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Species density distributions as null models for ecologically significant interactions of parasite species in an assemblage

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Abstract

A multiple-kind lottery model is presented for use in determining whether species density distributions in parasite species assemblages reveal regularly occurring species-to-species interactions. The model utilizes a recurrence vector algorithm to rapidly calculate expected frequencies of species per host classes in such assemblages. These calculations have been a computational problem because the probability of a host individual acquiring one species of parasite is not necessarily equal to that of acquiring another species. Thus although the number of possible ways for a host to acquire x parasite species of a possible n is given by the familiar binomial expansion term $n!/[x!(n-x)!]$, each of these ways can have a different probability. The model is applicable to any system that mimics a multiple-kind lottery in which (1) successes are independent events and (2) it is possible to fail completely to acquire any parasites or their analogs. The algorithm is thus a null model for species density distributions in general. Application of the model is illustrated by host/parasite systems involving snails and trematodes, fish and their protozoan and platyhelminth parasites, and a relatively rich assemblage of parasites in bats.

Keywords: Parasitism; Species interactions

1. Introduction

Parasite species assemblages present a number of problems that have made interpretation of field data somewhat frustrating. For example, hosts may differ significantly in the diversity of their parasite fauna (Kennedy et al., 1986), regional and local diversity may or may not be interrelated (Goater et al., 1987; Janovy et al., 1992), and the extent to which assemblage members are interactive is still a matter of controversy (Price, 1984, 1987; Holmes and Price, 1986). Numerous investigators have used similarity indices to compare parasites from various host species and populations (e.g. Bush, 1990). However, such comparisons do not lead naturally to further studies aimed at discovery of mechanisms by which assemblage structure is determined. Similarly, the concept of "core" and "satellite" species, at least as used by parasitologists, describes rather than explains the origin and nature of assemblage structure (cf. Pence and Windberg, 1984; Stock and Holmes, 1987a,b, 1988).

Species density frequency distributions con-

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structed from field data on species-poor parasite assemblages often fit a histogram predicted by a random selector model (Goater et al., 1987; Dobson, 1990; Janovy et al., 1990, 1992). In this lottery-type model the host selects parasites, at random, from a multiple-kind array in which (1) the relative probability of becoming infected may be different for each parasite species, and (2) the array is not completely filled with parasites (see fig. 5 in Janovy et al., 1992). Thus it is possible for a host to select a number of times, from the array, without getting infected. Independence of parasitic events, i.e. the occurrence of a species, is implicit in this model.

Although competition between assemblage members frequently has been inferred from field data on species density distributions (Dobson, 1985; Stock and Holmes, 1987a), the follow-up experiments generally have not been done, or sometimes cannot be done because of the logistical difficulties of working with certain systems, e.g. as in the migratory bird studies of Bush and Holmes (1986a,b). And in those cases where assemblage members appear to interact, the observations often can be explained by ecological factors (e.g. intermediate hosts share microenvironments) or heterogeneity in summarized published data sets (Goater et al., 1987; Janovy and Hardin, 1988).

Species density frequency distributions have not been presented very often either in original or review papers (but see Lotz and Font, 1985, 1991), although it is obvious from published data sets that the information necessary to calculate the theoretical frequencies, for comparison to observed ones, has been gathered (see references in Esch et al., 1990). These distributions are, however, potentially of great utility for four reasons: (1) they routinely fit discrete approximations of normal curves, thus allow rather standard parametric analyses (unlike many parasite population and community descriptors); (2) this property facilitates meaningful statistical comparisons between parasite assemblages in related, sympatric hosts, or in different populations (or subpopulations) of a single host species; (3) because of the second reason, they are easily incorporated into experimental designs; and (4) they provide a null model for use in testing for the role of species-to-species interactions in providing structure to a species assemblage.

The large number of parasite species found in some host species' populations, however, makes the direct calculation of expected frequencies prohibitively laborious without a time-efficient method, and the few workers who have used species density distributions as research tools have either fit them to Poissons (Goater et al., 1987) or derived them from Monte Carlo simulations (Lotz and Font, 1991). Although some parasite species density distributions fit a Poisson (Dobson, 1990), they are not in fact Poisson distributions because success and failure (p, $1-p$) vary with each species in the assemblage. For example, in an assemblage of n parasite species, the probability of a 3-species infection is not given by the familiar combination–permutation formula for n items taken 3 at a time multiplied by $p^3(1-p)^{n-3}$, but varies depending on which 3 species of parasites are involved. In addition, in the case of parasites, different transmission mechanisms and life cycles mean that infection events are not equivalent, regardless of their potential statistical independence. The calculations are a practical problem because many parasite species assemblages contain more than 10 species. Expected frequencies for an assemblage with 15 species, such as reported by Leong and Holmes (1981), require calculations for 32 768 combinations, a time-consuming task even for most personal computers.

