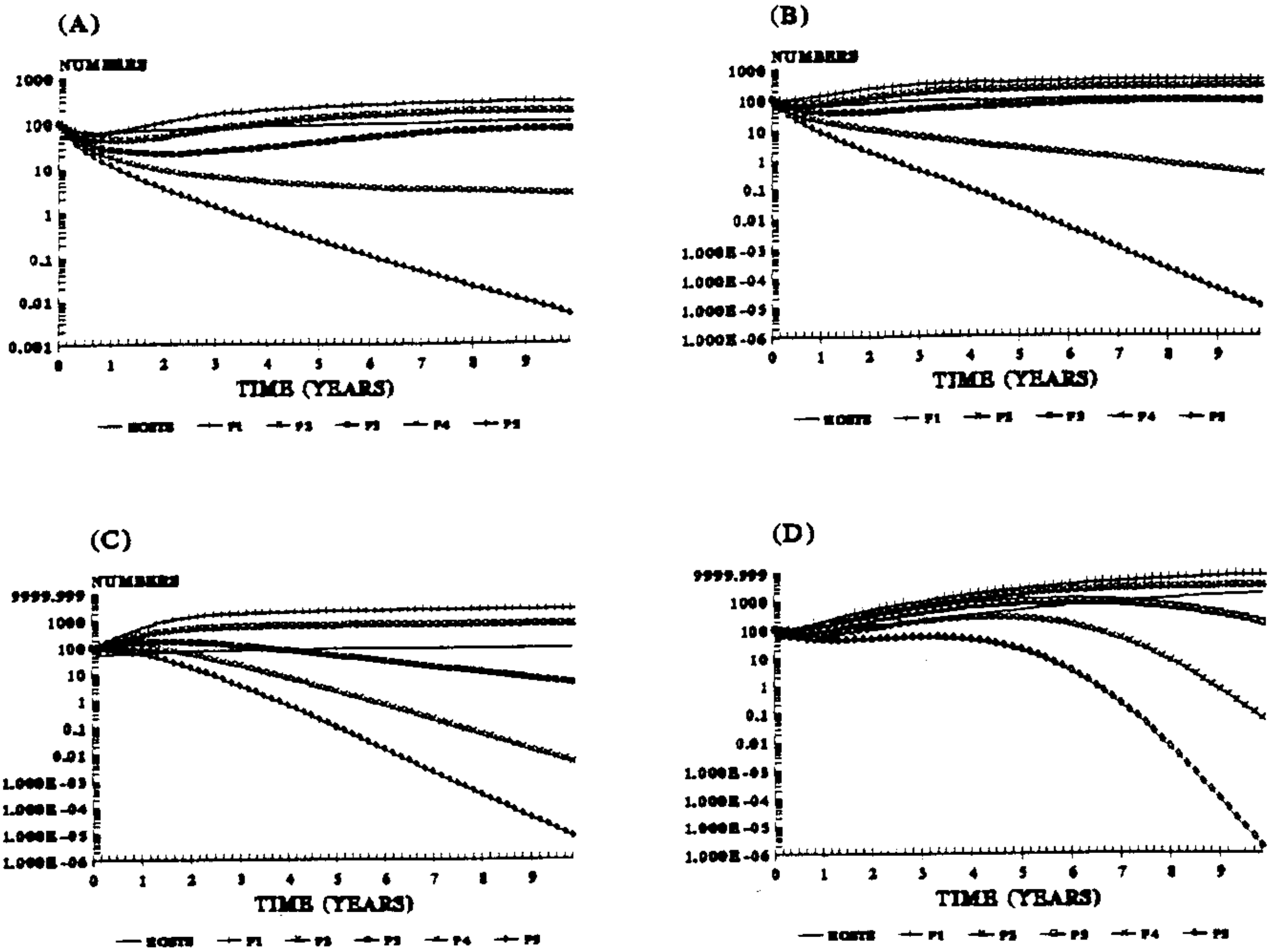

Fig. 4. Numerical solutions of the five parasite, one host species model for systematic variations in a number of key parameter values. In all cases we illustrate factors that reduce the diversity of the parasite community by altering one parameter value from the solutions for the stable five parasite community illustrated in Fig. 3 (A) The effect of host fecundity and mortality $a = 2{\cdot}5$ and $b = 2{\cdot}0$; $r = (a–b)$ still equals 0·5. (B) Reduced similarity between parasites species, the multiplication factor for parasite parameters has been set to 1·4. (C) The effect of reduced aggregation; $k_1 = 0{\cdot}02$. (D) Increases in host carrying capacity, $K = 500$.

one or two parasite species dominating a parasite community and causing the majority of economic losses.

The model may also be used to determine the equilibrium densities of parasites and hosts in more diverse parasite communities (Fig. 5). Notice that the model produces parasite communities that appear to have a 'core' of species that are always present in the community, and 'satellite' species that enter in higher density host populations. In each case species that might be classified as 'core' species are simply those with higher R_0 values, while those that might be classified as 'satellites' are those with the lower fecundity, survival or transmission rates leading to lower R_0 values. Species with high R_0 values invade the host community at lower population densities, and consistently have higher mean worm burdens than species which can only establish in higher density host populations. When mean parasite burden for any species is plotted against host population density, the resultant curves form a nested series with the core species with high R_0 values surmounting the satellite species with lower R_0 values.

COMPARISON WITH EMPIRICAL DATA FOR HELMINTH COMMUNITIES

Some aspects of the patterns observed in these models are seen in data collected from a study of the parasite community of Anolis lizards on different islands in the Caribbean (Dobson *et al.* 1992; Dobson & Pacala, 1992). A full description of the protocols used to collect these data is provided in the papers cited. As the Anolis species on these islands have evolved from a common ancestor, the data reflect some of the different ways in which the ancestral parasite communities have evolved. The data were collected from two host species (*Anolis bimaculatus* and *A. wattsi*) on ten islands ranging in size from 13 to 280 km², where different habitats allow the host population to exist at different densities. The data thus reflect a spectrum of parasite communities that runs from isolationist (Anguilla –

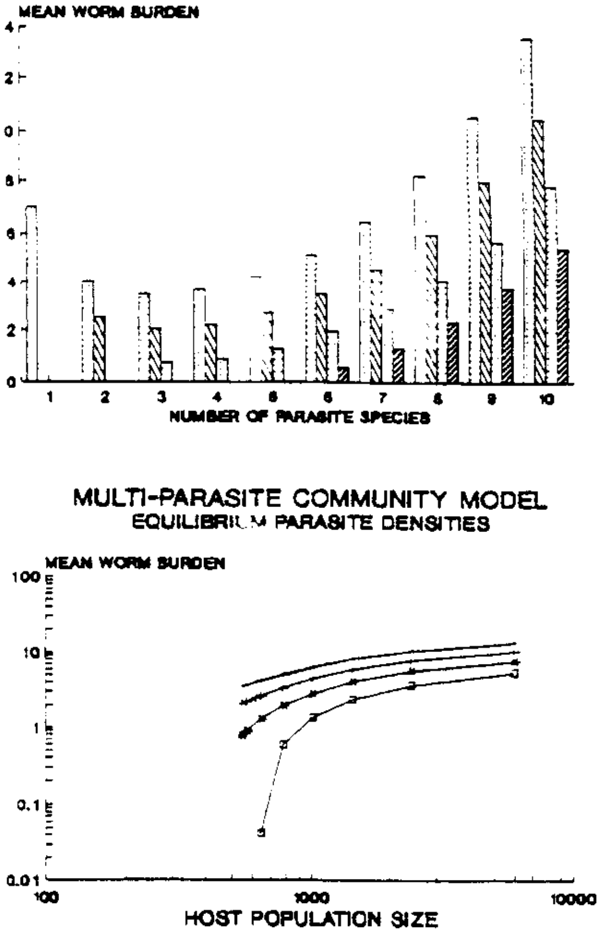

Fig. 5. The equilibrium solutions for a single host, ten parasite spec[illegible] community. The upper figure illustrates the abundan[illegible] f four 'core' species as new species with sequentially [illegible] ues are added to the community. [illegible] gure illustrates the relationship [illegible] veen host popu[illegible] size and mean worm burden [illegible] ame four 'core' species. Notice that these [illegible] rovide a nested set of abundances with each [illegible] entially establishing parasite species having both a higher threshold for establishment and a lower eventual mean worm burden. This result is similar to that conjectured from some earlier graphical work of Dobson (1990).

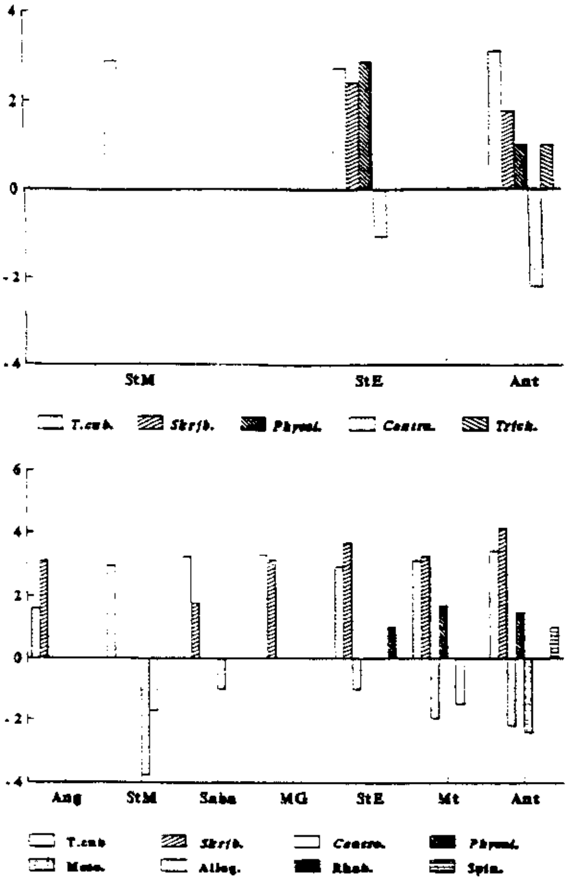

Fig. 6. The mean parasite burdens (number of worms per host) of different parasite species from *Anolis* lizards sampled on islands in the Lesser Antilles. The upper figure shows data for lizards of the '*wattsi*' series (only present on three islands), the lower figure shows data for the '*bimaculatus*' series. The seven islands (and their sizes) are: Anguilla (Ang, 91 km^2), St Maarten (StM, 88 km^2), Saba (13 km^2), Marie Galante (MG, 155 km^2), St Eustacius (StE, 31 km^2), Montserrat (Mt, 85 km^2), Antigua (Ant, 280 km^2). In each case the islands are arranged in increasing order of parasite diversity (from left to right). Abundance is on a logarithmic scale with 0 = no worms detected, 1 = 0·01 worms per host, 2 = 0·1 worms/host etc. The parasites are T.cub.-*Thelandros cubensis*; Skrjb.-*Skrjabinoden* spp.; Centro.-*Centrorhynchus* sp.; Physal.-*Physalopteridae* gen.sp.; Meso.-*Mesocoelium* sp.; Allog.-*Alloglyptus crenshawi*; Rhab.-*Rhabdias* sp.; Spin.-*Spinicauda amarili*; Trich.-*Trichospirura* sp.

