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Some roles of parasitic helminths in trophic interactions. A view from North America

Algunos papeles de los helmintos parásitos en interacciones tróficas. Una visión desde Norteamérica

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ABSTRACT

Parasites are seen as organisms that share physiological mechanisms with other species on a dynamic continuum of interactions with hosts, from detrimental to beneficial, that are not easily specified. Trophic and trophically mediated interactions between parasites and between parasites and their hosts are emphasized, especially recent North American literature dealing with helminths. Parasite-host interactions include the following: 1) behavioral alterations of parasitized hosts – some examples, and evolutionary and ecological considerations; 2) effects on host distribution and abundance – via reproductive effects or the mediation of interactions with other free-living species; 3) environmental influences – biotic and abiotic – on parasites; 4) parasitic castration; 5) population effects – host and parasite population regulation, transmission and host diet, hosts as selective influences on parasites; and 6) coevolution – sexual selection, the evolution of pathogenicity, and phylogenetic studies of host-parasite evolution. Consideration of parasite-parasite interactions at the infrapopulation level includes the study of density-dependent effects, mate location and physiochemical influences. At the level of parasite communities within a host species, a variety of hypotheses that may account for structure are reviewed.

Key words: Helminths, host-parasite interactions, parasite-parasite interactions, North America.

RESUMEN

Se considera a los parásitos como organismos que comparten mecanismos fisiológicos con otras especies en un continuo dinámico de interacciones con huéspedes, desde perjudicial a beneficiosas, las cuales son difíciles de especificar. Se enfatizan las interacciones tróficas, o mediadas tróficamente, entre parásitos y entre parásitos y sus huéspedes; en particular aquellas interacciones documentadas sobre helmintos en la literatura reciente. Se examinan las siguientes interacciones parásito-huésped: 1) Alteraciones conductuales de los huéspedes parasitados; con algunos ejemplos y consideraciones evolutivas y ecológicas. 2) Efectos sobre la distribución y abundancia de los huéspedes; vía efectos reproductivos o mediación de interacciones con otros organismos de vida libre. 3) Influencias ambientales, bióticas y abióticas, sobre los parásitos. 4) Castración parasitaria. 5) Efectos poblaciones; regulación poblacional de parásitos y huéspedes, transmisión y dieta del huésped, huéspedes como influencias selectivas sobre los parásitos. 6) Coevolución; selección sexual, evolución de la patogenicidad y estudios filogenéticos de la evolución parásito-huésped. Se consideran las interacciones parásito-parásito al nivel infrapoblacional, incluyendo efectos denso-dependientes, localización de pareja e influencias fisicoquímicas. Al nivel de las comunidades de parásitos dentro de especies huéspedes, se revisa una variedad de hipótesis que pueden explicar su estructura.

Palabras claves: Helmintos, interacciones huésped-parásito, interacciones parásito-parásito, Norteamérica.

INTRODUCTION

Parasites are generally thought to be organisms that live in close association with larger hosts, frequently exhibiting a metabolic dependency on that host. Occasionally, arguments have surfaced about how close the association must be to be considered parasitism, or how broadly the dependency can be characterized. But the definition is basically satisfying; it allows us to think we know what a parasite is.

Ecologists (*e.g.*, Odum 1971, Anderson & May 1978) usually view parasites as detrimental to their hosts. Some of the organisms discussed in this paper have yet to reveal their detrimental effects to inquiring scientists, however. The nature of their associations with hosts may change during host ontogeny. Even "harmful" parasites may have beneficial influences on their hosts. The definitions are not that realistic, and Van Beneden (1876:1) knew this when he wrote, "...the precise limit at which commensalism begins is not

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always easily to be ascertained". (See also Price *et al.* 1986). Read (1970:3) argued for a study of *symbiology, i.e.,* symbiosis, which he defined as "...the sharing of physiological mechanisms by different species, without specifying the relative benefits derived or outcome of the association". He argued that many associations that we classify as "parasitism" or "mutualism" do not readily fit these definitions, and the extent to which they do may depend on circumstances. Finally, he (Read 1970:8) observed that "Many of them [symbiotes] produce little or no disease; but as will become apparent, the status quo is an illusory concept in symbiosis."

The notion of symbiology has yet to catch on in the undergraduate curricula of most North American universities. The organisms I will discuss here are some of the subjects of parasitology courses, and are commonly called parasites. Please remember that in some cases, such designation is more a matter of convenience than an accurate description of the association. They are all, however, symbiotes.

Parasites are relevant to trophic interactions in a variety of ways. They themselves have long been considered a trophic level, but as such, they are surprisingly disparate, ranging from facultative predators on other parasites (Lie *et al.* 1965, Lie 1966), to "absorbers" (Bush & Holmes 1986b). Many of them are transmitted through food chains, sometimes by increasing a predator's encounters with prey, and they are also known to affect the feeding behavior of their hosts. Their ubiquity is equalled by their inconspicuousness in many instances, and we do not know how many reports of gastropod biomass are really largely reports of the trematode biomass they may contain (Duszynski, pers. comm.).

The ecology of symbiotes has been the subject of a fascinating book (Price 1980), and I approach the topic from a more restricted perspective. As indicated by the subject material of this conference, I have limited most of the review to research activity by North Americans. The excellent work being conducted on other continents is largely accessible through the bibliographies of the literature I cite herein. I emphasize areas in which trophic or trophically mediated interactions of either parasites or hosts are important, although I include some other areas of parasite ecology that are currently developing in North America. I focus on the recent (6-8 yr) literature, especially that pertaining to helminths. Other literature is included in a more eclectic fashion. Although the two areas can hardly be separated, I approach the material first from the perspective of parasite-host interactions, and then from that of parasite community interactions. In the former instance, I review literature pertaining to behavioral alterations involved in parasite transmission, parasite effects on host distribution, reproduction, and population, coevolution, and environmental influences on parasites. Under parasite community interactions, I consider factors influencing parasites at the infrapopulation (individuals of one parasite species within a single host; Esch *et al.* 1975), infracommunity (populations of all parasite species within a single host; Holmes & Price 1986) and component community (all infracommunities in a population of hosts; Holmes & Price 1986) levels. [See Holmes & Price (1986) for discussion of compound communities – all parasite populations in an ecosystem.]

This is an admittedly broad view that, it might be argued, goes beyond the topic of trophic interactions. I maintain that to the extent parasites influence the contours of host distribution and abundance, sometimes being transmitted by those same hosts, their ecology in its broadest sense directly affects trophic interactions at a variety of levels.