The algorithm presented in this paper solves the calculation time problem well enough to allow theoretical species density distributions to be used as a research tool even with highly diverse assemblages. This solution demonstrates the utility of handling parasite assemblage data as species density distributions fit to the null model of no interspecific interaction. The general methods presented are applicable to any analogous multiple-kind array.

2. The concept

Conceptually, the species density model consists of a multiple-kind array of slots, some of

which are filled, and some of which are empty. A host individual "selects" parasites from this array in a uniform random manner. Each kind (of parasite) has an equal range of slots. The parasite kinds can differ in the proportion of their allotted slots filled, i.e. in their relative probabilities of selection. In a three-parasite species array, for example, with species A, B and C, a host individual can be infected with two kinds of parasites in three different ways: A and B, A and C, B and C. The null hypothesis of no interspecific interactions demands that A, B and C be independent events. In contrast to the case of a binomial expansion, each of the three two-parasite species infections carries a unique probability (which are permitted, however, to be equal). Host classes are established on the basis of number of parasite species present (0, 1, 2,..., n). The number of such unique probabilities for any one host class is given by the familiar

$$n!/[x!(n-x)!],$$

where n is the number of parasite species in the array and x is a parasite species per host class. These unique probabilities must be summed to obtain the expected proportion of a host sample with x kinds of parasites. The number of kinds, or in this example parasite species, can vary according to the system under investigation.

A theoretical species density distribution is obtained by multiplying the parasite species per host class probabilities by the number of hosts in the sample. The parameter values of this discrete distribution will change with changing relative probabilities of infection. Observed frequencies can be tested against the expected by means of chi-square. Effective interspecific interactions should appear as departures from the expected, e.g. as when parasite species exclude one another or are transmitted together. Such interactions may not appear as departures from expected if occurrence probabilities of the interacting pair are very high or very low; however, in such cases, one must defend the assertion that interactions are of evolutionary or ecological significance. A rigorous test of the null hypothesis of no interspecific interaction requires that the same biological system be studied with a series of homogeneous samples, preferably taken over a range of abiotic conditions.

3. The algorithm

Expected species density distributions are founded on independent probabilities of successful infection for each parasite species in the community. This condition implies that the prevalence of a parasite species in a host population is equivalent to the probability that any given host in the population will be infected by that parasite species. As host sample size increases, the Central Limit Theorem suggests that prevalence becomes increasingly indicative of the true probability of infection. Therefore, the event of infection by a single parasite species in any given host is probabilistically a single Bernoulli trial in which success (p) is equal to the parasite species prevalence in the host population, and failure (q) is equal to one minus the parasite species prevalence in the host population. Consider a parasite community of N species: there exists a series of values that describes the probability of successful infection by each parasite species, $p_1,\ldots, p_N$, where p_1 = the prevalence of parasite species 1, p_2 = the prevalence of parasite species 2, etc. Expected species density distributions differ from Poisson distributions in that they are accumulations of multiple Bernoulli trials that do not share a common probability of success. None the less, as modified Bernoulli trials, the outcomes are still independent and binary in nature and are suitable for the generation of an expected frequency distribution.

The expected species density distribution for such a system is constituted by the expected frequency of host inclusion in each host class. Consider a host/parasite system with N parasite species and any number of host individuals, in which a host individual can be infected with 0, 1, 2,..., N parasite species. If host class, C, is defined by the number of parasite species present, then host class also takes its values from the range of whole numbers 0, 1,..., N. For each host class, C, $P(C)_N$ is the probability that any given host will be infected by exactly C of N

parasite species without regard to parasite species combination, that is, $P(C)_N$ = the probability of successful infection by C parasite species in any given host if there are N parasite species in the community at large. $P(C)_N$ is the accumulated probability of each unique combination of C parasites species drawn from N parasite species, each with a unique probability of infection as described above. The expected probability distribution for such a system can be calculated and stored in a recurrence vector using a series of iterative algorithms.

