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Introduction to Animal Parasitology

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Chapter 1

Introduction to Animal Parasitology

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Introduction

One of the most fascinating things that a person can experience in the complex realm of biology is the discovery of an animal living inside another animal. If this discovery takes place at an early enough stage in the development of a young person's view of the world, that is, before the rules and regulations of what of society thinks, and before what is good and what is bad are perfused into a learner's mind, the first discovery of living-motile trematode worms living inside the lungs of a frog or of tapeworms inhabiting the gut of a rodent can be exhilarating and a positively unforgettable experience. The questions that arise when these kinds of animals are encountered for the first time are innumerable and, if answered carefully and perhaps fully, may lead to more and more questions, and hopefully, more and more answers.

Many students of biology first begin to investigate parasites and parasitism via the initial study of the ecology, behavior, or systematics of a species of a free-living organism. That is, the free-living animal (pick your favorite species) is being studied for any of a myriad of reasons and during the investigations, those doing the work discover that there may be several species of parasites occurring in or on (or, more likely, both) their study animals. This discovery can occur for other reasons not related to **parasitology** at first, but then leads to investigation of parasitism.

True **parasitologists**—those who are intrigued with the intimate associations of parasites and are interested in the biology of the parasite itself—may become intensely focused on a single group, like tapeworms of rodents or gregarines of beetles or damselflies, for instance. Other students of parasitology may focus on the complete endoparasite fauna of a group of insects, fish, mammals, birds, amphibians, or reptiles. It is not unusual for a parasitologist to spend their whole career studying a single group of parasites pretty much to the exclusion of other parasites, as did Odile Bain, who worked on filarioid nematodes (phylum Nemata: superfamily Filarioidea) and Marie Claude Durette-Desset who works on trichostrongyloids (phylum Nemata: superfamily Trichostrongyloidea), both in the Laboratoire des vers, French National Museum of Natural History. Another example of a working parasitologist is Donald W. Duszynski from the University of New Mexico, who followed the path initially laid out by his mentor, William C. Marquardt at Colorado State University. Duszynski chose to focus the bulk of his entire career on protozoan parasites called the coccidia.

Humans—Including Scientists—Beginning to Notice Parasites

Even though the recognition of parasites and of parasitism had a recorded beginning in ancient Greece and China (Hoeppli, 1959), there is no doubt that parasites were known as part of the natural fauna by the earliest of peoples. For example, in the early 1950s, the nomadic Nunamiut Eskimo hunters in the Brooks Range of Alaska knew of and routinely recognized the strobilar (adult) stages of cestodes in the intestines of carnivores and other mammals and they recognized the larval stages of the cestodes in the viscera of the caribou that they prepared and used for food and shelter (Robert L. Rausch, personal communication; Rausch, 1993).

The first studies of parasites of animals and resulting scientific publications started during the late 1700s and early 1800s with formal publications by Johann Gottfried Bremser, Carl Asmund Rudolphi, Karl Moriz Diesing, Raphaele Molin, A. F. Schneider, R. von Drasche, Peter Simon Pallas (shown in Figure 1), Karl Theodor Ernst von Siebold, Johann August Ephraim Goeze, Karl Georg Friedrich Leuckart, Constantine Janicki, Otto von Linstow, and others. Much of the work that was originally published by Molin and Rudolphi originated from the collections made by Johann Natterer (see Guerrero, 2021) and Hermann von Ihering (see Klassen, 1992; Brooks and McLennan, 2002) during collecting expeditions into the

Figure 1. Portrait of Peter Simon Pallas. Source: Artist, Ambroise Tardieu; reproduced by Raikov, 1952; digitized by Kouprianov, 2006. Public domain.

Amazon region of Brazil. In the late 1800s, Leuckart trained many **helminthologists** in his parasitology laboratory in Leipzig, Germany including Henry Baldwin Ward and others.

