Regulation of Parasite Populations

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ACADEMIC PRESS, INC. New York London San Francisco 1977

A Subsidiary of Harcourt Brace Jovanovich, Publishers

Parasitism and r- and K-selection

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INTRODUCTION

The relationship between an organism and its environment can be studied in a number of ways. But for the most part, since suggested by Elton in 1927, the essence of ecology has been the examination of the distribution and abundance of plants and animals in nature. Such an approach can be made at the individual, population and ecosystem levels of biological organization.

While the accent in parasitology has largely been at the individual level and, hence, an emphasis on physiology and immunology, in recent times there has been an increasing interest in studying parasitism at the population and ecosystem levels. Andrewartha (1970) has said that the aim of population ecology is to explain the numbers of plants or animals which can be counted or estimated in natural populations. In seeking an explanation for the numbers of individual organisms, parasitic or otherwise, there are at least two problems which must be resolved. First, the numbers of organisms which may be present at a given point in time must be counted, or estimated, accurately. And second, the fundamental nature of change in numbers should be perceived, analyzed and related, if possible, to biotic and abiotic variables. In other words, changes in density in a temporal sense must be ascertained and then, an effort must be made to identify the factors which regulate or control the density changes. Obviously, there are a number of highly complex, contributing variables, but in many instances, these have been more than adequately defined and the result has been the formulation of meaningful interpretations, applicable to the regulation of population dynamics.

Many of the difficulties inherent in understanding the regulation of free-living populations are also critical in the consideration of parasite populations. However, the very nature of parasitism inexorably adds a diversity of problems unique to parasitic organisms and thus makes an understanding of regulatory phenomena even more difficult. Most significant among these problems is that the immediate environment of the parasite is alive and thus, potentially, is capable of responding in a negative manner such that further recruitment and establishment may be restricted. Conversely, other parasites are able, under certain circumstances, to induce host mortality, thereby eliminating their environment and preventing further recruitment. It should be clear, therefore, that the complexity of host-parasite interactions may pose very serious obstacles for understanding the nature of regulatory phenomena associated with parasite populations.

Prior to considering the host-parasite relationship and the regulation of parasite populations, a problem of immediate concern is to precisely define what it is that constitutes a parasite population. The definition is of importance since, if regulation is to be understood, suitable operational terminology must be employed. For example, it would generally be acceptable to define a population of free-living plants or animals as a group of organisms of the same species occupying a given space. As pointed out by Esch, Gibbons, and Bourque (1975), however, this definition is unsatisfactory for parasite populations. The problem, as represented by these authors, is whether "all members of a given parasite species within a single host constitute a population, or should all members of a species in all hosts within a given ecosystem be considered a population?" It also was noted that populations of free-living organisms increase in density through birth and/or immigration processes while, within a single host, the density of most species of helminth parasites is able to increase only through immigration (= recruitment).

In an effort to circumvent the difficulties attendant in defining parasite populations in the same terms as free-living populations, a new approach was devised by Esch, Gibbons, and Bourque (1975). They proposed that all individuals of a single parasite species within an individual host be regarded as an infrapopulation. In broader terms, they referred to all individuals of a given parasite species, in all stages of development, within all hosts of an ecosystem as a suprapopulation.

The justification for a new approach becomes more apparent when a search is made of the current literature dealing with the ecology of animal parasites. There has been a strong tendency, for example, to treat parasite population biology in terms of specific, isolated life cycle stages, without regard for other life cycle stages of the same species which may also be present within the same ecosystem. The result has been the generation of considerable, and generally useful, data which are essential for analysis of infrapopulation dynamics. It does not, however, provide information necessary for evaluating the dynamics of the suprapopulation. Exceptions to the more widely used approach are the elegant studies by Hairston (1965), who examined the population biology of the trematode, *Schistosoma japonicum*, at the suprapopulation level and Anderson (1974), who also used a more holistic approach in studying the population biology of the tapeworm *Caryophyllaeus laticeps*. The utility of these approaches and that of Esch, Gibbons, and Bourque (1975) should be obvious. It would not serve any useful purpose to study the population biology of a free-living species by examination of only the adults or only the juveniles. It is important that knowledge of all life cycle stages, free-living or otherwise, be obtained and assessed if an understanding of regulatory phenomena is to be gained. When individual life cycle stages, and therefore infrapopulations, are studied separately and information concerning each stage is then summarized and integrated, only then will it be possible to understand regulation at both the infra- and suprapopulation levels.

A useful method for considering the regulation of parasite infra- and suprapopulations was devised by Kennedy (1970). He formulated a "general systems theory" which he believed would assist in the analysis and understanding of those factors which are important in regulating parasite systems. While his efforts were more specifically directed at identifying the biotic and abiotic forces which operate in fish host-parasite systems, they are nonetheless useful in examining regulation in broader terms. Borrowing from Kennedy (1970) and adding the notions presented by Esch, Gibbons, and Bourque (1975), a simplified, yet general, description of regulation as applied to the host-parasite system, has been developed (see Figure 1).

INTRINSIC (TO THE HOST) VARIABLES AFFECTING REGULATION OF PARASITE INFRAPOPULATIONS

In order to perceive the processes involved in regulation of parasite infrapopulations, it is necessary to focus on the flow of parasites (Figure 1) into (recruitment) and out of (turnover) the host. When this is done, then it can be seen that the density of an infrapopulation is a function of several intrinsic (to the host) variables.

INHERENT HOST ACCEPTABILITY

The emphasis is on inherent, for it infers a genetically-based characteristic(s) which ultimately determines whether a parasite will become established once it has been recruited. Such factors are of obvious significance since they are directly related to the phenomenon of host specificity. Odening (1976) lists nine different criteria which may be useful in measuring the suitability of a given host for a given parasite and several of these are of significance in determining inherent host acceptability. Included among these

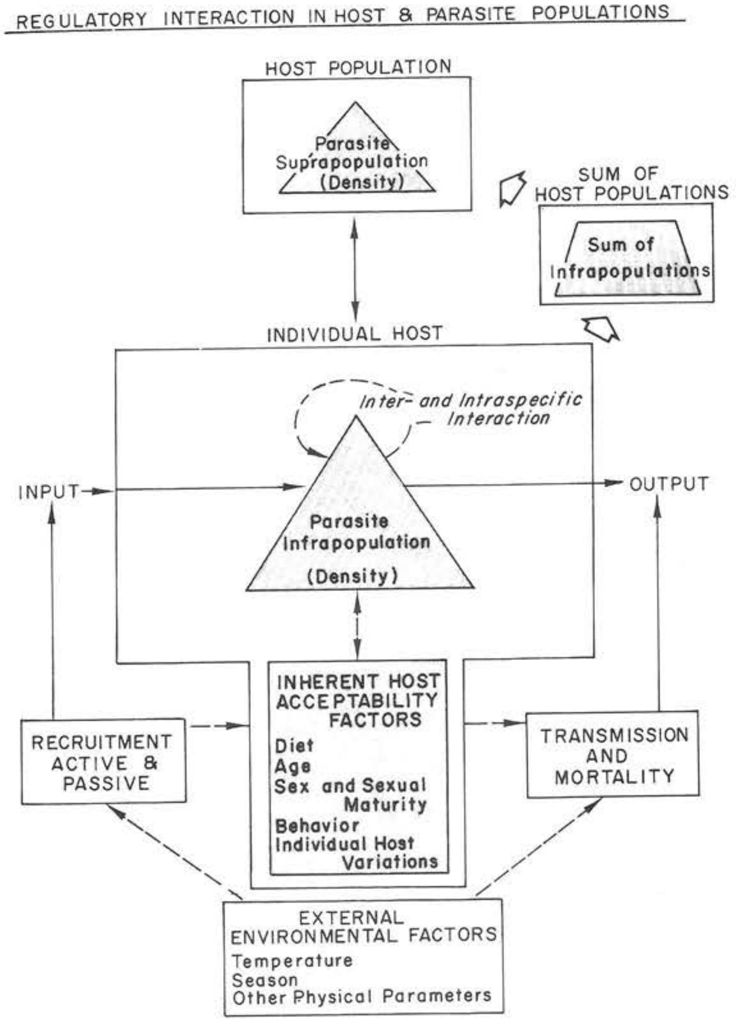

Figure 1. A schematic model showing the relationship between inherent host acceptability factors and external environmental factors in regulating parasite input and output at the infrapopulation and suprapopulation levels.

are the rate of parasite development, life expectancy of the parasite (and the host), reproductive potential of the parasite, intensity of the host's defensive response, ability of the host to withstand pathogenic insult, and the viability and transmissability of the reproductive forms of the parasite. Collectively, these criteria will be reflected in host and parasite compatability (or incompatability) and ultimately are the manifestations of a variety of morphological and physiological characteristics.

For each species of organism, parasitic or otherwise, there is an array of requirements which, in combination, represent a multidimensional space, or hypervolume. The physiological and morphological requirements of a parasitic organism, relative to all the biotic and abiotic factors which influence the host and parasite, represent the niche. For parasitic organisms occupying the intestine of a host, the requirements include a range of morphological, physical and biochemical factors. Smyth and Smyth (1968) reported, for example, that the variability in sizes of the crypts of Lieberkuhn could be of importance in the establishment of *Echinococcus granulosus* and *E. multilocularis* in various species of carnivores. Should the crypts be too narrow or shallow, then one of the species could not become established (even after recruitment), while the other exhibited a wider range of potential hosts since its establishment was not limited by the size of the crypts. An even better example was reported by Williams (1960). Thus, the fish, *Raja montagui*, *R. clavata* and *R. naevus*, have intestines with substantial morphological variability. Each fish species is parasitized by species of the tetraphyllidean tapeworm, *Echeneibothrium*, and, in each case, the cestode scolex is appropriately modified to conform with variations in villus depth as well as morphology of the crypts.

