A Parasitological Primer (with a focus on some theoretical issues): The Ten General Rules of Parasitism and Parasitology

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Here are some generalities about parasitism that probably should be kept in mind when assessing the contributions of various people working with host-parasite systems, especially when that work involves parasite population biology, host-parasite co-evolution, and epidemiology or epizootiology:

(1) The first and perhaps most important rule to remember is that the word "parasite" can, and in the primary literature does, refer to an enormous array of organisms ranging from viruses, bacteria, and fungi, to at least some members of all animal phyla (including vertebrates), and numerous plant species. Thus, to borrow a literary device from G. Stein: *a parasite is not a parasite is not a parasite is not a parasite* . . . The more conservative parasitologists would likely recognize at least a dozen or so different types of parasitic relationships; the most liberal parasitologists would probably claim that each host species + parasite species combination is unique in some important way, thus eco-evo-devo work on one system is probably not very applicable, conceptually, to other combinations. A minimal amount of work with any common system in nature, e.g. freshwater fish or amphibians and their parasite communities, shows that even when a single host species is involved, the population-level interactions between that host species and its several parasite species are likely to be parasite species-specific (see Fig. 1). The scientific names of the species involved, both hosts and parasites, are therefore exceedingly important, indeed integral, components of any study because these names are links to our understanding, or lack thereof, of life cycles, developmental requirements, transmission mechanisms, and the like. That is, these names are the search terms for use in gaining access to the primary literature.

(2) The second aspect of parasitism that is critical to an understanding of the phenomenon is host specificity. Thus a second general rule could read: some parasite species (the "specialists") are highly restricted in the kinds of hosts they will infect, whereas others (the "generalists") may be quite unrestricted, although virtually no parasites are universally infective. The extent of generalist and specialist properties may vary at the species level, with different species of a parasite genus exhibiting different levels of host specificity, even at different life cycle stages. One might ask, for example, whether a generalist parasite can indeed drive an evolutionary response from one of its several hosts? Or, perhaps a better question might be: What are the conditions under which a parasite species that routinely infects a dozen host species in nature would drive evolutionary change in only one of those host species?

(3) The third general rule of parasitism is that within any one generation, only a small fraction of genetic diversity among the parasites is displayed against a relatively small fraction of host genetic diversity. This rule is illustrated in Figure 2. The assumption that parasitism can drive evolutionary change also requires an assumption that whatever portion of the parasite's genetic diversity is displayed against a host's genetic diversity in nature is similar from generation to generation, although in nature, pure chance and often highly variable ecological conditions actually determine which fraction of the parasite's genetic repertoire

actually survives, and which fraction of the host species' genetic repertoire actually encounters the parasite survivors. In order to actually show that parasites are driving evolution in any species-to-species relationship, the following conditions must be met:

a. Genetic makeup of an infected host dictates course of infection to the extent of reducing host fitness.

b. The parasite is host specific and is either not affected by host defenses or is genetically variable enough to overcome these defenses in the short term.

c. Succeeding generations of hosts having increasing frequencies of susceptible genotype.

d. The parasite is at or near the top of the list of risk factors for the host; i.e., the parasite cannot be an inconsequential pest.

e. The parasite has to exert its fitness effects on hosts of, or prior to, reproductive age.

f. The ecological arena in which host and parasite encounter one another must be stable enough so that abiotic factors do not override biotic ones in determination of host fitness.

g. Other, co-infecting, parasite species must be shown to have no effects on host fitness.

(4) A fourth general rule is that symbiosis is the most common way of life on Earth and that every organism that has been studied seriously has been found to be occupied, at the species level, by at least one, and typically several, other, unrelated, species, i.e., the symbionts. Thus whatever one person means by the word "parasite," that meaning is likely to fall somewhere on a very large scale of symbiotic relationships ranging from benign and opportunistic to deadly and obligate, and may have little connection to whatever another person is calling a "parasite." The main obstacles to understanding of evolutionary relationships between hosts and parasites, therefore, are investigator ignorance and investigator agenda. The ignorance often limits an investigator's ability to put host-parasite relationships into their phylogenetic and/or a natural context; an agenda often drives a search for systems to further it.

