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PARASITOLOGY MEETS ECOLOGY ON ITS OWN TERMS: MARGOLIS ET AL. REVISITED*

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ABSTRACT: We consider 27 population and community terms used frequently by parasitologists when describing the ecology of parasites. We provide suggestions for various terms in an attempt to foster consistent use and to make terms used in parasite ecology easier to interpret for those who study free-living organisms. We suggest strongly that authors, whether they agree or disagree with us, provide complete and unambiguous definitions for all parameters of their studies.

Clear and effective communication must be the primary goal facing every scientist. The most significant discovery, the identification of a fundamental theorem, or the test of some critical hypothesis is meaningless if it is neither communicated nor understood. Unfortunately, effective communication can often be undermined in some disciplines by "jargon." When 2 jargon-prone disciplines such as parasitology and ecology meet, the result may be confusion. Perhaps recognizing this, Elmer Noble, President of the American Society of Parasitologists in 1981, commissioned an ad hoc committee to comment on the use of ecological terms in parasitology.

The resulting publication by Margolis et al. (1982) became a citation classic. Clearly, a need had been fulfilled, and whether authors agreed or disagreed with the proposed terminology, there existed, for the first time, a reference point. At the time the committee was commissioned, the focus of ecological parasitology was largely population biology. Understandably then, and despite its rather broad title, the paper by Margolis et al. (1982) was devoted to the use of ecological terms as they applied to populations of parasites. Since that time, studies on communities of parasites have become common. Recognizing extant, and perhaps impending, problems with ecological terms as applied to the community ecology of parasites, Gerald Esch, Editor of the *Journal of Parasitology,* asked one of us (A.O.B.) to "assemble a team of 'ecological types' to discuss the use of ecological terms as they apply to the ecology of parasite communities."

We perceived our goal as supplementing Margolis et al. (1982), not supplanting it. However, as ecologists, we recognize that community ecology without population ecology is like confession without sin: there really isn't much to talk about. Furthermore, we are aware, from our work and from comments made by colleagues during the past decade, that some of the suggestions in Margolis et al. (1982) "just don't work." Therefore, in this paper, we revisit Margolis et al. (1982), suggest some major and minor modifications, and then expand our coverage to a consideration of communities.

Our approach will be to discuss, first, words and concepts as human constructs (waxing philosophical if you will). Next, we revisit general terms and terms applied to populations of parasites, and we then discuss terms applicable to the community level. For the latter 2 topics, we provide, when relevant for illustrative purposes, published examples of term use. Accepting the cliché that a "picture is worth a thousand words", we present several figures in an attempt to clarify our presentation and amplify our discussion for some terms. Finally, we argue now, and conclude emphatically, that what we offer are only suggestions. We recognize there exist scientists who will disagree (some vehemently so) with us. Whether others agree or disagree with our suggestions, we strongly urge them to define explicitly their intended meaning for specific terms. If this paper serves as either a source of agreement or point of departure, as did the paper by Margolis et al. (1982), it will have served its utilitarian purpose.

We review all terms discussed originally in Margolis et al. (1982). Our choice of terms relating to communities is selective. We discuss several general descriptive terms, some specific terms that we feel are frequently used improperly, and other terms that we feel warrant a departure from traditional ecological terminology.

Although the distinction is not absolute, we consider 2 kinds of terms, observational (or objective) and theoretical (Hempel, 1965; Hull, 1974). Observational terms refer to something that is the same to 2 independent observers and can be generally understood without reference to a scientific theory. Therefore, by observational terms, we mean words that stand for things (traits and objects) that can be seen (widely interpreted), are descriptive, and often can be measured, e.g., prevalence, diet, range, diversity index, necrosis. Theoretical terms, on the other hand, apply to the more abstract and subjective concepts that a science, and its theories, are about, e.g., community, niche, habitat, species, population, diversity. Theoretical terms are often not directly observable, and the words are dependent on scientific theories for their meaning. For example, although 2 individuals might recognize all living organisms found in some prescribed area as a community, they might disagree substantively on a theory of how that community is maintained through ecological time. Because they hold different theories, they "see" different things; one might see a group of independent species, whereas the second might see a group of tightly interdependent species. Hence, the meaning of the word community is dependent upon the theory that each individual holds. In some cases, theoretical terms can be reduced to observational terms and thereby provide operational definitions of the theo-

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retical terms (Hempel, 1965). For example, diversity is an important trait of biological communities, and a great deal of theory has developed attempting to explain the diversity of communities. In those theories, diversity remains rather vague; however, in practice, several operational definitions of diversity are used, e.g., species richness, Simpson's index. In our opinion, the definitions of theoretical terms are often best left to the science and its theoreticians (although we feel obliged to deal with some that are in very broad use in parasitology), whereas observational terms are more amenable to definition by convention.

SOME GENERAL TERMS

Ecologists need the ability to describe an organism's surroundings. Parasites are not fundamentally different from other living organisms in this regard, but, because parasites often have complex life cycles, various descriptive terms can be rather misleading.