with only two parasite species), to more speciose and potentially interactive [illegible] Antigua, two host species with five and six [illegible] species detected respectively). The da[illegible] 6) illustrate several of the patte[illegible] the models. In particular, com[illegible] to Fig. 5. Those parasite species whose [illegible] stories allow them to persist in low den[illegible] ost populations (high R_0 values) are present [illegible] as where almost no other species are present. These are also the most common parasite species on islands with higher parasite diversity, where species with lower R_0 values have also managed to enter the community.

The relative abundance of each parasite species again produce patterns that are similar to those suggested by the model. As the diversity of the parasite community on an island increases, those species that are present on the species-poor island tend to be the most abundant parasite species on the species-rich island (for example *Thelandros cubensis* and *Skrjabinodon* spp., see Fig. 6). In contrast, those species that are absent from the species-poor islands, tend to be those that are present at low abundance on the species-rich island (for example *Centrorhynchus* and *Physalopteridae* spp., see Fig. 6). This suggests that the transmission and other life-history features of each parasite are important in determining their relative abundance in the community.

Stochastic effects are also important in determining the observed structure of the parasite communities

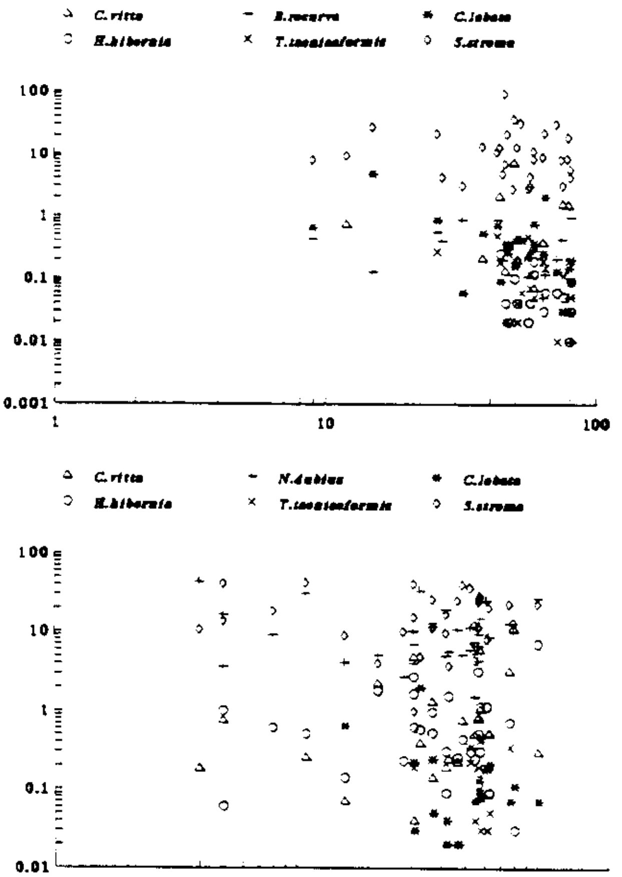

Fig. 7. These data illustrate patterns of abundance of parasitic helminths in two populations of mice in Northern Ireland, the upper figure is for a deciduous woodland site (Clanboyne), the lower figure is for a coniferous woodland site (Tollymore) (after Montgomery & Montgomery, 1988, 1990). The data in the original publication have been replotted to illustrate the relationship between the abundance of the each parasite species and host abundance.

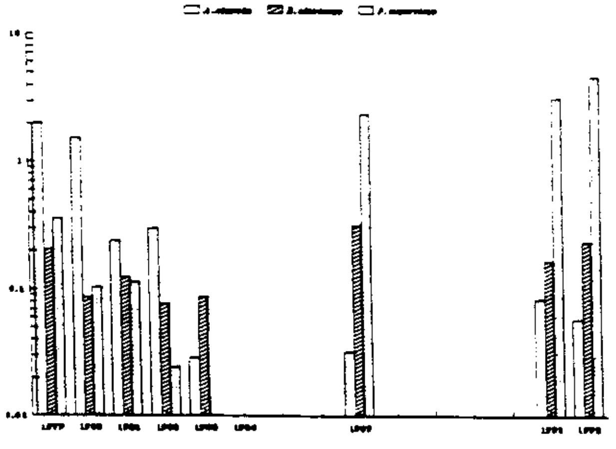

Fig. 8. The observed abundance of three species of parasite of eels (*Anguilla anguilla*) over a thirteen year study period (after Kennedy 1993). Although seven other species of parasite were recorded during the study, the abundance of the other species never rose above 5 % of the total parasites recorded.

on some islands. The sequences by which parasites enter the communities as we examine islands with larger Anolis populations are not perfect, and occasionally a parasite species is missing (for example *Skrjabinodon* spp. were not detected on St Maarten, see Fig. 6). The absence of a species may be due to a number of reasons: potentially it was present when the host population first colonized the island and has since become extinct; in other cases the parasite may have invaded the island since its colonization by the host and may then have become extinct; or alternative hosts in the life-cycle of parasites with complex life cycles may be missing from some islands and it has been unable to invade. This may be the case for the trematode parasite (*Mesocoelium* sp.) and potentially the acanthocephalans (*Centrorhynchus* sp.) seen on only some of the islands. Notice that the absence of a species does not seem to produce any detectable increase in the density of any potential competitors.

A complimentary set of data are available for the helminth parasite communities of small mammals in Northern Ireland. These data consist of a sequence of monthly samples of the parasites of *Apodemus silvaticus*, the wood mouse, at two locations (Montgomery & Montgomery, 1990). The long-term patterns of abundance are plotted as the relative abundance of each parasite species against host abundance (Fig. 7). Here we see a similar type of pattern to that predicted by the model (cf. Fig. 5). The core species, *Syphacia stroma*, *Catenotaenia lobata*, *Brachylaima recurva* (at Clanboyne) and *Nematospiroides dubius* (= *Heligmosomoides polygyrus*) (at Tollymore) are always present in low-density host populations, and are always present in higher abundances than species that are only detected at higher host population densities, such as *Taenia taeniaformis* and *Corrigia vitta*. Those species that require higher host population densities to establish, never achieve the densities of the parasites with the higher R_0 values that can invade at lower host population densities.

Although similar patterns can be seen in a long-term study of parasites community in eels (*Anguilla anguilla*), changes in the dominant species in this predominantly isolationist community occurred several times (Kennedy, 1992, 1993). In the early years of the study, *Acanthocephalus clavula* was the dominant species in the system (Fig. 8), after a transient period of low abundance when *Bothriocephalus claviceps* was the commonest species, the community became dominated by *Paraquimperia tennerrima*. These changes chiefly reflect changes in the river occupied by the parasites and their host, these have mainly been the result of human management for flood prevention (dredging), but pollution and eutrophication have led to pronounced changes in the invertebrate community that act as intermediate hosts for several of the parasite species

(Kennedy, 1993). The study emphasizes the importance of both host density and intermediate host availability in determining the transmission success of the parasite species that are present at any time. It is sobering that even parasite communities are easily perturbed by short-term anthropogenic activities.

DISCUSSION

A continuing debate in ecology is concerned with whether the structure of ecological communities is determined by interactive or non-interactive processes (Schoener, 1986). A recent review suggests that communities of parasitic helminths provide the main examples of communities where interactions between species are the primary process determining relative abundance (Cornell & Lawton 1992). The models described in this paper suggest almost the opposite conclusion; that interactions between parasites and their hosts are more important in determining community structure than direct interactions between parasite species. Indeed, direct interactions between parasite species may produce the opposite effect on diversity than would be assumed by cursory examination of the sign of the interaction. Competitive interactions tend to increase the diversity of parasite communities by reducing the impact of multiple infections on individual hosts. In contrast, synergistic interactions between parasite species lead to high worm burdens in individual hosts, and higher rates of host mortality that in turn lead to net reductions in the diversity of parasite species supported.

The models described here assume parasites have some detrimental effect on host survival and that this is crucial in determining observed mean worm burdens. This assumption is intrinsic to most models of parasitic helminth dynamics (Anderson & May 1978, 1991). As the impact of pathogenicity of any parasite species is reduced, the observed mean worm will increase. When assemblages of parasite consist of species which all have low rates of parasite induced host mortality, then high mean worm burdens will be observed if transmission rates are high. The high levels of diversity observed may lead to interaction between species in concomitantly infected hosts. However, the aggregated distributions of each parasite species will reduce the proportion of hosts which contain mixed species infections. Thus spatial aggregation, host longevity and population growth rate are the crucial mechanisms permitting increases in diversity in parasite communities. In contrast, the ability of any species to establish and invade the community is dependent upon its life history strategy, particularly its fecundity and transmission success. This suggests that 'supply-side' considerations are crucial in determining which parasite species are present in a host population. In more detailed models for parasite communities that include stochastic effects, it is likely that the huge fecundity and long life expectancy of parasitic helminths will also promote the coexistence of a variety of species (Warner & Chesson, 1985; Chesson & Warner, 1981).