As scientific knowledge of the natural world increased during the early 1800s, studies of the natural history of parasites produced increasing numbers of publications. Scientists wanted to know what these animals were and how they got where they were being discovered. It was soon revealed that some parasites had very complex **life cycles** and that parasites were extremely common in nature. Through time, as students of parasite diversity studied **transmission patterns**, **life histories**, and **pathologies**, and then much later, researchers put these together in **phylogenies**, more knowledge was generated that enabled new testable ideas to develop in ecology and evolution (Brooks and McLennan, 2002). The development of the ecological and evolutionary ideas that used parasites as indicators of both biogeographical and ecological relationships was aptly named **parascript** by Harold Winfred Manter (1966). Manter's research program in parasite **systematics** was foundational in the field of parasitology for the subsequent development of parasite phylogenetics and ecology which was ultimately articulated as a research program called **Historical Ecology** that was first outlined in a talk by Daniel R. Brooks (1985) at the Systematics Symposium of the Missouri Botanical Garden organized by Peter Raven. Brooks realized that Manter's insight was derived from his deep knowledge and understanding of the **biological diversity** of trematodes that occurred in marine fishes on both sides of the isthmus of Panama, even though at the time, there was not a firmly established method (in the English-speaking world) of consistent analysis of phylogeny (Manter, 1966). Subsequent groundbreaking work in the area of parasite phylogenetics and biodiversity was done in parasite systematics with the publication of the book Parascript: Parasites and the Language of Evolution by Brooks and McLennan (1993). For more information on the history of animal parasitology, see Janovy's chapter (Chapter 68) in this volume, as well as Sattmann (2002; in German) and Hoeppli (1959). As mentioned above, the parasitic way of life is one of the most common—if not the most common—way of protozoan and animal life that exists. It is likely that more than half of all species of organisms are parasites, and many are of very great economic and medical importance. Some of the most devastating diseases of humans, such as malaria, trypanosomiasis, and filariasis, are caused by parasites, and the economic loss caused by parasites of plants and animals worldwide reaches the equivalent of billions of United States dollars every year.

Definition of a Parasite

The concept of a **parasite** and its **host** essentially refers to the biological tension between 2 organisms that live physically adjacent to one another. With the classical definition of a **parasite** as **an organism living on or in another organism (the host) and usually causing some harm to the host**, the parasite sounds like it is merely a bad thing with respect to the host; and this definition works for the most part since most parasites probably *do* harm the host. In some species, the harm can be minuscule and undetectable, without causing discomfort to the host, or the damage can be significant, actually killing the host. For example, pinworm nematodes probably don't do very much to decrease the ability of their hosts to go about their daily lives or produce a normal number of offspring and live to old age. On the other hand, species of the phylum Acanthocephala, known as the thorny-headed worms, can cause a great deal of harm to their **definitive** or **final hosts** by penetrating the mucosal layer of the small intestine with their proboscis and sometimes the proboscis may penetrate the muscularis mucosa through the serosa into the peritoneal cavity, causing peritonitis, and when this occurs, the host usually dies.

Parasitism, beyond the classical definition provided above, can be defined in a very wide sense, that is, as **a close association between 2 organisms, in which a parasite depends on a host that provides some benefit to it** (usually nutrition or food, depending on the group of parasites), and the parasite does not always damage the host (as noted above, pinworms of rodents are good examples of this). A parasite can be very small relative to the size of the host—and most parasites *are* much smaller than the host; however, some parasites can reach huge sizes, and those that become numerous or are very large can even drain their host's blood of essential nutrients.

Parasitology is usually restricted to single celled eukaryotic, or protozoan (also called protistan) and multicellular or metazoan parasites, whereas many groups of organisms that lead a parasitic way of life, such as some fungi and bacteria, are usually instead included in the domain of microbiology, while viruses are studied in virology. However, it really depends on convention. In France, for example, fungi are often studied by parasitologists in addition to the helminths and protozoans or protistans.

Different authors use different definitions for parasitism, depending on their perspective or research interests. Thus, a medical parasitologist will stress that a parasite causes certain diseases and will exclude certain species from the definition which have no apparent ill effect on the host. A zoologist might be more interested in the physiological and morphological adaptations of a parasite to its host or of the host to its parasite. An ecologist may be more interested in the interactions of the parasite on its host and the animal populations with which parasites live, while an evolutionary biologist may be interested in the evolutionary interactions among parasites and their hosts without too much regard for the individual species of animals that are being studied. The definitions presented here are from the general perspective of a parasite **systematist**, one who is primarily concerned with the understanding of parasitism from the aspect of parasite biodiversity, how they evolved and are evolving, and any and all relationships among them (and their hosts).