(1) Site, location, and habitat. The terms site and location have a long history of use among parasitologists, and, to them, the terms may carry specific connotations. To others, such connotations are unknown or vague. We consider the site or location of a parasite to be the topological or spatial location in a host where a ***particular sample*** of parasites is collected. Site and location are thus anatomical parallels to geographic locality (see below). Habitat refers to the typical local environment in which parasites occur.

Remarks: We disagree with Margolis et al. (1982) that habitat should not be used to refer to "the tissue, organ or part of the host in [on] which a parasite was found." We suggest that, because organs and tissues provide the local environment (including physical, chemical, and biological surroundings), they are appropriately called habitats. In fact, we feel that the term habitat is preferable because it has a long history of similar use in the literature on free-living forms and it can easily be compounded, e.g., microhabitat, habitat-specific. Further, recognizing the complexity of many parasite life cycles, it will often be necessary to describe the surroundings of free-living phases, particularly in autecological studies. The use of habitat (rather than site or location) seems to make better sense when describing eggs in fecal pats, juveniles on blades of grass, or miracidia in a water column. As with most ecological words, scaling is important for the term habitat, and it is appropriate to refer to the intestinal veins as well as a rice field as habitat for *Schistosoma mansoni.* By way of contrasting location/site and habitat, consider Schad (1963), who examined habitat specificity of tortoise pinworms by recording the locations/sites of individual pinworms in the intestines of hosts.

(2) Locality. The term locality refers to a geographic locale of the external environment where the parasite is found.

Remarks: Locality is used widely for geographic position, and the term should be restricted to an identification of where, geographically, the individual, population, or community is obtained. Locality might be the spatial region where a host (or hosts) is (are) collected or it might refer to the spatial region where a substrate (or substrates) is (are) examined for parasites.

(3) Niche. The niche of a parasite refers to its role, and how it fits, within a particular community.

Remarks: We endorse Hutchinson's (1957) operational approach to the niche and agree with Brown (1995), who notes, "Hutchinson's concept of niche thus implicitly stresses the uniqueness of species in their ecological relationships. The fact that species exhibit distinctive patterns of abundance and distribution reflects their different requirements for environmental conditions. By Hutchinson's operational characterization, the niche is an attribute of species, not of environments. Thus, although extinct species had niches, there can be no unfilled niches."

Despite the above definition, and our reluctance to admit empty niches, we recognize that the phrase "empty niche" has been, and will probably continue to be, used by parasite ecologists to refer to the absence of a species from a system under investigation when that species is known to be present in a similar system elsewhere. The implication of such use is often that resources are therefore not limiting. This may or may not be true. Whether true or false, this claim is not relevant to our purposes. We point out only that the argument should be made without the phrase empty niche if niche is to be used according to the Hutchinsonian concept. The absence of a particular parasite may simply reflect that the parasite is unable to complete its life cycle in the system studied. Therefore, its absence in a host being studied in that system provides no evidence for, or against, resource availability.

When describing a niche, it is crucial to identify explicitly the scale to which one is referring. This might be a habitat within a host, an entire host, a host population, a host species, or some other level of taxonomy, geography, or demography.

PARASITE POPULATIONS

Here, too, parasites are not fundamentally different from other biological populations and a population of parasites comprises all of the individuals of a single parasite species at a particular place at a particular time.

Quantitative descriptors of parasite populations

Most quantitative descriptors such as prevalence and mean abundance are point estimates based on samples from the whole population of hosts. As a general comment, we note that although the value for each estimate can be determined accurately and unambiguously, its interpretation is usually made with reference to the source population and this introduces the element of uncertainty. ***We recommend strongly*** that authors publish an appropriate statistical measure, e.g., confidence intervals or standard errors, of how good the estimate is. In any event, the sample size should be identified clearly. When the data are subjected to a transformation, we recommend that the transformation be identified and that asymmetric confidence limits be reported in the original units.

(1) Prevalence. Prevalence is the number of hosts infected with 1 or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species. (We will use infect and its derivatives to include infest and its derivatives.) It is commonly expressed as a percentage when used descriptively and as a proportion when incorporated into mathematical models.

Remarks: Prevalence is intended as a descriptive statistic for presence–absence data on parasites in a sample of hosts and is used when it is desirable to classify hosts into 2 categories,

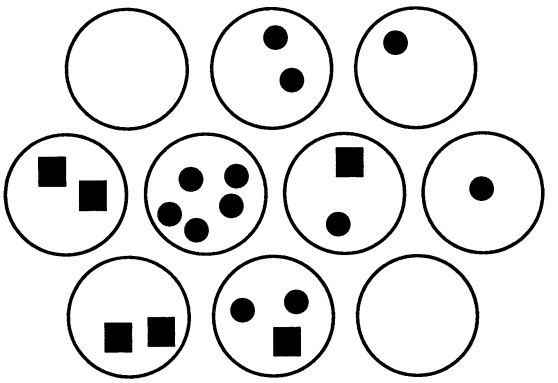

FIGURE 1. A generalized diagram of 2 parasite species distributed among 10 host individuals. Large open circles represent individual hosts. Small solid circles and squares represent individual parasites. Circle parasites are a different species than square parasites. All hosts and parasites live in the same locality. See text for quantitative details.

infected and uninfected, without regard to when the infected hosts acquired their infection. Prevalence is 1 of the most widely reported descriptors of parasitic infection because it requires only detection of the presence of the parasite and not enumeration of the individuals present.