Bile salts within the intestines of vertebrate species are known to vary both in composition and concentration. "Since a wide range of bile salts occurs in vertebrates, it may be expected that the composition of bile - along with other factors - may determine whether or not a particular species can develop in a particular host" (Smyth, 1969). For example, it was shown by Smyth (1962) that the tegument of *Echinococcus granulosus* is lysed by deoxycholic acid as well as by bile from several herbivorous, but 'unsuitable hosts', such as rabbit, sheep or hare, which have high concentrations of deoxycholic acid. On the other hand, bile from carnivorous animals such as fox, dog and cat, have relatively little effect since deoxycholic acid is virtually non-existent.

There are numerous other cases which could be used as examples to illustrate the notion of 'inherent' host acceptability following recruitment of a parasite. It is clear enough from these, however, that host and parasite morphology and physiology have evolved in such a way that compatability (or incompatability) with a specific host, or group of hosts, will be the outcome of recruitment. While the parasite has evolved morphologically and physiologically to conform to a prescribed set of host-provided environmental conditions, the host also has evolved in such a manner that it is capable of responding to recruitment of parasites. In general, this adaptation by a host to a parasite produces incompatability, or at least partially so. The thrust of this evolutionary process is defensive in nature and has resulted in the development of an immune capability which, unless reversed by the parasite evolving a counter strategy, e.g. molecular minicry (Damian, 1964), non-reciprocal cross-immunity (Schad, 1966), should produce mortality of the parasite or, at the least, make it more difficult for establishment once recruitment has occurred. The phylogenetic and ontogenetic consequences of immunity thus may be reflected either in compatability or incompatability of host-parasite systems.

HOST FACTORS

Inherent host acceptability could be considered as the single, basic, controlling element (excluding, of course, external environmental forces) in influencing recruitment and establishment of parasite infrapopulations. There are, however, several additional factors which can be considered independently even though they are actually modifiers of genetically based strategies. These factors include dietary considerations, host age, sexual maturation and behavior.

Diet

It can be said that, in general, the enteric parasite fauna of a host is a reflection of what is eaten. Moreover, as pointed out by Dogiel (1964), "the parasitological indicators of diet are among those clues which allow us to make deductions from the type of parasite fauna about various aspects of the ecology of the host."

There are numerous studies which have adequately shown the relationship between diet and the parasite fauna. Dogiel (1964), for example, noted that the parasite fauna of the herbivorous cyprinid, *Chondrostomus nasus*, was virtually devoid of enteric helminths while carnivorous cyprinids, within the same ecosystem had relatively 'rich' enteric faunas. Esch and Gibbons (1967) reported that sexually immature (carnivorous), painted turtles, *Chrysemys picta*, were much more heavily parasitized than herbivorous adults. In the case of both cyprinid fish and painted turtles, the obvious variations in parasite fauna were the result of differences in probability of ingestion of infected intermediate hosts.

In lacustrine ecosystems, ecological succession may proceed from oligotrophy through mesotrophy to a eutrophic condition. As might be expected, the successional changes are reflected in complex alterations in the biotic community. Wisniewski (1958), Chubb (1970) and Esch (1971) have all reported on the differences between oligotrophic and eutrophic ecosystems with respect to the diversity and density of the parasite fauna within the piscine community. Esch (1971) proposed that the nature of the changes during succession could be explained by examining the changes in predator-prey interaction. Thus, in an oligotrophic lake, the majority of parasites complete their life cycles within interacting species of the aquatic fauna; there is little aquatic-terrestrial interaction and, hence, the system is relatively closed in terms of predator-prey relationships. On the other hand, the parasite fauna of the eutrophic ecosystem reflects more extensive aquatic-terrestrial interaction with more parasites of fish completing their life cycles in terrestrial predators; the eutrophic system is thus more open. As the biotic community changes during succession, the predator-prey interactions also shift, resulting in both qualitative and quantitative changes in the parasite fauna. Support for this hypothesis was recently provided by Kennedy (1975a).

As proposed by Esch (1971), therefore, "the nature of predator-prey relationships should serve...as a potential biological index for predicting the structure of a parasite fauna in any given aquatic ecosystem." While this approach was directed mostly at long-term successional changes, the same principles should also apply to seasonal alterations in the biotic community within aquatic ecosystems. There are a number of typical transformations which occur on a seasonal basis in the biotic and physicochemical characteristics of (especially) temperate zone aquatic ecosystems. Many of these changes ultimately can be attributed to increase in temperature and light intensity; there is likewise a shift in quantity and quality of both producer and consumer species. It naturally follows that the dietary components of many consumer organisms will also shift. Concomitant seasonal changes in the density and diversity of the parasite fauna within various hosts should also occur and, in many cases where studied, such has happened. Conner (1953) reported a significant seasonal change in density of the tapeworm *Proteocephalus stizostethi* in pikefish, *Stizostedion v. vitreum*. He stated that tapeworms were variable in size in October and November and that recruitment did not occur later in winter. He indicated that the variability in size during fall was due to intermittent feeding on the intermediate host (presumably a cyclopoid copepod) and that the lack of recruitment in the winter was occasioned by the unavailability of the intermediate host in the diet. Lees (1962) regarded the seasonal changes in frog trematode density and diversity as being due to the seasonal changes in abundance of various insect intermediate hosts. Gerking (1962) reported that the diet of bluegill sunfish, *Lepomis macrochirus*, in an Indiana (U.S.A.) eutrophic lake, turned from a high proportion of *Daphnia* in July to a high proportion of midge larvae in August. Esch, et al. (1976) reported a significant shift in the recruitment of the acanthocephalans *Leptorhynchoides thecatus* and *Pomporhynchus bulbocolli* during an eight week period in the summer of 1973 and attributed the variation in recruitment to changes in diet.

Rysavy (1966) examined the cestode fauna of birds representing several different orders, as well as different food habits and habitat preferences. The study indicated that similarities in food and habitat preferences may result in similar or even identical cestode faunas even if the birds are phylogenetically widely separated. Conversely, species of birds which are closely related phylogenetically may have very diverse faunas if their diet and habitat preferences are widely divergent.

Age

Host age is an important factor in considering regulation of parasite infrapopulations. The patterns of change in parasite densities and diversity, as the host ages, are quite variable. In some cases, a given species of parasite will be intensively recruited while the host is young and then decline in numbers as the host ages. In others, the timing of recruitment will be reversed, with the parasite being absent in young individuals and appearing with greater frequency as the host ages. In yet another pattern, recruitment will begin while the host is a juvenile and persist throughout its lifetime. Changes in quality and quantity of the parasite fauna may be a consequence of several interacting variables, including diet, immunity, interspecific interaction among sympatric species and changes in foraging patterns as the host ages.

Lewis (1968) studied the changes in the parasite fauna of the long-tailed field mouse, *Apodemus s. sylvaticus*, in two contrasting habitats from Skomer Island, off the coast of England. Results indicated that *Nematospiroides dubius*, a nematode parasite not requiring an intermediate host, was maintained in adult hosts throughout the 15 month study period. Juvenile *A. sylvaticus* became infected during and after the breeding season in the summer and were responsible for maintaining the infection cycle into the following year when they themselves became adults. According to Lewis, "a striking feature here, however, is that the juveniles are less likely to be infected than the adults, a fact which is correlated with the life history of *N. dubius* and the limited foraging activities of the juveniles during and immediately after the breeding season." Since eggs of *N. dubius* are shed with feces, the density of the infective larvae "will obviously depend upon the size of the area over which the host moves, whether the host feces are distributed at random or are aggregated, a larger area of host movement will give rise to a low density of infective stages, resulting in a low level of infestation in the host. Even if the host's movements range over a large or small area, the adults due to their increased foraging activity, will probably harbor heavier worm burdens of *N. dubius* than the juveniles."

Hine and Kennedy (1974) reported a situation in which the acanthocephalan *Pomphorhynchus laevis* was more or less constantly recruited throughout the life of the definitive host, *Leuciscus leuciscus*. There was also an increase in the infrapopulation density of *P. laevis* as the host aged. Since, however, the parasite infrapopulation was found to be in a state of virtual dynamic equilibrium, i.e. constant recruitment and turnover, the increasing densities with age could not be attributed to the addition of newly recruited parasites to a previously established infrapopulation. Instead, the change in density with age was attributed simply to an increase in the level of feeding with increased age.

The allocreadid trematodes *Bunodera sacculata* and *B. luciopercae* in yellow perch, *Perca flavescens*, in Lake Opeongo, Ontario, Canada, were both reported to increase in infection percentage as the host aged (Cannon, 1972). In contrast to *P. laevis* which were in dynamic equilibrium (Hine and Kennedy, 1974), both allocreadid species were recruited and turned over on an annual basis. Presumably, greater recruitment in older fish was the result of higher probability of exposure through wider foraging or heavier feeding, or both.

