ANIMAL PARASITES

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Their Life Cycles and Ecology

Third Edition

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Illustrations by the author

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To my students of the past who have inspired me to learn how to teach parasitology in a more interesting and informative manner, as well as to those of the future who may rightly expect similar treatment of this fascinating subject, and to my wife, Ione Palfreyman Olsen, who encouraged me to do it for them.

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Preface

The third edition of *Animal Parasites* follows the format of the preceding ones. Much new information has been added, together with a large number of text figures. Most of the chapters have been rewritten to include recent advances. All references are given as complete citations. This edition is intended as a text and reference book for all persons interested in parasitology or concerned with it. It is a text for students of biology and parasitology, as well as a reference for veterinarians, extension agents, wildlife personnel, and investigators in advanced aspects of parasitology, including the protozoans and helminths.

The book presents what I consider the basic principles of parasitology essential to an understanding of the subject. They include (1) basic classification for understanding relationships of common parasites, (2) general morphology of adults and larval stages for recognition, (3) patterns of life cycles of the different groups for comprehension of how they live, (4) general ecological requirements of all stages of the parasites in the physical and biological environments, and (5) means of transmission of all stages.

An understanding of these fundamentals provides sound background for a career in applied parasitology or for investigating additional important and practical aspects of the subject. These include ecology of the parasites in the physical and biological habitats occupied by them; physiology of all stages of the parasites in their various microhabitats; investigation of ultrastructure of the different stages to recognize the organelles and the significance of their roles; nutrition of the various stages and how it is achieved; development of immune processes and their roles in limiting parasites in the hosts; host-specificity and the nature of its operation; geographic distribution of the parasites and their intermediate hosts; seasonal distribution of parasites; and, finally, the application of the great body of biological information to the development of methods of controlling parasites to prevent economic loss, morbidity, disease, suffering, and death.

The life cycles presented here have been chosen because they are representative types, are well known for the most part, and generally represent parasites that the students find in animals that they know and see about them. In selecting parasites from common hosts whose habits and ecological environments are familiar, students are able to understand and appreciate better the biological problems associated with the phenomenon of parasitism.

Parasites of humans are not excluded, but neither are they emphasized. Common species that are likely to occur, such as pinworms, entamoebas, taenias, and ascarids, are included. Other important species, such as the filarioids, medina worm, hookworms, and others known from man and treated extensively in texts on clinical parasitology, are represented here by closely related species found in domestic and wild animals of this country.

There is no extensive treatment of physiology, immunology, pathology, and medication. In cases where reference is made to these subjects, it pertains to the species under consideration and represents basic aspects of special interest.

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Parasitism

Animal parasitism is a way of life in which one species, the *parasite*, living in or on another species, the *host*, gains its livelihood at the expense of the latter. The host furnishes both the habitat and the food for the parasites which are physiologically dependent on it for life. Moreover, the parasite always does damage in some degree to its host.

Parasitology is the study of parasitism. It includes the morphology, classification, biology, and physiology of the parasites. In addition to these, it involves the relationships between the parasites and their hosts, as well as the reactions toward each other. Its purpose is to lead to a fuller understanding of these relationships and the results of them on both the host and the parasite.

Development of Parasitism

As phylogenetic groups of animals appeared in the beginning of our planet, they spread throughout the world, occupying all the available ecological niches of the physical environment. Their bodies, both inside and outside, constituted new ecological biohabitats ready for occupancy by those species that possessed the potential and capability of adapting to them. Many different phylogenetic groups of animals invaded this new living habitat but few were capable of adapting to it in a large measure of success. The protozoa, the helminths, and some of the arthropods were the most successful. They constitute the important groups of parasites known today. This biotic association is one of *symbiosis* in which animals live together in varying degrees of dependency between the *host* and the *symbiont*.

Symbiotic Relationships. Three degrees of symbiosis are generally recognized. They are *mutualism*, *commensalism*, and *parasitism*.