In Figure 1, 10 host individuals are infected with none, 1, or 2 species of parasites. The prevalence of the circle parasite is 6/10 = 0.6 (or 60%), and the 95% confidence interval would be 26–88%. The prevalence of the square parasite is 4/10 = 0.4 (or 40%), and the 95% confidence interval would be 12–74%.

Prevalence is 1 of the most commonly used, and least misused, of ecological terms in parasitology. Perhaps the most common problem associated with its use is in reporting its value to more significant digits than are warranted by the sample size of hosts. This can be remedied by the inclusion of confidence intervals. Sample sizes numbering into the hundreds are necessary to generate 95% confidence limits for percentages that are within 1% of the estimated value (Rohlf and Sokal, 1969). Yet, too often in the literature, prevalences are reported to the nearest 0.1%, or even 0.01%, based on sample sizes that might warrant reporting only to the nearest 5%.

Alternative terms for prevalence: Percent infected, percent infestation, extensity, or extent of infection, used most frequently in non-North American literature, may be considered synonyms for prevalence. Frequency has been used when it is desirable to focus on the absolute number of infected hosts in a sample (Bush and Holmes, 1986) rather than the proportion of the host sample they represent. Incidence (see below) is frequently used incorrectly as a synonym for prevalence (Durfee, 1978).

(2) Incidence. Incidence is the number of new hosts that become infected with a particular parasite during a specified time interval divided by the number of uninfected hosts present at the start of the time interval.

Remarks: Incidence is a descriptive statistic used to determine the risk of acquiring new infections by individuals in a population of hosts. Incidence is applicable only to the uninfected individuals in the host population, without regard to the number of hosts with existing infections. Durfee (1978) provided an example of the calculation of incidence. "In an epizootic of an acute viral disease on a dairy farm with a population of 100 susceptible cows, 7 became sick on day 1 of the outbreak, 15 on day 2 and 10 on day 3. The daily attack rates would be: 7/100 = 0.07 (7%), 15/93 = 0.16 (16%), and 10/78 = 0.12 (12%), respectively." Note the decrease in the denominator as hosts acquiring the infection in 1 time interval are now removed from the susceptible pool for subsequent intervals.

Incidence is most commonly used to monitor the spread of clinical disease in populations of humans or domestic animals because determining the number of preexisting cases of the disease is relatively easy (Durfee, 1978). Margolis et al. (1982) suggested that incidence has limited applicability for the study of feral populations because the number of individuals infected at the beginning of the time period is rarely known. However, the number of individuals infected at the beginning of the interval can be obtained from sequential estimates of prevalence. If P_0 is the prevalence at the start of a time interval, and P_1 is the prevalence at the end of the interval, then (assuming prevalences are expressed as percentages) incidence = $(P_1 - P_0)$ divided by $(100 - P_0)$. Although the calculation of confidence intervals on ratios is not trivial (see Cochran, 1977), the accuracy of the incidence can be assessed from confidence intervals of the individual prevalences.

The concept of incidence has greatest applicability to the study of the dynamics of parasite populations and thus may be encountered most often in epidemiological and modeling studies.

Alternative terms for incidence: Although incidence is often used incorrectly as a synonym for prevalence (Durfee, 1978), the reverse does not seem to be a problem. Attack rate, colonization rate, morbidity rate, and reporting rate are synonyms for incidence.

(3) Density. Density is the number of individuals of a particular parasite species in a measured sampling unit taken from a host or habitat, e.g., in units of area, volume, or weight.

Remarks: Density is used widely in the ecological literature and can be equally applied to parasites. When the sampling unit is an individual host, it would be proper to report infections as "A density of X parasites per infected host (or per host)." However, because of the frequency with which parasitologists use the host as the sampling unit, the terms intensity and abundance (see below), with their implied sampling units, are more concise and seem preferable. We, therefore, recommend that density be used when an accurate census of all parasites in a host is difficult or impossible to make. For example, an efficient density measure of *Trypanosoma lewisi* might be the number of flagellates per milliliter of rat blood. In any case, it is important to specify the denominator to avoid confusion.

(4) Intensity (of infection). Intensity (of infection) is the number of individuals of a particular parasite species in a single infected host, i.e., the number of individuals in an infrapopulation (see below).

Remarks: Intensity is a form of density with the sampling unit specifically defined as an individual infected host. Therefore, intensity is a convenient measure for parasitologists because hosts are discrete and natural sampling units.