(5) A fifth general rule related to parasitism is that systematics matter. This rule is the one often, if not typically, violated by people who are studying host-parasite systems in some agenda-driven manner. No matter what his/her interests, a biologist must respect the power of scientific names and understand clearly how those names are actually links to vast amounts of information, much of it of evolutionary importance. In addition, the names are the communication system by which we put our work into an evolutionary context. A scientific name carries with it a historical record, a set of observable properties, an assumed set of developmental events and requirements, an ecological niche, and a bunch of relatives, all of whom also have names. The word "parasite" is not a scientific name; *Haematoloechus coloradensis* is a scientific name; *H. coloradensis* is a parasite, but not all parasites are *H. coloradensis*. When people who understand the first four rules use the term *Haematoloechus coloradensis* in conversation, suddenly the evolutionary context is established, constraints on

and opportunities for transmission are understood, and participants in this conversation are able to screen out irrelevant information.

(6) A sixth general rule about parasitism is that the study of it, namely parasitology, is a highly integrated discipline. Thus all parasitologists understand that pathology, immunology, transmission, development, parasite genetics, physiological relationships between host and parasite, evolutionary history, geographic distribution, and the practical problems of diagnosis and identification, are all inextricably linked to one another. This understanding is the basis for parasitologists' breadth (usually forced on them by the discipline), although they all understand that specialization is necessary for a productive research career. You simply cannot study everything about even a single host-parasite system during a single lifetime.

(7) The seventh general rule is that the overwhelming majority of symbiotic organisms do not cause disease, or if they do, such disease is relatively mild compared to some other risks faced by a potential host. The risk of an embryonic or hatchling duck being eaten by a bull snake, for example, is many times, perhaps many orders of magnitude, greater than the risk of not mating, or not successfully completing migration a year later, because of a hundred tapeworms in its gut. So when assessing, or even contemplating, the potential damage that parasites can inflict on hosts, especially in an evolutionary context, it is important to consider the hosts' entire lives, including ecological requirements, predators, etc.

(8) The eighth general rule is that parasites are divided into two categories: microparasites and macroparasites. The former multiply inside the host individual in whatever developmental stage actually occupies that particular host. Malarial parasites, trypanosomes, amebas, and viruses are all good examples of microparasites. Macroparasites do not multiply inside the host in the developmental stage that occupies that host. Large roundworms and tapeworms are good examples of macroparasites; either group may produce staggering numbers of eggs that are subsequently passed in feces, but adult tapeworms typically do not produce more tapeworms within the original host. Whatever factors produce selection pressures on both hosts and parasites differ markedly between these two general types of parasites—micro- and macro-.

(9) The ninth general rule is that in nature, most host species are either uninfected with a particular parasite species, or are only lightly infected, and that most of the parasites are in a relatively few host individuals. This rule applies mainly to macroparasites, but with these kinds of parasites, it is the most important evolutionary consideration (again, see Figure 2).

(10) The tenth general rule is that in the case of parasitic organisms, persistence is the measure of success, not numbers. Thus when contemplating parasite properties, it is probably wise to begin with the life cycle, which is an inherited and evolved boundary condition, then ask how much reproductive potential must be maintained for the parasite species to persist in the long term. So any model that begins with assumptions about numbers must make sure that these assumptions focus on the life cycle steps that limit, or allow, persistence. This requirement for persistence as a measure of success means that host-parasite evolution

models must take into account the full range of ecological conditions under which hosts and parasites co-occur, including alternate or reservoir host species.