PARASITE-HOST INTERACTIONS

Behavioral Alterations

The emphasis of this workshop is on trophic interactions, and perhaps the most unusual way that parasites influence trophic interactions is by affecting the availability of their prey-item/intermediate hosts (hosts that harbor a juvenile parasite that must be eaten in order to reach adulthood in the predator/final host). In so doing, they may enhance their own probability of transmission to the final (definitive) host. Holmes & Bethel (1972) delineated four ways in which parasites might take advantage of definitive host foraging behavior and thus enhance transmission: they may alter host stamina, increase host conspicuousness by changes in appearance, disorient the host as a result of neurological damage, and alter responses to environmental stimuli. More recently, Radabaugh (1980a) has shown that social (schooling) behavior in minnows is affected by a trematode, *Ornithodiplostomum ptychocheilus,* that encysts in the brain (Radabaugh 1980b). Infected minnows may form less compact schools and may be more vulnerable to piscivorous birds.

When responses to environmental stimuli are altered, distributions of hosts may be affected, with infected animals moving into areas of increased predator-prey encounter (Holmes & Bethel 1972). Acanthocephalans are especially notable in this regard, altering such behaviors as activity, phototaxis, predator avoidance, exposure, substrate color choice and vertical distribution. In some parasite-host associations, these alterations have been shown to affect predation intensity in a laboratory setting (see Moore 1984a, b for reviews). Moore (1983) showed that an acanthocephalan, *Plagiorhynchus cylindraceus,* was also implicated in increased starling predation on the terrestrial isopod intermediate host (*Armadillidium vulgare*) under field conditions. What this says to ecologists in general is that parasites can affect the distribution of animals in nature, and do so in a way that alters trophic interactions. Thus, two communities that exhibit similar isopod relative abundances, but vary in the prevalence (% infected hosts; Margolis *et al.* 1982) of *P. cylindraceus,* could yield different rates of avian predation on these isopods.

Acanthocephalans are not alone in this respect, and a wide range of parasites have been shown to use a variety of means in altering host behavior and thereby possibly affecting transmission probabilities. Moore & Lasswell (1986) showed that when infected with an immature nematode (*Dispharynx nasuta*), the isopod *A. vulgare* exhibited altered behaviors other than those accompanying acanthocephalan infection. They tentatively concluded that in at least one of these host-parasite associations (acanthocephalan or nematode), the changed behavior was peculiar to the association and not a generalized isopod response to infection. Other examples of parasites that alter invertebrate host behavior include the larva of the trematode, *Brachylecithum mosquensis,* which encysts in the supraesophageal ganglion of carpenter ants. These ants behave in a sluggish, highly visible manner and may be more easily preyed upon by birds (Carney 1969). Unlike *B. mosquensis,* which is transmitted when the ant containing it is eaten, *Plasmodium gallinaceum* is transmitted when its mosquito host (*Aedes aegypti*) feeds. This malarial parasite affects the quality of the vector's saliva, necessitating increased probing activitv (Rossignol *et al.* 1984).

In the case of vertebrate hosts, Rau & Caron (1979) showed that *Echinococcus* hydatids may increase the likelihood of a moose being shot by a hunter (see also Mech 1966). Rau (1983a, b, 1984a) discovered that mice infected with *Trichinella spiralis* are less active and more likely to exhibit subordinate behavior that could lead to predation and parasite transmission. He did not find this with *T. pseudospiralis* (Rau 1984b). Different predators may be involved in this parasite's life cycle. Stibbs (1984) showed that rats infected with *Trypanosoma brucei gambiense* had levels of serotonin, dopamine and 5 - hydroxyindoleacetic acid that differed from those of uninfected controls. Activity levels in the two groups also differed.

The cestode plerocercoid of *Schistocephalus* affects the respiration of its stickleback intermediate host. These fish require more oxygen, move to shallower water, and may be easier prey for piscivorous birds (Lester 1971). The swimming abilities of some intermediate hosts are impaired by the trematode, *Nanophyetus salmincola,* with a similar possible result (Butler & Millemann 1971). Changes are not always specific, however, and Brassard *et al.* (1982) found that *Diplostomum* increased guppy susceptibility to brook trout, which are not suitable hosts for the parasite. They speculated that such a risk may be part of the cost of lowering guppy activity levels and thus possibly enhancing general predation, including that from birds.

The examples I have reviewed here have covered a wide range of behavioral alterations – altered responses to environmental stimuli, neurological damage, and debilitation. Conspicuous intermediate host appearance is another way that predation risk may be increased (Holmes & Bethel 1972). Oetinger & Nickol (1982) have shown that there are differences in ommochrome fractions between uninfected *Asellus intermedius* and *A. intermedius* infected with *Acanthocephalus dirus.* These differences support the idea that the acanthocephalan may compete with the isopod for compounds used in ommochrome synthesis, thus resulting in pigment dystrophy. Brattey (1983) has recently reported that *Asellus aquaticus* exhibits darkened respiratory opercula when infected with *Acanthocephalus lucii.* In his laboratory studies, perch ate a disproportionately large number of infected *A. aquaticus.*

The evolutionary history of behavioral changes associated with parasitism is unclear. Holmes & Bethel (1972) considered alteration of host behavior to be a parasite strategy. Smith Trail (1980) hypothesized that under some conditions, behavioral changes could be a kin-selected host adaptation. Through suicidal behavior, the host individual could eliminate the parasite from the host population. Parasite transmission might later be favored by such suicide. Moore (1984a) argued that this was unlikely in the case of acanthocephalans. She noted that in at least one case, (*Polymorphus paradoxus* in *Gammarus lacustris;* Bethel & Holmes 1974) the behavioral switch does not occur until the acanthocephalan is infective for the final host, a trait that clearly benefits the parasite. In addition, many intermediate hosts that suffer altered behavior when infected with acanthocephalans are not thought to occur near their kin, and some of them are reproductively functional, thus increasing the cost of suicide considerably (see also Wilson 1977). Studying non-helminth parasites, Stamp (1981) found the behavior of gregarious caterpillars containing parasitoids to be inconsistent with the host suicide hypothesis. Horton (ms. in prep.) has explored the possibility of individual host defense mechanisms playing a role in the evolution and maintenance of altered behaviors found in a wide range of host-parasite associations.

The likelihood of parasite transmission may also affect social behavior. Freeland (1976) has suggested that primate social behavior, including aspects such as xenophobia, group size, infant handling, and sexual fidelity, may have been influenced by correlates of pathogen transmission. Current news sources speculate that human social behavior may be undergoing modification in response to risk of parasite acquisition.

Evidence for behavioral changes that are important in parasite transmission is abundant, especially among cases where predator-prey interactions are necessary for parasite life cycle completion. Less well known is the fact that changes in host behavior may also alter the role of the host as a consumer in community trophic interactions. Curtis (1985) showed that after the breeding season the carrion response of the snail, *Ilyanassa obsoleta,* was affected by a variety of trematode larvae. This was not thought to be related to transmission efficiency, as the snails were first intermediate hosts for the parasites, which will actively leave the snails in search of the next host. Compared to uninfected conspecifics, *Helisoma trivolvis* infected with *Echinostoma revolutum* is less attracted to food (Boland & Fried 1984), and exhibits reduced radular activity (Moore, unpubl.). Female grasshoppers infected with *Nosema locustae,* a protozoan, consume less food than conspecifics (Oma & Hewitt 1984). For general reviews of the physiological aspects of such host-parasite interactions, see Vinson and Iwantsch (1980), Thompson (1983), and Beckage (1985).