Mutualism constitutes one type of relationship in which the host and the symbionts are physiologically dependent upon each other and the relationship is mutually beneficial. Termites and their intestinal protozoa are an example. The termites provide the habitat and the food in the form of wood (cellulose) which they cannot digest. The protozoa in the intestinal habitat, however, are capable of hydrolyzing the wood for their own and the termites' use. Ruminants and other herbivores with their rich flora of bacteria and fauna of protozoa are additional examples of mutualism wherein both the host and the symbionts are physiologically dependent on each other.

Commensalism is the condition in which the host provides the habitat and food for its symbionts which live without benefit or harm to it. The symbionts, however, are physiologically dependent on the host for their existence. The host, on the other hand, is not dependent on them. Certain of the protozoa living in the alimentary canal of man or on the bodies of hydra are examples of commensals. Other examples of commensalism appear among the marine animals, particularly sea anemones and crabs.

Parasitism is that relationship in which the symbiont is physiologically dependent on the host for its habitat and sustenance and at the same time may be harmful to it. All of the trematodes, cestodes, acanthocephalans, and many of the protozoa and nematodes are examples of true animal parasites.

Kinds of Parasites

The degree to which parasites are dependent on their hosts ranges from intermittent visits for food, as in the case of mosquitoes, to one of complete dependence inside the body with no free-living stage, as occurs in the plasmodia and trichinella. Several groups of parasites are recognized, depending on their relationship to the host.

Location *on* or *in* the body of the host serves as one basis for dividing parasitic animals into two groups. *Ectoparasites* live on the external surface of the body of the host or in cavities that open directly onto the surface. They include monogenetic trematodes, lice, mites, and ticks. *Endoparasites* live in the bodies of the hosts, occurring in the alimentary canal, lungs, liver, and other organs, tissues, cells, and body cavity. Examples are tapeworms, digenetic trematodes, nematodes, and protozoa.

The amount of time spent on or in the host serves as temporal basis for dividing parasites into two major groups. *Temporary parasites* visit the host for food. Having satisfied their hunger, they leave. Bloodsucking arthropods and leeches are examples. *Stationary parasites* spend a definite period of development on or in the body of the host. They may be divided into groups, according to the amount of time spent with the host. Those which remain with the host for only a part of their development and then leave to complete it and continue a nonparasitic life are known as *periodic parasites*. Botflies and mermithid nematodes represent this group. Parasites that spend their entire existence in hosts except for the times they occur free while transferring from one host to another are designated as *permanent parasites*. The trematodes, cestodes, acanthocephalans, nematodes, and protozoa are examples.

Parasites found in unusual hosts, or unusual places in normal hosts, are designated by terms indicating the nature of their abnormalities. *Incidental parasites* are those which occasionally appear in unusual hosts under natural conditions. The double-pored tapeworm of dogs is found sometimes in children, or the common liver fluke of sheep occurs in dogs or cats. *Erratic* or *aberrant parasites* are individuals of a species that wander into unusual places in the normal host. Ascarids of swine and man may wander from the intestine into the liver, body cavity, or nostrils.

All of the parasites listed in these categories are *obligate parasites*. They are unable to exist without some degree of development on or in the host. A few normally free-living animals, on the other hand, are able to exist for short periods in the bodies of other animals when accidentally introduced into them. They are spoken of as *facultative parasites*. Representatives of them are certain free-living nematodes of the genera *Rhabditis* and *Turbotrix*, and fly maggots such as those of the cheese skippers (*Piophila casei*) and some of the blowflies.

Properties of Parasitism

The basic properties of parasitism appear in the many adaptations necessary for the parasite to live in its biotic environment, to reproduce, and to infect new hosts. These interactions between the two living organisms give rise to both consequences and specializations for each participant, which become fixed through inheritance.

Adaptations for Parasitic Life. The basic physiological requirements of a parasite are similar to those of free-living animals. They are habitat, food, and reproduction. The problems in achieving these requirements under the conditions of parasitism are complex, and special adaptations have evolved to meet them. Probably the one basic underlying characteristic of parasitism is that of adaptation. One writer has called it the hallmark of parasitism.