In Figure 1, 6 hosts are infected with circle parasites, and the intensities are 1, 1, 1, 2, 2, and 5. Four hosts are infected with square parasites, and the intensities are 1, 1, 2, and 2.

The potential confusion of intensity with other forms of density makes it necessary to define it following initial use.

Alternative terms for intensity: Although a few authors will likely continue to use synonyms (worm burden, parasite load, and degree, level, or extent of infection), we recommend the use of intensity.

(5) Mean intensity. Mean intensity is the average intensity of a particular species of parasite among the infected members of a particular host species. In other words, it is the total number of parasites of a particular species found in a sample divided by the number of hosts infected with that parasite.

Remarks: In Figure 1, the mean intensity (±SE) for circle parasites is 12 divided by 6 or 2.0 ± 0.6, whereas for square parasites it is 6 divided by 4 or 1.5 ± 0.3. Because it is derived solely from infected hosts, mean intensity should always be reported in conjunction with prevalence.

It is prudent to consider that mean intensity is often not a reflection of a typical infection because parasites are usually aggregated (or clumped) among their hosts. We are aware that some parasitologists hold the opinion that mean intensities should always be reported to the nearest integer because there is no such thing as part of a parasite. We disagree because the mean is a derived datum but note that the number of decimal places reported should not exceed that warranted by the sample size.

The greatest potential for misunderstanding is to confuse mean intensity with mean abundance (see below) by using all hosts (infected and uninfected) in the denominator. In some cases, median intensity or modal intensity will be appropriate substitutes for mean intensity.

(6) Abundance. Abundance is the number of individuals of a particular parasite in/on a single host regardless of whether or not the host is infected.

Remarks: Abundance is also a form of density, and it differs from intensity in that, by definition, an intensity of 0 is not possible whereas an abundance of 0 is appropriate. In Figure 1, the abundances of the circle parasites are 0, 0, 0, 0, 1, 1, 1, 2, 2, and 5, and the abundances of square parasites are 0, 0, 0, 0, 0, 0, 1, 1, 2, and 2.

We find the distinction between intensity and abundance to be useful because, in some studies, only the infected host subpopulation is of interest; in other studies, the whole host population (including those hosts carrying parasite infrapopulations of size 0) is of interest. Often in community studies, one might wish to examine phenomena such as co-occurrences where 0-sized populations are important. For example, Lotz and Font (1994) examined whether the presence of parasites could alter the habitat to favor establishment of additional parasite species.

(7) Mean abundance. Mean abundance is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts of that species examined (including both infected and uninfected hosts). It is thus the average abundance of a parasite species among all members of a particular host population.

For example, in Figure 1, the mean (±SE) abundance of circle parasites is 12 divided by 10 or 1.2 ± 0.5; for square parasites, it is 6 divided by 10 or 0.6 ± 0.3.

Remarks: With apparently little enthusiasm, Margolis et al. (1982) proposed using the terms relative density or abundance for mean abundance. We see no advantage to the phrase relative density and see pleasing parallels among mean density, mean intensity, and mean abundance. We would reserve relative density to be parallel to relative abundance in the ecological literature. The commonly used phrase "relative abundance" has a specific use in ecology and refers to a standardized comparison of the numbers of each of the several species in a community or collection. Relative abundance in parasite ecology would refer to a similar standardized comparison of the numbers for an infracommunity, component community, or supracommunity (see below). The phrases "relative mean abundance" and "relative mean intensity" provide counterparts to ecological use and are informative characteristics of parasite communities.

Mean abundance is equivalent to mean intensity multiplied by prevalence. Mean abundance, in conjunction with its variance, can yield an indication of the dispersion of parasites among hosts. In some cases, median abundance or modal abundance will be an appropriate substitute for mean abundance.

(8) Density dependence (independence). Density dependence (independence) is the tendency for intraspecific characteristics (particularly vital rates such as birth and death) to change (or not) as a function of the density of that population.

Remarks: As an example of density dependence at the infrapopulation level, Croll et al. (1982) found a decline in per capita egg production with increased density of *Ascaris lumbricoides* in humans.

For many parasites, crowding, host immune response, or intensity-dependent mortality can lead to density dependence. Margolis et al. (1982) recommended the term intensity dependence as a substitute. Because the term density dependence has such a long tradition in ecology, we see an advantage in not redefining the concept for parasitology. Furthermore, the factors that affect parasite populations may be as much a function of parasite density (see above) as parasite intensity (see above).

(9) Intensity dependence (independence). Intensity dependence (independence) refers to the interspecific effect (or lack thereof) that a parasite's intensity has on a host, e.g., behavior, pathology.

Remarks: An example of intensity dependent mortality is the increased overwinter mortality of young sunfish heavily infected with *Uvulifer ambloplitis* (Lemly and Esch, 1984).