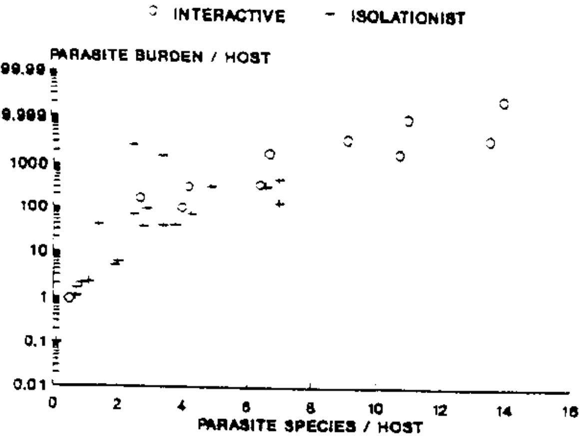

Fig. 9. The relationship between parasite community richness (average number of species per host) and parasite burden per host for a collation of studies of parasite communities (Sousa, 1994). The communities that were designated as 'interactive' by the original authors are marked 'Int' in the diagram.

Most empirical sets of data for parasite communities suggest that local abundance (the burden of worms carried by any individual host) is determined by regional abundance (Dobson, 1990; Dobson & Pacala, 1992). The models described here provide an important insight into the debate about whether parasite communities are 'isolationist' or 'interactive' (Holmes & Price, 1986), and whether the parasite species in a community can be defined as 'core' or 'satellite' species, as well as the larger debate which considers this phenomenon in populations of free living species that live in patchy or fragmented environments (Hanski, 1982; Nee, Gregory & May, 1991). Sousa (1994) has suggested that 'isolationist' and 'interactive' communities as defined by Holmes & Price (1986) are probably two ends of a hypothetical spectrum of parasite communities. When the data collated by Sousa (1994) are plotted as graphs of parasite abundance against parasite diversity (Fig. 9), no clear demarcation occurs between isolationist and interactive communities. Although most of the more diverse communities have been classified as interactive, there are many communities of intermediate diversity, that have been classified as isolationist. The models presented here suggest that the diversity of a parasite community is strongly determined by the growth rate and longevity of the host population; later extensions of the model will examine how age-structure in the host population, fine scale niche partitioning within the host and heterogeneity in the external habitat contribute to the levels of diversity that can be maintained.

In more homogeneous habitats, parasite distributions will be less aggregated and hosts are more likely to contain mixed species infections. This may select for more antagonistic interactions between parasite species. It is intriguing to note that one of the best documented examples of antagonistic interactions between parasite species come from the intertidal mollusc communities studied by Sousa (1992, 1993). Long-term studies of this system conclude that recruitment processes still primarily determine the composition and relative abundance of species in these communities (Sousa, 1993). However, the homogeneous habitat and high fecundity of the host population may select for interference competition in the parasitic trematodes that dominate the parasite community. In contrast, long lived vertebrates tend to live in complex habitats which will produce high levels of aggregation of the parasites in the host population (Pence & Windberg, 1984; Bush, Aho & Kennedy, 1990; Esch, Bush & Aho, 1990; Goater & Bush, 1988; Bush & Holmes, 1986*a*). Differences between the general levels of diversity observed in fish and bird parasite communities (Kennedy, Bush & Aho, 1986) may simply reflect the combination of differences in habitat heterogeneity and host life expectancy. The parasite species in these communities are not usually pathogenic, so high levels of parasite abundance and diversity can be supported by the host.

The basic reproduction number of a parasite (R_0) is fundamental in determining the population dynamics of simple single-parasite one host communities. Modifications of parasite survival, fecundity, transmission and behaviour affect R_0. Fully understanding the life history consequences of changes in parasite behaviour therefore requires the derivation of an expression for R_0 (Dobson 1988, Anderson 1994). Once obtained, these expressions allow us to examine the role of parasite life-history strategies in determining the success of a parasite in a host population. Extending the models to more than one parasite species in a community allows us to examine the role of parasite life-history strategies in determining the relative abundance and diversity of different species in parasite communities. A parasite's fecundity and transmission success are the two key determinants of its life-history strategy which determine whether it can invade a host population and its abundance once established in that population. The diversity and patterns of relative abundance observed in any collection of parasite species in a community are thus more likely to reflect the life-history strategies of each individual species in the community, rather than interactions between the species.

This work was developed while the authors took part in the programme on epidemic models at the Isaac Newton Institute for Mathematical Sciences, University of Cambridge. We are deeply grateful to the organisers for allowing us to take part in the programme, and to the participants for many interesting discussions on this topic. In particular we would like to thank Bryan Grenfell and Hans Heesterbeek in this regard. Clive Kennedy, Gary Smith and Wayne Sousa all made helpful and insightful comments that greatly improved this manuscript. MGR also received financial assistance from a Trimble Agricultural Research Fellowship and MSD-AgVet Ltd.

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The Population Dynamics of Communities of Parasitic Helminths

M. G. ROBERTS
AgResearch, Wallaceville Animal Research Centre, P.O. Box 40063, Upper Hutt, New Zealand

AND

A. P. DOBSON
Ecology and Evolutionary Biology, Eno Hall, Princeton University, Washington Road, Princeton, New Jersey 08544-1003

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ABSTRACT

This paper considers the dynamics of a host (animal) species that would grow exponentially in the absence of parasitism, and a community of parasite species that may regulate this growth. The model consists of a single differential equation for the host and one for each of the parasite species. This level of simplicity is achieved by assuming that each parasite species has a negative binomial distribution within the host population, with either zero covariance between the species (exploitation competition), or a specified covariance structure (interference competition). Conditions on the model parameters that determine the abundance of the different species are formulated, as are conditions that determine when a parasite species can invade a community and when a species is likely to be squeezed out. The results show that highly aggregated parasite species are more likely to coexist, but are less able to regulate their host population. A negative correlation between the distributions of the parasite species enhances both their ability to coexist and their ability to regulate the host population. The results of this analysis apply more generally to other systems where communities of exploiter species coexist on discretely distributed hosts, for example, insects on plants.

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1. INTRODUCTION

Anderson and May [2] demonstrated with the aid of a simple differential equation model that a parasite species could regulate the size of a host population that would otherwise grow exponentially. In constructing the model they assumed that the distribution of the parasites within the host population was negative binomial and invariant with time.

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Since then several attempts have been made to relax this requirement [1, 15, 16, 24], but these alternatives are less mathematically tractable than the original Anderson and May model that continues to make a significant contribution to the subject [27]. In contrast to the scrutiny that the assumption concerning the distribution of parasites has received, the assumption that a single parasite species is present has attracted little critical attention. Dobson [10, 11] used a two-species version of the Anderson and May model to describe the interaction between two parasite species that utilize the same host and classified the types of interaction as *exploitation* or *interference* competition. For the former the parasite species utilize the same resource independently, and hence the covariance between their distributions is zero. For interference competition external factors determine that the presence of one species influences the probability of the presence of the other, and hence there is a nonzero (positive or negative) covariance between their distributions. In this paper we extend the work of Dobson [11] to an arbitrary number of parasite species in a community and relax some of the constraints on parameter values. The treatment throughout is phenomenological in that no mechanisms for the generation of the probability distributions are included in the model.

Anderson and May [2] assumed the parasites to have a negative binomial distribution within the host population, that is the probability generating function

$$F(m,k,z) = \left(1 + \frac{m}{k}(1-z)\right)^{-k}$$

with mean m and variance $m(1 + m/k)$. They modeled the dynamics of the host population size (H) and the total size of the parasite population (P) by the differential equations

$$\frac{dH}{dt} = (a-b)H - \alpha P$$

$$\frac{dP}{dt} = \frac{\lambda PH}{H_0 + H} - (b + \mu + \alpha)P - \frac{\alpha(1+k)}{k}\frac{P^2}{H}. \qquad (1)$$

Here the birth and death rates of the host are a and b, respectively, the death rate of the parasite is μ, the increase in the rate of mortality of the host due to a single parasite is α, and λ is the rate of production of transmission stages per parasite. The proportion of transmission stages that become adult parasites is $H(t)/(H(t)+H_0)$. This factor incorporates all parts of the life cycle external to the host, for example the dynamics of free-living or intermediate stages. A full description of the assumptions that lead to (1) may be found in [2].

The long-term behavior of solutions of (1) may be summarized as follows [9,27].

If

(i) $0 \leqslant \lambda < b + \mu + \alpha$ $\qquad H \to \infty, \quad P \to 0$

(ii) $b + \mu + \alpha < \lambda < a + \mu + \alpha$ $\qquad H \to \infty, \quad P \to \infty$

$P/H \to 0$

(iii) $a + \mu + \alpha < \lambda < \Lambda = a + \mu + \alpha + (a-b)/k$

$H \to \infty, \quad P \to \infty$

$P/H \to k$

$(\lambda - (a + \mu + \alpha))/\alpha > 0$

(iv) $\lambda > \cancel{\Gamma}$ $\qquad H \to H_0 \cancel{\Gamma}/(\lambda - \cancel{\Gamma}),$

$P/H \to (a-b)/\alpha.$

$P/H \to$

$k(\lambda - (a+\mu+\alpha))/\alpha > 0$

Λ (u.c. lambda)
3 times

In words, the four possibilities are, for increasing values of λ:

(i) The parasite population becomes extinct and the host population grows without bound;

(ii) Both host and parasite populations grow without bound, but the mean number of parasites per host tends to zero. This is known as "washout";

(iii) Both host and parasite populations grow without bound, and the mean number of parasites per host tends to a positive finite limit;

(iv) Both host and parasite populations tend to a bounded steady state. For this fourth possibility the parasite regulates the host population to a constant density.

In order to develop an n-dimensional version of (1) it is not necessary to specify the generating function for a multivariate negative binomial distribution although this can be done in a variety of ways (see Appendix). For the results in this paper we need only assume that when the n individual parasite species are distribut~~ion~~ with mean m_i, their variances are $m_i(1 + m_i/k_i)$ and the covariance between species i and species j is $m_i m_j / l_{ij}$ and $l_{ij} \geqslant k_i, k_j$.