In order to live on or in a host, the parasite must evolve structures for adhering to it. Such adaptations appear in the tarsi of Anoplura for holding on to hairs. Monogenetic trematodes and acanthocephalans have rigid hooks for attaching to the host. Suckers for the same purpose are highly developed by trematodes and cestodes.

Living in a host necessitates means of leaving it in order to reach new ones. Parasites of the alimentary canal, lungs, liver, and reproductive system utilize the natural outlets of these organ systems as avenues of exit for cysts or eggs. Those living in the bloodstream and tissues generally utilize other animals or means to leave their hosts. Bloodsucking arthropods serve as the route by which malaria and related protozoans and the microfilariae of filarioid nematodes escape from the body and in which further development occurs. Dracunculid worms in the subcutaneous tissues vesiculate the epidermis, forming openings through which the female releases active larvae into the water. Others (trichinella, cestodes, and trematodes) depend on the digestive processes of predators or scavengers which serve as definitive hosts to release them from the tissues of their intermediate hosts. *Capillaria hepatica* eggs in the liver of rodents may be freed by postmortem decomposition of the host or digestion of it by another animal, after which development of them proceeds under favorable conditions in the physical environment.

Means of survival and development are essential during the interval of transfer from one definitive host to the next. This transfer involves a period of development in the soil or water, in the case of parasites having a *direct* life cycle, or development in the body of one or more intermediate hosts with those having an *indirect* cycle. In parasites with a direct life cycle, protective cysts, thick egg shells, or the retained cuticle of larvae are adaptations to protect the stages free in the soil against the hazards of desiccation and freezing. Species having an indirect life cycle may depend on some of the features listed above for protection during the time of transfer between their several hosts. But since practically all of their development takes place in the body of one or more intermediate hosts, their adaptational requirements must be adjusted to the biotic environment of the bodies of several species, often from different phyla. An example is the lancet fluke, *Dicrocoelium dendriticum*, which lives and develops successively in sheep, snails, and ants.

Transmission of the infective stage of the parasite to the next host in the developmental cycle is accomplished by one of three methods. They are *passive*, *active*, or *inoculative*. Passive transmission occurs when the infective stages of the parasites contaminate or infect the food or water of the host and are swallowed with them. Examples are the eggs of ascarids, cysts of *Entamoeba*, and larvae of trichostrongyles. Infection of food occurs in the larval stages of trematodes, cestodes, acanthocephalans, and many nematodes. Active transfer occurs in the hookworms, and the miracidia and cercariae of trematodes. These parasites actively penetrate the bodies of their hosts upon coming in contact with them. Often responses such as thermotropic, geotropic, as in the case of hookworm larvae, or chemotropic, as occurs in miracidia toward their snail hosts, aid in bringing the host and parasite together. Inoculative transmission occurs when the infective stage of the parasite has developed in the body of a bloodsucking arthropod, as with *Plasmodium* in mosquitoes. Transfer back to the vertebrate host is accomplished when the arthropod inoculates the parasites into the host while feeding upon it.

Survival within the host is dependent upon the ability of the parasites to withstand the destructive action of the digestive juices and the immunological reactions of the host against them, or to reach microhabitats within the host where the required nutrients for growth and reproduction are available in adequate amounts.

The most successful parasites have evolved a biotic potential of great capacity in order to compensate for the tremendous losses of eggs or larvae, or both, incurred in the completion of their complicated life cycles. This is accomplished by an increased production of eggs, as in the ascarids and cestodes, the duplication of sex organs in segments, as in cestodes, or vegetative reproduction extending over long periods of time such as occurs in the sporocysts or rediae of trematodes and scolices in cestodes (*Echinococcus* and *Multiceps*).