Nelson (1959) reported that *Schistosoma haematobium* was primarily an infection of children and that evidence of infection in adults is difficult to demonstrate. Clarke (1965), as reviewed by Kagan (1966), indicated that, with increasing age, there was a decrease in the level of infection accompanied by a decline in egg production. The pattern was attributed to an increasing level of acquired immunity in the population under consideration. Age related immunity to several other species of parasitic helminth has been reported (Horak, 1971; Soulsby, 1963; Kassai and Aitken, 1967; Michel, 1969). In the majority of cases, immunity is acquired through exposure to infective larval stages. In this way, as the potential host ages, the probability of exposure increases but immunity also increases. The outcome is heavier infections in younger age groups and a decline in older ones. As pointed out by Michel (1969), "population increase of a parasite which completes its life cycle within the same host tends to follow a constant pattern. Characteristically, the increase is exponential during early stages of infection while the host offers an ideal environment. Subsequently, when the host becomes resistant and represents a less suitable environment, the rate of increase declines to zero and the population then rapidly decreases."

Sex and Sexual Maturity

In some host-parasite systems there may be a strong correlation between the onset of sexual maturity and the density and diversity of the parasite faunas; with other systems, there appears to be a relationship between host sex and the intensity of infection. In either situation, the relationship between sex and parasitism could be due to variation in recruitment by males and females, or it may be due to the quantity or quality of steroid hormones (presumably, mainly androgens and estrogens) which differentially affect establishment of parasites after recruitment. The relationship between host sex and the establishment and maintenance of parasites has a long history of documentation although, in virtually all cases, there is a complete lack of evidence to indicate that such a correlation is *directly* causal.

Studies by Addis (1946), Beck (1952), Esch, (1967), Culbreth, Esch, and Kuhn (1972) and Novak (1975) have shown that the sex of the host can variously affect establishment, growth, egg production or asexual reproduction in an array of helminth parasites. Fischer and Freeman (1969) reported that the plerocercoids of the tapeworm *Proteocephalus ambloplitis* are stimulated to migrate from parenteric sites into the intestine of the smallmouth bass, *Micropterus dolomieui*. The cue for migration was suggested to be rising water temperature. Interestingly, however, they also reported that migration, and subsequent maturation to the adult stage, did not occur unless bass were sexually mature. Their findings were later confirmed by Esch, Johnson, and Coggins (1975). The implication of these studies is clear, i.e. sexual maturity coincides with increased production of sex hormones which may well be involved in stimulating migration, or subsequent growth and development of the tapeworm. It should again be emphasized, however, that evidence to support a direct causal relationship between steroids and recruitment and establishment of parasites in any vertebrate host is lacking.

Behavior

Host behavior may play a very significant role in the regulation of parasite population dynamics. The role is manifested to the greatest extent by influence on recruitment, rather than establishment, once exposure has occurred. Any behavioral characteristic which ensures, or prevents, contact between a host and a parasite would thus be of importance. It should also be emphasized that the behavioral attributes of either the host or the parasite may be of significance. The literature in this area is replete with examples and thus only a few will be mentioned here.

One of the best studies on the behavior of a free-living parasite larval stage was conducted by Donges (1963). By varying light intensity and water turbulence it was shown that the swimming behavior of the cercaria of *Posthodiplostomum cuticola* could be significantly altered. When cercaria were maintained under relatively stable light intensity and then, suddenly, light intensity is reduced to zero, followed by restoration to the original level, there was a significant increase in swimming activity. On the other-hand, a linear reduction in light intensity over a two second interval produced complete inhibition of swimming activity. It was suggested that the sudden drop in light intensity simulated a shadow produced by a swimming fish and that the increased swimming activity of the cercaria would increase the probability of contact. Similarly, water turbulence was said to simulate currents created by a swimming fish and also thus increase the chance of contact between the fish and parasite. A slow decrease in light intensity produced no response. It was suggested that the slow decrease in light intensity would be similar to that which might occur with changing cloud cover. Biologically, the significance of the cercarial swimming behavior would rest in the preservation of limited glycogen reserves in the non-feeding larval stage.

In a recent review, Holmes and Bethel (1972) described a number of host-parasite systems in which the host behavior was modified to such an extent that the probability of parasite transmission to a subsequent host in the life cycle was significantly increased. They detailed a series of studies in which the behavior of the amphipod, *Gammarus lacustris*, was altered when infected with the cystacanth larval stage of the acanthocephalan, *Polymorphus paradoxus*. Thus, when infected, *G. lacustris* exhibited a striking, positive phototaxis in conjunction with a strong clinging behavior such that they tightly attached to floating vegetation, remaining even when vigorously agitated. The consequence of the abnormal response was that infected *G. lacustris* became vulnerable to predation by mallard ducks, the definitive host for the parasite. According to Holmes and Bethel (1972), "the combination of the different behavior patterns of infected and uninfected gammarids, and the feeding behavior of mallards, resulted in a disproportionately large number of infected gammarids being eaten" during the course of a series of prey selection experiments.

A number of other cases of behavioral modification as a result of parasitism were also reviewed by Holmes and Bethel (1972). Thus, van Dobben (1952) reported that approximately 6.5% of a population of roach, *Rutilis rutilis*, were infected with plerocercoids of the tapeworm, *Ligula intestinalis*, while 30% of the roach in the diet of the cormorant definitive host were infected; this would imply that infected roach were more vulnerable to predation. Lester (1971), suggested that the behavior of sticklebacks infected by plerocercoids of the tapeworm *Schistocephalus solidus* was altered in such a way that predation by piscivorous birds was increased. Previous studies by Arme and Owen (1967) had shown that the gonadal-hypophyseal hormonal axis was altered by a secretion from the plerocercoids. In effect, the fish became stunted and reproductively sterile while the larval tapeworm continued growing, ultimately occupying substantial space in the body cavity thereby affecting the ability of the fish to swim in an upright manner; the outcome was increased predation by the fish-eating definitive host.

A recent review by Croll (1975) and earlier ones by Rogers and Summerville (1963) and Michel (1969) have most adequately described various features of the behavior of larval nematodes, particularly in terms which would apply to the regulation of parasite populations. In general, it can be stated that nematode larvae exhibit responsive capabilities to a large number of chemical, mechanical, thermal and light stimuli. In being able to respond to this array of stimuli, nematode larvae are able to seek, penetrate and establish within appropriate intermediate and definitive hosts, thereby contributing to the regulation of infrapopulations.

INTER- AND INTRASPECIFIC INTERACTIONS

The density (and diversity) of parasite infrapopulations may be affected by inter- and intraspecific interactions. Thus, several investigators (Holmes, 1961; Schad, 1963; Chappel, 1969), studying quite different host-parasite systems under both laboratory and field conditions, have shown that enteric parasite populations can be affected by competition for space or nutrients (additional comments regarding these studies and other related ones will be made subsequently).

EXTRINSIC (TO THE HOST) FACTORS AFFECTING THE REGULATION OF PARASITE INFRAPOPULATIONS

Input and output from the infrapopulation are the manifestations of recruitment, transmission and mortality (refer to Figure 1). Recruitment may be characterized as being active or passive. Active recruitment would require an expenditure of energy on the part of the host, i.e. energy expended by a predator in seeking prey which may harbor an infective larval stage for the definitive (predator) host. In other cases, active recruitment would occur when a potential host accidentally ingests an egg or larva along with other food material (there would still be an expenditure of energy by the host in recruitment of the parasite). Passive recruitment would occur when a parasite expends energy in order to seek and penetrate a host; in this case, the host is passively involved in recruitment.

Output from an infrapopulation may result from parasite mortality, or it may occur when an infrapopulation is transmitted to a new host either by direct predator-prey interaction or via direct inoculation of a parasite by an insect vector. Mortality among parasite populations may be the result of normal senescence which can occur seasonally, or at irregular intervals. Mortality may also be a reflection of host and parasite incompatability such as might be induced through immunologic means. A change in diet by a host can have profound affects on enteric physiology and may, as a result, create local environmental conditions which are incompatible with continued existence of an established parasite infrapopulation - the result would be parasite mortality and output. Transmission may also affect the density of an infrapopulation. The density may decline partially, or completely, depending on the specific nature of the parasite's life cycle. For example, the host might be serving as an intermediate for the parasite which must be consumed by the appropriate definitive host in order to complete its life cycle. Obviously, the outcome of this kind of transmission is a decrease in the infrapopulation density. These kinds of changes would be of significance when the sum of similar infrapopulations is under consideration, or when the density of subsequent life history stages and infrapopulations is considered, or when the dynamics of the suprapopulation is the focus of attention.

Recruitment (whether active or passive), as well as mortality and transmission, are influenced by an array of abiotic and biotic factors; any variable impacting on the physiology and behavior of either the host or the parasite, or both, may be important in regulation. As stated by Esch, Johnson, and Coggins (1975), "the result of the collage of interacting host and environmental variables is the establishment of isolated parasite infrapopulations which collectively represent an important segment of the suprapopulation." The number of these factors is large and would be cumbersome either to list or thoroughly comment upon, so the following are noted as examples only.