Host Distribution

Parasites can affect the distribution of their hosts on a variety of scales, both locally and globally, and not all of these involve parasite transmission probabilities or host foraging. Curtis & Hurd (1983) showed that trematode parasites were an important component of the local spatial heterogeneity exhibited by the snail, *Ilyanassa obsoleta.* Because of large spatial differences in prevalence of trematodes, there were spatial differences in *Ilyanassa* reproductive output. "Heavily infected snails are little more than 'sacks' of parasites with especially gonads, and sometimes digestive glands, virtually absent" (Curtis & Hurd 1983:823). Curtis & Hurd asked if such parasites can be keystone species in the sense of Paine (1969).

Parasites can clearly affect the distribution of their hosts on a global scale. The meningeal worm, *Parelaphostrongylus tenuis,* is benign in whitetail deer, but pathogenic for some other cervids (Karns 1967, Anderson 1972). Range expansion of whitetail deer has resulted in decreases in other cervid species. Barbehenn (1969) hypothesized that parasites may give a host a competitive advantage against other animals for which the parasite is more pathogenic (see also Cornell 1974). Freeland (1983) expanded upon this idea at the community level and suggested that the notable phylogenetic, morphological and ecological differences among coexisting animals that are often attributed to competition might result from the influence of parasites. Such differences could act as barriers to parasite transmission and thus allow coexistence.

There is certainly evidence that parasites can modify the effects of host species on one another (reviewed by Holmes 1979, 1982, Holmes & Price 1986), and Park's (1948) classic work on *Tribolium castaneum* and *T. confusum* showed clearly that parasites can reverse the outcome of competition between two species. Price *et al.* (1986) have recently reviewed the literature concerning ecological interactions that are mediated by parasites (broadly defined). They observed that the results of such "germ warfare" were unlike those of more direct interaction, in that the effects of parasites could be far greater than their cost to the original host and could be observed over large distances. They maintained that parasite-mediated ecological interactions are quite common, and cited numerous examples of such phenomena as endosymbiosis, asymmetrical effects on hosts (*e.g. P. tenuis*), protection against other parasites, diet selection that includes parasiticidal elements, and mediation of predator-prey interactions (*e.g.* acanthocephalans). They observed that when biotas are introduced, animals in one biota that have no apparent ecological equivalent (competitor) in the other may nonetheless go extinct. In many cases, this occurs in the smaller of the groups, and is consistent with the notion that more pathogenic organisms can be successfully propagated in larger groups. Thus, over evolutionary time, parasites may have been a selective force on many aspects of biology, from the molecular to the biogeographic level (Price *et al.* 1986).

Environmental Influences

The temperature at which the host lives can influence the likelihood of being parasitized. Most helminths have transmission stages that must survive and in some cases, develop outside a host. Clearly, ambient conditions would be of great importance to these life history stages. Sankurathri & Holmes (1976) reported that high temperatures associated with thermal effluents had a negative effect on two subspecies of *Chaetogaster limnaei,* an oligochaete associated with the gastropod *Physa gyrina.* These annelids were observed to eat larval stages of the trematode *Echinoparyphium recurvatum,* and a decrease in annelids coincided with an increase in *E. recurvatum* infection.

Temperatures external to the host can affect both the state of the parasite and its effect on the host, even where homeothermic hosts are concerned. Novak (1979) showed that the cestode *Mesocestoides corti* in mice exhibited greater biomass at colder temperatures. Also in mice, the cestode *Hymenolepis microstoma* was heavier, produced more eggs, and reached patency (egg production) sooner at colder temperatures (Evans & Novak 1983). This tapeworm also influenced the weight of the liver (as did temperature and, to some degree, host sex) and the weight of the bile duct (Evans *et al.* 1985; see also Novak *et al.* 1986 for effects of temperature and *Hymenolepis nana* infection on mouse small intestine). In a field study of habitat variables and parasitism, Pence & Windberg (1984) found extrinsic factors such as seasonality to be influential in populations of coyote parasites.

Holmes (1979) examined the effects that biotic influences on hosts might have on their parasites. He noted that not all hosts were of equal quality where a parasite was concerned and delineated the following three types of hosts: 1) *required* – the parasite is well-adapted to this host, which is necessary for its survival; 2) *suitable* – the parasite can mature in this host, but cannot maintain its population with this host alone; and 3) *unsuitable* – the parasite can establish, but cannot reproduce. Holmes (1979) observed that because parasites can often be exchanged among host, the host community composition should influence that of the parasites, and that such current ecological conditions might obscure historical host-parasite associations (Holmes 1983). (Other influential factors in his model included parasite fecundity, rate of establishment and maturation, life span, and host mortality). For instance, if a competitor of the definitive host were introduced, the suprapopulation of the parasite (all the parasites of that species in the host populations; Esch *et al.* 1975) would be expected to decrease. The infrapopulation levels might increase, however, if diet were restricted and more intermediate hosts were eaten. In another scenario, the introduction of alternate prey might serve to decrease infrapopulations if fewer intermediate hosts were eaten. This might not affect the suprapopulation if it allowed an increase in the definitive host population.

The introduction of a predator on the definitive host could decrease the parasite population in at least two ways: 1) transmission rates might decrease due to the combination of fewer definitive hosts and an increased number of individuals of the intermediate host species; and 2) if parasites exhibited a clumped distribution in the definitive host, along with an adverse effect on its ability to escape predators, predation on heavily-infected hosts could destroy a large proportion of parasites. In a similar vein, Pence *et al.* (1983) suggested that the "secondary community" of parasites within a host (those shared by other host species) might be more likely to be involved in parasitic outbreaks and epidemics than the "primary community" in that host, in part because members of the secondary community did not depend on that specific host for survival. Clearly, external conditions – both biotic and abiotic – and their effect on trophic interactions can influence parasites tucked away and unseen within their hosts.

Reproductive Alterations

The castration of a host by its parasite is one of the more dramatic ecological effects that parasites can have and its impact has been considered in the contexts of individual evolutionary strategy (*e.g.* Baudoin 1975, Sousa 1983, Minchella 1985) and population influences (*e.g.* Obrebski 1975). Kuris (1974) considered the trophic role of a parasitic castrator and stated it was similar to that of a parasitoid, among other things, "killing" one host per parasite. Baudoin (1975) noted that parasitic castration could enhance parasite fitness through the increase in host growth and survivorship that resulted from reduced reproductive effort. In addition, parasitic castration has a variety of effects other than reduced reproduction. These can include alterations in internal chemistry, secondary sexual characteristics, internal organs, and sexual/parental behavior. Baudoin (1975) noted that castrated hosts often grew more than noncastrated conspecifics.