Specific Host-Parasite Relationships. Parasites normally do not infect different species of animals at random under natural conditions but show varying degrees of preference for hosts and for habitats within them. Thus parasites of horses, cattle, dogs, or humans are most likely to be found in their respective hosts. Moreover, parasites of the intestine, the liver, or tissues occur with marked regularity in these sites. This condition is designated as *host specificity*, *organ specificity*, or *tissue specificity*, as the case may be.

Specificity of Host-Parasite Relationships. Specificity of host-parasite relationships is determined by the success of the parasite to invade, occupy, and reproduce in certain microhabitats inside or on the outside of the bodies of hosts. The factors involved in the development of host specificity among parasites are opportunities for contact between them and their hosts, followed by entrance, adaptation, establishment, nourishment, and reproduction in them.

Opportunities for infection of the host are present only when it and the parasite come in contact with each other under favorable conditions. This occurs during periods when developmental, kinetic, or behavioral activities of the parasite and the host bring them together.

Ability to invade the host and survive in it involves the capabilities, requirements, and susceptibilities of the parasite. Structural properties of the integument may be beyond the capability of the parasite to penetrate, thereby serving as a barrier. The physiological properties of the tissues or organs may not meet the requirements of the parasite, making growth and development impossible. Susceptibility to antibodies produced by the host in response to the presence of the parasite may prove lethal to it or produce an environment unfavorable to growth and reproduction.

Chemotropic response by parasites to substances elaborated by hosts leads to host, organ, or tissue specificity. The miracidia of trematodes are attracted to their specific snail hosts by certain substances in the mucus secretions. Parasites in the body of hosts are directed to specific organs or tissues through their chemotropic responses to them. Young liver flukes, *Fasciola hepatica*, *Dicrocoelium dendriticum*, and *Clonorchis sinensis*, liberated from their cysts in the small intestine of the definitive host, find their way to the bile ducts, each by its own route, doubtless being directed by different stimuli originating in the liver. In cases where distribution is directed by chemotropic responses, parasites accumulate in specific hosts or tissues within them. In the absence of such responses, they occur at random in species or tissues. The cercariae of echinostome flukes encyst in a number of species of snails, and trichinella larvae may be found in the skeletal muscles of many species of mammals.

A single species of parasite may be limited to one species of host, as in the case of the beef tapeworm *Taeniarhynchus saginatum* in man. On the other hand, a species occurs in hosts as widely separated as orders, such as the trematode *Plagiorchis muris* in birds, rats, and humans.

Substances in certain organs or tissues become inimical to parasites and interfere with their development in them. After chicks become a few weeks old, the goblet cells of the mucosal lining of the intestine develop and secrete mucus which hinders the establishment and development of the larvae of *Ascaridia galli*.

The specific nutritional requirements of parasites must be satisfied if they are to succeed. These are developed through the evolutionary processes of host and parasite, resulting in host specificity.

Effect of Parasitism on the Evolution of the Host Species

Parasitism may be considered as an evolutionary pressure in which the host and parasite adapt to each other through a selective process. Since parasitism has a deleterious effect on the host, it may be manifested in lowered vitality, reduced rate of reproduction, slower growth, or death of infected individuals. This can result in extinction of a species or it can lead to a change in the population through the selection of resistant species or strains. Host adaptation to parasitism develops from selective pressure resulting in strains better adapted to resist or tolerate parasitism. This is accomplished through the evolution of antibody responses on the part of the host.

Effect of Parasitism on Individual Host

The effect of parasitism on the individual host may be *injurious* or *defensive*. Injurious effects show a wide range of severity, leading to manifested disease often resulting in the death of the host. When parasites, such as hookworms in man or trichostrongyles in cattle and sheep, affect the entire population, the effect of the disease is masked and often not recognized. The less severe effects of parasitism are kept in repair by the host, and therefore are not readily detectable. The mechanisms of injury are mechanical, chemical, inflammatory, and the introduction of pathogens.