TEMPERATURE

In general, the effect of temperature is measured in terms of its influence on the rate of enzymatically catalyzed metabolic activities, but it also affects such non-catalytic activities as diffusion and osmosis. Operating within this framework, temperature affects a wide variety of growth and development processes, any one of which may effectively influence recruitment, transmission and mortality, and thus be involved with regulation of parasite populations. In some cases, addition of thermal effluent may exacerbate what may be considered as normal temperature effects.

Not surprisingly, temperature and its role in controlling egg hatching, development of intramolluscan trematode stages, and the subsequent release of cercaria are all known to affect the regulation of trematode populations. In an excellent review, Ollerenshaw and Smith (1969) described the use of meteorological factors in the forecasting of helminthic disease in a number of animals, for example, fascioliasis in sheep. Employing observations by Ollerenshaw (1959), they described "a time-table showing the seasonal distribution of eggs on pasture, infected snails, infected herbage and disease in sheep...(which) was based solely on the response of the parasite to seasonal variations in temperature." Spall and Summerfelt (1970) reported that higher water temperature increases both the maturation rates of the intramolluscan larval stages of *Posthodiplostomum minimum* and the release of cercaria. Both of these developmental processes play important roles in determining rates of passive recruitment and densities of metacercarial infrapopulations within piscine intermediate hosts.

Kennedy (1975b) has correctly pointed out that there are a number of fish parasites in which egg production by the adult and the maturation cycle as a whole can be closely correlated to annual changes in the water temperature cycle. And, as indicated by Chubb (1967), the correlation suggests a causal relationship. Since, however, there is no supportive experimental evidence, Kennedy (1975b) urges caution in drawing conclusions with respect to the influence of temperature on these growth processes.

Bauer (1959) reported that the development time of the protozoan parasite of fish, *Ichthyopthirius mutifiliis*, was inversely correlated with rising temperature; and, indeed, this may be true for many protozoan parasites. Recently, Esch, et al. (1976) reported a striking seasonal periodicity in infection of largemouth bass, *Micropterus salmoides*, by the peritrich ciliate *Epistylis* sp. This periodicity of infection was very closely tied with seasonal changes in mean temperature. Seasonal changes in body condition of the host fish were, however, also reported; it was suggested that the body condition of the host may be of overriding significance in affecting the epizootiology of *Epistylis*. This observation supports the generalizations made by Kennedy (1975b) that correlations between temperature and growth and development of parasites do not necessarily indicate a direct causal relationship between temperature and changes in parasite population dynamics.

In a series of studies by Fischer (1967) and Fischer and Freeman (1969) on the biology of the tapeworms *Proteocephalus fluviatilis* and *Proteocephalus ambloplitis* in smallmouth bass, a strong case was made for a correlation of several growth factors with temperature. In the first instance, the eggs of *P. fluviatilis* were reportedly killed by low winter temperatures, and since infection is then precluded in either copepods or bass, infrapopulation densities in both hosts decline (Fischer, 1967). Fischer and Freeman (1969) implicated temperature as a force in inducing the parenteric plerocercoids of *P. ambloplitis* to migrate into the intestine, thus resulting in enteric recruitment of adult tapeworms.

In a reservoir (Par Pond, Aiken, S. C., U.S.A.) receiving thermal effluent from a nuclear production reactor, Eure and Esch (1974) reported that while infection percentages did not vary between locations, the densities of *Neoechinorhynchus cylindratus* (Acanthocephala) infrapopulations in largemouth bass, were significantly higher in bass taken from thermally altered areas as compared to those taken in ambient areas. They attributed the difference to heavier feeding activities of bass subjected to elevated temperature and not to any direct effects of temperature on the parasite. In the same reservoir system, Bourque and Esch (1974) reported a similar thermal effect with respect to *Neoechinohynchus* spp. in the yellow-bellied turtle, *Psuedemys s. scripta*. Turtles in areas receiving thermal loading had significantly higher infrapopulation densities than those taken in ambient areas. They also attributed the differences to increased feeding by the turtles. However, the diversity of the parasite fauna was less among turtles from the thermally altered areas even though densities of the remaining parasite species were high. The reduced diversity was probably due to a decline in species diversity of the ostracod intermediate host, since similar changes in density and diversity had previously been noted in other members of the biota of that reservoir (Parker, Hirshfield, and Gibbons, 1973). Aho, Gibbons, and Esch (1976), who also studied parasitism in the Par Pond system, reported a significant difference in metacercarial infrapopulations in the mosquitofish, *Gambusia affinis*, in relation to thermal effluent. Their results showed that while infection percentages were similar in *G. affinis* throughout the reservoir, fish taken in heated areas had higher worm burdens of the metacercaria of *Ornithodiplostomum ptychocheilus* than in those from ambient areas. Conversely, *G. affinis* from ambient areas of Par Pond had larger infrapopulation densities of the metacercaria of *Diplostomulum scheuringi* than did fish from thermally altered areas. Interestingly, recruitment of these parasites by *G. affinis* is passive, while recruitment in the hosts studied by Eure and Esch (1974) and Bourque and Esch (1974) was active. Clearly, further efforts are needed to evaluate the impact of thermal effluent on recruitment and turnover of parasites by poikilothermic vertebrates as well as invertebrates.

DISPERSION

The phenomenon of dispersion is exceedingly important in considering those factors involved in the regulation of parasite infrapopulations. In terms of parasitic organisms, Crofton (1971) was the first to call attention to the relationship between regulation and dispersion. Indeed, he attempted to incorporate the concept of dispersion into a comprehensive definition of parasitism. The essential features of his definition were: (1) that parasites are physiologically dependent on their hosts, (2) the parasite kills heavily infected hosts, (3) the parasite species has a higher reproductive potential than its host, and (4) the infection process produces or tends to produce an overdispersed distribution of parasites within the host population. Whether all four tenets are accepted or not is not essential to this discussion. The important feature is the last, i.e. overdispersion. Since Crofton's 1971 paper, there has been a series of reports (Pennycuick, 1971; Schmid and Robinson, 1972; Bourque and Esch, 1974; Boxshall, 1974; Anderson, 1974) which have directed attention to overdispersion as a characteristic of various parasite populations.

Indeed, as was shown by Anderson (1974), the overdispersion of infected intermediate hosts, in conjunction with feeding behavior of the definitive host, may directly influence recruitment of parasite infrapopulations and thus be of significance in regulation. He reported that the overdispersion of adults of the tapeworm *Caryophyllaeus laticeps* in the European bream could be described by a negative binomial model. He suggested that the overdispersed infrapopulation densities of the adult tapeworms were not due to the compounding of random successive waves of invasion by infective stages acquired by predation of randomly scattered infected intermediate hosts (benthic tubificid worms). Instead, he attributed the overdispersed infrapopulations to the spatial heterogeneity of infected intermediate hosts within the benthic community. The spatial distribution, when coupled with non-random feeding behavior of the bream, was sufficient to produce overdispersion of adult worms in the definitive host.

REGULATION AT THE SUPRAPOPULATION LEVEL

If successful recruitment by an appropriate host occurs for a particular life cycle stage in any given host-parasite system, then an infrapopulation may become established. It will then be maintained for an appropriate period of time after which individuals within the infrapopulation may senesce and die or the entire infrapopulation may be transmitted to the next host in the life cycle, becoming a new infrapopulation or part of an existing one. The relationships among the factors which regulate at the infrapopulation and suprapopulation levels are exceedingly difficult to analyze, in part because the complexity of the regulatory phenomena acting at these levels is frequently compounded by the existence of multiple life cycle stages involving a variety of intermediate and definitive hosts.

One of the few analyses of suprapopulation dynamics yet published examined was based on the digenetic trematode *Schistosoma japonicum* (Hairston, 1965; Pesigan, et al., 1958). The outcome of these studies showed that field rats maintained the schistosome suprapopulation at such a level that if all humans were to be removed from a given area and replaced by the same number of uninfected individuals, then only a few years would be required for infrapopulations within humans to reach previous levels. For an excellent consideration of regulation at the suprapopulation level, see Holmes, Hobbs, and Leong (this volume).

r- AND K-SELECTION

Among host-parasite systems there is a series of selection forces (biotic and abiotic) which, acting in concert with genetic variability of both the hosts and the parasites, ultimately determines the success of individuals, populations and species. Thus, selection pressure(s) and genetic variability within the host and parasite are reflected in regulation. Some of the ideas inherent in the notion of natural selection and regulation of parasite populations can be suitably joined in the concept of r- and K-selection which has produced considerable discussion, both pro and con, among ecologists in recent years. It is not the intention here to enter the controversy centering on r- and K-selection. Instead, use will be made of the concept only for the purpose of generating new, even perhaps incautious, ideas concerning the factors involved in the regulation of parasite populations. Liberal use will also be made of the notions presented in the previous section dealing with the schematic model shown in Figure 1.

The concept of r- and K-selection was initially proposed by Dobzhansky in 1950. Writing in American Scientist, Dobzhansky suggested that natural selection in the tropics favored low fecundity and slow development while, in temperate zones, competitive advantage was bestowed on those species with higher fecundity and more rapid development. Pianka (1970) pointed out that "Dobzhansky's ideas were framed in terms too specific to reach the general ecological audience and have gone more or less unnoticed until fairly recently."