Sousa (1983) studied the interactions of several trematode species with the marine prosobranch *Cerithidea californica* in the field. He discovered that these infections did not necessarily result in gigantism, but that their effect on growth was related to the age of the snail, with enhanced growth most readily observed in sexually mature snails. He hypothesized that among such snails, life history attributes could affect the occurrence of gigantism in trematode-snail associations. In the case of short-lived gastropods (predominantly freshwater), reproduction is an energy-intensive activity and the elimination of that activity by parasitic castration may liberate many resources for enhanced growth. Iteroparous, long-lived snails (usually marine) may have a smaller proportion of their energy budget devoted to reproduction. Elimination of the gonads in these animals, as well as in sexually immature snails, liberates less energy and may not result in notably increased growth. Sousa emphasized the diversity in snail-trematode interactions and qualified his model with the observation that no single model was likely to describe all such interactions. Working with a bivalve, *Transennella tantilla,* Kabat (1986) also concluded that distribution of reproductive activity over time could influence the outcome of trematode-mollusc interactions. Castration was not complete in these animals, which are sequential brooders (*i.e.*, not all brooded offspring are at the same developmental state). Kabat speculated that total castration may be more likely for a synchronous brooder, perhaps because of a threshold in the energy required.

Minchella (1985) discussed possible molluscan responses to parasitism and asked why resistance to infection was not more common. Minchella & Lo Verde (1983) determined that in the presence of susceptible snails *and* schistosome miracidia (the infective stage), resistant snails exhibited lower reproductive success. Minchella (1985) then noted that the evolution of resistance depended not only on the presence of appropriate genotypes, the effect of the parasite and the probability of encountering it, but also on the cost of resistance as compared to those factors. Other responses are available to molluscs, and these include fecundity compensation (early reproduction prior to castration) and gigantism, which he expected to encounter as a host adaptation primarily in long-lived snails with some possibility of outliving the infection.

Population Effects

In a series of papers, Anderson and May have explored host-parasite interactions at the population level (Anderson & May 1978, 1979, May & Anderson 1978, 1979, May 1983, 1985a). (The reader is urged to consult these papers for detail). In their models, Anderson and May assumed that host mortality rates increase with parasite levels. Using this and other assumptions about transmission rates and effects of parasite density and distribution, they emphasized the importance of threshold host densities (for parasite persistence), host mortality rates, and, in the case of macroparasites, parasite reproductive rates in the regulation of host populations. (Unlike those of microparasites, the propagules of macroparasites do not remain within the host). They found at least three stabilizing influences in host-parasite relationships. First, some types of functional relationships between parasite-induced death and parasite burden are stabilizing; others are not. Second, this relationship is linear and if parasites are clumped in distribution, they may regulate host population growth. Finally, density-dependent constraints on parasite populations acting within the host can have a stabilizing influence. May and Anderson also discovered destabilizing influences, which included a negative effect of parasites on host reproduction, temporal lags between transmission and reproduction of parasites, and within-host parasite reproduction that enhances parasite population size.

Anderson and May listed at least four factors that influence disease patterns: 1) the host as parasite habitat, 2) host mortality, 3) immunity, and 4) transmission. They noted that because of changes in virulence, the ability of a parasite to regulate the population of its host may vary over time. Cyclic variation in prevalence itself can result from stochastic fluctuations in prevalence or temporal variation in transmission.

May & Anderson (1978) indicated that the results of these models may be useful for public health consideration of chemotherapy. They further explored the role of immunity in host populations (Anderson & May 1985a), mathematically modelling helminth population dynamics in a host population whose individuals are heterogeneous in their ability to acquire immunity. (See Wassom *et al.* 1974 and Arnason *et al.* 1986 for other considerations of host heterogeneity in susceptibility). In such a case, mass chemotherapy may result in an increased average worm burden. They suggested selective treatment for individuals that are predisposed to heavy infection (but see Cheever 1986, Anderson *et al.* 1986). Schad & Anderson (1985) presented evidence that in the case of hookworms in humans, which occur in clumped distributions, pre- and post-treatment hookworm levels were significantly associated, suggesting that targeted treatment might be efficacious. Host genetics has also been shown to be important in the distribution of cestodes in the white-footed deer mouse (Wassom *et al.* 1974, 1986).

In a review of population models of human-parasite interactions, Anderson & May (1985b) and May (1985b) listed areas of research that are important for future progress. These include basic aspects of helminth demography (reproduction, longevity), the influences of host age and parasite density, and the origin and implications of aggregated distributions.

Holmes (1982) agreed that parasites do injure and kill their hosts. He indicated that additive mortality (above that experienced by a parasite-free host population) was likely in invertebrate host-parasite associations and in the case of some introduced species associated with native faunal extinctions, but he questioned whether the effects of parasites were additive for vertebrate host populations (but see Toft 1986). If disease, similar to some forms of predation, primarily strikes low-status, "surplus" animals, then ensuing mortality is compensatory – it replaces other risks – and is not additive. In such a case, parasites might act as agents of selection but fail to exert a regulatory influence. Holmes (1982) agreed with Anderson and May on many points, but argued that parasites, in many instances, were probably a source of compensatory mortality, not additive mortality, and stressed the need for more field studies. Getz & Pickering (1983) also urged increased study of individual host-parasite associations.

Recent field work on parasite-induced mortality has supported this call for knowledge of specific systems. For instance, Uznanski & Nickol (1980) observed no effect of the acanthocephalan, *Leptorhynchoides thecatus,* on the growth, reproduction or survivorship of its amphipod intermediate host. (They did not examine behavioral effects or predation risk). Keith *et al.* (1985) found no consistent, single relationship between the prevalence of a variety of parasites of snowshoe hares and the cyclicity of the host population. They felt that their indicator (prevalence – *i.e.*, presence/absence) might be too coarse and that parasite species might differ in the combinations of factors that could influence population size. Keith *et al.* (1986) did find intensities of some parasites related to decreased body weight, and intensity of *Obeliscoides cuniculi* was positively associated with likelihood of death from trapping, handling or predation. Granath & Esch (1983) determined that mosquitofish mortality from *Bothriocephalus* was influenced by several factors, including temperature-dependent growth and size. In a study that clearly showed the importance of multiple influences on parasite-host relationships, Lemly & Esch (1984) found that heavily infected juvenile bluegill sunfish died as a result of the interaction of decreasing temperatures (with associated decreasing feeding) and of lipid depletion associated with trematode larvae. If temperatures remained high, bluegill continued to feed and replaced lipids. McPhail & Peacock (1983) observed that seasonal differences in prevalence can affect the impact of the parasite on the host population. In their cestode (*Schistocephalus solidus*) – stickleback system, cestode larva prevalence was highest after the fish reproductive season. They noted that this could be a result of selection or simply coincidental with other factors in the pond.

In considering the regulation of parasite populations, Holmes *et al.* (1977) stated that there were two prerequisites for population regulation: 1) reproductive activity must have the potential to increase population size, and 2) a feedback mechanism that prevents such increase must exist. They cited Bradley (1972, 1974) in emphasizing transmission and immunity as important limits to parasite population growth. To this they added the influence of parasite-parasite competition. In a modelling/simulation exercise, they showed that a parasite suprapopulation might be regulated by the occurrence of competitive interactions in only one host species, provided the other species were inadequate to maintain the parasite population.