Infection by any of N parasite species is an independent Bernoulli trial, thus parasite species can be added to the expected distribution one-by-one, without regard to the order of their addition. For computational purposes we can build the expected distribution using a step-wise recurrence vector, beginning with the distribution for single available parasite species and expanding the distribution as each parasite species is added. Such a vector can be visualized as an array of N elements, where each element conceptually represents a host class, C. On completion of the vector, each element contains $P(C)_N$, the probability of successful infection by any unique combination of C parasite species in any given host if there are N parasite species in the community at large. The vector is built using the following set of iterative algorithms:

Where

N = the number of parasite species that have been added to the distribution;

$P(n)_N$ = the probability of infection by n parasite species when N parasite species have been added to the distribution;

p_i = the probability of successful infection by the ith parasite species; and,

q_i = $(1-p_i)$ = the probability of no infection by the ith parasite species.

When the first parasite species is added, the vector is established:

For $N=1$:

$$P(0)_N = P(0)_1 = q_N = q_1, \quad (1)$$

$$P(1)_N = P(1)_1 = p_N = p_1. \quad (2)$$

When each additional parasite is added to the vector host class is incremented, and three algorithms are used to recalculate the distribution. For all $N>1$, where C goes from 0, 1,... N, if $C=0$:

$$P(C)_N = P(0)_N = P(0)_{N-1}q_N; \quad (3)$$

if $0<C<N$:

$$P(i)_N = P(i-1)_{N-1}p_N + P(i)_{N-1}q_N \quad (4)$$

for all i, where i goes from 1 to $N-1$;
if $C=N$:

$$P(C)_N = P(N)_N = P(N-1)_{N-1}p_N. \quad (5)$$

The following example demonstrates the algorithms for a system with three parasite species. When the first parasite species is added, the vector is established with two classes (0 and 1) using Eqs. 1 and 2:

$$P(0)_1 = q_1,$$

$$P(1)_1 = p_1.$$

When the second parasite species is added, the 0 class is calculated using Eq. 3:

$$P(0)_2 = P(0)_1 q_2 = q_1 q_2$$

The 1 class is calculated using Eq. 4:

$$P(1)_2 = P(0)_1 p_2 + P(1)_1 q_2 = q_1 p_2 + p_1 q_2.$$

The 2 class is calculated using Eq. 5:

$$P(2)_2 = P(1)_1 p_2 = p_1 p_2.$$

When the third parasite species is added, the 0 class is calculated using Eq. 3:

$$P(0)_3 = P(0)_2 q_3 = q_1 q_2 q_3.$$

The 1 class and the 2 class are calculated using Eq. 4:

$$\begin{aligned} P(1)_3 &= P(0)_2 p_3 + P(1)_2 q_3 \\ &= q_1 q_2 p_3 + q_3(q_1 p_2 + p_1 q_2) \\ &= q_1 q_2 p_3 + q_1 p_2 q_3 + p_1 q_2 q_3, \end{aligned}$$

$$\begin{aligned} P(2)_3 &= P(1)_2 p_3 + P(2)_2 q_3 \\ &= p_3(q_1 p_2 + p_1 q_2) + p_1 p_2 q_3 \\ &= q_1 p_2 p_3 + p_1 q_2 p_3 + p_1 p_2 q_3. \end{aligned}$$

The 3 class is calculated using Eq. 5:

$$P(3)_3 = P(2)_2 p_3 = p_1 p_2 p_3.$$

The recurrence vector now holds four classes: class 0 holds the probability of no infection, class 1 holds the probability of infection by exactly one

parasite species, class 2 holds the probability of infection by exactly two parasite species, and class 3 holds the probability of infection by all three parasite species. The summation of these four probabilities approaches 1. The expected frequency distribution is obtained by multiplying each class probability by the total observed host sample size.

The recurrence vector is stored in a double precision matrix with one element for each parasite species present in the system. The algorithm presented here has been implemented by the authors using QuickBASIC 4.5 (Microsoft Corporation, Redmond, WA).