The terms r-selection and K-selection were actually coined by MacArthur and Wilson (1967). Their intent was to characterize temperate and tropic zone selective mechanisms but, as Pianka (1970) indicated, these two types of selection are not at all restricted to the tropics or temperate climates. In 1970, Pianka presented a summary of the concepts of r- and K-selection. His view was that there is an r-K continuum, with the r-end point representing a situation in which the optimum strategy is to place 100% of the matter and energy of an organism into reproduction, with a minimum into each individual offspring so as to produce the maximum number of progeny (strategy in this paper is used to indicate a genetically fixed adaptation or characteristic, as in the sense of Harper, 1967). The outcome of r-selection would thus be high productivity. Continuing, Pianka (1970) indicated that at the other end of the continuum, K-selection would lead to highly efficient utilization of environmental resources. Density effects would be maximized and the environment would be saturated with organisms; in other words, the population would be at capacity for a given amount of space or nutrient level. Under such conditions, competition would be keen, with the best survival strategy being to shunt all available resources into self-maintenance and to produce highly fit progeny. As McNaughton (1975) stated, "in the ecological void, the optimal adaptive strategy channels all possible resources into progeny, thereby maximizing the rate at which resources are colonized. At ecological saturation, on the other hand, the optimal strategy channels all possible resources into survival and production of a few offspring with highly competitive ability."

The population growth curve for a K-strategist can be written in the form shown in Figure 2 (top). The

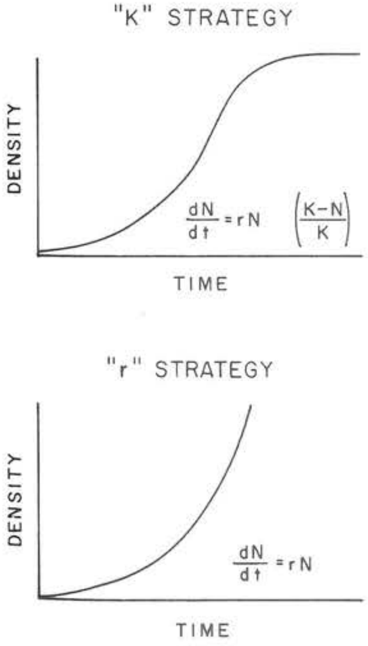

Figure 2. Population growth curve for a K-strategist (at the top) and an r-strategist (at the bottom).

curve can be described by the familiar Verhust-Pearl logistic equation. The equation, in essence, says the following: the rate of population increase $(\frac{dN}{dt})$ is equal to the maximum growth rate times the number in the population (rN), times the degree of realization of maximum rate $(\frac{K-N}{K})$ (Odum, 1971). In this equation, K represents the upper asymptote, or the carrying capacity; K-selection relates to competitive ability or, in other words, the manner in which the instantaneous increase of a population will change in relation to changing levels of competition.

The population growth curve for an r-strategist will be recognized in Figure 2 (bottom) as the expotential phase of the previous logistic equation where a population is increasing (or decreasing) expotentially. The r-term in the equation represents what is commonly called the intrinsic rate of natural increase; it is a constant, but it may take any value. According to Hariston, Tinkle and Wilbur (1970), "it thus represents in a single number all of the physiological response of all members of the population to a given set of environmental conditions since, ultimately, all physiological responses must be relatable to the ability to reproduce, or the ability to survive."

As previously indicated, the concept of r- and K-selection has not been universally accepted (for a discussion of some objections, see Hariston, Tinkle, and Wilbur, 1970). In spite of their criticisms (which may or may not be well taken) there is obvious significance in its acceptance in general terms and, especially, in the sense presented by Pianka (1970; 1972). It has gained wide acceptance by a variety of investigators because it does focus on an ecologically important problem, i.e. "allocation of resources between competitive and reproductive functions" (McNaughton, 1975). Other investigators who have utilized the concept in one way or another in the past several years include Gadgil and Bossert (1970), Gadgil and Solbrig (1972), Barclay (1974), Forsyth and Robertson (1974), and McNaughton (1975).

The use and application of the concept of r- and K-selection in considering host-parasite relationships has been non-existent until recently. Seidenberg, et al. (1974) suggested that the nematode *Longistriata adunca*, an enteric nematode of the cotton rat, *Sigmodon hispidus*, exhibited characteristics of an r-selected species since adult males died soon after copulation thus reducing the overall population density and increasing resource availability (both nutrients and space) to egg-producing females. More recently, Jennings and Calow (1975), in an excellent paper, reviewed the relationship between fecundity and the evolution of endoparasitism. They indicated that "r-strategists, with high fecundity, can be expected to have low calorific values because their resources are channeled into production of the maximum number of progeny, while K-strategists will have high calorific values based on lipid reserves which buffer adults against possible reductions in food supply." They provide evidence which suggests that the relationship between fecundity and caloric content in r- and K-strategists can be seen after comparing various members of the phylum Platyhelminthes, some of which are parasitic and others free-living. Endoparasitic flatworms exhibit high fecundity in combination with low caloric values, while free-living species show the opposite (low fecundity and high caloric values); ectocommensalistic forms were reported to be similar to free-living platyhelminths. They argue, however, "that parasites, particularly endoparasites, follow both an r- and K-strategy at the same time and that this is only possible because of the stable, nutrient-rich environment provided by the host. Evolutionary theory dictates that all species would follow an r- and K-strategy simultaneously but environmental conditions force them into one alternative or another. Consequently the high fecundity of endoparasites, which has hitherto been viewed as a specific adaptation to endoparasitism, is now viewed as an automatic consequence of the conditions provided by the parasitic environment."

A traditional approach among parasitologists has been to view high fecundity as an adaptation for a parasitic mode of life. In an earlier paper Calow and Jennings (1974) disputed this contention by saying that "an interesting consequence of our interpretation of the relationship between the nature of the food reserve, mode of life and level of fecundity, is that parasitism, and especially entoparasitism can be regarded simply as adaptive devices which favor high fecundity." They indicate that free-living flatworms tend to have higher concentrations of stored lipid with concomitant higher calorific values and lower fecundity as compared to parasitic flatworms. In the latter group, the high fat levels are reduced and replaced by higher levels of glycogen which are relatively lower in calorific values than lipid. Previous literature had suggested that the high glycogen and low lipid levels in parasitic flatworms were the result of low oxygen concentration in the enteric environment. Calow and Jennings (1974) argue that it is an "adaptation for high fecundity, necessitated by the mode of life." They point out, however, that the high glycogen level in endosymbionts does represent a pre-adaptation to relative anaerobiasis. They further indicate that while there is a direct relationship between glycogen levels, low levels of oxygen and a modified intermediary carbohydrate metabolism among endosymbiotic flatworms, "the relationship is seen to be proximate rather than ultimate in nature."

While the ideas presented by Calow and Jennings (1974) and Jennings and Calow (1975) are intriguing, they may not be completely acceptable. As pointed out by Boddington and Mettrick (1976), there are too few data which support their contention and "of the data for the free-living forms, 50% are artificially inflated because they were for animals in the well-fed state, while the values for the parasitic forms were all field data to which no nutritional significance could be attached." The latter point could be of major significance in calculating calorific values of any parasitic helminth, flatworm or otherwise. For example, starvation of *Fasciola hepatica* for 24 hours resulted in the virtually complete depletion of parenchymal glycogen, which in turn would effectively alter the relative dry weight percentage of carbohydrate, lipid and protein (von Brand and Mercado, 1961); obviously, the calorific values would also change. Calow and Jennings (1974) state, "thus our results confirm the evolutionary trend within the Platyhelminthes, assuming that the free-living forms are primitive, has been toward a reduction in the amount of lipid stored per unit weight with a concomitant reduction in calorific values." In 1966, von Brand summarized the lipids in percent of dry weight of tissues for a wide variety of parasitic flatworms. The values ranged from a low of 1.35% (Goil, 1958) for *Gastrothylax cremenifer*, a trematode of the rumen of water buffalo, to a high of 34.6% (Goodchild and Vilar-Alvarez, 1962) for *Hymenolipis diminuta*, a tapeworm of rats. Very recently, Yusufi and Siddiqi (1976) reported that the lipid in percent of dry weight of tissues of *Gastrothylax cremenifer* was 10.5%. This latter value and the one given by Goil (1958) for the same fluke are an order of magnitude different and, while conversion to calorific values was not made, it is certain that these would also be significantly different. It is also worth noting that *Fasciola hepatica*, a bile duct trematode of sheep, has a lipid content of 13.3% (Weinland and von Brand, 1926) while the closely related *Fasciolopsis buski*, an intestinal fluke of pigs, was found to have a lipid content of 50.4% (Yusufi and Siddiqi, 1976). The variability (as noted above) in lipid, as a percentage of dry weight, could be due to (1) nutritional conditions at the time of sampling, (2) reproductive condition of the parasite, (3) inherent species-specific differences in the parasites tested, (4) age of the parasite and (5) as pointed out by Yusifi and Siddiqi (ibid), the technique used for lipid extraction. Any of these variables could have influenced the findings of Calow and Jennings (1974) and, in turn, would influence the validity of their hypothesis.

While the notions presented by Calow and Jennings (1974) should be viewed with caution, they are of exceptional value if they do nothing more than stimulate debate and challenge accepted dogma among parasitologists. Furthermore, even in view of the proper criticisms by Boddington and Mettrick (1976) concerning the absence of adequate controls in their test animals, it is quite conceivable, even likely, that a relationship between r- and K-selection, relative nutrient and calorific values, and evolutionary strategies among free-living and parasitic flatworms may exist as suggested by Jennings and Calow (1975).