As has been recognized, the host may influence infrapopulation size by a complete or partial immune response. Parasitologists have discovered even more subtle and unexpected host influences on parasite levels. Possibly related to host immunity is the phenomenon of arrested development, a condition seen in some nematodes that temporarily cease development within the host until some future time. Schad (1977) reviewed this literature, and while he noted that arrested development might be controlled by host resistance or be a parasite response to adverse conditions, he emphasized its role in parasite population regulation.

In the case of mammals, populations of parasites may also appear where they're least expected – in neonates – as a result of transmammary transmission from infected mothers. Stone & Smith (1973) reviewed this literature, which deals primarily with nematodes. Recently, cestodes (*Mesocestoides corti;* Conn & Etges 1983) and trematodes (*Alaria marcianae;* Shoop & Corkum 1983) have also been shown to enter new hosts in this manner (see also Miller 1981). Transplacental transmission is also known to occur in some species (*e.g.*, Hibler *et al.* 1972, Todd & Howland 1983).

Host diet can influence levels of parasites that are transmitted in the food chain (Price & Clancy 1983). Campbell *et al.* (1980) documented relationships between the foraging habits of some deep sea fish species and their parasite fauna. They also noted that differences in host habitat and age-related dietary shifts influenced this fauna, as did host community diversity. In a study of flatfish, Scott (1982) noted the roles of host diet, age, sex, and geographic distribution in parasite community composition. Amin (1985) found that the numbers of the acanthocephalan *Echinorhynchus salmonis* in hosts increased with host age while other acanthocephalans decreased, a trend he attributed, in part, to host diet. [See also George-Nascimento & Vergara (1982) for Southern hemisphere corroboration of host dietary influence on levels of the nematode *Proleptus acutus*].

Recently, Kennedy *et al.* (1986) have compared intestinal helminth communities in fish and birds (plus one mammal). They found the ectotherms to be relatively depauperate in both richness and abundance, and concluded that a variety of factors contribute to helminth community diversity. While these factors certainly include breadth of host diet, as well as inclusion of intermediate host species in that diet, they also encompass the diversity of habitats visited by the host and the exposure to penetration by parasites that enter through non-dietary means. The increased energy requirements and intestinal differentiation of endotherms are yet other factors that may favor rich communities.

Coevolution

The evolution of virulence/avirulence is an active area of research emerging from evolutionary theory that is closely related to the work described in the previous section. This is in part because virulence and parasite reproductive rate are used synonymously, a habit that may give a parasitologist pause, for the effect that a parasite has on its host is often determined by factors far more numerous and complex than the number of offspring it produces. The reasoning behind the equation of these two terms is nonetheless logical: In the case of two parasites that share nearly identical biology and host-parasite attributes, the one that produces more offspring will probably demand more host resources. [See Bremermann & Pickering (1983) for a more complex definition of virulence that includes parasite reproduction, infectiousness, and disease severity]. At any rate, the traditional view that well-adapted, coevolved host-parasite relationships tend to be benign has little factual or theoretical basis.

Holmes (1983:178) asked, "Because the net reproductive rate of the parasite is a function of both its reproduction per unit time and its length of life, under what circumstances should a parasite be selected to emphasize the former?". He suggested that increased reproductive rate would be favored by factors such as the presence of a large, expanding population of susceptible hosts, life cycle attributes that include host death as a necessary part of transmission, and short-lived hosts. Holmes (1983) discussed the following three models of host-parasite coevolution: 1) The mutual aggression model, in which the parasite increases exploitation and the host increases defense; 2) the prudent parasite model, in which parasites are favored that limit damage to the host; and 3) the incipient mutualism model, in which both parasite and host are selected to benefit one another.

Anderson & May (1982) reviewed the host-parasite coevolution and pathogenicity literature that has been based on population genetics models and epidemiological models. They cautioned that many coevolutionary outcomes are possible, given a variety of relationships between virulence and transmission. May & Anderson (1983) concluded that polymorphisms probably result from the coevolution of hosts with a wide variety of parasites and that "well-balanced" associations are not necessarily avirulent. Levin & Pimentel (1981) theorized that a combination of intra- and interdemic selection pressures to increase and decrease virulence, respectively, could yield intermediate levels of pathogenicity. (see also Lewontin 1970). Bremermann & Pickering (1983) showed that within-host competition among parasites could affect the evolution of virulence.

In specific studies of the evolution of virulence, protozoa have received more attention than have helminths. Ewald (1983) predicted that vector-transmitted pathogens should be more severe, for the transmission cost involved in immobilizing the host is reduced. He tested this and some related predictions using a correlative, comparative approach, and concluded that vector-borne diseases are more severe than those without vectors. According to Ewald, the implications of this for public health include the following predictions: 1) severity can be expected from currently pathogenic vector-transmitted diseases and new benign vector-transmitted diseases, and 2) diseases of recent origin that do not depend on vectors should tend towards avirulence.

Gill & Mock (1985) studied the trypanosomes of the newt, *Notophthalmus viridescens,* in an attempt to discover if hosts and parasites could mutually regulate their populations and if there were evidence for decreased virulence. They reviewed the literature in this area and noted that if there were a period in a host's life during which transmission could not occur, parasite avirulence would be favored by natural selection during this time. In the eft stage of newt development, trypanosome prevalence is low and trypanosomes cannot be transmitted until the newt reenters the pond some years later. They surmised that the trypanosomes allowing the eft to live until this time would be favored by natural selection, and that the trypanosome population of a pond would then be influenced by these entering, avirulent protozoans. Gill and Mock predicted increases in virulence as ponds age. They outlined three general models of pathogen evolution: 1) increasing pathogenicity in the presence of simultaneous infection by alternative genotypes, 2) interdemal selection that incorporates transmission difficulties associated with host death, and 3) avirulence favored by lack of transmission opportunities.

Hamilton (1980) and Rice (1983) have hypothesized that sexual reproduction may be favored by short-lived, rapidly-evolving parasites. Hamilton observed that frequency-dependent selection mediated by parasites would be most severe against the most common genotype, and that in the presence of increasingly intense selection and moderate fecundity, sexually reproducing animals are at an advantage. Rice noted that a genetically divergent offspring might escape the pathogens accumulated by its parents.

Hamilton & Zuk (1982) extended the role of parasites to that of an influence in sexual selection. In their model, the host and the parasite population each have two alternative genotypes (*H, h* and *P, p*). *H* confers resistance to *p,* susceptibility to *P,* and *h* does the opposite, producing a stable limit cycle. Hamilton and Zuk proposed to evaluate resistance *via* plumage and fur quality, the appearance of bare skin patches, and courtship behavior involving energy expenditure or urinary marking. They stated that their hypothesis – that animals exhibiting well developed epigamic traits should be subject to a wide variety of parasites – would be refuted if, within a species, preferred mates had the most parasites, and would be supported if, among species, those that exhibit the greatest evidence of sexual selection are those especially subject to parasitism. A comparison of the occurrence of six blood parasites and three passerine courtship displays revealed significant associations that are consistent with the Hamilton and Zuk model. "For the present we conclude that eugenic sexual selection can work and may be common, and that our results hint at chronic disease as one agitator of the dynamic polymorphism that such selection requires". (Hamilton & Zuk 1982:386).