Associations Related to Parasitism

Some types of ecological associations resemble parasitism in various aspects and cannot always be unambiguously distinguished from a parasitic relationship, either because little is known about a particular species or because intermediate forms exist. Such ecological associations include: Predation, commensalism, phoresis, mutualism, and symbiosis sensu stricto (meaning, in the strict sense). In the case of **predation**, the predator usually kills and eats another animal, the prey. In the case of **commensalism**, an organism associated with a host uses food found in the internal or external environment of the host and there may be no close phylogenetically determined relationship with the host or host group. For example, many species of barnacles and isopods can take up residence on the external surfaces of whales. These can then be termed **ectocommensals** (**ecto** = outside of the host). In **phoresis**, one organism uses another only for transport and/or protection. Barnacles can again serve as an example: Some species live attached to the skin of whales, by which they are carried around finding new sources of pelagic food (plankton). A **mutualistic** association is one in which both host organism and the associated species benefit. The Australian mistletoe bird *Dicaeum hirundinaceum* feeds on the seeds of mistletoes which are plants that derive most of their sustenance from their host plants, and the mistletoe depends on the bird for dispersal of its seeds through space. **Symbiosis** (sensu stricto) is an extreme form of mutualism, in which the association is compulsory, that is, both partners (symbionts) benefit and cannot live without each other. Very ancient examples of symbiosis are organelles (specialized cell components) of all protozoan (unicellular) and metazoan (multicellular) animals and plants, which are thought to have arisen by the joining of originally free-living organisms. However, the term symbiosis is also occasionally used in a wider sense that can include the phenomena of parasitism, commensalism, phoresis, and mutualism.

That a distinction between the various kinds of associations is sometimes difficult to make is shown by the observation that the same organism may sometimes be a parasite, commensal, mutualist, or predator, depending on the circumstances. Thus, oftentimes, the amoeba *Entamoeba histolytica* may feed on bacteria in the intestine of humans without causing any damage, or it may live as an often-fatal pathogenic parasite ingesting red blood cells and sometimes penetrating through the gut wall into the abdominal cavity, with fatal consequences. Some parasites may even improve the well-being of their hosts when infection intensities are low, but this is an understudied area.

Kinds of Parasitism

Lice, ticks, fleas, some monogeneans, and many crustaceans such as isopods and barnacles, as alluded to above, are **ectoparasites** that live on the surface of animals. Nematodes (such as species of Oxyurida or Oxyuroidea), tapeworms (such as fish, beef, and pork tapeworms), flukes (also known as trematodes, such as liver flukes, eye flukes, and blood flukes), and coccidian parasites (such as *Plasmodium*, which causes the disease malaria in humans) are examples of **endoparasites** found in the tissues or within the organs of their hosts. Cestodes and trematodes are **obligate**

parasites which cannot survive without a host at least for part of their life cycle, whereas some maggots (larvae of flies that usually feed on decaying organic matter) may be **facultative parasites**, which infect living animals only occasionally (note that there are plenty of species of flies in which their larval stages are parasitic in vertebrates and cannot live anywhere else). **Permanent parasites**, such as most parasitic helminths, including trematodes, cestodes, and nematodes, are organisms that are parasitic on or in a host over long time spans, whereas **temporary parasites,** such as most leeches, are parasitic only intermittently.

An example of a **sexually dimorphic** parasite is the chigoe flea *Tunga penetrans* Linnaeus in which only the female is a permanent parasite—usually on the toes of some hapless human or some other mammal—and the male may move around from toe to toe and from host to host. Some species of parasites are selective in their parasitic existence such as species of the phylum Arthropoda that range in diversity from marine gnathiid isopods (phylum Arthropoda: subphylum Crustacea: class Isopoda) to terrestrial chigger mites (class Acari: family Trombiculidae). Some species in these 2 groups are parasites only as larvae, thus they are referred to as **larval parasites**. In this example, the isopod larvae live on marine fish and suck their blood, yet when they molt to the adult stage they live the rest of their lives eating detritus in the benthic zone of the sea floor. The trombiculid mites (family Trombiculidae) exist as adults that eat detritus in the soil and they lay eggs there that hatch into larvae called chiggers that are the torment of humans and other mammals worldwide. Other larval parasites include the cysticercoids of hymenolepidid tapeworms (phylum Platyhelminthes: class Cestoda: family Hymenolepididae) that live in mites or beetles as larvae and mature to adults in their rodent final or definitive hosts. However, many organisms are **parasitic only as adults** and they are associated with a host for all, or at least part, of their sexually reproductive phase.