The relationship between r- and K-selection, parasitism, and regulation of parasite populations can also be viewed within the broader context developed by Dobzhansky (1950), MacArthur and Wilson (1967) and Pianka (1970). For example the biology of colonization, succession and the vicissitudes of ecosystem stability and complexity in relation to parasitism and r- and K-selection could be examined, but have not. Thus, there are several approaches which may be taken. The framework for the present approach is provided by the schematic model shown in Figure 1.

There are three questions which will be considered in the following analysis. First, and probably most important, is it feasible to consider parasitism and parasites in terms of r- and K-selection? Second, if parasites can be characterized in this manner, can they be identified as more r-selected or K-selected, or do they constitute a spectrum between the extremes and thus parallel the r-K continuum? And third, are there any unique life history strategies associated with parasites in general which might re-enforce any general conclusions which may be made regarding the case for parasites as being either r- or K-selected?

The aim of the analysis will not be simply to identify selection strategies in association with particular parasite species. The objective instead will be to examine the strategies in such a way that a different and, perhaps, more useful perspective may be gained with regard to the behavior and regulation of parasite populations within a variety of environmental conditions.

An ideal point of departure for considering the questions posed above is to analyze a set of correlates created by Pianka (1970) for the purpose of comparing and contrasting r- and K-strategies. The correlates are based on such variables as climate, mortality, survivorship, population size, competition, development time, body size, length of life, etc.

Climate: r-selection - "variable and/or unpredictable: uncertain" (Pianka, 1970).
K-selection - "fairly constant and/or predictable: more certain" (Pianka, ibid).

Within the biosphere there is a continuum of environments ranging from those which are more or less constant and predictable to those which are variable and unpredictable. Organisms existing in the latter may be subjected to heavy mortality, on an irregular basis. In general, such species survive under conditions which would be less competitive than for those existing in more stable environments. The ideal strategy (r-strategy) under less stable conditions would be to produce as many progeny as possible. The more stable environment, on the other hand, would be saturated. The outcome would be intense competition with maximum energy directed at development of maintenance and competitive skills with less effort directed at production of large numbers of progeny. These species would thus exhibit characteristics of a K-strategist.

After examination of the correlate for climate, it was felt that Pianka (1970) intended to refer to the role of temperature, humidity, rainfall, soil conditions, etc., in influencing the life history and physiological characteristics of free-living organisms. For many parasitic animals, the impact of environmental variability would be similar to those of free-living organisms since most parasites have free-living life cycle stages. However, most of the life of a parasite is spent within a host and could, therefore, because of various homeostatic processes associated with the host, be considered as life within a relatively stable environment. In spite of this, it is generally true that environmental instability is the rule.

Take, for example, the life cycle of a digenetic trematode, beginning with the release of the egg into an aquatic environment (assuming, of course, that the egg requires the interposition of an aquatic environment, and that the egg is shed therein - thus the initial vagary). On hatching, a free-living larval stage (the miracidium) emerges. The miracidium is subjected to the same set of environmental variables with which the free-living organisms must also contend. These would, of course, include temperature, osmotic pressure, pH, etc. While the larval trematode has evolved a remarkable array of physiological and behavioral adaptations in order to survive such conditions, it is unquestionably true that the majority die in a relatively brief period of time (see section on survivability).

Utilizing chemotatic responses, the miracidium locates and penetrates an appropriate intermediate host and therein is subjected to significant environmental changes, including especially pH and osmotic pressure. Perhaps even more significant, the parasite is subjected to the potential of a host response which could result in mortality. In some cases, there is even evidence for predation of newly penetrated trematodes by previously established larval stages of other digenetic trematodes (Lie, Heyneman, and Kostanian, 1975). If the miracidium is successful in becoming established, dramatic morphological and physiological changes then occur with the outcome being the development of asexually reproducing sporocysts and/or redia, depending upon the species. The intramolluscan larvae then produce yet another larval stage which exists from the molluscan sanctuary. These larvae, called cercaria, enter the aquatic environment and, like miracidia, must cope with significant changes in temperature, pH and osmotic pressure. And, as with miracidia, cercaria survivability is low and longevity is brief (on the order of a few hours).

Employing a complex set of physiological and morphological adaptations, the cercaria seek out and penetrate an appropriate intermediate host. (Note that this route varies according to parasite species since some cercaria may encyst in the open on vegetation or other substrates, while other cercaria may penetrate directly the definitive host). On penetration of the intermediate host, the parasite usually encysts, becoming a metacercaria. Within the host the parasite is subject, once again, to significant changes in temperature, pH and osmotic pressure. And, again, the parasite must cope with host immune responses. The metacercaria then remains until the intermediate host is consumed by the appropriate definitive host. While the metacercaria is essentially quiescent, there are indications that the host continues to respond to the parasite and that, at least in some cases, the parasite may be overwhelmed and killed in the process.

When finally ingested by the definitive host, the metacercaria is subjected to a new set of environmental changes which, in many ways, may be the most hostile. Thus, when the metacercaria excysts in the stomach, it encounters a pH of about 1-3 and a complex of protein-digesting enzymes. On entering the small intestine, the parasite is exposed to new environmental conditions, with different enzymes, an array of bile salts and a pH of 7.0. If the parasite and host are suitable to each other, the trematode will undergo sexual maturation and egg production will follow quickly.

From the foregoing account, it should be clear that the parasite must be well adapted to the rapid and dramatic shifts in environmental conditions which occur throughout the life cycle. This is also obvious from the literature which shows the large number of parasites in animals from virtually all possible habitats (Yamaguti, 1958). This description of a generalized, trematode life cycle, however, also serves as an indication of the high degree of variability and unpredictability of the parasite's environment. It is safe to state that most parasite species are exposed to more environmental or climatic variability than virtually any other group of animals. From the standpoint of climate, therefore, it must be concluded that parasites are subject to selection forces which are characteristic of r-strategists.

<u>Mortality</u>: r-selection - "often catastrophic, non-directed, density-independent" (Pianka, 1970).
K-selection - "more directed, density-dependent" (Pianka, ibid).

At both the suprapopulation and infrapopulation levels, parasites are regulated by density-dependent and density-independent processes. For evidence of density-independent regulation of parasite infrapopulations, the study by Kennedy (1974) on the acanthocephalan *Pomphorhynchus laevis* is illuminating. Utilizing the common goldfish as an experimental host, Kennedy reported that when "infections with different population densities of parasite were given to fish on one occasion only and on several occasions with different time intervals between infection," that "the parasites established and grew in experimental hosts at rates comparable to those in natural hosts on all occasions." He stated further that "the proportion establishing did not increase with increasing population size and bore no relationship to the presence of an existing population." He concluded that parasite mortality was not subject to feedback control and was of little consequence in regulating the size of parasite infrapopulations. Awachie (1966) reached similar conclusions regarding the regulation of *Echinorhynchus truttae* densities in *Salmo trutta*.

Recognizing the potential for both positive and negative relationships between hosts and parasites, Bradley (1974) proposed three mechanisms by which parasite populations are regulated. Bradley's Type I regulation involved factors which are related to transmission of the parasite from one host to another; essentially, this form of regulation would be density-independent and would be controlled by extrinsic, environmental forces. An example given by Bradley was of "malaria in an epidemic area, such as the Punjab, where ambient temperature, humidity, distribution of surface waters, vegetation shading those waters, number insectivorous birds, may all affect transmission but are scarcely or not at all affected by transmission."

Those situations in which parasites are regulated at the host population level are referred to as Type II regulation (Bradley, 1974). In a very real sense, this kind of regulation is density-dependent and is related to two phenomena, i.e. immunity and overdispersion. Since overdispersion will be considered subsequently, it will be only briefly alluded to here. According to Crofton (1971), the overdispersion of parasite infrapopulations is an inherent property of host-parasite systems. In effect, most parasites within a group of infrapopulations are found within a small number of hosts. Because of overdispersion, there is a potential to increase the density of a given infrapopulation to such an extent that it will eventually cause the host to die. If this occurs, then the density of the infrapopulations is reduced. Hence, there is negative feedback by the parasite; overdispersion (and, therefore, density) is the operational factor. Bradley (1974) did suggest, however, that overdispersion may not produce stability for densities of helminth parasites among vertebrate hosts though it may for parasites among invertebrate populations. Immunity (in this case, complete immunity) was also considered as a density-dependent factor in regulating parasite populations. Thus, a situation could arise in which a single infrapopulation would become large enough to induce complete immunity in a host and preclude subsequent reinfection. Should this occur, the impact would be the same to the parasite as if the host were non-existent, or dead. In effect, the density of the parasite infrapopulations would be self-regulated except that the host population would be mediating the regulation through the immune response.

Type III regulation is considered by Bradley (1974) as the most efficient in maintaining stability of parasite infrapopulations since the densities are regulated by individual hosts. Thus, he states, "consider a helminth whose usual transmission rate is 100 worms inoculated per host and the host has a means of preventing the worm load exceeding 10, then over a tenfold fall or indefinite rise in transmission the parasite population will be perfectly regulated. This is the ultimate in regulation: highly efficient transmission combined with 'premunition' or some similar process of parasite regulation by each host." This form of regulation would be density-dependent and, according to Bradley, "is seen to a varying degree in many parasitic systems."