λ ed distributed

The equations for the dynamics of the host population and the n species of parasite are

$$\frac{d\cancel{H}}{dt} = (a-b)H - \sum_{i=1,n} \alpha_i P_i$$

λH $\quad$ $\boxed{\frac{dH}{dt}}$

$$\frac{dP_j}{dt} = \frac{\lambda_j P_j H}{H_0 + H} - (b + \mu_j + \alpha_j)P_j - \frac{\alpha_j(1+k_j)}{k_j}\frac{P_j^2}{H}$$

$$- \sum_{i=1,n;\, i\neq j} \frac{\alpha_i(1+l_{ij})}{l_{ij}}\frac{P_i P_j}{H}$$

for $j = 1$ to n. These equations are easier to analyze following the transformations $X = H/(H + H_0)$, $Y_j = m_j = P_j/H$, which lead to

$$\frac{dX}{dt} = H_0 X(1-X)\left[r - \sum_{i=1,n} \alpha_i Y_i\right]$$

$$\frac{dY_j}{dt} = Y_j\left[\lambda_j X - s_j - \sum_{i=1,n} \frac{\alpha_i}{l_{ij}} Y_i\right], \tag{2}$$

where $r = a - b$, $s_j = a + \mu_j + \alpha_j$, and $l_{ii} = k_i$. The variable Y_j is the mean number of parasites of species j per host (intensity of species j), and X is an increasing measure of host population size, $0 \leqslant X < 1$, $X \to 1$ as $H \to \infty$. In contrast to Dobson [11] who assumed a common natural mortality rate μ for each parasite species, we only assume the parameter H_0 to be the same for all species. A relaxation of this latter requirement will be discussed in a subsequent paper.

In Section 2 the properties of (2) with $n = 2$ are discussed, and in Section 3 the equations for n species of parasite are analyzed. The model addresses the following questions:

(1) What determines the abundance of the different parasite species in the community?

(2) Are life history constraints on parameter values important in determining a parasite's ability to invade a community, or in permitting it to exclude other species?

(3) When can a parasite species invade a community and when is a species likely to be squeezed out?

(4) Is there a limit to the diversity of parasite communities, and which features of parasite host ecology determine observed levels of diversity?

2. THE INTERACTION BETWEEN TWO SPECIES OF PARASITE

When restricted to two species of parasite, the equations in (2) become

$$\frac{dX}{dt} = H_0 X(1-X)[r - \alpha_1 Y_1 - \alpha_2 Y_2] \tag{3}$$

$$\frac{dY_1}{dt} = Y_1\left[\lambda_1 X - s_1 - \frac{\alpha_1}{k_1} Y_1 - \frac{\alpha_2}{l} Y_2\right] \tag{4}$$

with a similar equation for Y_2. We first analyze (3), (4) for the case of exploitation competition, where $l = l_{12} \to \infty$. For this case the only interaction between the parasite species is through the dynamics of the host population ((3)).

2.1. *EXPLOITATION COMPETITION*

2.1.1. The Steady States

When $1/l = 0$ Equations (3), (4) have the uninteresting trivial solution ($X = Y_1 = Y_2 = 0$), and seven different steady state solutions:

S1 $X = 1, \quad Y_1 = Y_2 = 0.$

S2 $X = 1, \quad Y_1 = k_1(\lambda_1 - s_1)/\alpha_1, \quad Y_2 = 0.$

S3 $X = 1, \quad Y_1 = 0, \quad Y_2 = k_2(\lambda_2 - s_2)/\alpha_2.$

S4 $X = 1, \quad Y_1 = k_1(\lambda_1 - s_1)/\alpha_1, \quad Y_2 = k_2(\lambda_2 - s_2)/\alpha_2.$

S5 $X = (r + k_1 s_1)/(k_1 \lambda_1), \quad Y_1 = r/\alpha_1, \quad Y_2 = 0.$

S6 $X = (r + k_2 s_2)/(k_2 \lambda_2), \quad Y_1 = 0, \quad Y_2 = r/\alpha_2.$

S7 $X = (r + k_1 s_1 + k_2 s_2)/(k_1 \lambda_1 + k_2 \lambda_2),$
$Y_1 = k_1(\lambda_1 X - s_1)/\alpha_1, \quad Y_2 = k_2(\lambda_2 X - s_2)/\alpha_2.$

$\lambda 2$ S_2

Although all seven steady states are mathematical properties of the system for any parameter values, they are only biologically feasible if the parameters are such that the values of X, Y_1, and Y_2 are within their feasible regions, $0 < X \leqslant 1$, $0 \leqslant Y_1, Y_2$. The parameter values that lead to each of the steady states S1–S7 being feasible are indicated on the diagram of the (λ_1, λ_2) plane presented as Figure 1.

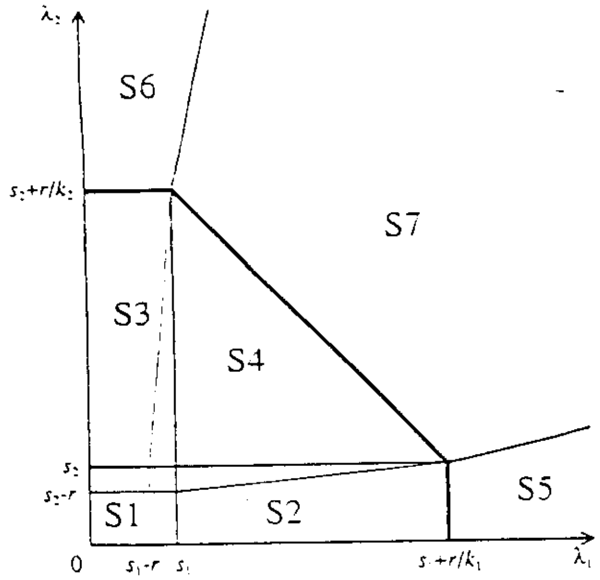


FIG. 1. Regions in the (λ_1, λ_2) plane for which each of the seven possible steady state solutions to (3), (4) are locally stable when $1/I = 0$.

2.1.2. *Local Stability Results*

The Jacobian matrix of the system (3), (4) is

$$J = \begin{pmatrix} H_0(1-2X)[r-\alpha_1 Y_1-\alpha_2 Y_2] & -\alpha_1 H_0 X(1-X) & -\alpha_2 H_0 X(1-X) \\ \lambda_1 Y_1 & \lambda_1 X - s_1 - \dfrac{2\alpha_1 Y_1}{k_1} & 0 \\ \lambda_2 Y_2 & 0 & \lambda_2 X - s_2 - \dfrac{2\alpha_2 Y_2}{k_2} \end{pmatrix}.$$

For steady states S1–S4, $X = 1$, the matrix J has eigenvalues $-H_0(r-\alpha_1 Y_1-\alpha_2 Y_2)$, $\lambda_1 - s_1 - 2\alpha_1 Y_1/k_1$, and $\lambda_2 - s_2 - 2\alpha_2 Y_2/k_2$, and hence the regions in parameter space where the steady states are locally stable are readily discerned. For steady state S5 J has two negative eigenvalues, and a third equal to $\lambda_2 X - s_2$, which is negative when $\lambda_2/s_2 < \lambda_1/(s_1 + r/k_1)$. Similarly, steady state S6 is locally stable when $\lambda_1/s_1 < \lambda_2/(s_2 + r/k_2)$. Finally direct analysis of J reveals that the steady state S7 is locally stable in the region for which it is biologically feasible, that is, the region where $0 < X < 1$ and $Y_1, Y_2 > 0$ as defined above for S7. Hence the regions in the (λ_1, λ_2) plane where steady states S1–S7 are locally stable are all readily determined. These are illustrated in Figure 1.

2.1.3. *The "Washout" Phenomenon*

For steady states S1–S3 Y_1 and/or Y_2 are zero, and the size of the host population H tends to infinity. For these cases either the total number of parasites of the relevant species (P_1 or P_2) may tend to zero, or ~~tend to a finite limit, or~~ grow at a slower rate than the host population. The situation where the parasite intensity (Y_j) tends to zero, but the total number of parasites of the same species (P_j) does not tend to zero is known as "washout," because the growing host population *washes out* the parasite population. To investigate this phenomenon rewrite (3) as

$$\frac{dH}{dt} = H[r - \alpha_1 Y_1 - \alpha_2 Y_2].$$

For S1 $Y_1, Y_2 \to 0$, and hence $H \sim e^{rt}$. From (4) $Y_1 \sim \exp[(\lambda_1 - s_1)t]$ and hence $P_1 = HY_1 \to 0$ if $\lambda_1 < s_1 - r$. Similarly species two becomes extinct if $\lambda_2 < s_2 - r$, but washes out if $s_2 - r < \lambda_2 < s_2$.