Female mosquitoes and some fly larvae like the Congo floor maggot (*Auchmeromyia luteola*; see Zumpt, 1965) are **periodic parasites** which visit a host periodically. In this example, the *A. luteola* maggot comes out of its daytime hiding place in the evening and fills up on the blood of a sleeping human, and then goes back into the floor to wait until the next feeding session. When individuals of the same species parasitize other individuals of the same species, they are referred to as **intraspecific parasites**. This type of parasitism is not very common but does occur. An example is that of males of some deep sea fish that live permanently attached to females of the same species, absorbing food and deriving physical protection from the female. **Hyperparasites** (of the primary, secondary, tertiary, etc. degrees) are parasites of other parasites. For example, some protozoans infect helminths (worms) in the intestine or tissues of fishes, and this also occurs in nematodes that have flagellated protozoa (*Histomonas meleagridis*) in the uterus of females that are actually transmitted to the next galliform bird host such as chickens and turkeys (class Aves: order Galliformes) and are protected in the eggs of the nematode. **Kleptoparasites** are animals which force others to regurgitate or drop their food and then steal and eat their prize, and this is an example of behavorial parasitism. Frigate birds and some hawks chase other birds in flight. Cowbirds and about 50 species of cuckoos are **brood parasites**, that is, they lay their eggs in the nests of other birds where they are incubated by and cared for by the parental birds of the nest they have invaded. **Microparasites** include viruses, bacteria, protozoans, and some small worms (helminths), which reproduce in or on the host, sometimes inducing immune responses in vertebrate hosts. **Macroparasites**, that is, large-bodied parasites, include most helminths and arthropods; most do not multiply within the host.

There are many species of hymenopterans (phylum Arthropoda: class Insecta: order Hymenoptera) that are considered **parasitoids.** These are animals that lay their eggs in insect or other arthropod hosts and the egg hatches and begins to feed on the host tissues. Here, the host may survive for some time before it is eventually killed by the feeding and growing larval parasitoid. In some cases, several levels of **hyperparasitism** have been identified in which parasitoids are parasitized, such as by a wasp.

Mechanisms of Infection

Specific **mechanisms of infection** are truly numerous and are well-studied in many species of parasites (Table 1). Some species of parasites possess conspicuous morphological adaptations that increase the probability that the life cycle will be completed. For example, eggs of some blood flukes of humans (namely, schistosomes causing schistosomiasis also known as bilharzia or bilharziasis) have spines which contribute, together with enzymes produced by the larva within the egg, to eroding the walls of blood vessels where the adults live, thus facilitating escape of eggs produced by the female directly into the bloodstream. The eggs then travel from the bloodstream through the walls of the blood vessels into the feces or urine, depending on the species of *Schistosoma* (adults of *S. haematobium* live in blood vessels around the urinary bladder while adults of *S. mansoni* live in the blood vessels of the intestines).

Adaptations to Parasitism

Each parasite species has adaptations that increase the probability of the parasite to infect, or make it to, a new host

Mechanism	**Example organism(s)**
Autoinfection (for example, eggs hatching and the larvae maturing in the host's intestine)	*Taenia solium* or *Strongyloides stercoralis*
Contact transfer	Mange mites of various species
Fecal contamination of wounds, mucosa, or lacrimal surfaces	*Trypanosoma cruzi* transmitted by reduviid bugs/kissing bugs
Ingestion of infected intermediate hosts	Trematodes and cestodes of various species
Ingestion of parasite eggs	*Trichuris*, *Ascaris*, *Taenia*, *Echinococcus*
Ingestion of parasite cysts from undercooked muscle of vertebrates	*Toxoplasma*, *Taenia*, *Echinococcus*
Ingestion of spores and trypomastigotes	Protozoans of various species
Ingestion of transport hosts, such the muscle of uncooked, never-frozen fish	Anasakine nematodes
Inhalation and swallowing of eggs	Phylum Nemata: Species *Enterobius vermicularis*
Inoculation	*Plasmodium* spp. transmitted by mosquitoes
Kissing	Flagellated protozoan *Trichomonas tenax*
Penetration into the nasal passage	Protozoan *Naegleria fowleri*
Penetration through skin	Phylum Nemata: Family Ancylostimatidae
Sexual intercourse	Flagellated protozoan *Trichomonas vaginalis*
Transmammary transmission via milk	Nematodes of various species
Transplacental transmission	*Plasmodium*, *Toxoplasma*, *Ancylostoma*, *Toxocara*