4. Application

This species density model, the algorithm, and the underlying ideas, are applicable to systems beyond those involving parasites and hosts. In addition, the short calculation time suggests this algorithm may prove particularly useful in systems involving large numbers of species. Virtually any sampling scheme, e.g. a grid, that mimics selection from a multiple kind array can be tested for fit to the null hypothesis of independence using an algorithm such as the one presented. For example, studies of immigration after disturbance, e.g. as in those of heterogeneity in burned prairie (Collins, 1992), typically use grids or census points on transects. Each potential immigrant species has a probability of successfully occupying a sampling unit. Thus census points and grid squares are the analogs of host individuals. Regardless of the system to which the model is applied, however, the major requirement is for homogeneity. For example, assume one is replicate sampling a grid and assessing the species density distributions of grid units. A homogenous field sample would consist of a single census conducted within a time shorter than the least time required for species replacement or colonization of an individual grid square. The study design would have to include enough, presumably replicate, census points to generate a meaningful distribution. That number is dictated in part by the potential number of colonizing species. Given these constraints, a series of homogeneous samples over time should reveal whether dynamic

Table 1
Observed (O) and expected (E) species density distributions for the parasite species assemblage in a pulmonate snail (*Physa gyrina*)

Sampling date	Species/host classes							Chi-sq	p_{fit}
	0	1	2	3	4	5	6		
Apr 91 (O)	86	23	7	0	0				
Apr 91 (E)	82	32	3	0	0			8.060	ns
May 91 (O)	41	64	15	1	0				
May 91 (E)	43	58	17	2	0			1.449	ns
June 91 (O)	37	65	11	0	0				
June 91 (E)	42	55	15	1	0			4.480	ns
July 91 (O)	44	54	20	0	0				
July 91 (E)	43	57	16	2	0			3.181	ns
Aug 91 (O)	65	47	7	1	0				
Aug 91 (E)	66	45	9	1	0			0.548	ns
Sept 91 (O)	78	35	9	0	0				
Sept 91 (E)	82	37	3	0	0			12.303	< 0.05
Oct 91 (O)	56	50	11	1	0				
Oct 91 (E)	57	48	12	1	0			0.184	ns
Nov 91 (O)	94	17	3	0	0				
Nov 91 (E)	94	19	1	0	0			4.211	ns
Dec 91 (O)	106	10	0	0					
Dec 91 (E)	106	10	0	0	0			0	ns

Data from Snyder and Esch (1993). Expected frequencies calculated according to the algorithm presented in this paper. Parasite species are larval trematodes.

processes are at work to alter the species density profile of the system.

Biological phenomena should be manifested as species-dependent density distributions. Interspecific interactions significant enough to influence the species makeup of an assemblage over evolutionary time should be evident in stable but unexpectedly high or low frequencies of certain classes, i.e. departure from the null model, manifested over a range of abiotic conditions. The data must be collected and analyzed as a series of homogeneous samples. Failure to obey the homogeneity requirement results in data sets in which potential species-to-species interactions are masked, or false interactions are suggested, by heterogeneous host–parasite encounter conditions. Types of interactions other than co-occurrence are not addressed by this paper. Nor is any claim made that the species density distribution is the only device for detecting or analyzing interspecific interactions.

Data sets to illustrate the application are presented from a variety of host/parasite systems (Tables 1–3). In no case is a mechanism for structuring the species density distribution proposed, but in every case departures from the null model are recognized as proximal, sometimes isolated, events, resulting from perturbations of a random selector/multiple-kind array system. Thus the overall dynamic pattern in these systems is one in which species density distribution – one aspect of community structure – is dictated by relative probabilities of infection (colonization). Claims for other organizing forces, e.g. competition, should be supported by regular and similar departures from that predicted by the null model, in a series of homogeneous samples.

The snail data (Table 1) are from a study of larval trematode species in *Physa gyrina* from a single pond (Snyder and Esch, 1993). Snail/trematode systems are of interest in this context because of the well-established fact of interspecific competition between larval trematodes in snails, specifically a hierarchy of predation based in part on larval size (a genetically determined trait) (Kuris, 1990). In the Table 1 data, the single departure from the null model predictions, among a series of homogeneous samples, is one in which there are more heavily infected hosts than predicted, hardly evidence for serious interspecific competition. In general, in snail/trematode systems, prevalence of any one parasite species is low and on that basis, multiple infections are thus predicted to be few, regardless of the fate of co-occurring species.