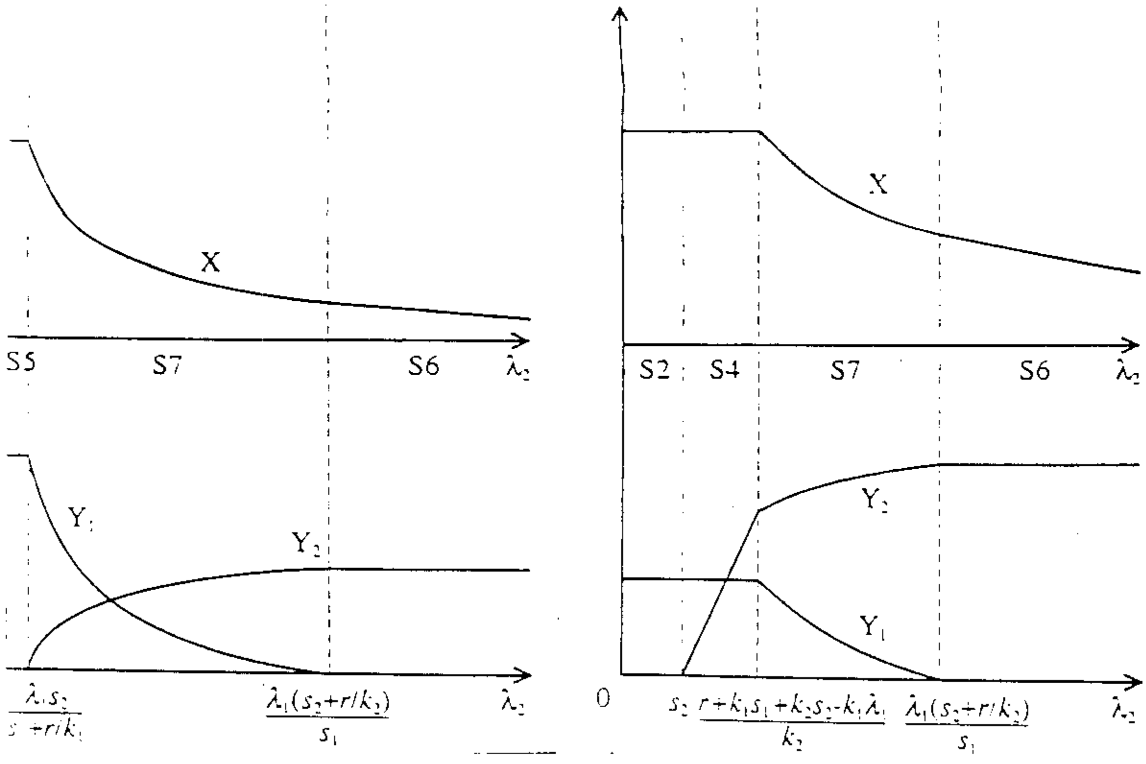
Applying a similar argument to the steady state S2 reveals that parasite species two washes out if $r + k_1 s_1 + \lambda_2 > s_2 + k_1 \lambda_1$, boundary of which is a line in the (λ_1, λ_2) plane joining the points $(s_1, s_2 - r)$ and the points $(s_1 + r/k_1, s_2)$, and hence continuous with the washout boundary in the region where S1 is stable. A similar analysis defines the boundary for S3. A typical example of the boundary between parasite population washout and extinction is shown in Figure 1. For the remainder of this paper we will not make a distinction between the two types of behavior as $Y_j \to 0$.

/ the

2.1.4. *Conditions for Invasion Success, Competitive Failure, and Coexistence*

In Sections 2.1.1–2.1.3 we catalogued the dynamical behavior of solutions to (3), (4), and hence the process of exploitation competition. The interesting points to note are the conditions under which the presence of one parasite species influences the dynamics of the other.

Figure 2a illustrates the locally stable steady state values of X, Y_1, and Y_2 plotted as functions of λ_2 with all other parameter values fixed and $\lambda_1 > s_1 + r/k_1$. Hence we are tracing a line parallel to the λ_2 axis in Figure 1, through the regions where the steady states S5, S7, and S6 are stable in turn. As λ_2 increases from zero species one is present, but species two cannot invade until the first threshold is reached. Above this threshold species two can "invade," and for increasing λ_2 the intensity of species one and the size of the host population decrease, while the intensity of species two increases. At the second threshold the intensity of species one is zero, and above it the intensity of species two



(a) (b)

FIG. 2. Locally stable steady state values of X, Y_1 and Y_2 calculated from (3), (4) for realistic values of H_0, r, α_i, k_i, and s_i, $i = 1,2$; plotted as a function of λ_2 for (a) $\lambda_1 > s_1 + r/k_1$ and (b) $\lambda_1 < s_1 + r/k_1$.

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remains constant while the host population size continues to decrease as λ_2 increases. Hence the lower threshold specifies a condition which must be met in order for species two to invade, and the upper threshold the condition for species one to be expelled. Between these thresholds the two species coexist and jointly regulate the host population.

Figure 2b shows similar information, but for the situation where the host population is not regulated by species one alone. There are now three thresholds corresponding to the boundaries in the (λ_1, λ_2) plane where S2, S4, S7, and S6 are locally stable in turn. For values of λ_2 below the first threshold species two cannot invade. As λ_2 increases through this threshold species two invades, but the intensity of species one remains constant until the second threshold is reached. Above this the parasite species regulate the host population, with the intensity of species one reaching zero at the third threshold. Above this species two is constant with increasing λ_2 (cf., Figure 2b). Hence if species one is present in an increasing host population, the lower threshold specifies the criterion for species two to invade, the middle threshold the criterion for the parasite species to jointly regulate the host population, and the upper threshold the criterion for species one to be expelled.

The condition for two parasite species to coexist in a regulated host population corresponds to the condition for the existence of the steady state S7. The boundaries between the region where this state is stable, and the regions where S5 and S6 are stable, subtend an angle θ at the origin of the (λ_1, λ_2) plane (see Figure 1), where

$$\tan\theta = \frac{(s_1 + r/k_1)(s_2 + r/k_2) - s_1 s_2}{s_1(s_1 + r/k_1) + s_2(s_2 + r/k_2)}.$$

$\lambda 2$ $\boxed{S_2}$

Hence there is always a region in the (λ_1, λ_2) plane where the two species can coexist, but this region is "squeezed" as the k_j get bigger. Small values of the k_j correspond to a high degree of aggregation, and hence aggregated species have a better chance of coexisting in a population. Analogous results have been found in other studies [3, 11, 21]. It is also apparent from Figure 1 that small values of the k_j increase the size of the region in the (λ_1, λ_2) plane where the host population is not regulated. Hence, a low degree of aggregation (large k_j) increases the ability of the parasites to regulate the host.

Finally, when two species coexist (S4 or S7) we have the relationship

$$\frac{\alpha_1}{k_1\lambda_1} Y_1 - \frac{\alpha_2}{k_2\lambda_2} Y_2 = \frac{s_2}{\lambda_2} - \frac{s_1}{\lambda_1}.$$

Hence, to a first approximation, the relative magnitudes of the two species are determined by the relative magnitudes of $k_1\lambda_1/\alpha_1$ and $k_2\lambda_2/\alpha_2$.

2.2. *INTERFERENCE COMPETITION*

Interference competition is characterized by a nonzero (positive or negative) correlation between the two parasite species, and hence $1/l \neq 0$ (see (4)). For biological realism we assume that the covariance between the distributions of the two species is small compared to their individual variances, which means mathematically that $l \gg k_1, k_2$. If the intensity of one parasite species is zero then the steady state values of X, Y_1, and Y_2 are unchanged from their values when $1/l = 0$ (see Section 2.1.1). Hence the steady states S1–S3, S5, and S6 are the same as those for exploitation competition. The state S4 is replaced by S4′, where $X = 1$ but

$$Y_1 = \frac{k_1}{\alpha_1}\,\frac{(\lambda_1 - s_1) - k_2(\lambda_2 - s_2)/l}{(1 - k_1k_2/l^2)}$$

and a similar expression holds for Y_2. The steady state S7 is replaced by S7′, where

$$X = \frac{r(1 - k_1k_2/l^2) + k_1s_1 + k_2s_2 - k_1k_2(s_1 + s_2)/l}{k_1\lambda_1 + k_2\lambda_2 - k_1k_2(\lambda_1 \cancel{-} \lambda_2)/l} \qquad \lambda +$$

$$Y_1 = \frac{k_1}{\alpha_1}\,\frac{(\lambda_1 X - s_1) - k_2(\lambda_2 X - s_2)/l}{(1 - k_1k_2/l^2)}$$

with a similar expression for Y_2. The Jacobian matrix of the system (3), (4) is

$$J = \begin{pmatrix} H_0(1-2X)[r - \alpha_1Y_1 - \alpha_2Y_2] & -\alpha_1H_0X(1-X) & -\alpha_2H_0X(1-X) \\ \lambda_1Y_{\cancel{1}} & \lambda_1X - s_1 - \dfrac{2\alpha_1Y_1}{k_1} - \dfrac{\alpha_2Y_2}{l} & -\dfrac{\alpha_2Y_1}{l} \\ \lambda_2Y_2 & -\dfrac{\alpha_1Y_2}{l} & \lambda_2X - s_2 - \dfrac{2\alpha_2Y_2}{k_2} - \dfrac{\alpha_1Y_1}{l} \end{pmatrix}. \qquad \lambda_1 \quad \boxed{Y_1}$$

For steady states S1–S3 and S4′, J has one eigenvalue equal to $-H_0(r-\alpha_1 Y_1-\alpha_2 Y_2)$, and two others which are negative if

$$\left(\frac{2}{k_1}+\frac{1}{l}\right)\alpha_1 Y_1+\left(\frac{2}{k_2}+\frac{1}{l}\right)\alpha_2 Y_2>(\lambda_1-s_1)+(\lambda_2-s_2)$$

and

$$\begin{vmatrix} \lambda_1-s_1-\dfrac{2\alpha_1 Y_1}{k_1}-\dfrac{\alpha_2 Y_2}{l} & -\dfrac{\alpha_2 Y_1}{l} \\ -\dfrac{\alpha_1 Y_2}{l} & \lambda_2-s_2-\dfrac{2\alpha_2 Y_2}{k_2}-\dfrac{\alpha_1 Y_1}{l} \end{vmatrix}>0.$$

The regions in the (λ_1,λ_2) plane for which ⁁ of these steady states is locally stable are then readily determined from the values of Y_j given above. For steady state S5 two eigenvalues of J are negative, and the third is negative when $\lambda_2(s_1+r/k_1)<\lambda_1(s_2+r/l)$ (recall that S5 can only exist if $\lambda_1>s_1+r/k_1$). A similar result holds for S6. For the steady state S7′ the eigenvalues of J are the roots of the cubic polynomial

⁁each

$$\begin{aligned} w^3&+\left(\frac{\alpha_1 Y_1}{k_1}+\frac{\alpha_2 Y_2}{k_2}\right)w^2\\ &+\left(\alpha_1\alpha_2 Y_1 Y_2\left(\frac{1}{k_1 k_2}-\frac{1}{l^2}\right)+H_0 X(1-X)(\alpha_1\lambda_1 Y_1+\alpha_2\lambda_2 Y_2)\right)w\\ &+H_0 X(1-X)\alpha_1\alpha_2 Y_1 Y_2\left(\frac{\lambda_1}{k_2}+\frac{\lambda_2}{k_1}-\frac{\lambda_1+\lambda_2}{l}\right). \end{aligned}$$

As the coefficients are positive, and the product of the coefficients of w^2 and w exceed the constant term, the roots of the cubic equation have negative real part. Hence the steady state S7′ is locally stable whenever it exists. The regions of the (λ_1,λ_2) plane for which ~~each of the~~ seven steady states ~~exist~~ and are locally stable are specified in Table 1, and illustrated in Figure 3. The steady states are labelled S2′–S7′ to emphasize that although ~~in some~~ cases the values of X, Y_1, and Y_2 are the same as when $1/l=0$, their regions of stability in the (λ_1,λ_2) plane are different.