and increases the chance of survival in it. For example, *Plasmodium* species in birds cannot normally survive in primates, and the species of human pinworm (oxyurid nematode) *Enterobius vermicularis* is known only from humans, although other species of *Enterobius* occur in primates with 1 species being reported from rodents (Brooks and McLennan, 2002). In other words, each of these species possesses characteristics enabling it to complete its life cycle using these hosts. Such characteristics (in the very few cases analyzed in some detail) determine not only the species of host(s) used, but also the degree of **host range**, that is, how many host species a parasite can utilize (Brooks et al., 2022).

Like all animal species, parasites must be able to disperse, as populations with a small numerical density and limited geographic distribution may be at risk of extinction when environmental conditions become unfavorable or they may succumb to inbreeding depression via loss of genetic heterozygosity, and (perhaps) run the risk of overinfecting a local and restricted animal-host population. In parasites, dispersal may be mostly, or even entirely, passive; that is, the parasite is spread to new geographic areas and new hosts via the geographic dispersal of the host. Many parasites have elaborate dispersal mechanisms, such as flotation organs of larval flukes (cercariae), polar filaments on the eggs of some cestodes that live in water birds, and some parasites can even modify the behavior of their host to increase the probability that the parasite will make it to the next host.

Aggregation, Hermaphroditism, Parthenogenesis, and Asexual Reproduction

Surveys of the distribution of parasites in animal populations always find that not all potential host individuals are infected to the same degree. Most parasites are usually concentrated in a few individuals of the host population. This is what is meant by distributions being **aggregated** or **overdispersed**. There has been some debate about whether aggregation has a biological function, such as facilitating the finding of mates, or limiting the damage done overall to the host population. Statistically speaking, in the negative binomial distribution, the variance is greater than the mean, so the variance divided by the mean is greater than 1. Since these are counts of numbers of parasites in hosts that were examined, the fact that few hosts have many parasites shows an overdispersed or an aggregation distribution of the parasites in or on a few hosts. The parasites are not dispersed evenly throughout the host population. Whenever the variance/mean is greater than 1, it is said that the distribution is overdispersed or aggregated.

Overdispersion characterizes a phenomenon of aggregation of a majority of parasites in a minority of the host individuals in a certain population. Thus, the majority of hosts have no or few parasites. A very small number of hosts, however, carry a great number of parasites. Crofton (1971) first showed that overdispersion was present for parasite populations. Since then, overdispersion has been defined as axiomatic among parasites of a variety of vertebrate and invertebrate hosts (Knight et al., 1977; Anderson and May, 1985; Crompton et al., 1984). Patterns of overdispersion have also been discovered in populations of managed species of wildlife (Shaw et al., 1998; Wilson et al., 2002).

Additional research shows that the same general pattern occurs across several other species of animals. For example, cestodes of the species *Triaenophorus nodulosus* (class Cestoda: family Bothriocephalidea) in perch fish (*Perca fluviatilis*) show less aggregated distributions with only 54% of these worms occurring in 18.5% of hosts with 81.5% of fish remaining uninfected or lightly infected. Data accumulated relative to infections by the nematode *Porrocaecum ensicaudatum* (phylum Nemata: superfamily Ascaridoidea) in populations of the European starling (*Sturnus vulgaris*) from 1 study, 89% of the hosts were uninfected or lightly infected, and 69% of the parasites were recorded in just a few (11%) of the hosts. In pond frogs *Rana nigromaculata* harboring nematodes of the species *Spiroxys japonica* (phylum Nemata: class Spirurata: family Gnathostomatidae), it was found that 70% of the parasites were recorded in just 4% of the frogs examined while 88% of the frogs were found to be uninfected and 8% had light infections (Shaw et al., 1998).