It is apparent that both regulatory mechanisms (density-dependent and density-independent) operate, depending on the specific host-parasite system involved. Indeed, it is conceivable that both may operate for a given host-parasite system, with one form of regulation influencing the density of parasites within an intermediate host and the other form at the level of the definitive host. It is probably true, that with respect to this correlate, parasitic organisms lie along the r-K continuum and not exclusively at either endpoint.

Survivorship: r-selection - "Often Type III (Deevey, 1947)," Pianka (1970).
K-selection - "Usually Type I and II (Deevey, 1947)," (Pianka, ibid).

Type I survivorship (Pearl, 1928) is reflected by an age specific death rate which is expressed by a hyperbolic function. Western man exhibits a Type I survivorship curve, i.e. there is relatively low mortality in early age classes with subsequent mortality continuing to remain low until near the limit of normal longevity. The Type II survivorship curve is linear (Caughley, 1966), with mortality rates proceeding at the same rate regardless of age; birds commonly exhibit such a survivorship curve. According to Pianka (1970), these two types of survivorship are characteristic of K-selected species.

A Type III survivorship curve follows an inverse hyperbolic function; it is produced by high initial mortality with a gradual decline and subsequent lower mortality among older individuals. According to Caughley (1966), this kind of survivorship is typical of fish and insects. Type III survivorship is characteristic of r-selected species, although Pianka (1970) also states that fish may span the entire r-K continuum.

Intuitively, it might be guessed that survivorship of parasites would be best characterized by a Type III curve. However, there have been too few studies on age specific mortality throughout an entire life cycle. Such an assessment is further complicated since many parasite species have life cycle stages in which asexual reproduction occurs. Anderson and Whitfield (1975) noted a high initial mortality of cercaria of *Transversotrema patialensis*, a trematode using fish as the definitive host. After 26 hours, survivorship was about 50%; this was followed by complete mortality after 44 hours as glycogen reserves were depleted. In this case, survivorship was not linear and might be best considered as a modified, Type III curve.

At the suprapopulation level, it is speculated that survivorship for most parasite species probably fits a Type III curve. Intuitively, this would be correct in view of the prodigious reproductive capacities of most parasites as compared with the relatively low chances for success of a single egg completing the entire cycle. In view of the survivorship criterion, it seems appropriate to characterize most parasitic organisms as r-strategists.

Population size: r-selection - "Variable in time, nonequilibrium; usually well below the carrying capacity of the environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year." (Pianka, 1970).

K-selection - "Fairly constant in time; at or near carrying capacity of the environment; saturated communities, no recolonization necessary." (Pianka, ibid).

Populations of r-strategists are generally of variable nature, at well below the carrying capacity. Typically, r-strategists are capable of rapid, annual recolonization which also implies they will move into an ecological vacuum with facility. In terms of host-parasite systems, it is reasonable to consider a non-parasitized host as an ecological vacuum and, for many parasite species, recolonization is a typical annual strategy. Many helminth parasites are seasonal, infecting the definitive host in spring, producing eggs, and senescing in late summer or fall. The densities of many parasite infrapopulations are thus highly variable within a single 12 month period.

While annual recolonization is a typical strategy for many parasite species, this tendency may well be tempered by the state, or level, of existing immunity within the potential host. As suggested by Bradley (1974), the level of immunity, or 'premunition', may be one of the most significant elements in regulating parasite densities. Indeed, the level of immunity, in conjunction with finite space and nutrient resources, may be considered as the primary limiting factor in determining the carrying capacity of an individual host. In many cases, it is conceivable that space and nutrient resources would not ever be fully exploited because of the overriding effect of immunologic factors. Under these conditions, the density of the parasite infrapopulation would remain below the 'apparent' carrying capacity of the host. It is also possible that some parasite infrapopulations may never reach the 'apparent' carrying capacity, since death of the host may occur before K is reached. On the other hand, as has already been suggested, some parasite populations remain in a state of dynamic equilibrium on an annual basis, i.e. recruitment and turnover within the parasite infrapopulations are constant.

Since very little is known about carrying capacities for parasite infrapopulations under natural conditions, this correlate must be viewed with some caution. It would appear, however, that most parasite species exhibit characteristics of an r-strategist when such factors as density variability, equilibrium versus non-equilibrium, recolonization, etc., are considered.

Intra- and interspecific competition: r-strategist - "Variable, often lax" (Pianka, 1970).
K-strategist - "Usually keen" (Pianka, ibid).

Both intra- and interspecific competition are known to occur among and between various parasite species. Roberts (1966) reported stunting of *Hymenolepis diminuta* when infrapopulations were at high densities. Ghayal and Avery (1974) indicated that when infrapopulation densities were high, that length, weight and egg production decreased for cysticercoid-derived and egg-derived infections of the cestode *Hymenolepis nana*. The tapeworm *Diphyllobothrium dendriticum* is smaller when at high infrapopulation densities in both hamsters and gulls (Halverson and Anderson, 1974). Holmes (1961) showed that densities as low as 10 worms per host would result in both reduced length and weight of *Hymenolepis diminuta*.

In an elegant study, Holmes (1961) conclusively demonstrated competitive exclusion of one parasite species by another. In concurrent infections by the tapeworm *Hymenolepis diminuta* and the acanthocephalan *Moniliformis dubius* in the white rat, he was able to show clearly that (1) growth of the tapeworm was retarded and (2) the tapeworm attached to the wall of the intestine at a site other than the one observed in single species infections. He also showed that established populations of *H. diminuta* migrated away from the initial site of infection on the appearance of *M. dubius* at that site. While Holmes' study was conducted under laboratory conditions, Chappel (1969) provided field evidence for competitive exclusion of the tapeworm *Proteocephalus filicollis* by the acanthocephalan *Neoechinorhynchus rutili* in three-spined sticklebacks. In both of these studies, competitive interactions resulted in longitudinal redistribution of the affected parasite species. Working with the European tortoise, *Testudo graeca*, Schad (1963) clearly demonstrated that competitive interaction would also effect changes in the radial distribution of several species of enteric, parasitic nematodes and that the apparent operational factor in producing the changes in location was likely due to differential food preferences among the affected species.

From the studies cited above, it is apparent that intra- and interspecific competition do occur among various species of parasitic helminths. Indeed, Kennedy (1975) states that "nearly all species of cestodes appear to show crowding effects." In spite of this sweeping statement, just how common competition is among different species of parasitic organisms is actually difficult to assess, since far too few investigators have reported on efforts to obtain evidence which would address this question. Since overdispersion is an inherent characteristic of parasitism and, thus, the potential for competitive interaction is certainly extant for most parasitic organisms, there is opportunity for generating data to provide support for a generalization such as Kennedy's (ibid). Until more information is available, it would seem judicious to wait before attempting to categorize parasites as r- or K-selected in terms of intra- and interspecific competition.

Longevity: r-strategists - "Short, usually less than one year" (Pianka, 1970).

K-strategists - "Longer, usually more than one year" (Pianka, ibid).

When the correlate for population size was being discussed, it was stated that seasonal fluctuation in population density was a common attribute for parasites. In part, this observation is correct because the generation time of most parasites is less than one year. There is, however, some variability. For example, the trematode *Fascioloides magna* may survive for more than five years in the livers of deer (Blazek, Erhadová-Koctila, and Kortley, 1972), while the closely related fluke *Fasciola hepatica* has a life span of only six months in sheep (Boray, 1969). Life spans of the nematodes *Ascaridia dissimilis*, *Heterakis gallinarum*, *Capillaria caudinflata* and *C. obsignata* are all less than nine months while that of *Syngamus trachea* was shown to be 126 days in turkeys and 92 days in chickens (Barus, 1966). Other parasites, such as some taeniids and schistosomes, are said to be rather long-lived, spanning several years.

It is safe to say that the life span of most helminth parasites is less than one year; the same is true for most protozoa which may have a life span ranging from a few hours to a few days. It would thus be reasonable to conclude that most parasites exhibit an r-strategy in terms of life span.

OTHER CONSIDERATIONS

At the outset of the discussion of r- and K-selection and parasitism, three questions were posed. The first was directed at the feasibility of fitting parasites within the concept of r- and K-selection. The second question referred to the position of parasites within the r-K continuum. Based on the foregoing analysis, it is, first, clear that parasites can be considered within the conceptual framework provided by the notions of r- and K-selection and, second, it is safe to conclude that selection among parasite species has favored the evolution of life history strategies, morphological characteristics and physiological traits which *collectively* suggest the spector of r-selection. This statement must be qualified by noting that some of these features suggest that certain parasites are not at the r- endpoint, but instead lie along the r-K continuum.

The third question was directed at the possible existence of any unique attributes of parasites which would re-enforce conclusions regarding the nature of selection forces which may affect parasites. There are several attributes which may be considered as unique. Foremost among these is the phenomenon of dispersion.

The dispersal and dispersion patterns of a population, or the description of how an organism is dispersed in space and time and the pattern of the eventual distribution of these organisms, are of considerable ecological importance (Cassie, 1962). In describing the dispersion of organisms within a particular habitat, there are three general types of frequency distribution which are recognized. These are (1) a uniform, or underdispersed, population, (2) a randomly distributed population, or (3) an aggregated, or overdispersed, population. On examination of the dispersion patterns of various populations, it has become increasingly evident that most species do not exhibit a uniform, or underdispersed distribution. Exceptions to this generalization might arise when competition for resources is severe or when chemical substances might be produced such that other organisms are prevented from becoming established nearby. If a population is randomly distributed, then the mean density and variance, per unit area, will be equal. Random distributions can be described by the Poisson frequency distribution model. Randomly distributed populations are also apparently rare in nature (Cassie, 1962). The most commonly observed frequency distribution pattern is one of overdispersion, i.e. contagion. In this type of distribution, organisms within the population are found in groups or clumps and the variance exceeds the mean density.