In Figure 3a it can be seen that where there is a positive correlation between the parasite species; the region in parameter space where two species can coexist is reduced, as is the region where the host population is regulated. Alternatively, it can be seen in Figure 3b that a

TABLE 1

The Regions in the (λ_1, λ_2) Plane of the Regions Where the Steady State Solutions of (3), (4) Exist and Are Locally Stable

S1	$0 < \lambda_1 < s_1, 0 < \lambda_2 < s_2$
S2′	$s_1 < \lambda_1 < s_1 + r/k_1, 0 < \lambda_2 < s_2 + k_1(\lambda_1 - s_1)/l$
S3′	$0 < \lambda_1 < s_1 + k_2(\lambda_2 - s_2)/l, s_2 < \lambda_2 < s_2 + r/k_2$
S4′	$\lambda_1 > s_1 + k_2(\lambda_2 - s_2)/l, \lambda_2 > s_2 + k_1(\lambda_1 - s_1)/l,$ $k_1(1 - k_2/l)(\lambda_1 - s_1) + k_2(1 - k_1/l)(\lambda_2 - s_2) < (1 - k_1k_2/l^2)r$
S5′	$\lambda_2(s_1 + r/k_1) < \lambda_1(s_2 + r/l), \lambda_1 > (s_1 + r/k_1)$
S6′	$\lambda_1(s_2 + r/k_2) < \lambda_2(s_1 + r/l), \lambda_2 > (s_2 + r/k_2)$
S7′	$\lambda_1(s_2 + r/k_2) > \lambda_2(s_1 + r/l), \lambda_2(s_1 + r/k_1) > \lambda_1(s_2 + r/l)$ $k_1(1 - k_2/l)(\lambda_1 - s_1) + k_2(1 - k_1/l)(\lambda_2 - s_2) > (1 - k_1k_2/l^2)r$

negative correlation between the parasite species results in an enlarged region where they can both coexist and an enlarged region where the host population is regulated. Synergistic interactions between parasites are thus likely to reduce diversity or require hosts with enhanced population growth rates. In contrast, competition increases diversity but reduces the abundance of individual parasite species.

The boundaries between the regions in the (λ_1, λ_2) plane where S5′ and S7′, and S6′ and S7′ are locally stable subtend an angle θ at the origin, where

$$\tan\theta = \frac{(s_1 + r/k_1)(s_2 + r/k_2) - (s_1 + r/l)(s_2 + r/l)}{(s_1 + r/l)(s_1 + r/k_1) + (s_2 + r/l)(s_2 + r/k_2)}.$$

Although this region is "squeezed" even more when $l > 0$, there is still always a region where the species can coexist. A negative correlation between the parasite species facilitates coexistence, whereas a positive correlation reduces the area of parameter space where this is possible.

3. THE INTERACTION BETWEEN n SPECIES OF PARASITE

We now generalize the analysis of Section 2 in order to examine the dynamics of n interacting species of parasite. Equations (2) have the uninteresting trivial steady state, $2^n - 1$ different steady states with $X = 1$, and another $2^n - 1$ with $X < 1$. The weight of analysis can be reduced by imposing an ordering on the parasite species according to whether their steady state intensity is positive or zero.

3.1. *EXPLOITATION COMPETITION*

When $1/l_{ij} = 0$ for $i \neq j$, and $l_{ii} = k_i$, the equations in (2) have the steady states where all parasite species are present: $X = 1$, $Y_j = k_j(\lambda_j -$

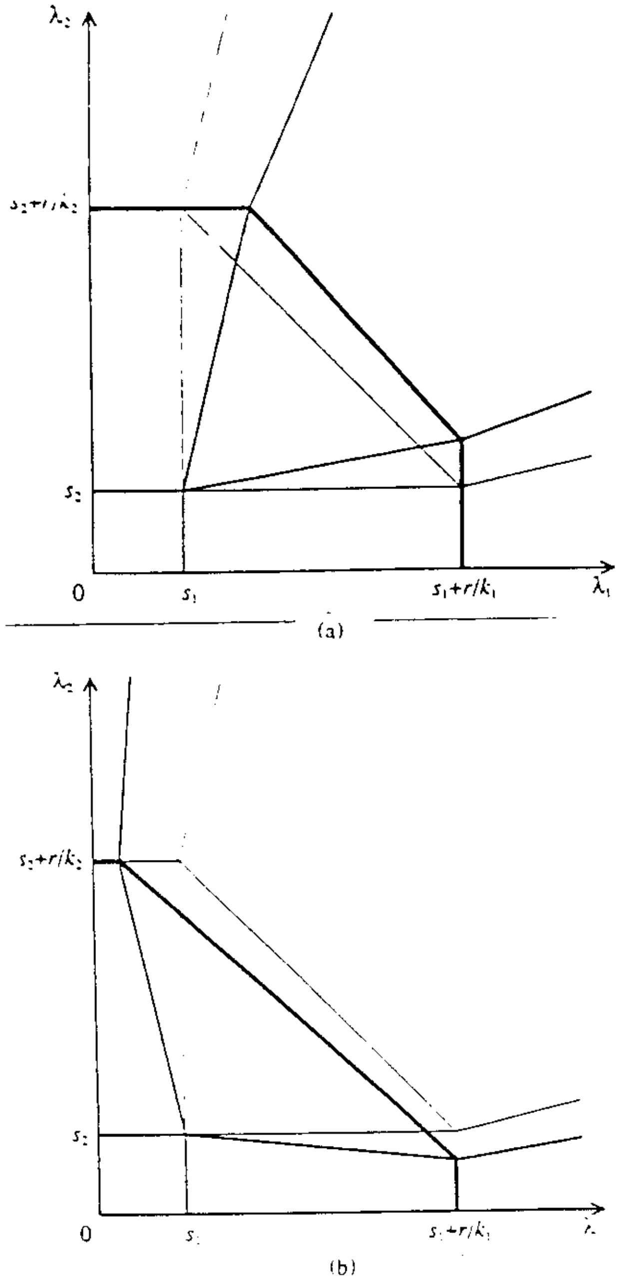

FIG. 3. Regions in the (λ_1, λ_2) plane for which each of the seven possible steady state solutions to (3), (4) are locally stable, with (a) $l > 0$ and (b) $l < 0$. The boundaries in Figure 1 are shown as faint lines.

$s_j)/\alpha_j$ for $j = 1$ to n; $X = (r + \Sigma_{i=1,m} k_i s_i)/\Sigma_{i=1,m} k_i \lambda_i$, $Y_j = k_j(\lambda_j X - s_j)/\alpha_j$ for $j = 1$ to n; and the steady state values where some of the species are absent: $X = 1$, $Y_j = k_j(\lambda_j - s_j)/\alpha_j$ for $j = 1$ to m, $Y_j = 0$ for $j = m + 1$ to n, for all $m = 1$ to $n - 1$; and $X = (r + \Sigma_{i=1,m} k_i s_i)/\Sigma_{i=1,m} k_i \lambda_i$, $Y_j = k_j(\lambda_j X - s_j)/\alpha_j$ for $j = 1$ to m, $Y_j = 0$ for $j = m + 1$ to n, for all $m = 1$ to $n - 1$. The biologically realistic steady states are those with $X \leqslant 1$ and $Y_j \geqslant 0$ for $j = 1$ to n.

When there are m parasite species present, the Jacobian matrix of the system J has the principal $(m + 1) \times (m + 1)$ submatrix

$$J' = \begin{pmatrix} H_0(1-2X)[r - \Sigma_{i=1,m}\alpha_i Y_i] & -\alpha_1 H_0 X(1-X) & -\alpha_2 H_0 X(1-X) & \cdots \\ \lambda_1 Y_1 & \lambda_1 X - s_1 - \dfrac{2\alpha_1 Y_1}{k_1} & 0 & \cdots \\ \lambda_2 Y_2 & 0 & \lambda_2 X - s_2 - \dfrac{2\alpha_2 Y_2}{k_2} & \cdots \\ \cdots & \cdots & \cdots & \cdots \\ \lambda_m Y_m & \cdots & \cdots & \cdots \end{pmatrix}$$

diagonal elements $J_{ii} = \lambda_i X - s_i$ when $m + 1 < i \leqslant n$, and all other entries zero.

For the steady states where the host population is not regulated $(X = 1)$, the eigenvalues of J are $-H_0(r - \Sigma_{i=1,m}\alpha_i Y_i)$, $-\alpha_i Y_i / k_i$ for $1 \leqslant i \leqslant m$, and $\lambda_i - s_i$ for $m + 1 < i \leqslant n$. Hence the regions in parameters space where each of these steady states are locally stable are easily determined. In particular, species i can or cannot persist according to whether λ_i is greater or less than s_i, subject to the overall condition $r > \Sigma_{i=1,m}\alpha_i Y_i$. If this last condition is contravened, then the host population is regulated by the m species.

