THE ECOLOGY OF ENDOPARASITISM IN WILDLIFE POPULATIONS

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Ecology has been defined as the science which deals with lives and habits of organisms in relation to other living organisms and to their environments. This concept has been regarded as a dynamic fluctuating equilibrium including the effects of the environment upon the organism in all phases of its life, its metabolism, and its reproduction (Otto, 1958). It would also include the effect the organism has upon its environment.

The living together of animals of different species, which the ecologist calls animal associations, has intrigued biologists for many years. These symbiotic associations reflect varying degrees of interaction between the species as exemplified by the three types of symbiosis: commensalism, mutualism, and parasitism.

A parasite may be defined as an organism which lives on or in another organism known as the host, and at the expense of the latter. This implies that the parasite does harm to its host. Many individuals view parasites as obnoxious and thus should be eliminated. Still others regard parasitism as a way of life which can be appreciated scientifically. Because the parasite obtains its food from the body of its host, it is physiologically dependent upon the host. The fact that an animal parasite lives within another animal necessarily implies that it is fitted to live in such a habitat. Such fitness is demonstrated by morphological and physiological adaptations. These are organs of attachment, cuticular adaptations which prevent digestion or destruction by antibody action, secretions which neutralize or inhibit the action of the host's enzymes, or behavioral responses which avoid the counteractions of the host.

Parasites are where you find them. There is no disputing this statement, but we may wonder how the parasites were successful in reaching their specific habitats. The endoparasite must be adapted to maintain its existence, and it must be able to feed, metabolize, and reproduce. It must be transmitted to another host in order to preserve the species.

The study of the ecology of endoparasites includes many disciplines: taxonomy, morphology, physiology and biochemistry, pathology, immunology, and epidemiology.

Today we wish to limit our discussion to certain aspects of transmission. What are some of the factors concerned in the transmission of parasites from one host to another? Fundamental to such a study is a knowledge of the life histories of parasites. There are two general types of life-cycles: the direct and the indirect.

A parasitic animal which passes directly from one host to another is said to have a direct life-cycle. It lives in a host where it produces eggs or larvae which leave the host and become adult parasites in another host. In the indirect life-cycle we find at least two biologically different hosts. The host in which the adult parasite lives and reproduces sexually is known as the definitive host. The animal in which the larval stage or stages develop to infectivity is known as the intermediate host. The infective stages in the intermediate host may gain entrance to the definitive host by ingestion, or by penetration of the skin or by being injected into blood or skin by arthropod vectors.

Both types of life-cycles are demonstrated by nematodes, trematodes and cestodes, but the direct cycle is more often utilized by roundworms than by flukes and tapeworms. A group of nematodes, known as the ascarids, demonstrates both types of life-cycles. *Ascaris lumbricoides,* a common parasite of pigs, has a direct life-cycle. The adults live in the small intestine where they feed on its contents, and the females lay eggs. These eggs embryonate outside of the host, and infection of the host is by ingestion of embryonated eggs, the larvae hatching in the small intestine. The larvae immediately penetrate the small intestine and enter the blood stream, and are carried successively to the liver, heart, and lungs. In the lungs they develop to the fourth stage larvae which break out of the lung capillaries into the alveoli and travel through the branches of the "respiratory tree" to the trachea and from thence to the pharynx, and then it is swallowed a second time. It remains in the small intestine and matures. The direct life-cycle is utilized by many species of nematodes such as the strongylids, oxyurids, and trichurids, but they may or may not migrate within the definitive host before taking up their sojourn in the intestine.

Another species of ascarid, *Ascaris columnaris,* which is found in carnivores, utilizes a rodent as an intermediate host. In some of the sea mammals we find a further modification of the ascarid life-cycle as exemplified by *Porrocaecum oecipiens.* The eggs of this worm are eaten by crustacea, which in turn are eaten by fish, a source of food for the definitive host, the seal.