Overdispersion was also recorded for 4 species of the most common human-infecting **geohelminths** (Croll and Ghadirian, 1981) and a search of the literature shows that almost invariably, parasites are distributed through animal populations in a non-random way, but what determines this is still poorly understood. For summaries of this topic in helminth parasites, see Churcher et al. (2005) and Lester (2012).

General Reproductive Biology of Parasites

Common among parasites are the various methods of reproducing that are found in the Kingdom Animalia, including: **Hermaphroditism** (1 individual has fully functioning male and female organs), **parthenogenesis** (females are able to produce offspring without mating), and **asexual reproduction** (an individual reproduces by budding or spores in which there is no recombination of genes on the chromosomes). Thus, in asexual modes of reproduction, the resulting new individuals are clones of the original organism. Among most species of parasites, only a single individual or very few individuals will reach and successfully infect or colonize a new host. In this case, populations of parasites may establish and then increase in numerical density from just a few founder individuals, or even from a single founder individual, that makes it to a new animal that it can then utilize as a host. It is a paradigm of evolutionary theory that sexual reproduction creates new combinations of genes that provide the raw material for evolution via natural selection (Williams, 1966; Williams, 1992). However, in reproduction that requires no mating and thus no sexual recombination of genes via the mixing of chromosomes, the advantage of rapid population growth from a single propagule in a new environment may in the short term outweigh the advantages of sex (Ghiselin, 1969; Williams, 1992; Kearney, 2022).

An example of **asexual reproduction** in a parasite occurs in species of *Plasmodium* (the causative agent of malaria in people). This example illustrates the stage that occurs in the vertebrate intermediate host, in the red blood cells after the infective stages first multiply in liver hepatocytes and are released into the bloodstream. In the bloodstream, these parasites develop in the red blood cells (RBCs) and multiply by mitotic division of the nucleus and other cell organelles but not the cytoplasm. These then escape the RBCs into the bloodstream to invade more RBCs and undergo more cycles of development and multiplication (depending on the species).

Parasitic platyhelminths, including trematodes, cestodes, and monogeneans, with a few exceptions, are hermaphroditic and individuals can, if necessary (such as when there are no mates nearby), fertilize their own eggs, although they usually cross-fertilize due to several morphological and developmental stages that decrease probability of self-fertilization in these groups. Some species of nematodes, including those in the genera *Steinernema* and *Heterorhabditis* (entomopathogenic nematodes, namely, those that infect insects as part of their life history) also have hermaphroditic stages (Cao et al., 2022). Many other species have been shown to exhibit various methods besides sexual reproduction and some of these are reviewed in Triantaphyllou and Hirschmann (1964) and Maggenti (1981).

Parthenogenesis is the growth and development of an animal from an ovum without fertilization and this occurs commonly in species of *Strongyloides* (phylum Nemata: family Strongylidae) which infect mammals (see Cable, 1971; also see the definition of parthenogenesis in Maggenti, 1981).

Host Range

Some parasites are known to occur in or on a few or, in some cases, only 1 species of free-living animal. Definitions are always problematic, and defining species of parasites with limited host range (formerly, or at times still, referred to as host specificity) depends on vast knowledge that can only be based on extensive collections of animals conducted over broad geographic spaces and includes complete data for the specimens of both parasites and their hosts (note that if an animal is not parasitized, it is not a host, but is only a potential host). In order for these data to be useful, the specimens that are collected and processed and their associated data must be deposited in museums that maintain both specimens and their data in perpetuity. The reason that the host and parasite are both stored in museums after collection is to enable tests of the hypotheses of host-range by actually looking at, and using data for, both the host and parasite. Many times, the host group is misidentified in the field and the species name can only be positively known by comparative methods using museum collections (Brooks et al., 2015; Galbreath et al., 2019).

Most species of parasites show some level of limited host range, although the extent of limits among species is variable. For example, the large human nematode *Ascaris lumbricoides* (phylum Nemata: order Ascaridida) has a direct life cycle and occurs in both humans and pigs (Araújo et al., 2015). The apicomplexan protozoan *Toxoplasma gondii* (phylum Apicomplexa: family Sarcocystidae) has been shown to occur in a wide range of mammals and birds and shows broad infectivity on those groups of potential hosts (Dubey, 2008).