The Jacobian matrix about the regulated steady states has the principal $(m + 1) \times (m + 1)$ submatrix

$$J' = \begin{pmatrix} 0 & -\alpha_1 H_0 X(1-X) & -\alpha_2 H_0 X(1-X) & \cdots \\ \lambda_1 Y_1 & -\dfrac{\alpha_1 Y_1}{k_1} & 0 & \cdots \\ \lambda_2 Y_2 & 0 & -\dfrac{\alpha_2 Y_2}{k_2} & \cdots \\ \cdots & \cdots & \cdots & \cdots \\ \lambda_m Y_m & \cdots & \cdots & \cdots \end{pmatrix}$$

with the other elements zero apart from $J_{ii} = \lambda_i X - s_i$ for $m + 1 < i \leqslant n$. The eigenvalues $\lambda_i X - s_i$ for $m + 1 < i \leqslant n$ determine the stability of the steady state when the corresponding $Y_i = 0$. The other eigenvalues of the Jacobian matrix correspond to those of J'. Let w be an eigenvalue of J', and let the corresponding eigenvector have components u_{j-1} for $j = 0$ to $m + 1$. The u_j solve the equations

$$wu_0 + H_0 X(1 - X) \sum_{j=1,m} \alpha_j u_j = 0 \tag{5}$$

$$\lambda_j Y_j u_0 - \left(w + \frac{\alpha_j Y_j}{k_j} \right) u_j = 0. \tag{6}$$

First suppose w real and positive. If u_0 were zero, then from (6) all u_j for $j = 1$ to m would be zero. Hence without loss of generality assume $u_0 > 0$. Equation (6) then implies that $u_j > 0$ for $j = 1$ to m, but (5) then implies $u_0 < 0$. A similar contradiction follows from the assumption that w is complex with positive real part. Hence all eigenvalues of J' are negative, or complex with negative real part, and the stability of steady states where the host population is regulated is determined.

Given a set of parameters $\{r, k_i, s_i, \alpha_i, \lambda_i, i = 1 \text{ to } n\}$ it is now possible to determine which steady state exists and is locally stable. The process is presented below in the form of an algorithm.

```
1.  Order the species so that $\lambda_i / s_i \geq \lambda_{i-1} / s_{i-1}$ for $i = 1$ to $n$.
2.  $m := \max\{i: 1 \leq i \leq n$, such that $\lambda_i > s_i\}$;
3.  For $i = m + 1$ to $n$: $Y_i := 0$;
4.  $X := (r + \Sigma_{i=1,m} k_i s_i) / \Sigma_{i=1,m} k_i \lambda_i$;
5.  If $X < 1$ then {Host population is regulated}
6.      For $i = 1$ to $m$: $Y_i := k_i(\lambda_i X - s_i)/\alpha_i$;
7.      If $Y_m < 0$ then
8.          $Y_m := 0$;
9.          $m := m - 1$;
10.         Go To Step 3;
11. Else {Host population is not regulated}
12.     $X = 1$;
13.     For $i = 1$ to $m$: $Y_i := k_i(\lambda_i - s_i)/\alpha_i$;
14. End;
```

The invasion problem may be solved by examining the stability of the steady state where just one of the Y_i ~~are~~ zero. Assume that the host population is regulated by $m = n - 1$ parasite species, and the intensity of species n is zero. Hence $X = (r + \Sigma_{i=1,m} k_i s_i)/\Sigma_{i=1,m} k_i \lambda_i$, and $J_{nn} = \lambda_n - s_n$. If $J_{nn} > 0$ this steady state is unstable. Species n will then invade and the host population will subsequently be regulated by the n parasite species. Note also that, by direct differentiation $\partial X / \partial k_j < 0$ whenever $\lambda_j X > s_j$, and hence when a parasite species regulates its host

is

population, the host population size is smaller when the degree of aggregation is less. As noted in Section 2.1, a low degree of aggregation in individual parasite species increases the ability of the parasites to regulate the host population.

3.2. INTERFERENCE COMPETITION

We now introduce a nonzero covariance, i.e., for at least one pair (i, j), $i \neq j$, $0 < i, j \leqslant n$, $1/l_{ij} \neq 0$. As before we assume covariances to be small compared to variances. The full steady state solutions of (2) are now difficult to construct explicitly, but approximate solutions may be found by looking for small perturbations about the solutions for exploitation competition.

$\lambda \neq$ not equal to

Consider first the case where there is no population regulation, for which the steady state solution is $X = 1$ $(H \to \infty)$ and

$$Y_j + \sum_{i=1,n;\, i \neq j} \frac{\alpha_i l_{jj}}{\cancel{\alpha_j} l_{ij}} Y_i = \frac{l_{jj}}{\alpha_j}(\lambda_j - s_j) = Y_j^*,$$

$\times$

$\lambda \propto$ alpha

α_j

where Y_j^* is steady state solution for exploitation competition. Defining $\epsilon = \max\{l_{jj}/l_{ij};\ i, j = 1 \text{ to } n;\ i \neq j\}$ we obtain

$$Y_j = Y_j^* - \sum_{i=1,n;\, i \neq j} \frac{\alpha_i}{\alpha_j} \frac{l_{jj}}{l_{ij}} Y_i^* + o(\epsilon) \tag{7}$$

and hence if all covariances are positive, and other parameters remain unchanged then the intensity of each parasite species is reduced in comparison with that for exploitation competition. Similarly, if all covariances are negative the intensities are increased.

When population regulation occurs, define $x = X - X^*$, $|x| \ll 1$. Where $Y_j \neq 0$ the steady state values must solve

$$\sum_{i=1,n} \frac{\alpha_i}{l_{ij}} Y_i = \lambda_j (X^* + x) - s_j$$

and hence

$$Y_j = Y_j^* - \sum_{i=1,n;\, i \neq j} \frac{\alpha_i}{\alpha_j} \frac{l_{jj}}{l_{ij}} Y_i^* + \frac{l_{jj}}{\alpha_j}\left(\lambda_j - \sum_{i=1,n,\, i \neq j} \frac{l_{jj}}{l_{ij}} \lambda_i\right) x + o(\epsilon). \tag{8}$$

Substituting in $\Sigma_{i=1,n}\alpha_i Y_i = r$ we obtain

$$x = \frac{\displaystyle\sum_{j=1,n}\;\sum_{i=1,n;\,i\neq j} \alpha_i \frac{l_{jj}}{l_{ij}} Y_i^*}{\displaystyle\sum_{j=1,n} l_{jj}\lambda_j} + o(\epsilon). \tag{9}$$

Hence steady state values may be found. If all covariances are positive then $x > 0$, and the host population is regulated at a higher density than it would be if the covariances were zero. Note, however, that if Y_j is the steady state intensity of species j under interference competition, and Y_j^* is its intensity under exploitation competition, then

$$\sum_{j=1,n} \alpha_j (Y_j - Y_j^*) = 0$$

and hence interference competion will always increase the intensity of some species and decrease the intensity of others.

3.3. *EXAMPLE* $n = 3$

First consider three parasite species exhibiting exploitation competition. In accordance with the algorithm order the species so that $\lambda_1/s_1 > \lambda_2/s_2 > \lambda_3/s_3$. If $\lambda_3 > s_3$ then $m = 3$ and we calculate $X = (r - \Sigma_{i=1,3}k_i s_i)/\Sigma_{i=1,3}k_i\lambda_i$. If $X < 1$ the host population is regulated by the three parasite species. Explicit expressions for the Y_i are

? λ_3 $\Sigma_{i=1,3}$

$$\begin{aligned} Y_1 &= \frac{k_1}{\alpha_1}\left(\frac{r\lambda_1 + k_2(\lambda_1 s_2 - \lambda_2 s_1) + k_3(\lambda_1 s_3 - \lambda_3 s_1)}{k_1\lambda_1 + k_2\lambda_2 + k_3\lambda_3}\right)\\ Y_2 &= \frac{k_2}{\alpha_2}\left(\frac{r\lambda_2 + k_1(\lambda_2 s_1 - \lambda_1 s_2) + k_3(\lambda_2 s_3 - \lambda_3 s_2)}{k_1\lambda_1 + k_2\lambda_2 + k_3\lambda_3}\right)\\ Y_3 &= \frac{k_3}{\alpha_3}\left(\frac{r\lambda_3 + k_1(\lambda_3 s_1 - \lambda_1 s_3) + k_2(\lambda_3 s_2 - \lambda_2 s_3)}{k_1\lambda_1 + k_2\lambda_2 + k_3\lambda_3}\right). \end{aligned} \tag{10}$$

By the ordering of the parasite species Y_1 and Y_2 are positive, if $Y_3 < 0$ as calculated by (10) we reset $Y_3 = 0$, $m = 2$ and recalculate X. When $m = 2$ the steady states are the same as for the two-species model, except that from (10) the states where the host population is regulated are only stable when

$$\frac{\lambda_3}{s_3}(r - k_1 s_1 - k_2 s_2) > k_1\lambda_1 + k_2\lambda_2.$$

When the host population is not regulated the steady states are $X = 1$ and $Y_i = k_i(\lambda_i - s_i)/\alpha_i$ if $\lambda_i > s_i$, otherwise $Y_i = 0$. The steady states ~~and their~~ regions of stability in the $(\lambda_1, \lambda_2, \lambda_3)$ octant are summarized in Table 2.

~~The~~ changes to these steady states due to a nonzero correlation between the species may be determined from Section 3.2. When the host population is not regulated ($X = 1$), then from (7)

$$Y_1 = Y_1^* - \frac{\alpha_2}{\alpha_1}\frac{l_{11}}{l_{12}}Y_2^* - \frac{\alpha_3}{\alpha_1}\frac{l_{11}}{l_{13}}Y_3^*$$

TABLE 2

The Regions in the $(\lambda_1, \lambda_2, \lambda_3)$ Plane ~~of the Regions~~ Where the Steady State Solutions of (2) Exist and Are Locally Stable, with $n = 3$, $1/l_{ij} = 0$ if $i \neq j$, $l_{ii} = k_i$ and $\lambda_1/s_1 \geqslant \lambda_2/s_2 \geqslant \lambda_3/s_3$

