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An evolutionary definition of parasitism

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The original concept of parasitism defined the relationship as the use of one organism, the host, as both habitat and a source of nourishment by another organism, the parasite (Leuckart, 1879 as cited in [1]). The tendency of current authors [2–4] to restrict their definition to the trophic aspect of the relationship has resulted in the acceptance of parasitism as a relative term that can be used in any manner, as long as each worker defines separately their concept of the relationship [4]. Parasitism is not viewed as a discrete association, but rather as one that merges into other interspecific relationships [5], allowing Ewald [6] to describe the unique relationship of parasitoids with their hosts as merely the lethal endpoint of an endoparasitic continuum and to equate ectoparasitism with predation along a shared continuum of body size.

The limitations of characterising parasitism as merely a trophic relationship can be easily gleaned from a definition proposed by MacInnis [7], where a parasite is one partner of an interacting pair of species that is dependent on a minimum of one host gene or its products for survival. This open-ended definition has prompted some textbook authors [8–10] to include a section differentiating parasites from predators as part of their definition of a parasite, although none so elegant as the comment by British ecologist Elton that predators live on capital, whereas parasites live on income [11].

Crofton [12] included the harmful consequence of the metabolic interaction between host and parasite in his definition of parasitism, requiring that a true parasite must have the potential to kill the host. This addition has been adopted by several authors [9, 13–15], despite the admonishment by Filipchenko (1937 as cited in [1]) that it is incorrect to characterise one entity by an attribute belonging solely to another entity. Moreover, inter- and intraspecific differences in host responses to parasitism make the concept of harm virtually unquantifiable, and thus of little or no use as a defining character.

There appears to be a general consensus among parasitologists that there is no distinct morphological, physiological, ecological or evolutionary character that distinguishes all parasites from all non-parasites [16]. This lack of a clear definition of parasitism robs us of the ability to make any generalisations regarding the relationship. Noble and Noble [17] argued that the lack of general rules exists for the simple reason that none are specifically applicable. Read [18] refused to accept this verdict, alleging that the failure to produce generalising concepts is a failure of the methods used to approach the phenomenon of symbiosis as a special interaction between species. The term parasitism encompasses both the host and the parasite [11], and the problem in defining the relationship involves the determination of the degree and extent of the integration [18].

The recognition that parasites form a biological and not a systematic group (Braun, 1883 as cited in [1]) forces the realisation that parasitism is purely an ecological concept, and indeed Filipchenko (1937 as

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cited in [1]) has suggested that parasites form an ecological group of the same significance as terrestrial or aquatic animals. Thus, in order to resolve the degree of integration between a host and a parasite, it is necessary to consider the host as habitat, and not simply a meal (Pavlovski, 1934 as cited in [1]). This reasoning led Dogiel [1] to the conclusion that parasites are those animals that use other living animals as habitat and a source of nourishment, surrendering, in whole or in part, the regulation of relationships with the external environment to their host. Thus, "parasitology should concern itself not only with the parasite and host, but also with the relationships and adaptations which arise as the result of one animal living in another" [1].

The role of the host as both habitat and nourishment explicitly separates parasitic organisms from both insidious (e.g., mosquitoes) and consumptive predators. The separation of parasitoids from parasites also becomes more intuitive, as only the larvae of parasitoids are tied obligately to the host, whereas with parasites the adult is the stage constrained to the host habitat. Thus, the distinction between parasitoids and parasites is not whether they kill the host, which suggests a continuum rather than a separation, but rather whether the adult stage is free living or not. This classification groups insects whose life-cycles are characterised by obligatory myiasis (e.g., screw worms, bot flies and warbles) together with the parasitoid wasps, based on a shared life-history trait. The differences in the effect parasitoids have on the host may merely be an artefact of the relative size of the parasitoid and, therefore, not a defining character.

Using the "host as habitat" criterion requires some means of establishing the level of intimacy of a given symbiotic relationship. Read [11] recognised three main properties of parasitism: infectiousness, establishment and transmission. Infectiousness is a short-term process involving a degree of tolerance to an instantaneous exposure to a new environment [11], while transmission is ultimately dependent upon successful establishment (i.e. growth and persistence). The three are interdependent, and yet only establishment separates parasitism from all other associations of organisms with their habitat. In order to become established in an environment dictated and delineated by another organism, there is one key adaptation that all successful parasites must possess: the ability to tolerate or evade the immune response of the host organism. The immune response must be viewed as an environment that has an acute effect on the evolution of the host–parasite relationship [19], as it is the one unique barrier to the colonisation of all host organisms.

The distinction of being able to evade the immune response of the host not only demarcates parasitic relationships among extant taxa, but also allows the origin of parasitism to be identified within a given lineage. The common theme of parasitic origins involving a transition from phoresy or commensalism to parasitism provides little insight into a definitive modification of the nature of a given symbiotic relationship. Viewing the elusion of an immune response as a key adaptation that facilitates the invasion of a new habitat marks the point where other symbiotic relationships end and parasitism begins. Unfortunately, this concept will remain little more than an adaptationist argument until it can be demonstrated from the standpoint of historical ecology [20] that the origin of the mechanisms used by parasitic organisms to evade the immune response coincides with the inception of the parasitic habit.

The use of the immune response to determine the relationship between two organisms is effective because it quantifies many aspects of the relationship from the perspective of the "habitat". The generation of an immune response is a manifestation of the intimacy of the association between two organisms, as well as an indication that this association is potentially harmful to the host. However, as has been suggested previously, one must look at characteristics belonging to the parasite in order to define parasitism. The host's immune response does establish the parasite's intimacy with the habitat and the potential to harm, but only the evasion of that response is indicative of being adapted to survive the host habitat. Defining parasites as organisms that have the ability to evade the immune response of another organism places all parasites within a shared evolutionary framework, with the host immune response as a constant and powerful selective factor.

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