As a more detailed example of host range, the nematode *Ransomus rodentorum* (phylum Nemata: superfamily Strongyloidea) had been reported to occur only in the cecum of pocket gophers while a related species of *Ransomus* occurs in species of mole rats in China and perhaps Mongolia. The pocket gophers are rodents with a subterranean lifestyle restricted to North America, Central America, and extreme northern South America (Nearctic). Chinese mole rats are also subterranean rodents, but they have a distribution in the Palearctic and northern Ethiopian regions with no known history of either the Chinese mole rats occurring in the Nearctic nor of the pocket gophers occurring in the Palearctic (Thenius, 1972). Relative to *R. rodentorum* in pocket gophers, this strongyloid species has never been reported from other sympatric species of rodents within the geographic ranges of the nematode, and despite intense field collecting in several areas in North America, this species has never been shown to occur in rodents that are phylogenetically close to gophers. It is interesting that no instances of infection with these nematodes have been reported from rodents that share burrow systems with pocket gophers, even from those that are phylogenetically related, such as the kangaroo rats or pocket mice. These groups are related at a basal level, all with a common ancestor linking the heteromyids (such as kangaroo rats) with the geomyids (pocket gophers) in the superfamily Geomyoidea, one major shared derived trait (**synapomorphy**) being external fur-lined cheek pouches. This is a case where the other species of rodents are both **sympatric** (meaning, occurring in the same geographic space; Brooks and McLennan, 2002) and **syntopic** (meaning, occurring in the same ecological space; see the definition of syntopic in Rivas, 1964. See also an explanation synapomorphy in Chapter 2.).

Attempts to understand patterns of diversity of parasites that have both wide and narrow host ranges have been ongoing with concentrated work and summaries presented first by Baer and Mayr (1957). This work has been one of the foundations of systematic and ecological parasitology since the beginning of the scientific study of parasites (Guerrero, 2021; Hoeppli, 1959); however, the collections of individual parasites from vertebrates representing myriad species and their deposition into museums (as well as depositing individual host animals) has not kept pace with the same work on the vertebrates themselves (Galbreath et al., 2019). In a summary of mammal collections in museums in the United States (Dunnum et al., 2018), there were estimated to be about 5,275,000 individual cataloged mammal specimens distributed through 395 active mammal collections. However, there are only a handful of major collections of parasites of mammals in the United States and, of those, only 2 collections have significantly large reciprocal collections of both mammals and the parasites that were found during geographically focused surveys and inventories of the mammals themselves. Thus, without excellent reciprocal collections of parasites and their hosts with their data available in museums, it is difficult to say very much about host range. Until more data are collected, certain questions will remain unanswered.

Rausch (personal communication) considered that the concept of host specificity was imprecise at best because the noun *specificity* implies an unvarying quality, and he considered that the degree of specificity cannot be easily expressed or measured and any experimental test of the concept would be biased in so many different ways that the results of tests would be invalid, or at best equivocal. Phylogenetic specificity was a term that was used by Baer (1951) to refer to helminths and their hosts that were shown to have coevolved. Baer considered ecological specificity to occur when opportunistic infections were involved. This is what is now called **ecological fitting** sensu Janzen (1985).

Species Richness of Parasites and Distribution of Parasites

Arndt (1940) was the first ecologist who counted the number of parasites as a proportion of a total fauna. In Germany, he found 10,000 parasitic species out of a total of 40,000 species, but did not include insects parasitizing plants, as he classified them as herbivores. Price (1977) included such species but excluded temporary parasites (for example, mosquitoes and leeches) in his survey of the British fauna. Price estimated that more than half of all British species are parasitic.

Thirteen large taxa (phyla, subphyla, or classes) consist entirely of parasites, and many other groups include a high proportion of parasitic species. Even among the vertebrates several species are parasitic, such as the sea lamprey *Petromyzon marinus*.

Virulence of Parasites

Virulence of parasites can be defined as the degree of damage done by the parasite to the host. There are 2 opposing trends which determine the degree of virulence: 1) Usually it is not a selective advantage to severely damage or kill its host, because this would also affect the fitness of the parasite;

2) parasite transmission to another host may be facilitated by such damage: A weak host may be easier prey for a predatory final host than a strong one. Therefore, evolution will lead to an increase or a decrease in the virulent nature of various parasites, depending on the circumstances.