	Steady state values	Locally stable iff
$m = 0$	$X = 1$, $Y_i = 0$, $i = 1$ to 3	$\lambda_i < s_i$, $i = 1$ to 3
$m = 1$	$X = 1$, $Y_1 = k_1(\lambda_1 - s_1)/\alpha_1$, $Y_2 = Y_3 = 0$	$s_1 < \lambda_1 < r + s_1/k_1$ $\lambda_2 < s_2$, $\lambda_3 < s_3$
	$X = (r + k_1 s_1)/k_1\lambda_1$, $Y_1 = r/\alpha_1$, $Y_2 = Y_3 = 0$	$\lambda_1 > r + s_1/k_1$ $\lambda_i < s_i + r/k_i - k_1(s_1 - \lambda_1)/k_i$ $i = 2, 3$ $\Sigma_{i=1,3} k_i \lambda_i > r + \Sigma_{i=1,3} k_i s_i$
$m = 2$	$X = 1$, $Y_i = k_i(\lambda_i - s_i)/\alpha_i$, $i = 1, 2$, $Y_3 = 0$	$\lambda_1 > s_1$, $\lambda_2 > s_2$, $\lambda_3 < s_3$ $k_1\lambda_1 + k_2\lambda_2 < r + k_1 s_1 + k_2 s_2$
	$X = (r + k_1 s_1 + k_2 s_2)/$ $(k_1\lambda_1 + k_2\lambda_2)$, $Y_i = k_i(\lambda_i X - s_i)/\alpha_i$, $i = 1, 2$, $Y_3 = 0$	$\lambda_1 > s_1$, $\lambda_2 > s_2$ Either $\lambda_3 < s_3$ and $k_1\lambda_1 + k_2\lambda_2 > r + k_1 s_1 + k_2 s_2$ Or $\lambda_3 < s_3(k_1\lambda_1 + k_2\lambda_2)/(r + k_1 s_1 + k_2 s_2)$ and $\Sigma_{i=1,3} k_i \lambda_i < r + \Sigma_{i=1,3} k_i s_i$
$m = 3$	$X = 1$, $Y_i = k_i(\lambda_i - s_i)/\alpha_i$, $i = 1$ to 3	$\lambda_i > s_i$, $i = 1$ to 3 and $\Sigma_{i=1,3} k_i \lambda_i < r + \Sigma_{i=1,3} k_i s_i$
	$X = (r + \Sigma_{i=1,3} k_i s_i)/$ $\Sigma_{i=1,3} k_i \lambda_i$, $Y_i = k_i(\lambda_i X - s_i)/\alpha_i$ $i = 1$ to 3	$\lambda_1 > s_1$, $\lambda_2 > s_2$, $\lambda_3 > s_3(k_1\lambda_1 + k_2\lambda_2)/(r + k_1 s_1 + k_2 s_2)$ and $\Sigma_{i=1,3} k_i \lambda_i > r + \Sigma_{i=1,3} k_i s_i$

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to order ϵ, with similar equations for Y_2 and Y_3. It is apparent that the steady state intensity of infection of species 1 is reduced if

$$\frac{l_{22}}{l_{12}}(\lambda_2 - s_2) + \frac{l_{33}}{l_{13}}(\lambda_3 - s_3) > 0.$$

When population regulation does occur, the change in the host population density is found from (9) as

$$x = \frac{(l_{22}/l_{21} + l_{33}/l_{31})\alpha_1 Y_1^* + (l_{11}/l_{12} + l_{33}/l_{32})\alpha_2 Y_2^* + (l_{11}/l_{13} + l_{22}/l_{23})\alpha_3 Y_3^*}{l_{11}\lambda_1 + l_{22}\lambda_2 + l_{33}\lambda_3}$$

and the changes in the intensity of each parasite species may then be found from (8).

4. DISCUSSION

The results presented in this paper have implications for both the structure of parasitic helminth communities, and the structure of communities of other organisms that utilize patchily distributed dynamic resources [3,20,31,32]. Similar models apply to many other ecological systems (for example, insects on plants, coral reef fishes, and on a longer time scales birds in woodlands). In particular, the models are appropriate for any system where communities (or assemblages) of species with relatively high birth and death rates repeatedly colonize and utilize the individuals of a species with slower rates of population turnover. The results suggest that spatial heterogeneity may be as crucial a mechanism in determining the diversity of ecological communities of other free living systems as it is for parasitic helminths. Other workers have recently derived similar results for microparasites such as viruses and bacteria utilizing hosts as resources [35], Drosophila using fruit as a resource [3,29,30,31], and plant species utilizing space as a resource [35,36]. It is suggested that the coexistence of parasite species that utilize the same host population is mainly mediated by the aggregate distribution of each parasite species within the host population, which effectively "frees up" unoccupied areas of host-space for colonization by other species.

The results show that highly aggregated parasite species are more likely to coexist, but are less able to regulate their host population. The conditions that determine which of two parasite species (or both) is able to persist in a host population have been presented in two ways: as regions in parameter space (Figure 1) and as bifurcation diagrams (Figure 2). A negative correlation between the distributions of two parasite species enhances both their ability to coexist and their ability to regulate the host population (Figure 3). The analysis for exploitation competition (zero covariance) has been extended to three (Table 2) or more parasite species, and the results generalized to interference competition (nonzero covariance) using a perturbation technique. In more detailed models for parasite communities that include stochastic effects, it is likely that the high fecundity and long life expectancy of parasitic helminths will also promote the coexistence of a variety of parasite species [6,36].

The algorithm that describes whether or not a species can invade the parasite community provides insights into the continuing debate about "core and satellite" species in parasite communities [5,10,14], and the larger debate which considers these phenomena in populations of free-living species that live in naturally discrete patchy or fragmented environments [17,26]. Essentially, these invasion criteria suggest the community will be dominated by species with large basic reproduction ratio ($R_0 = \lambda_i / s_i$) and that a continuous spectrum of strategies exist in any community; at one end are "core" species with high R_0 values and at the "satellite" end are species with low R_0 values.

A continuing debate in ecology is concerned with whether the structure of ecological communities are the result of interactive or noninteractive processes [28]. Most data sets for parasite communities suggest that local abundances (the burden of worms carried by individual host animals) are determined by regional abundance [10,12], but a recent review suggests that communities of parasitic helminths provide the main examples of communities where interactions between species are the primary process determining relative abundance [8]. A simulation study has suggested that (in at least one system) interactions between parasite species play only a minor role in determining the structure of the parasite community [22]. Empirical studies present evidence for both positive and negative interactions between parasites in natural communities [4,7,11,12,13,18,19,25]. The models described in the present paper suggest that interactions between parasites and their hosts are more important in determining community structure than direct interactions between the parasite species. Indeed, direct interactions between parasite species may produce the opposite effect on diversity than would be assumed by cursory examination of the sign of the interaction.

These results demonstrate the importance of individual life histories in determining whether a parasite will establish in, and potentially regulate, a host population. The importance of life history payoffs in determining the structure of ecological communities and assemblages, and the trade-offs within the life histories of the different species that allow the~~y~~ to coexist, has been emphasized in a number of recent

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studies [29,30,35]. For example, a detailed study of trematode communities in snails has shown that even where interactions between parasite species are pronounced, the fecundity and colonization rates of individual species are crucial in determining their abundance in the parasite community [33]. The work described in the present paper suggests that similarities in the life-history strategies of parasitic organisms are important in determining which species will establish in a host population. Small differences between species will then be important in determining which species will coexist. Recent studies have suggested that parasite communities can be classified as either isolationist, where interactions between species are infrequent, through to interactive, where interactions between parasite species have pronounced effects on diversity [20,23] (compare the distinction between exploitation and interference competition in the present paper). In addition, a recent review of parasitic helminths in vertebrate hosts suggests that parasite communities fall along a spectrum from completely isolationist to highly interaction [34]. The results presented in this paper compliment that review in suggesting that fecundity and recruitment dominate interactions between parasite species in determining the observed levels of diversity and abundance in parasite communities.

APPENDIX

A candidate for a probability generating function for a community of n parasites is

$$\mathcal{F} = \prod_{i=1,n} F(m_i, k_i, z_i) + \sum_{j=1,n} \sum_{i<j} \frac{[1 - F(m_i, k_i, z_i)][1 - F(m_j, k_j, z_j)]}{l_{ij}}, \qquad \text{(A1)}$$

where $F(m,k,z)$ is the generating function for the negative binomial distribution (see Section 1). We establish conditions for $\mathcal{F}$ to be a generating function, i.e., conditions that ensure that $\mathcal{F} = 1$ when $z_i = 1$ for all i, and that the coefficients of the Taylor expansion of $\mathcal{F}$ in the z_i are positive. The first condition follows directly from the fact that F is a generating function, hence $F(m,k,1) = 1$. The second condition is similarly easy to verify when $1/l_{ij} = 0$ for all i, j (exploitation competition), but does not hold for all values of l_{ij}.

For notational convenience let the coefficient of z_i^p in the expansion of $F(m_i, k_i, z_i)$ be $F_p^{(i)} > 0$. The probability that a host animal has no parasites of any species is

$$\prod_{i=1,n} F_0^{(i)} + \sum_{j=1,n} \sum_{i<j} \frac{\left[1 - F_0^{(i)}\right]\left[1 - F_0^{(j)}\right]}{l_{ij}}. \tag{A2}$$

The probability that a host animal has p parasites of species i, and no parasites of any other species is

$$F_p^{(i)}\left(\prod_{j=1,n;\, i \neq j} F_0^{(j)} - \sum_{j=1,n;\, i \neq j} \frac{\left[1 - F_0^{(j)}\right]}{l_{ij}}\right), \tag{A3}$$

and the probability that a host animal has p parasites of species i, q parasites of species j, and no parasites of any other species is

$$F_p^{(i)} F_q^{(j)}\left(\prod_{w=1,n;\, w \neq i,j} F_0^{(j)} + \frac{1}{l_{ij}}\right). \tag{A4}$$

For $\mathcal{F}$ to be a generating function (A2)–(A4) must be positive, which for (A3) and (A4) requires that the expressions in parentheses are positive.

For the case where $n = 2$ conditions (A2)–(A4) simplify to

$$-\frac{1}{\left(1 + \frac{m_1}{k_1}\right)^{k_1} - 1} \times \frac{1}{\left(1 + \frac{m_2}{k_2}\right)^{k_2} - 1} < \frac{1}{l} < \frac{1}{\left(1 + \frac{m_1}{k_1}\right)^{k_1} - 1}$$

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$$-1 < \frac{1}{l} < \frac{1}{\left(1 + \frac{m_2}{k_2}\right)^{k_2} - 1}. \tag{A5}$$

Equations (A5) show that $\mathcal{F}$ is not a valid generating function for all values of l and m_i. As Y_i ($= m_i$, see (2)) tends to infinity in (A5), $1/l$ must tend to zero for the inequality to hold. However, as pointed out in the text the results do not depend on the precise generating function, only on the stated variance and covariance to mean relationships.

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