The *Fundulus zebrinus* data (Table 2) are from a long-term study of parasite population and assemblage dynamics in that species in the Platte

Table 2
Observed (Obs) and expected (Exp) species density distributions for the parasite species assemblage in a freshwater fish (*Fundulus zebrinus*)

Sampling date/site	Species/host classes								Chi-sq	p_{fit}
	0	1	2	3	4	5	6	7		
July 19, 1982–Aug 2, 1982 (Roscoe)										
Obs	0	0	0	0	9	10	19	4		
Exp	0	0	0	1	5	16	18	3	6.84	ns
July 21, 1982–Aug 5, 1982 (Maxwell)										
Obs	1	4	8	12	7	9	2	1		
Exp	0.2	2	7	13	13	7	2	0.2	11.96	ns
July 25, 1983 (Roscoe)										
Obs	0	2	2	2	5	7	2	1		
Exp	0	1	4	7	6	2	0	0	23.24	< 0.05
June 19, 1988 (Roscoe)										
Obs	0	4	8	6	5	0	0	1		
Exp	0	4	8	7	3	1	0	0	3.48	ns

Data from Janovy and Hardin (1988) and unpublished collections. Expected frequencies calculated according to the algorithm presented in this paper.

River of Nebraska, a braided river with substantial fluctuations in streamflow over several time scales. The first five years of this work was published in Janovy and Hardin (1988), and a diversity model developed to explain long-term assemblage dynamics used an additional two years' worth of data. At present, the parasite assemblages from 49 homogeneous samples of *F. zebrinus*, have been analyzed, covering an 11-year period (1982–1992 inclusive) and involving 995 fish from a single collecting site. Forty seven of those 49 samples fit the null model of a multiple-kind array sampler described in this paper and in Janovy et al. (1992). The two assemblages that did not fit were from July 25, 1983 and August 18, 1992; the former had more heavily infected fish than expected, the latter had more fish in the 3- and 4-species/host classes than expected (out of 7 possible species). Both departures are interpreted as being of abiotic origin. The July 25, 1983 sample is one of those given in Table 2.

Table 3 shows the results of applying the algorithm to host/parasite systems that are much richer in parasite species than either the pulmonate snail or *F. zebrinus* ones. The bat data in Table 3 are from Lotz and Font (1991), although from sub-sets assumed to be homogeneous because of collection dates and localities. The entire samples reported in Lotz and Font (1991) may be homogeneous, but because they were collected over an extended time period, were not used in Table 3. The bat parasite assemblages have up to 18 parasite species per sample, although obviously the mean number of parasites per host is much lower than that figure.

These three data sets (Tables 1–3) are illustrative of the general structure of parasite species assemblages over a wide variety of systems. In virtually all published parasite survey data sets, prevalence of a parasitic infection varies with the parasite species. Thus the probability of infection, estimated by the prevalence, also varies by parasite species. Data from Janovy and Hardin (1988) further indicate that parasite species vary in their response to large abiotic changes, e.g. order of magnitude fluctuations in a river's streamflow over monthly and yearly periods. The parasite species density distributions (Table 2), however, still tend to fit those predicted by the multiple-kind array model, as well as the distributions

Table 3
Observed (Obs) and expected (Exp) species density distribution for the parasite species assemblage in Wisconsin bats

Sampling date	Species/host classes												
	0	1	2	3	4	5	6	7	8	9	10	11	12
MLUC: May 5–June 10, 1981													
Exp	0	0	0	0	1	3	5	5	3	1	0	0	0
Obs	0	1	0	1	1	3	3	3	3	1	0	0	2
Chi sq = 7.60(11) = ns													
MLUC: June 7–July 13, 1986													
Exp	0	0	1	3	6	6	4	2	0	0	0	0	0
Obs	0	1	2	2	5	4	2	2	2	0	1	0	0
Chi sq = 5.17(11) = ns													
EFUS: January 11–March 19, 1980													
Exp	0	0	1	4	6	7	5	3	1	0	0	0	0
Obs	0	0	3	3	5	7	4	4	2	0	0	0	0
Chi sq = 5.95(11) = ns													
EFUS: November 10–January 15, 1981													
Exp	0	0	1	2	3	4	3	2	1	0	0	0	0
Obs	0	1	1	1	3	1	4	2	2	0	0	0	0
Chi sq = 7.41(11) = ns													

Bat species are abbreviated by capital letters: MLUC = *Myotis lucifugus*; EFUS = *Eptesicus fuscus*; MLUC from 1986 were all collected in Dunn County, Wisconsin; the rest were all collected from Eau Claire County, Wisconsin. Data are from the large collections reported in Lotz and Font (1991). Expected frequencies calculated according to the algorithm presented in this paper.

generated by the algorithm presented in this paper, although the means and variances of these distributions vary with time and streamflow.

