Evolutionary Ecology of Parasites: From Individuals to Communities

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BOOK REVIEW . . .

Evolutionary Ecology of Parasites: From Individuals to Communities. By R. Poulin, Chapman & Hall, New York. 1998. 212 pp. US $107.00 (hardcover), US $54.00 (paperback) from amazon.com.

Ecology is the study of organisms and their environments (Begon et al., 1996); therefore, if animal hosts can be viewed as part of the environment for their parasites, the synthesis of ecology and parasitology is a logical extension of each discipline. In this book Robert Poulin laments the lack of crossover between the two sciences. Intended as a reference to parasitologists, this book bridges this gap and stimulates the kind of cross-fertilization that has so often in the past led to new insights when two disciplines intermingle. Poulin approaches this task from an evolutionary framework that neatly encapsulates his arguments. Poulin describes the ecology of parasites at three scales: the individual, the population, and the community. He begins by discussing the evolution of parasitism and the processes that guide its structure. Concepts of population ecology are then introduced, particularly in light of the unique circumstances that parasite populations experience. Finally, he expands to the level of parasite communities and the interspecies interactions through which they develop. The resulting monograph is a cohesive introduction to ecological principles for parasitologists, as well as a guide to the parasite niche for ecologists.

The most fundamental question any evolutionary ecologist must ask when confronted with a particular behavioural or morphological trait is, "what is its evolutionary significance?" Poulin repeatedly returns to this foundation. When describing the ecology of parasites at the scale of the individual, Poulin never deviates far from a evolutionary perspective. For example, Poulin asserts that two conditions are required in order for parasitism to evolve: (1) morphological and behavioural mechanisms must have existed that allowed a protoparasite to take advantage of the parasite niche, and (2) the fitness benefits of such a change in life style would have to outweigh the costs. Further, he argues at length that the evolution of complex life cycles (i.e., addition of one or more intermediate hosts) was an adaptive, rather than accidental, modification to the life history of various parasites.

The most interesting application of an evolutionary perspective is the discussion of the evolution of virulence, which is usually associated with parasite fecundity. Poulin argues that virulence should be a parasite-centred concept, as "from the parasite's perspective . . . what happens to the host as a consequence of its exploitation by the parasite may be of no importance." (p. 67). In the same paragraph, he continues this argument: "Our notion of virulence originates from medical science and is focused on impact on host fitness, whereas selection in parasites acts on rates of host exploitation irrespective of effects on host fitness." Poulin reviews extensive evidence that suggests virulence (whether it is defined as fecundity of the parasite or effect on host productivity) does not necessarily attenuate with common evolutionary history among parasite and host as previously thought. A parasite-centred concept of virulence does not preclude a positive correlation between parasite virulence and fecundity; however, the relationship should not be defined by such a correlation.

Poulin also addresses the widespread assumptions that transition from free-living to parasitic life styles incurs a concurrent reduction in body size and an increase in fecundity. He points out methodological biases that have prevented proper comparison among parasites and their free-living sister taxa (i.e., lack of correction for phylogeny during analysis and incompletely described taxa). Further, he provides extensive empirical evidence suggesting that both body size and fecundity are life history traits that can increase or decrease during this transition, depending on the particular selection pressures. This is an example of Poulin's meticulous attack of incorrect assumptions that is refreshing and brings this book to a higher level than simply a review text.

Poulin does an admirable job of bringing ecological tools for describing the distribution and demography of populations to parasitology. Concepts such as the causes and consequences of aggregation, population persistence, standard epidemiological models, and density dependence are described coherently and comprehensively.

Poulin describes how terminology differs among disciplines. For example, he notes that an "overdispersed" distribution is clumped or aggregated to parasitologists, but to ecologists overdispersion describes a uniform distribution. Unfortunately, Poulin fails to explicitly define "regulation," a fundamental term in ecology. A regulating factor is any density-dependent process that keeps populations within predictable density ranges. Regulating factors are a density-dependent subset of limiting factors that quantifiably affect population growth. There has been much confusion in ecological

literature as a result of vague or inaccurate use of the term regulation (e.g., Sinclair, 1991). An explicit definition in this volume would have prevented this misunderstanding in ecological parasitology.

An opportunity for further bridging the gap between the terminology of ecology and parasitology was missed in this text. Poulin uses the term "infrapopulation" to define all the parasites of a particular species occurring within the body of a single host individual (Margolis et al., 1982). This is in contrast to the "suprapopulation," which encompasses all the parasites of a single species, regardless of developmental stage, that occur within hosts within an ecosystem (Margolis et al., 1982). If an individual host is viewed as "habitat" for a parasite infrapopulation, these terms are directly analogous to the ecological terms, "local population" (a set of individuals living in the same habitat patch) and "metapopulation" (set of local populations which interact via dispersing individuals among local populations; Hanski, 1996), respectively. The analogy of metapopulation dynamics has been used extensively to describe the epidemiology of measles in humans (e.g., Grenfell and Harwood, 1997; Finkenstädt and Grenfell, 1998) and the distribution of strongylid nematodes in mammals (Arneberg et al., 1998; see review by Begon et al., 1996 for other examples). The metapopulation concept brought many innovations to ecology, and the opportunity to generate new ideas may have been because the concept was excluded here. For example, Poulin (1998) emphasizes that regulation occurs via processes acting within infrapopulations. Regulation of metapopulation size is a function of the colonization rate of new habitats, the proportion of habitats occupied, and the extinction rate within each habitat. The respective processes of infection, prevalence, and recovery or mortality of host individuals are analogous in light of the metapopulation concept. Dispersal among habitats (hosts) clearly affects both colonization (infection) and extinction (host recovery or mortality), and density of habitat patches (hosts) is a major determinant of dispersal. Therefore, density of hosts should be a primary determinant of parasite abundance. In fact, Arneberg et al. (1998) demonstrated that density of mammalian hosts influences strongylid nematode abundance, in contrast to the common view that regulation occurs primarily through infrapopulation density-dependence (Poulin, 1998).

A community is a collection of species in the same place and time. Poulin effectively describes interspecific interactions (e.g., competition, facilitation etc.) that serve to modify the abundance and distribution of parasites within a community. Further, Poulin provides a comprehensive review of the evidence surrounding creation of community structure, effectively whether, "the structure of parasite infracommunities differs from that of random assemblages." (p. 145). This has been a central question in ecology since Frederic Clements proposed in 1916 that plant community succession results in an "organic entity" or functional super-organism (Clements, 1916). Gleason (1926) vehemently opposed this thesis, and proposed that associations among plants were coincidences driven by similar resource needs. Poulin's review suggests that infracommunity development also may be the result of similar resource needs.

Poulin concludes the book by discussing the influence of human activities, namely habitat alteration and parasite control (which he points out is merely changing the parasites' habitat). As with all ecology, it is evident that our analytical toolbox suffers from a severe lack of predictive power, consequently the consequences of our actions are largely unknown. Maybe, as Poulin predicts, the use of comparative studies to develop testable hypotheses will allow the development of a "holistic, evolutionary perspective of parasite biology."

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