Digenetic trematodes characteristically demonstrate the indirect type of life-cycle. An example is the life-cycle of *Metorchis conjunctus,* a fluge which lives in the bile ducts of piscivorous mammals such as the mink. The eggs are laid in the bile ducts, reach the intestine, and pass out with the feces. The droppings must be deposited in water in order for the eggs to continue their development in certain aquatic snails. The eggs are eaten by the snails and several intermediate stages are produced through polyembryony. This reproduction eventually results in the formation of a large number of cercariae. These leave the snail and penetrate into the skin of fish and encyst in its flesh. The infected fish is then eaten by the definitive host. In this particular life-cycle we have demonstrated two necessary intermediate hosts. Characteristically all digenetic trematodes utilize a mollusc as the first intermediate host. The second intermediate host varies. It may be another snail, a fish, frog, snake, turtle, crayfish, or insect—many different types of intermediate hosts are utilized by different species of trematodes. Some species encyst upon vegetation; and, obviously, these are limited to herbivorous or omnivorous animals.

Tapeworms utilize intermediate hosts in their life-cycles. We can mention the life-cycle of *Echinococcus granulosus,* which has been the subject of considerable study in Alaska and also here in the states. The adult worm lives in the intestine of carnivores, particularly of the Family Canidae, and produces eggs which are eaten by herbivorous animals from contaminated vegetation. Within the herbivore the eggs develop into hydatid cysts, which proliferate many scolices, the infective stage of tapeworms. In North America it occurs generally in deer which are eaten by carnivores. Deer which are killed by hunters are sources of infection of the hunter's dogs which may in turn infect their masters. Obviously, the cycle will be stopped if man becomes infected with the hydatid cyst. The normal cycle then is from carnivore to herbivore and back to carnivore. In *Echinococcus multilocularis* we have a similar cycle; but the intermediate host is a rodent, the cycle going from fox to rodent back to fox. The larval stage of this particular species is not commonly found infecting man, although man may upon occasion become infected with the cyst.

These are only a few examples of the many kinds of life-cycles demonstrated in trematodes, cestodes, and nematodes.

Closely correlated with the life-history of the parasite is the bionomics of the host. Where does it live, how does it live, what does it eat, what are its defecation habits?

Food is the hub of the wheel of life (Chandler, 1955). Many parasites have taken advantage of the food habits of their hosts in getting from host to host. Protozoa and some nematodes with a direct life-cycle utilize a cystic or egg stage as the means of transmission. Such parasites are abundant where there is considerable fecal contamination of the host's habitat. Is the host a cat or a dog? Does it practice sanitary disposal of its excreta? Does it practice coprophagy? This practice facilitates the transmission of some nematodes and protozoa. Host population density affects the degree of contamination of an area, and thereby influences the chances for infection. It is well known that the raising of cattle on permanent pastures year after year results in heavy infections with helminths. The same is true in the raising of poultry, the artificial propagation of quail and pheasants, and the raising of fur-bearers in captivity. This has been demonstrated also in wildlife populations. Erickson (1944) has shown that as the snowshoe hare population increases the percentage of infected animals becomes greater and the worm burden heavier. It must be remembered, however, that much variation in degree of parasitism is seasonal or geographical (Rausch and Tiner, 1949). This brings us to a consideration of climatological and edaphic factors. The effects of moisture, relative humidity, and temperature are very important to the viability of those stages of a parasite which reach the outside world. Characteristically, there is an increase in worm burden during the spring of the year when moisture and temperature are favorable. Summer heat and drought check the parasitic invasion of hosts because of the decimating effect upon the "free-living" stages. Here knowledge of the bionomics of the eggs and/or larvae is essential. What are the minimum, maximum, and optimum temperatures for the development of eggs and/or larvae? How much moisture and/or relative humidity are necessary for survival of these stages? What are the optimum amounts, and what are the maxima? Human hookworm does well in those areas of the world where there is a minimum of approximately 40 inches of rainfall per year. Moreover, this must be evenly spaced. Excessive rainfall is detrimental to hookworm larvae. The type of soil is important for hookworm larvae which do best in a sandy loam. Vegetation may favor their development and survival because it shelters them from the injurious effects of heat, sunlight, and drying.