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References

Bush, A.O., 1990. Helminth communities in avian hosts: Determinants of pattern. In: G.W. Esch, A.O. Bush and J.M. Aho (Editors), Parasite Communities: Patterns and Processes. Chapman and Hall, New York, NY, pp. 197–232.

Bush, A.O. and Holmes, J.C., 1986a. Intestinal helminths of lesser scaup ducks: Patterns of association. Can. J. Zool., 64: 132–141.

Bush, A.O. and Holmes, J.C., 1986b. Intestinal helminths of lesser scaup ducks: An interactive community. Can. J. Zool., 64: 142–152.

Collins, S.L., 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology, 73: 2001–2006.

Dobson, A.P., 1985. The population dynamics of competition between parasites. Parasitology, 91: 317–347.

Dobson, A.P., 1990. Models for multi-species parasite–host communities. In: G.W. Esch, A.O. Bush and J.M. Aho (Editors), Parasite Communities: Patterns and Processes. Chapman and Hall, New York, NY, pp. 261–288.

Esch, G.W., Bush, A.O. and Aho, J.M. (Editors), 1990. Parasite Communities: Patterns and Processes. Chapman and Hall, New York, NY, 335 pp.

Goater, T.M., Esch, G.W. and Bush, A.O., 1987. Helminth parasites of sympatric salamanders: ecological concepts at infracommunity, component and compound community levels. Am. Midl. Nat., 118: 289–300.

Holmes, J.C. and Price, P.W., 1986. Communities of parasites. In: D.J. Anderson and J. Kikkawa (Editors), Community Ecology: Patterns and Processes. Blackwell Scientific Publications, Oxford, pp. 187–213.

Janovy, J. Jr. and Hardin, E.L., 1988. Diversity of the parasite assemblage of *Fundulus zebrinus* in the Platte River of Nebraska. J. Parasitol., 74: 207–213.

Janovy, J. Jr., Ferdig, M.T. and McDowell, M.A., 1990. A model of dynamic behavior of a parasite species assemblage. J. Theor. Biol., 142: 517–529.

Janovy, J. Jr., Clopton, R.E. and Percival, T.J., 1992. The roles of ecological and evolutionary influences in providing structure to parasite species assemblages. J. Parasitol., 78: 630–640.

Kennedy, C.R., Bush, A.O. and Aho, J.M., 1986. Patterns in helminth communities: Why are birds and fish different? Parasitology, 93: 205–215.

Kuris, A., 1990. Guild structure of larval trematodes in molluscan hosts: Prevalence, dominance and significance in competition. In: G.W. Esch, A.O. Bush and J.M. Aho (Editors), Parasite Communities: Patterns and Processes. Chapman and Hall, New York, NY, pp. 69–100.

Leong, T.S. and Holmes, J.C., 1981. Communities of metazoan parasites in open water fishes of Cold Lake, Alberta. J. Fish Biol., 18: 693–713.

Lotz, J.M. and Font, W.F., 1985. Structure of enteric helminth communities in two populations of *Eptesicus fuscus* (Chiroptera). Parasitology, 63: 2969–2978.

Lotz, J.M. and Font, W.F., 1991. The role of positive and negative interspecific associations in the organization of communities of intestinal helminths of bats. Parasitology, 103: 127–138.

Pence, D.B. and Windberg, L.A., 1984. Population dynamics across selected habitat variables of the helminth community in coyotes, *Canis latrans*, from south Texas. J. Parasitol., 70: 735–746.

Price, P.W., 1984. Communities of specialists: vacant niches in ecological and evolutionary time. In: D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle (Editors), Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, NJ, pp. 510–523.

Price, P.W., 1987. Evolution in parasite communities. Int. J. Parasitol., 17: 203–208.

Snyder, S.M. and Esch, G.W., 1993. Trematode community structure in the pulmonate snail *Physa gyrina*. J. Parasitol., 79: 205–215.

Stock, T.M. and Holmes, J.C., 1987a. *Dioecocestus asper* (Cestoda: Dioecocestidae): An interference competitor in an enteric helminth community. J. Parasitol., 73: 1116–1123.

Stock, T.M. and Holmes, J.C., 1987b. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). Can. J. Zool., 65: 669–676.

Stock, T.M. and Holmes, J.C., 1988. Functional relationships and microhabitat distribution of enteric helminths of grebes (Podicipedidae): The evidence for interactive communities. J. Parasitol., 74: 214–227.