Using intensity-dependent mortality is preferable to using density-dependent mortality to describe the effects of a parasite on a host because the latter might be confused with effects of host density on host mortality. Because the mortality observed by Lemly and Esch (1984) does not lead to transmission of the trematode, this is an example of a density-dependent effect of a parasite population on itself (parasites in dense infections are more likely to die) and an intensity-dependent effect of the parasite on the host population.

For comparison, the effect of rhizocephalan barnacles on their host crabs is also intensity independent (Kuris, 1974) and shows that the effect need not be linear; 1 barnacle castrates the host as completely as do several barnacles.

The nesting of parasite populations

(10) Infrapopulation. A parasite infrapopulation includes all individuals of a species in an individual host at a particular time.

Remarks: In Figure 1, there are 10 host individuals, but only

8 hosts have infrapopulations; there are, however, 10 infrapopulations: 6 of circle parasites, 4 of square parasites. The uninfected hosts are probably still of interest depending on the nature of the study (see mean abundance above).

The elemental subunits of the parasite suprapopulation are the infrapopulations. This is unchanged from Margolis et al. (1982).

(11) Component population. A parasite component population refers to all of the individuals of a specified life history phase at a particular place and time.

Remarks: We introduce this term upon consideration of the 2 misapplications of the term suprapopulation that Margolis et al. (1982) identified: "(1) to denote all of the individuals of a species of parasite occurring in only one of its host species in an ecosystem, and (2) to indicate all of the individuals of a particular stage in an ecosystem."

Our use of component population is mainly for (2), but we would not object to a study of only 1 of several host taxa being called a study at the component level. We would, however, suggest that, if such a study were meant to be a study of the component population, explicit reference be made to the fact that the sample may be severely biased concerning the complete component population. A study addressing (1) is not necessarily "bad." There are perfectly legitimate reasons to study, say, the population of adult *Fasciola hepatica* in cattle without addressing the adults that occur in other mammals. In any event, it is important that the bounds of the study be understood by the researcher and communicated to the reader.

A component population can often be designated by reference to host taxa that harbor the phase of interest. However, component population may also be applied to the free-living phases of a species. A component population is a subset of the total number of subpopulations that make up a suprapopulation.

(12) Suprapopulation. A parasite suprapopulation includes all developmental phases of a species at a particular place and time.

Remarks: Margolis et al. (1982) defined a suprapopulation as "all individuals of a species of parasite in all phases of development within all hosts in an ecosystem." We emend their definition to include free-living phases by dropping the "within all hosts" phrase. In addition, their use of the term "ecosystem" does not seem to provide any more precision than the phrase "particular place and time."

Types of populations

Both component populations and suprapopulations are metapopulations because they are found in spatially discontinuous habitats (often hosts). Besides being spatially discontinuous, they are compositionally heterogeneous and usually include segregated phase classes. As an illustration, we offer a generalized digenean life cycle (Fig. 2). Adults are found in vertebrates, rediae and sporocysts in molluscs, and metacercariae in or on a variety of animals and plants. In addition, eggs, miracidia, and cercariae are free-living. The 3 parasitic phases and the 3 free-living phases provide the stage-structuring. The specificity of the ontogenetic phases for particular taxa of hosts that often occur in different habitats (aquatic for molluscs, terrestrial for some vertebrates) ensures that the subpopulations of phases are segregated.