In a simulation study addressing this hypothesis, Kirkpatrick (1986) found that the alleles for male secondary sexual traits and female preference for these traits will not necessarily spread if they are rare. If female preference for male traits is common enough, however, then a "runaway" process is possible. [See Kirkpatrick (1986) for further discussion].

Hosts have been shown to exert a selective influence on their parasites, as well. After 16 generations of *Hymenolepis citelli* in *Tribolium confusum,* Schom *et al.* (1981) found reduced infectivity of the parasite. This corresponded with reduced host mortality. LoVerde *et al.* (1985) found that the allelic frequencies of a strain of *Schistosoma mansoni* formerly kept in baboons and passed for four generations through mice became similar to frequencies found in a strain that had inhabited mice for twelve years.

Brooks (Brooks *et al.* 1981, Brooks & Glen 1982, Mitter & Brooks 1983, Brooks *et al.* 1985, Glen & Brooks 1986) has approached the study of coevolution from the standpoint of phylogenetic systematics. Brooks (1979) identified two processes that might commonly be considered coevolution: *co-accomodation* without speciation, and *co-speciation* with concomitant host-parasite speciation. In the papers cited above, Brooks and various coworkers have used phylogenetic analyses of parasites and their hosts to investigate such divergent topics as biogeography and speciation of freshwater stingrays and their parasites, competing hypotheses of hominoid phylogeny, and the importance of adaptive radiation *versus* developmental constraint in digenean trematodes. Such approaches may also be informative in the study of communities, as we shall see in subsequent sections.

PARASITE COMMUNITIES

Because no parasite community exists independently of the host it occupies, parasite community interactions have a host component. The work I review below, therefore, is not meant to be cast as independent of host biology, but it does emphasize the role of other parasites in parasite ecology. Conversely, the nature of a parasite community may influence the host: A diverse community may exert a protective influence against the effects of a heavy monospecific infection (Holmes 1979, 1983).

Infrapopulations

Parasites can affect one another's reproductive success in a density-dependent way, a phenomenon long observed in cestodes and studied in detail by Read (*e.g.*, 1951, 1959) and Roberts (*e.g.*, 1961, 1966). [See also Nollen (1983) and Fried & Freeborne (1984) for recent work on crowding in the trematode *Philophthalmus gralli*]. Lejambre *et al.* (1971) showed that fecal nematode egg output was correlated more closely with total worm weight than number Recently, Insler & Roberts (1980), Roberts & Insler (1982), and Zavras & Roberts (1984, 1985) have performed a series of experiments in an attempt to isolate factors that could contribute to stunted growth in crowded cestodes (*Hymenolepis diminuta*). Zavras & Roberts (1985) concluded that among other influences (*e.g.*, pH, carbohydrate availability), substances such as succinate, acetate, D-glucosaminic acid and cGMP that are released by parasites may contribute to the crowding effect by reducing the growth rates of other worms.

Taxa of parasites may differ in the extent to which they can exhibit responses to the environment in terms of body size and reproductive success. Dobson (1986) found that both nutrition and parasite density contributed to variation in body size and reproduction, and that cestodes and acanthocephalans differed in their responses to changes in carbohydrate level, perhaps because of differences in degree of flexibility possible in their body plans. He emphasized that natural selection acts on such individual variation.

Resource use is an important aspect of all community studies and in the case of parasites, location in the host is commonly used as an indicator of resource use. Within hosts, intestines can be viewed as resource gradients and the distributions of many environmental factors therein are highly correlated (Read 1971). Location is therefore an important indicator of resource use and bears discussion here prior to examination of parasite community interactions. Holmes' (1973) extensive review of helminth site selection focussed on this aspect of parasite communities.

One influence on location is mate-finding. Bone (1982a, b) has reviewed much of the literature dealing with pheromones of Platyhelminthes, Nematoda and Acanthocephala. Most Platyhelminthes are monoecious, but outcrossing appears to be common and in some species, single-worm infections may not mature readily. Mate-location mechanisms are common among trematodes, and are especially important for schistosomes, which are dioecious. Such mechanisms are not always flawless, and Fried & Wilson (1981) have shown that interspecific pairing between the trematodes *Zygocotyle lunata* and *Echinostoma revolutum* occurs at frequencies comparable to those of intraspecific pairing in the two species. Bone (1982a) speculated that chemical releasers for this behavior may not be specific and other factors may contribute to reproductive isolation. Much less is known about reproductive behavior of cestodes. In the case of nematodes (dioecious), five zooparasitic species have been studied, with most attention devoted to *Nippostrongylus brasiliensis* and *Trichinella spiralis*. Male response to chemical attractants in these species is stronger than that of females. In the case of *Moniliformis dubius* (Acanthocephala), chemical recognition may be important for determining both species and sex of potential mates (Bone 1982b). In the latter instance, males place copulatory caps on both females and other males, but inseminate only females, a behavior which may be a product of sexual selection. Capped males are unable to reproduce (Abele & Gilchrist 1977).

In addition to modifying location in response to sexual cues, parasites select locations based on physicochemical cues. Initially, workers did not consider parasite mobility within the host small intestine, but Read & Kilejian (1969) demonstrated circadian migratory activity modified by host feeding schedule in the cestode *H. diminuta.* Such movements have both ontogenetic and circadian components (Cannon & Mettrick 1970). Arai (1980) has reviewed more recent work on migration in this worm and its relatives. Sukhdeo & Mettrick (1984) noted that major gradients were those of food and gastric, pancreatic and biliary secretions. They altered the location of these substances through ligation or surgery. They concluded that these cues were interactive and none was of singular importance. Moreover, the scolex of the worm was not always sensitive to the same substances that influence the rest of the biomass.

Site selection of nematodes has also been investigated. Sukhdeo & Croll (1981a) determined that bile was important for both establishment and location of *Nematospiroides dubius.* In the case of *Heligmosomoides polygyrus,* bile influenced larval site selection, but adult location was more sensitive to stomach content entry sites (Sukhdeo & Mettrick 1983). Sukhdeo & Croll (1981b) found that although surgically implanted *T. spiralis* larvae could establish anywhere in the small intestine, the location of orally transmitted worms was influenced by intestinal motility, inoculum size, and size of the delivery apparatus.