Mechanical injury involves destructive action such as perforation of an organ (ascarids, acanthocephalans), destruction of cells (coccidia, plasmodia), piercing tissues (whipworms, mosquitoes), chewing (Mallophaga), obstruction of a lumen (ascarids, cestodes), or the interference in transfer of foods across cell membranes (*Giardia*).

Chemical injury results from secretions by the parasites. Hookworms secrete substances from the cephalic glands that interfere with the blood. One of them is an anticoagulant that causes the blood to flow freely, even after the worms detach and move to new sites, and another depresses hematogenesis. *Cysticercus fasciolaris* of the cat tapeworm is carcinogenic in the liver of rats.

Parasites rob the host of essential nutrients. Trichostrongyles and hookworms feed on blood. Moreover, the injection of the anticoagulant factor by hookworms while feeding results in a great loss of blood through bleeding into the intestine. The broad fish tapeworm, *Diphyllobothrium latum*, of man absorbs vitamin B_{12} from the tissues of the intestinal mucosa and stores it in its own body.

The introduction of pathogenic organisms such as bacteria (*Clostridium novyi*) by the common liver fluke into the liver of sheep, rickettsiae (*Neorickettsia helminthoeca*) into the tissues of the intestine by the salmon poisoning fluke of dogs, or protozoa (*Histomonas meleagridis*) through the eggs of the cecal nematode into the alimentary canal of turkeys results in a high mortality among these hosts.

Defensive reactions to invasion or attack by parasites are aspects of physiological or conscious responses by the host against them. Inflammatory responses of a general or local nature are often the first reaction to the presence of parasites. They are primarily cellular and are divided into relatively distinct but overlapping stages of 1) temporary localization and destruction of parasites, as in the case of the cercariae of blood flukes of birds that infect humans, causing papules; 2) walling off or encapsulation of the invaded area, as seen in infection by the large American liver fluke, *Fascioloides magna*, of Cervidae in cattle; and 3) repair of damaged tissue, as occurs in light infections of amebiasis. Antibodies may destroy, localize, neutralize, or interfere with the reproduction of parasites and thereby serve as secondary defenses. Conscious efforts are made by the host to avoid parasitism by fleeing, as cattle do from botflies, or bunching, in the case of sheep as a protective measure against nose bots.

Evolutionary Effects of Parasitism

Once parasitism has been achieved, it proceeds by its very nature to exert a definite directive influence on the evolution of the host and the parasite. In the biotic environment, the parasite is isolated in the body of the host and confronted with the dynamic defensive mechanisms of it. The host, which constitutes the environment, is attacked and injured by the parasite. Improved relations on the part of each are indicated. In order to be successful, the evolution of parasitism must be toward better adaptation between the host and parasite. Any other course would lead to the ultimate destruction of one or both.

The direct force in achieving better adaptation between parasites and hosts is natural selection. The conditions for it are excellent. Through isolation of the parasites in the host, a population of genotypes of parasites is evolved that is adapted to meet more successfully the resistive efforts of the host. By the same selective forces, strains of genotypes of host animals appear whose antibody systems have evolved to cope more adequately with the destruction caused by the parasites in them. Thus, through the processes of isolation and natural selection, populations of parasites and hosts with specific tolerances for each other have developed.

Life Cycles of Parasites

The life cycles of parasites are complex and the physical and biological requirements for completing them are manifold and exacting. In order to surmount the many adverse conditions encountered in the course of maintaining themselves, parasites have developed a great reproductive potential together with the means of protection against physical hazards. In spite of the great odds, sufficient numbers of them succeed to assure continuity of the species.

The life cycles fall into two basic types. They are 1) the direct one with only the definitive host, and 2) the indirect one with a definitive host and one or more intermediate hosts. Parasites with a direct life cycle have a free-living phase, except for a few species, during which they develop to the infective stage. Those with an indirect life cycle usually, though not always, have a free-living stage between some of the hosts.