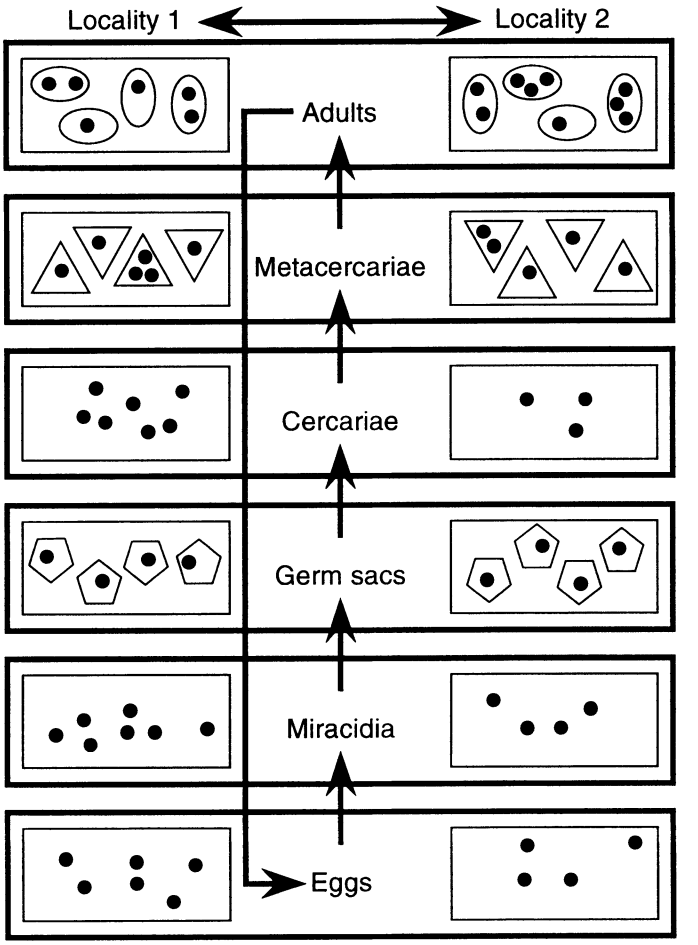

FIGURE 2. Structure of a generalized digenean parasite population from 2 localities (left and right columns). Filled circles represent individual ontogenetic stages of a single parasite species. Open ovals, triangles, and pentagons represent, by orientation, 2 species of hosts for each parasite stage of the ontogeny. Small rectangles circumscribe single-locality component populations, and large bold rectangles circumscribe combined-locality component populations. Double-tipped arrow indicates bi-directional (horizontal) flow of individuals between localities. Single-tipped arrows indicate unidirectional (vertical) flow of individuals among component populations.

(13) Colonization. Colonization (for parasites) is the phenomenon of a parasite establishing a population where none was present at the time. An uninfected host is colonized when it gets an infection.

Remarks: We recommend that the term colonization be restricted to mean the transformation of a host from an uninfected to infected state, that is, from harboring 0 parasites to harboring at least 1 individual. It is an antonym of extinction of a parasite or recovery of a host. We recommend that it not be used as a synonym for transmission, which refers to the conveyance of a parasite to a host no matter whether the host is carrying any individuals of that species.

Just as extinction and recovery could be used at several scales, so too could colonization. Colonization can be applied to an individual host, to a host population, or to a host species. An individual is colonized when the uninfected host becomes infected or reinfected, a population is colonized when the parasite is introduced or reintroduced to the population, and a spe-

cies is colonized when the parasite becomes established or reestablished in a species.

PARASITE COMMUNITIES

The concept of a community has a rich historical use in ecology. In its most ***fundamental*** sense, it refers simply to >1 population of different organisms living together in some spatiotemporal unit. (However, because of the unique, nested nature of parasites, communities of size 0 and 1 may be important at higher levels of analyses as we argue for infrapopulations of size 0 at higher levels.) The term community need not invoke interactions (see Fauth et al., 1996) as some would imply, e.g., Janovy et al. (1992); such modification is better left to adjectives. We agree with Palmer and White (1994) when they noted "We suggest that community ecologists define community operationally, with as little conceptual baggage as possible, so that we can put the debate about their existence behind us." In their most fundamental sense, parasite communities are not different from other biological communities. And just as populations of parasites can be viewed hierarchically, so too can communities.

Quantitative descriptors of parasite communities

(1) Diversity. Diversity is the concept that describes the composition of a community in terms of the number of species present and some factor that weights the relative evenness of distribution of each species. It is defined in practice by the particular diversity index chosen to describe it.

Remarks: Pielou (1977) noted that because a diversity index depends on 2 independent properties of a collection, some ambiguity in its meaning is inevitable. Species richness is the number of species present in a collection. Evenness is a measure of disparity in the number of individuals that represent each species. Communities with a higher species richness, evenness, or both are generally considered more diverse in comparison with communities with lower species richness, evenness, or both. However, because diversity is often described by a single datum, we agree with Simberloff and Moore (in press) that too much information is lost, limiting the types of comparisons that one can make. We include diversity here because it is used in some manner in most studies of parasite communities and thus may be necessary for comparative purposes (assuming the same index is used).

The variety of indices that have been developed to quantify the concept of diversity is evidence that subtle, yet important, variations exist among researchers in what they consider the concept to be. The contribution of each species may be weighted equally without regard to the number of individuals of each species found (in which case diversity is described by the species richness component alone) or in some fashion according to the number of individuals. In the latter case, relatively greater weight might be given to the more common species (as with Simpson's index) or to the rarer species (as with Shannon's index). Traditional views of diversity consider an individual of 1 species to be of equal importance to an individual of any other species. Cousins (1991) suggested that the concept of diversity can be broadened to include functional aspects of species, such as their body size or trophic level, that allow species to be ranked in importance.

The concept of diversity is applicable at any scale appropriate to the level of community organization being studied, whether infra-, component, or supracommunity. Different types of diversity are recognizable in the ecological literature (Istock and Scheiner, 1987) and reflect whether the concept is being applied to a collection as a whole or to patterns of change in diversity along a gradient or within some defined region.

Discussion of the more commonly used diversity indices, their properties, and problems with their estimation can be found in Krebs (1989) and Pielou (1977).

Finally, however, and as we note above, because indices obscure data, we see no compelling reason to recommend any of the different indices of diversity over (1) species richness and a variance measure on that richness and (2) a measure of mean abundance and a variance measure on that abundance for each species.