Multiple Species

The community ecology of parasitic helminths is a field with much controversy, most of it centering on the role of competition. Holmes (1973) reviewed research on parasitic communities within hosts, and noted that competitive exclusion was apparently common and that "interactive site segregation" (spatial niche shift in the presence of possible competitors) was relatively rare; "selective site segregation" (non-overlapping niches) was observed more commonly and Holmes viewed this as an indication of the general maturity of helminth communities. Holmes (1973) hypothesized that interactive site segregation characterized more recent community associations and that when parasites are long-lived and commonly coexist, it is replaced by genetically based selective segregation (see also Bush & Holmes 1983). Price objected to the contention that parasite communities are mature, claiming that parasites generally form nonequilibrial communities. Positive association among parasites has also been observed (Holmes 1973, Hobbs 1980, Lotz & Font 1985).

Some workers have emphasized aspects of helminth communities other than competition. In a review primarily of monogenetic trematodes, Rohde (1979) observed that selective niche restriction could result from intraspecific selection (*e.g.,* mate location). Brooks (1980a, b, 1985) emphasized the role of phylogeny in structuring parasite communities. Holmes & Price (1980) did not deny this role, but did object to Brooks' assignment of major importance to it. Toft (1986) has hypothesized that competition should be relatively less important for parasites than for predators.

Recently, Holmes (1986a) has cast this controversy in a different perspective, asking *not* "Do interactions among helminths structure communities of intestinal helminths?" but "Under what conditions do interactions become particularly important in structuring such communities?". Holmes & Price (1986) have enlarged upon these remarks explicitly considering the assumptions that underlie a range of hypotheses about parasite communities and the predictions that emerge from those hypotheses. They view parasite-parasite interactions in at least three ways – at the level of the infracommunity (within host individual), the component community (within host population or species), and the compound community (within host community, especially over several habitats). The elements of this hierarchy are interdependent. For instance, Holmes (1986b) noted that interactions within hosts are important in terms of predictable community structure and possible coevolution only when the species involved regularly co-occur. Although interactions occur in the infracommunity, the degree of co-occurrence must be measured at the component and compound community levels. Concepts diminishing the importance of infracommunity interactions are usually characterized by assumptions that minimize co-occurrence, and Holmes suggested that structure might be more readily observed if dominant species groups or guilds were the object of greatest attention. I will review infracommunity and component community work here, but studies of compound communities are beyond the scope of this paper. At the compound level, species specificity (Pence & Eason 1980) and relative numbers of hosts (Leong & Holmes 1981) contribute to community composition. See Holmes & Price (1986) for further discussion.

Infracommunity

It is at this level that individual parasites interact. Individuals of a species of host can be considered replicate communities, and one can examine presence/absence data, intensity, growth, maturation, fecundity and location (both shifts and differences in dispersion) as indicators of interactions. Such interactions can even appear in low diversity communities, provided species use similar resources. Holmes (1986b) found Hanski's (1982) concepts of core species (those occuring at high densities in most patches) and satellite species (low densities, few patches) to be useful in studying replicate communities (see Bush & Holmes 1986a). He cautioned against summing across communities for evidence of within-host interaction and noted that the positive association often observed between core species could result from similar exposure of the host to associated parasite groups, similar aspects of host quality for the groups, or mutualism.

In a thorough and thoughtful review, Holmes & Price (1986) delineated three hypotheses relevant to the study of infracommunities. The *competition hypothesis* states that competition has been and continues to be an important organizing force in parasite communities. The *population concentration hypothesis* emphasizes that niche restriction might be necessary for successful mate location. The *individualistic response hypothesis* states that coevolutionary processes and increasing specialization on the part of parasites can result in adaptation to narrow niches that is independent of other parasite species.

Holmes & Price (1986) observed that the competition hypothesis was compatible with what they called *interactive* communities, characterized by species that readily colonized the host, resulting in high populations of animals that commonly co-ocurred. These are equilibrial, saturated communities. *Isolationist* communities, unsaturated and nonequilibrial, characterized by low probabilities of colonization and co-occurrence and by low population levels, are appropriately aligned with the remaining two hypotheses. Interactive and isolationist communities can be seen as the extremes of a continuum along which parasite communities occur. [I urge the reader to consult Holmes & Price (1986) for greater detail about this and other levels of parasite communities].

The most detailed recent work on infracommunities includes that of Bush & Holmes (1986b) and Lotz & Font (1985). Bush and Holmes studied a complex, diverse community of intestinal helminths of lesser scaup. They found all parts of the small intestine occupied by the 29 species that made up 99% of the parasite individuals. In an association analysis (Bush & Holmes 1986a), they were able to identify core and secondary species, and in their study of infracommunities (Bush & Holmes 1986b), they found that in individual birds, each of these species occupied only a small portion of its potential range. This result, along with the shortage of vacant niches and the evenly dispersed locations and ranges of helminths, led Bush and Holmes to conclude that these communities were interactive. Differences in radial distribution were also observed (see also Schad 1963), and three guilds were identified: small, paramucosal absorbers (cestodes and acanthocephalans), larger mid-lumenal absorbers, and active ingesters (trematodes). In these communities, the core species were the most abundant and exhibited the earliest and fastest colonization. Most of the core species specialized on scaup. They were in the absorber guilds and used one of two commonly consumed intermediate hosts, resulting in high levels of co-occurrence. The secondary species occupied spaces left open by core species. They were moderately abundant and exhibited moderate colonization rates. Satellite (rare) species arrived later and were essentially random in location.

Detailed analyses of infracommunity structure may well be necessary for understanding helminth community structure. Bush & Holmes (1986b) noticed that Holmes and associates, in earlier studies of the same host-parasite system on a coarser scale, had failed to find evidence for interactive segregation.

In a detailed study that compared parasite communities (largely trematodes) in two host populations, Lotz & Font (1985) found little evidence for parasite-parasite interaction. They used different analytical methods from those of Bush & Holmes (1986a, b) and their communities did not contain as many parasites. They concluded that the host immune response kept parasites at population levels below those at which competition might occur. Referring to some related parasites of European bats, Lotz and Font speculated that some within-host distributional characteristics of at least one species were perhaps of historical origin in that they were shared by a European congener.

Positive associations among parasites have been observed (*e.g.*, Hobbs 1980, Lotz & Font 1985). The mechanisms that support these are often not clear, and possibilities range from mutualistic interactions (*e.g.*, Ewing *et al.* 1982) to similar habitat requirements (Hobbs 1980) or use of the same intermediate host (Bush & Holmes 1986a, b). In fact, precise mechanisms of parasite-parasite interactions, whether positive or negative, are often unknown. The influence of the host immune system can act in either direction and is a feature unique to parasite communities. Holmes (1983) reviewed examples of the immune system enhancing (immunosuppression) or depressing (*e.g.*, cross-immunity, Schad 1966) parasite-parasite co-occurrence. Bristol *et al.* (1983, and references therein) describe such interactions between vastly different taxa (nematodes and protozoa).

Dobson (1985) recently considered the relationship of competition and parasite population dynamics, emphasizing the importance of parasites' distributions among hosts, together with pathogenicity, as an influence on continued coexistence. He noted that as aggregation intensified, intraspecific interactions would become increasingly important relative to interspecific interactions and that the pattern of parasite distribution among hosts may be at least as important as resource use in parasite communities. Such an approach involves not only scrutiny of the infracommunity, but also consideration of component and compound communities.