The Protozoa have both types of life cycles among their members. In the Sporozoa, which have both types of life cycles, there are intermediate stages such as trophozoites, merozoites, sporozoites, and gametocytes which may occur in a single host in the case of the direct type of cycle or in two hosts in the indirect type (Plate 33).

Among the Trematoda, the Monogenea and most of the Aspidogastrea have the direct type of life cycle. The stage hatching from the egg is a larva that develops directly into the adult. Others of the Aspidogastrea and all of the Digenea have an indirect life cycle involving mollusks. In the Digenea, the egg produces a miracidium whose development in a mollusk produces the sporocyst, rediae, and cercariae. The cercariae, with the exception of several families of blood flukes, encyst on objects or in other animals and develop into metacercariae which are infective to the definitive host upon entering the alimentary canal (Plate 83).

In nearly all cases, the Cestoda have one or two intermediate hosts in the life cycle. The eggs hatch into a six- or ten-hooked larva. In the Proteocephala and Pseudophyllidea, there is a procercoid and plerocercoid larval stage, usually each in a different intermediate host (Plate 100). The Cyclophyllidea have three basic types of larvae in the intermediate hosts (Plates 92, 100). They are the cysticercoid, the dithyridium, and the vesicular types. The vesicular type has such variations as the cysticercus, strobilocercus, coenurus, and hydatid.

All species of Acanthocephala have an intermediate host. An acanthor hatches from the egg in the intestine of the intermediate host and develops into an acanthella and a cysticanth in succession. Species infecting aquatic vertebrates usually have aquatic invertebrates as the intermediate host; those in terrestrial vertebrates usually have terrestrial invertebrates as the intermediaries.

The Nemathelminthes have both a direct (Plate 141) and an indirect (Plate 142) type of life cycle. The larvae pass through a series of four molts to become adults. Some of the molts take place in the egg, in the free-living phases, and others in the intermediate and definitive hosts.

While these are basic patterns on which broad principles of the parasite life cycles can be based, the individual cycles in each of them often vary greatly within the fundamental plan. Some parasites, such as the sporozoans, trypanosomes, trichinella, and filarioids, with intermediate hosts, have no free-living stages. In others, such as *Probstmyria viviparus* and *Hymenolepis nana* (Plate 98), the eggs may hatch and the larvae develop to sexual maturity without ever leaving the definitive host.

The life cycle of each parasite presents its own peculiarities. Solution of it requires a broad knowledge of the physiology, biology, and ecology of the parasite and all of the hosts involved. The elucidation of the life cycle of a parasite, or, indeed, a part of it, is a distinct challenge and a gratifying achievement.

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Ecology of Parasitism

Ecology refers to the relationship of an organism to its environment for essentials necessary for the life processes. In the case of parasitic animals, the requirements for development and survival in the physical environment outside their hosts include favorable temperature, adequate moisture, sufficient oxygen, and, in some parasitic stages, nutriment. In addition, there must be protection from the lethal effects of freezing, heat from direct sunlight, and desiccation. For some species, the physical environment provides stimuli for 1) hatching of the eggs of many trematodes and nematodes, 2) direction of movement, such as cercariae swimming to or away from light, 3) periodic activity, shown by trichostrongyles that migrate up and down grass blades in response to light intensity, diurnal periodicity of microfilariae, and time of day when cercariae leave their snail hosts, and 4) molting of first and second stage strongyles and trichostrongyles.

The internal, or biological, environment in or on the bodies of host animals provides parasitic animals with stimuli for hatching of eggs and growth of larval stages, nutriment, site-finding, and a habitat favorable for reproduction. The biological environment, like the physical, may be inhospitable in some respects. The host may react toward the presence of the parasite by producing antigens that prevent it from becoming established and reproducing.

Only when conditions in the external and internal environments are met at an adequate level can parasitic animals survive, develop to the reproductive stage, and be transmitted to other hosts.

The ecological adaptations of parasites of terrestrial hosts have evolved to meet the exigencies of the external environment. They include thick-shelled eggs, ensheathed larval