(2) Core and satellite species. Core and satellite species are predictions of a hypothesis about the mechanisms that influence the distribution of a species within a region. If there is stochastic variation in the rate of colonization or extinction (or both) of habitat patches within the region, and if the probability of extinction within a patch declines as population size in the patch increases, then each species within a community will tend towards 1 of 2 opposite states. Some species will tend to colonize most patches and be found at high numbers within a patch. These regionally common and locally abundant species are termed core species. Other species will tend to colonize few patches and, where found, are in low numbers. These regionally uncommon and locally rare species are termed satellite species.

Remarks: The core–satellite hypothesis (Hanski, 1982) explains 2 empirical patterns of species distribution: (1) a positive correlation between distribution and abundance and (2) a bimodal distribution of species within a geographic region. This hypothesis predicts that core species, but not satellite species, should be well dispersed in niche space. The core–satellite hypothesis was introduced to parasite ecology by Bush and Holmes (1986), who represented the regional dispersion of parasites by prevalence and local abundance by intensity. They explicitly tested for a positive distribution–abundance correlation and examined the modes of the distribution before assigning parasite species to core or satellite status and evaluated the linear niche relations of the 2 groups. We discourage the use of core and satellite simply as synonyms for high prevalence and low prevalence, which has been a tendency in recent years (Nee et al., 1991). We recommend that the use of core and satellite be restricted to situations in which the assumptions or predictions of the core–satellite hypothesis are being tested and that the full set of criteria used to assign species within each study be stated explicitly.

The core–satellite hypothesis remains controversial (Hanski, 1991; Nee et al., 1991), and other mechanisms capable of producing the same empirical patterns have been suggested.

(3) Guild. Guilds are a subset of species in a community that are functionally similar or exploit environmental resources similarly (Root, 1967, 1973).

Remarks: This is a general term used by ecologists who study free-living and parasitic communities. The broader term community (which may often be comprised of >1 guild) is sometimes used when a more narrowly defined guild might be more appropriate. Membership in a guild should not be defined by taxonomy, and it should not be based exclusively on occur-

rence in a common habitat. For example, a host may be found to have nematodes and cestodes in the small intestine. If the intent of the study is to discuss how organisms use space, these might be considered a single enteric guild. However, if the question addresses nutritional adaptations, because cestodes are absorbers and nematodes engulf their food, they would represent 2 functional guilds.

(4) Isolationist community. The term isolationist community was coined initially by Holmes and Price (1986) to characterize a community that fits a number of assumptions and predictions of 2 hypotheses (the population concentration hypothesis and the individualistic response hypothesis) at the infracommunity level. Those assumptions include nonequilibrial communities that are unsaturated because of low transmission rates and where species are individualistically dispersed and are insensitive to the presence of other guild members.

Remarks: This, and the related term interactive community (see below), have been much abused, seemingly because many investigators ignore the assumptions and predictions leading to their formation. There seems to be a tendency, when one examines a host depauperate in parasites, to label the communities as isolationist without regard for the implications. Isolationist communities can result from either (or both) ecological, e.g., host exposure, or phylogenetic, e.g., host lineage, factors. Further, simply finding a depauperate community does not mean that either positive or negative interactions do not exist or that they are unimportant, e.g., Ewing et al. (1982) and Patrick (1991), respectively.

(5) Interactive community. The term interactive community was coined by Holmes and Price (1986) to characterize a community that fit the assumptions of the competition hypothesis at the infracommunity level. Those assumptions include that parasites have high transmission rates, interspecific competition is and has been important, individualistic responses are weak, and the communities are equilibrial.

Remarks: Speciose infracommunities need not be interactive communities. This is perhaps best exemplified by the studies of Lotz and Font (1985). Interactive communities are engendered when transmission rates for some parasite species are high, and thus large numbers of those parasites (species and individuals) are likely to co-occur within a habitat. This sets the ***potential*** for interspecific interactions to be an important structuring mechanism by some species. The concept of an interactive community does not preclude some parasite species showing random colonization or transmission. We would emphasize that when parasitologists use terms such as isolationist and interactive communities, they should do so with full recognition of the implications of the predictions for such communities and not use them as synonyms for speciose or depauperate communities.

The nesting of parasite communities

(6) Infracommunity. An infracommunity is a community of parasite infrapopulations in a single host. All community data are acquired at this level.

Remarks: In Figure 3, there are 15 hosts and 11 infracommunities. (Note that 4 hosts are apparently appropriate habitats in which a community has not established.) If individuals do respond to the presence of other species, it is at this level that any selection pressures will occur.