Component Communities

Students of component communities are concerned with community interactions at the host species level. Holmes & Price (1986) identified four hypotheses that have been put forward to account for patterns at this level. The *cospeciation* hypothesis was formulated by Brooks (1980a, b) and is based on the idea that parasite communities cospeciate with the host group and reflect historical events. The *island size hypothesis* is rooted in the MacArthur & Wilson (1967) theory of island biogeography and predicts that larger islands should have more species of parasites. (There is, however, some confusion about what "island size" should be – host range? host population size?). The *island distance* hypothesis, also emerged from the theory of island biogeography, holds the likelihood of reaching a host as a major influence on parasite communities. Finally, the *time hypothesis* states that increasing species number requires time, and older communities will have more parasite species.

Holmes & Price (1986) noted that as formulated by Brooks (1980a), the cospeciation hypothesis is largely independent of ecological interactions. The island biogeographic hypotheses yield predictions about species number, not about more subtle interactions. Nonetheless, in young communities characterized by larger island distances, isolationist traits might be expected. Holmes & Price (1986) also noted that one implication of the cospeciation hypothesis is that no island/host species is ever empty, a problem for the time hypothesis.

In fact, the use of hosts as islands has engendered a lively debate in the ecological literature. Students of herbivorous insect communities have explored this concept most widely. Freeland's (1979) study of primate social groups as islands is one of the more notable endoparasite studies using this approach. He found that number of protozoan species was related to *Cercocebus albigena* group size, that entry of nonmembers into *Cercopithecus mitis* groups increased protozoan species richness, but that all groups of *Papio anubis* had equivalent protozoan fauna. This last species, living in the savannah, had a higher rate of intergroup exchange than forest-dwelling primates. Freeland speculated that disease-related selection on such social behavior may vary across habitats. [See Betterton (1979) for a consideration of mainland *versus* island effects on species richness].

Kuris *et al.* (1980) objected to the use of hosts as islands. They reviewed the literature on that topic and delineated three ways of approaching host-islands: individual hosts, host populations, and host species. At each of these levels, hosts differ from true islands. Thus, unlike islands, individual hosts may defend against colonist parasites, which in turn may threaten the existence of the host. Interisland distance may fluctuate and there may be seasonal and ontogenetic differences in host quality. The host itself may be short-lived, and its parasite community may not reach equilibrium. At the level of host populations, Kuris and coworkers criticized the use of agricultural systems as islands, and noted that features such as host density, range, variation, dispersion, and overlap with other host species can all affect the application of island biogeographic theory to host-parasite systems. At the level of the host species, they stressed that coevolved characteristics could substantially influence the fit of island biogeographic theory to these systems. Other workers (*e.g.*, Lawton *et al.* 1981, Rey *et al.* 1981) rose to the defense of the application of island biogeographic theory to host-parasite systems, and the disparate views have yet to converge.

In general, nothing but an island is truly an island. All other sorts of disjunct habitats are simply analogous to islands and share some, but not all, of their attributes. If the extension of island biogeographic theory to these analogous situations is to be pursued in a reasonable manner, then the analogy must be formulated in a way that makes good biological sense for the specific communities in question. Some hosts are long-lived enough to acquire what appears to be a full complement of parasites; others are not. In the case of some types of parasite transmission, island distance and its analogues are much more meaningful than for other transmission modes. The objections of Kuris *et al.* (1980) should be studied and kept in mind in the attempt to combine productive questions with tractable systems.

Price & Clancy (1983) studied checklists of the parasitic helminth fauna of British freshwater fishes, questioning how diet and area of host range were related to parasite species number. They found that host range accounted for most of the variation (68%) in number of parasite species. Host length was a significant influence only in the cases of acanthocephalans and nematodes. For all parasites but the Monogenea, which are not transmitted through feeding, the feeding class of the host accounted for a significant amount of variation in parasite species number. (Feeding class was taken to mean major class of food – invertebrates, plants, fish, et cetera. Thus, both biogeographic and dietary factors were shown to affect species richness.

The cospeciation hypothesis has been directly addressed by Brooks (1980a, b, 1985, Brooks & Wiley 1986 and Holmes & Price (1980). Holmes (1971) published a study of two blood flukes of rockfish that occupied different sites in the fish's heart, a difference he found to be intensified in concurrent infections. Holmes (1973:341) said, "...niche segregation between the two appears to be basically genetically entrained, but reinforced by interactive site segregation". Brooks (1980a, b) noted that while Holmes (1973), Rohde (1979) and Price (1980), came to different conclusions about historical influences on current parasite communities, none had considered the role of parasite-host coevolution and phylogeny in the structure of these communities. Citing the rockfish (Holmes 1971) example specifically, he developed phylogenetic models that could account for these observations without involving the historical influences of colonization, competition or sexual selection, respectively.

Holmes & Price (1980) agreed that phylogenetic considerations would illuminate ecological studies, but concluded that an evolutionary study of the blood flukes of rockfish (*e.g.*, Holmes 1971) showed that one species had entered as a relatively recent colonist, and that this system had not experienced lengthy coevolution. They argued that the abundance of parasite species with little host specificity generally indicated a large potential for host shifts and colonization, and that Brooks' arguments were limited to lengthy, coevolved host-parasite associations. They speculated that while entire communities had probably not coevolved, perhaps subunits had, and they developed criteria for distinguishing between non-interactive and saturated communities.

Mitter & Brooks (1983) addressed the phylogenetic techniques useful in studying coevolved communities, using specific examples such as primate pinworms, lower vertebrates and their trematodes, termites and termitophilous beetles and some phytophagous insects and their host plants. They emphasized differences in patterns produced by colonization *versus* association by descent. Brooks (1985) and Brooks & Wiley (1986) have continued to explore aspects of historical ecology. Brooks (1985) disagreed with the phylogeny produced by Holmes & Price (1980), and in his analysis, found host and parasite cladograms to be congruent. He concluded that the rockfish trematode community described by Holmes (1971) was historically determined. Brooks & Wiley (1986) urged the testing of competition hypotheses against historical models.

CONCLUDING REMARKS

In a narrow sense, parasites influence and participate in trophic interactions when they alter the encounter rates between predators and their prey or host feeding patterns. Beyond such alterations, they can affect the abundance and distribution of their hosts through effects on host reproduction, direct pathogenicity, or mediation of interactions between free-living organisms. [As Holmes and Price (1986) observed, parasites both respond to and engender patchy biotic environments]. Because many parasites are transmitted through host diets, they can be indicators of host foraging habits. Hosts, by their dietary preferences, can influence parasite community characteristics. Although parasites are often considered a trophic level, they are diverse in their nutritional requirements. The parasite interactions that may result from such requirements in a limited environment can, along with other factors, influence the array of parasites available to a host or host community and, by extension, the ecology of the host (s).

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