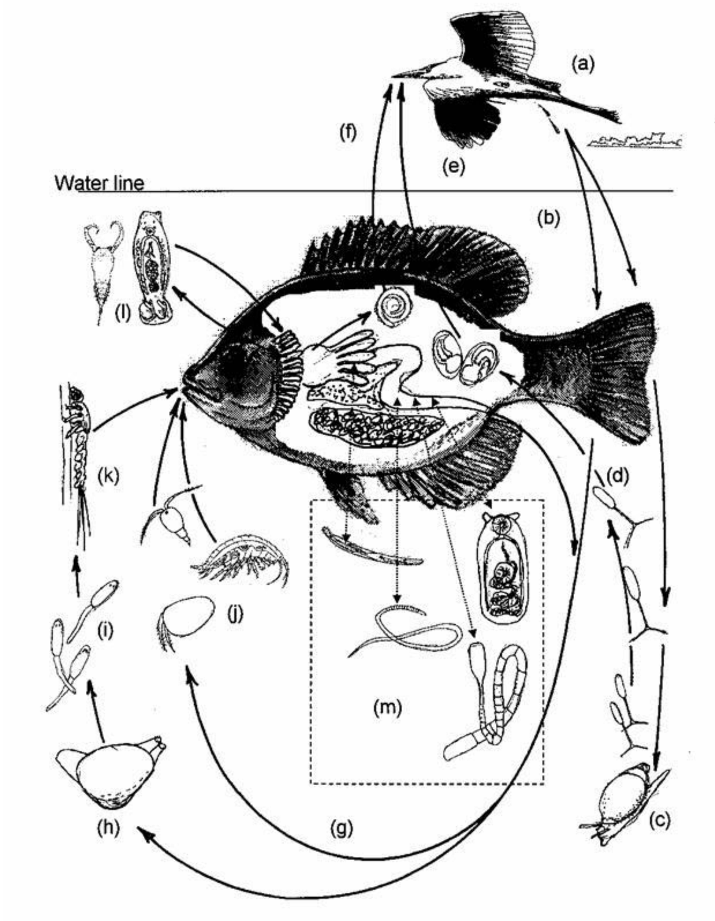

Figure 1. Ecology of parasitism in a typical North American freshwater pond.
(a) Fish-eating heron, the habitat of several adult helminth parasites that use bluegill as second intermediate hosts. (b) Trematode and nematode eggs being passed in heron feces and dropping into the water. (c) Snails that serve as first intermediate hosts for most trematodes. (d) Trematode cercariae emerging from snails; cercariae penetrating the fish, where they encyst as metacercariae. (e) Heron becoming infected with trematodes upon eating a fish containing metacercariae. (f) Heron becoming infected with a nematode upon eating the same fish that also contains an encysted juvenile worm. (g) Passage of helminth eggs from both heron and fish feces into the water. (h) Fingernail clams that first intermediate hosts for adult trematodes in bluegill. (i) Cercariae emerging from fingernail clam to penetrate and infect a mayfly nymph (k). (j) Community of small crustaceans serving as intermediate hosts for nematodes that live in both heron and fish, acanthocephalans from fish, and tapeworms from fish. (l) Ectoparasitic flatworms and crustaceans that occupy the fish's gills and have direct life cycles. Within the box (dotted line) are acanthocephalans from the fish's pyloric cecae, and nematodes, trematodes, and cestodes from the fish's intestine.

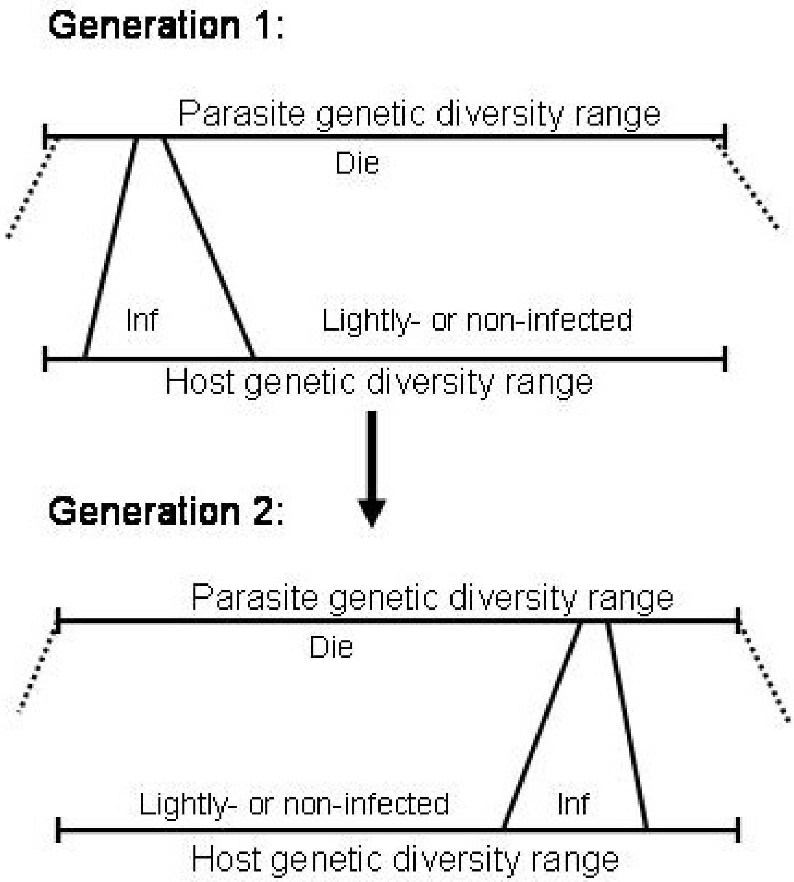

Figure 2. An illustration of the typical flow of parasites into hosts
Most parasites have enormous reproductive potential, but the probability of any one parasite surviving to infect another host is relatively small. In addition, within the vast majority of host species' populations, the majority, and often a large majority, are either not infected or are only lightly infected. The exceptions are, of course, the disease cases that we are inordinately interested in, and even in those situations, parasites are often distributed quite unevenly across time (thus the term "epidemic.")