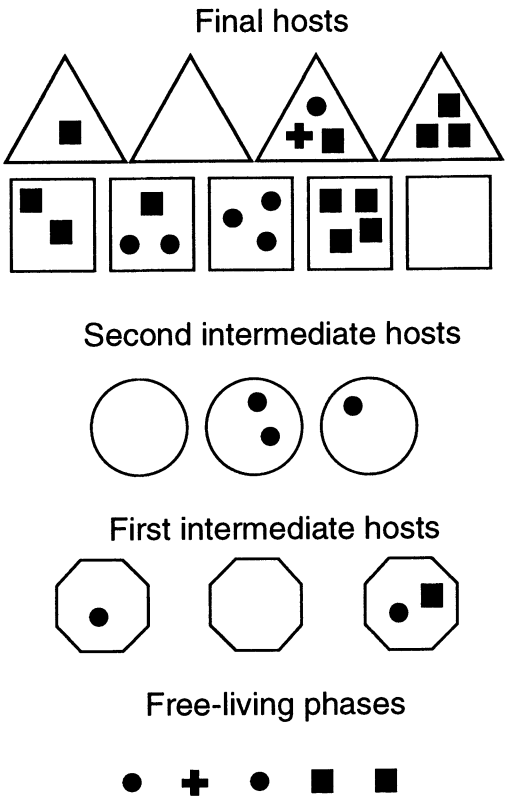

FIGURE 3. Stylized parasite communities. Large open geometric shapes represent hosts. Hosts having the same shape represent the same species. Small solid shapes represent parasites. Parasites with the same shape represent the same species. "Plus" parasites have a direct life cycle, "square" parasites require 1 intermediate host, and "circle" parasites require 2 intermediate hosts. All hosts and parasites live in the same locality. This is a much simplified community. For example, were any of the parasites digenes, there would be additional free-living phases; were any of the parasites transmitted by a vector, there would be no free-living phases. See text for quantitative details.

(7) Component community. A component community refers to all infrapopulations of parasites associated with some subset of a host species or a collection of free-living phases associated with some subset of the abiotic environment.

Remarks: In Figure 3, there are 5 component communities: triangle and square final hosts, octagonal and circle intermediate hosts, and free-living phases. Considering only square hosts, species richness is 0, 1, 1, 1, and 2 (mean ± SE = 1 ± 0.3). The abundances of circle parasites in square hosts are 0, 0, 0, 2, and 3, and the mean abundance (±SE) is 1 ± 0.6. The same parameters for square parasites in square hosts are 0, 0, 1, 2, and 4 with a mean (±SE) abundance of 1.4 ± 0.8. Circle parasites within square hosts have a prevalence of 40% (95% C.I. = 5–85%), intensities of 2 and 3, and a mean (±SE) intensity of 2.5 ± 0.5. Square parasites within square hosts have a prevalence of 60% (95% C.I. = 15–95%), intensities of 1, 2, and 4, and a mean (±SE) intensity of 2.3 ± 0.9.

The subset is typically a host species and may be further restricted to specific organs or organ systems. The term may also be applied to stage-structured host populations such as specific gender or age. It is at this level that most studies on par-

asites of free-living animals are published, e.g., surveys. Component community would also apply meaningfully to the community restricted to a particular abiotic microhabitat at a locality, e.g., the component community of free-living phases of nematodes associated with specific samples of soil.

(8) Supracommunity. A parasite supracommunity comprises parasite suprapopulations.

Remarks: In Figure 3, a study at the supracommunity level in this predefined locality would involve studying all hosts and free-living phases in the diagram.

Although this was originally called a compound community by analogy with Root (1973), we recommend that community terms share parallels with population terms. Therefore, we prefer supracommunity over compound community. The supracommunity can be viewed as a community of ontogenies or life cycles. It would thus include all potential hosts (intermediate, paratenic, vectors, and definitive) as well as free-living phases. In theory, the use of the term would be appropriate when one extended a component community study to include virtually all phases of the parasites found in the host(s) being studied. Scale will be very important, ranging from a local supracommunity, e.g., a small pond, to all other possible hosts and free-living phases found in the biosphere. We suspect that supracommunity analyses will be tractable, at best, only on a local scale.

Parallels between populations and communities

At the infra- and supracommunity levels, the organization of parasite communities generally parallels that of parasite infra- and suprapopulations. However, at the component level, communities and populations can be contrasted. A component community is devised after a consideration of habitat/host subdivisions, whereas a component population is devised after a consideration of ontogenetic subdivisions.

A final caution on the nesting of parasite populations and communities

Ironically, most parasitological data are acquired at the level of component populations or component communities, the 2 most subjective and artificial constructs of those we present. There are ***no*** discrete boundaries at the component level; they are, in fact, nothing more than the sum of infrapopulations or infracommunities (or, for free-living phases, some subset of the abiotic environment). They are thus vague and their identification and "size", e.g., the number of infrapopulations or infracommunities (or abiotic subsets) examined, will be mandated by the interests and resources of the investigators. To that end, we cannot overemphasize that authors identify explicitly what they are circumscribing when they use the term component.

CONCLUDING REMARKS

In summary, we suggest preferred usage for a number of objective terms commonly applied to ecological discussions of parasites. We also provide comment on some terms because they are so often (mis-) used in papers on parasite ecology. However, even among the 4 of us, there was not unanimous agreement on all terms. What we hope is that authors will heed our collective concerns for effective communication and define any potentially ambiguous terminology either through reference to the literature or, preferably, through definition within the body of their text.

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