Referring to our discussion on food habits of the host, some parasites are able to live in many species of animals but are normally not found because the host is not exposed to them. Its food habits are such that the parasite does not gain entrance. The rabbit can serve as a host for the trichina worm but is not infected naturally because it is not a flesh eater. Man in the USA is not infected with the common lung fluke of many of our mammals because he does not eat raw crayfish. This fluke, *Paragonimus kellicotti,* lives in a number of animals which eat crayfish and is a common parasite of man in the Orient where the second intermediate host, freshwater crabs, are commonly eaten uncooked. Also of importance in this regard is the habitat of the host's home range. Pearse (1930) in his study on Nigerian rodents and insectivores found a close correlation between parasites and the host's habitat and habits as did Kuns and Rausch (1950) in Wyoming voles. Closely related species with different habitats characteristically harbor certain parasites which are distinctive to each species. Trematodes requiring aquatic snail intermediate hosts will be found in appreciable numbers, if at all, only in those animals which frequent streams, ponds, or lakes. Anoplocephaline tapeworms, which utilize oribatid mites as intermediate hosts, will be significant only in habitats where there is a heavy population of such mites.

On the other hand, some parasites are very host specific. They live only in closely related animals and can live in no other animal. They are fitted to live only in the environment afforded them by their normal hosts.

To adequately understand the ecology of the parasites of any given host, one should be familiar with all the parasites in an area. Undoubtedly a particular host is exposed to parasites which do not infect it. "Much can be learned of the interrelationships involved when it is known just which host species and which parasites are present in a given area" (Rausch and Tiner, 1949).

In summary, we have noted certain aspects of the ecology of parasitism: life-histories, bionomics of host, eggs, and larvae, climatic and edaphic factors and the habitat. These are but a few of the factors concerned in a comprehensive ecological view of parasitism.

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PRESENT STATUS OF KNOWLEDGE ON THE ECOLOGY OF EASTERN ENCEPHALITIS VIRUS IN THE UNITED STATES

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THE DISEASE

The virus of eastern encephalitis (EE) produces highly fatal disease in humans, horses, and ring-necked pheasants (1-4). Outbreaks have occurred chiefly in states bordering the Atlantic and Gulf coasts. Less than 100 cases of human disease have been reported but mortality exceeds 60% and a large proportion of survivors are seriously and permanently disabled. Thousands of horses have been killed by the disease, usually in localized epidemics involving less than 100 cases; however, over 14,000 cases occurred in Louisiana in 1947. Mortality in horses is about 90% of the clinical cases. EE has produced many epidemics among captive ring-necked pheasants, with mortality of over 80% of involved flocks being common.

Epidemics have always occurred during summer months, chiefly in July, August, and September. In more southern areas they may begin as early as April.

It was suspected on epidemiological grounds as early as 1935 that wild birds were natural hosts and disseminators of the virus and that mosquitoes were natural vectors (5, 6). This suspicion has been amply substantiated by later work (7-11).

THE VIRUS IN NATURE

EE virus has been isolated from more than 20 species of naturally infected wild birds and specific antibody has been detected in more than 50 species. Field studies have shown wide spread of infection through wild bird populations during summer months (11-14). For example, in Massachusetts in 1956 and EE epidemic involved humans, horses, and ring-necked pheasants. EE virus was isolated from 3 of 152 wild birds collected in the affected area and antibody was present in 45%. During the same year in New Jersey, epidemics occurred in horses and ring-necked pheasants. EE virus was isolated from 7 of 143 birds and the antibody rate in resident birds increased from 14% in July to 54% in September. Other studies indicate comparable virus activity in Louisiana and Alabama.

Epidemics have usually occurred during hot, wet seasons when mosquito populations are high. Species of *Aedes, Mansonia,* and *Psorophora* mosquitoes are suspected of being epidemic vectors, but definite proof is lacking. There is strong evidence, however, that *Culiseta melanura* is the primary vector for bird-to-bird transmission of EE virus (8, 10). This species breeds in specialized areas of fresh water swamps and bogs (15). Seventeen virus isola-