Even though the vast majority of studies on population distributions have focused on free-living organisms, dispersion analysis is also applicable to parasites. While Li and Hsu (1951) were among the first to examine the frequency distributions of parasites within a host population, Crofton (1971) was the first to employ parasite dispersion as a means for explaining regulation of parasite populations. Through his efforts and those of more recent investigators (James and Srivastavy, 1967; Pennycuick, 1971; Schmid and Robinson, 1972; Boxshall, 1974; Anderson, 1974), it has been clearly shown that overdispersion is an inherent characteristic of parasite systems.

A number of theoretical models, e.g. Polya-Aeppli (Polya, 1931), double Poisson (Thomas, 1949), Neyman Type A (Neyman, 1939), log series, log normal, and negative binomial, have been used to describe the frequency distributions of parasite infrapopulations. However, in most cases where studied, the negative binomial model has provided the best fit to the observed distribution.

According to Pennycuick (1971) (also see Crofton, 1971), the distribution of parasite infrapopulations within a host population "may be a negative binomial if there is a departure from randomness caused by any of the following factors:

1. The host is exposed to several waves of infection, each of which attacks randomly, giving rise to a series of Poissons.
2. The infective stages of the parasite are not randomly distributed.
3. The presence of a parasite in a host increases or decreases its chances of acquiring further infections.
4. The sampling units are unequal; for example, the hosts are of different ages.
5. The sampling units change during sampling; for example, if the sampling takes a long time, the age of the hosts will change."

The concept of overdispersion has proved quite useful in understanding the regulation of parasite populations (Crofton, 1971). It is also possible to view the overdispersion concept in terms of competition and, thus, r- and K-selection. Pianka (1970) stated that selection for a K-strategist favors slower development, lower resource thresholds, delayed reproduction, larger body size and iteroparity. These characteristics maximize competitive ability. Conversely, selection for an r-strategist favors rapid development, higher resource thresholds, rapid reproduction, smaller body size and semelparity which, collectively, minimize competitive ability. Most parasites exhibit each of these latter characteristics. Thus, they develop rapidly in response to appropriate environmental cues, they generally reproduce quickly after reaching sexual maturity, they are small in body size and many are semelparous, that is to say, they reproduce but once in their lifetime. Even tapeworms, which are usually considered as being iteroparous, or continuous reproducers, may be thought of as semelparous since sexual reproduction in each proglottid apparently occurs only once.

It can be argued that overdispersion of parasite infrapopulations results in a reduction, or minimization, of competition. At first glance, this assertion may appear paradoxical, especially when it is noted that in many cases, 50-60% of the parasites in a given host population may be recovered from as few as 20-30% of the hosts. For example, approximately 60% of the metacercaria of *Crepidostomum cooperi* are found in 40% of the subimagoes of the burrowing mayfly, *Hexagenia limbata*, at the time of their emergence from Gull Lake, Kalamazoo County, Michigan (Esch, et al., unpublished observations). In this case, the metacercaria are overdispersed and the distribution can be fitted to the negative binomial (the mean metacercaria densities are 7.48 per female mayfly and the variance is 54.76; N = 1100). It must be noted, however, that in this, as well as other host-parasite systems, most of the hosts (70-80%) are fully exploitable in the sense that both space and nutrient resources are capable of sustaining recruitment of new parasites as well as maintaining established infrapopulations. It is also possible, if not probable, that this 70-80% of the hosts are the most likely to be immunologically ineffective in preventing further recruitment of parasites into the infrapopulation. While the majority of parasites would be found in hosts where resources could become limiting, the high r_{max} of *all* parasites, including especially those within the relatively unexploited 70-80% of the host population, would be more than likely capable of supplying the reproductive requirements of the suprapopulation, even if overdispersion produces death in heavily parasitized hosts. Thus, the advantage of overdispersion to the parasite would be in restricting, or reducing, competition in a relatively few infrapopulations. The advantage of such a strategy is clear, since most of the space and nutrient resources required by the parasite species would remain available for exploitation to a substantial portion of the parasites. If overdispersion can be considered in these terms, then it is concluded that it minimizes competition and, in doing so, is a strategy characteristic of r-selection.

Many parasite species display other life history characteristics which may also be considered as strategies for avoiding or minimizing competition so that maximum utilization of resources can be effected. One of the more unique ploys is associated with the host immune responsiveness. It would generally be agreed that immune responsiveness of a host to a parasite is a useful mechanism to protect against over-infection. While probably evolved as a defense system by the host, the outcome of immunity may also provide survival value for the parasite. Bradley (1974) has already pointed out that the host immune response should be considered as an important mechanism in regulation of parasite populations and, thus, in producing stability. Since the immune response is also effective in preventing heavy parasite loads within a host, the resulting reduction in size of the infrapopulation also minimizes the potential for competitive interaction among parasites and should, therefore, be considered as an r-strategy by parasitic organisms (mediated, of course, by the host).

There are a number of mechanisms which insure that parasitic animals have mating partners. These include hermaphroditism, monoeciousness, and protandrous hermaphroditism. For parasitic animals employing such reproductive strategies, there is survival value. An obvious advantage is that mating partners are guaranteed. However, the same strategies also minimize the competition for resources. Thus, the density requirement of a breeding infrapopulation could be reduced by as much as half for species of parasites which reproduce in one of the ways listed above. The same infrapopulation would also cut by a similar fraction the requirement for space and nutrient resources. Disproportionate sex ratios and early death of male parasites following copulation (Chan, 1952; Crofton and Whitlock, 1969; Seidenberg, et al., 1974) could also be considered as selection mechanisms which would minimize the potential for competitive interaction among some parasite species.

The general conclusion has been that parasitic animals exhibit many characteristics of an r-strategist. It is also clear that some species cannot be categorized more toward one end-point than the other and, therefore, occupy a position along the continuum. Indeed, it also seems conceivable that within a single suprapopulation, there could be a variety of genotypes, representing a genome with a high degree of variability with respect to r- and K-strategies. Genotypic variability would be of interest if parasitism is examined in terms of stress, or in terms of epizootic outbreaks within a given ecosystem.

Though somewhat afield of parasitism, Gadgil and Solbrig (1972) presented quantitative evidence that a population of one species of dandelion, occupying a given space, was actually separated into several ecotypes, differing in seed output, proportion of biomass devoted to reproductive tissues, and competitive ability, according to the degree of perturbation within the area. In effect, some ecotypes were more typical of r-strategists, while others were more characteristic of K-strategists.

If the observations of Gadgil and Solbrig (ibid) can be extended to host-parasite systems, then it is possible to see how the concept of r- and K-selection could be used in evaluating the relative stability of a parasite suprapopulation within an ecosystem, or in how the concept could be employed in explaining sudden and unpredicted epizootics. For example, it is conceivable that r- and relatively K-selected biotypes of a parasite species might co-exist within the same suprapopulation. Under more or less constant environmental conditions, individuals exhibiting a predominantly K-strategy would be selected for and the parasite suprapopulation would remain stable. While the K-strategists would dominate within the ecosystem, some individuals, possessing characteristics of an r-strategists would nonetheless persist. Then, suppose the ecosystem is perturbed in a manner in which, rapidly, selection favors the allocation of resources into more progeny rather than fewer. Under such circumstances, the r-strategist would be favored. The result would be a sudden, exponential expansion of the population and, in effect, an epizootic outbreak. In cases where epizootics have been known to occur, a sudden crash in the density of the parasite population has also been reported. In some instances, the sudden decline in parasite density could be associated with the withdrawal or removal of the perturbation. In these situations, selection forces might again favor K-strategists within the suprapopulation. Ultimately, the suprapopulation density would stabilize on reaching the K-asymptote, or carrying capacity. While selection would continue to favor the K-strategist, some r-strategists would remain and the entire sequence of events could reoccur should conditions change.

CONCLUDING REMARKS

To summarize, the basic aim of this presentation has not been to develop a case for support or rejection of the notions or concepts associated with r- and K-selection. Rather, the aim was to examine the physiologic, morphologic and life history characteristics of a functionally similar group of animals, namely parasites, and determine if the analysis will permit a comparison of this group with other groups which may appear dissimilar but which may nonetheless exhibit similar selection strategies. Perhaps such an approach will contribute to the development, or modification, of current views of regulation as they pertain to parasite population biology.

ACKNOWLEDGEMENTS

We want to express our appreciation to Mrs. Lila Spencer and Mrs. Yancey Smith for their tireless effort in deciphering and typing the manuscript. We also thank Mrs. Jean Coleman for preparation of the figures. Preparation of this manuscript was supported, in part, by Contract E(38-1)-900 between Wake Forest University and the United States Energy Research and Development Administration (ERDA) and by Contract E(38-1)-819 between the University of Georgia and ERDA. We should also like to thank Dr. Ronald Dimock for his reading and criticism of the manuscript.

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