Life Cycles

Many parasites have a **direct life cycle** (lice, fleas, monogenean flukes, and many nematodes) and they use a single host which harbors larval/juvenile stages as well as adults. Other parasites have **complex life cycles** and use a final (= **definitive**) host which harbors the mature stage, as well as 1 or several **intermediate hosts** which harbor the larvae, that is, they have **indirect life cycles** (for example all digenean flukes, all of which are from class Trematoda). An example of a trematode with 2 intermediate hosts is the lancoleate trematode *Dicrocoelium dendriticum*. In certain parasite species, alternative life cycles are possible. For example, in the aspidogastrean fluke *Aspidogaster conchicola*, both a direct and an indirect life cycle are possible: Adult worms in the mollusc produce eggs which are inhaled by other molluscs, but fish can also become infected by eating infected molluscs. In other aspidogastreans, and in the amphilinid tapeworm *Austramphiina elongata*, among many others, the life cycle is always indirect, involving both an intermediate and final host. In the amphilinid tapeworm, turtles serve as final hosts, eggs escape from the host in an unknown way, larvae hatch in freshwater and penetrate into a crayfish intermediate host, which is then eaten by a turtle.

Many species of parasites possess varied and diverse **behavioral adaptations** that facilitate completion of their life cycle and entrance into the next host in the cycle. Adult *Dicrocoelium dendriticum* (phylum Platyhelminthes: class Trematoda: subclass Digenea) infect the liver mainly of sheep, but other ungulates are also parasitized by these trematodes. These trematodes produce eggs which pass out of the host with the feces and are eaten by land snails, in which various larval stages are produced. The last stage is the tailed larva, or cercaria, many of which cluster in slime balls which are left behind in the mucus trail of the snail as it speeds to its objective, whatever that may be. If the trematode larvae are lucky, these slime balls are then eaten by ants. If not eaten, they dry up and die. After being ingested, the cercariae move from the intestinal tract to various parts of the ant. The first cercariae getting into an ant penetrate into the ant's subesophageal ganglion, inducing the ant to climb up a grass stem and, when the temperature drops, the cercaria induces cramp-like behavior in the ant, which consequently clings to the grass stem with its mandibles. This behavior increases the likelihood of the infected ant being eaten by a passing sheep or another ungulate.

Host-Parasite Interactions, Example: Cleaning Symbiosis

A considerable range of behavioral patterns leading to (or thought to lead to) the removal of parasites has been observed among animals. They include **preening and bathing of birds** in dust and water, and **passive and active anting**, where ants are allowed to passively crawl over the body, or where ants are actively squeezed over the plumage. Also, dogs rubbing their skin against rough surfaces, jumping of fish and whales out of water, and so on, may have a cleaning function. Best known is **cleaning symbiosis**, in which one animal (the cleaner) cleans another (the host) from parasites and diseased (necrotic) tissues. For example, cleaning behavior has been observed in birds which remove ectoparasites from cattle, hippopotamuses, large marine fish floating on the ocean surface, several species of shrimp, and some freshwater fish. Hosts are freshwater and marine fishes, whales and dolphins, and invertebrates, among others. Many cleaner fish possess special morphological adaptations which enable them to pick parasites off of the host skin or even gills (the mouth is located terminally to facilitate picking up of parasites, the anterior teeth are fused to form cutting plates, and color patterns are conspicuous, useful in signaling to hosts: "I am a cleaner!"). The cleaner fish *Labroides dimidiatus* even performs a cleaning dance to attract host fish. Invitation postures of hosts signal, in turn, to the cleaner that they are ready to be cleaned.

Generalization of Parasitism: Stockholm Paradigm

Parasites can be specialists or generalists depending on how much of their fundamental **host fitness space** is occupied in a population of animals (Agosta et al., 2010; Brooks et al., 2019). The smaller the fitness space being occupied by a parasite, the more specialized the parasite appears. The following is a short summary of the general ideas of the **Stockholm Paradigm** that deals with host-range and parasite use of animal populations. A more detailed explanation can be found in the book of the same title by Brooks et al. (2019). See also Agosta (2022) and Brooks et al. (2022).

The concept of host range infections has undergone rapid change in the past few years with the ideas of Brooks et al. (2015; 2019) forging new ground towards the interpretation of parasite-host relationships. It now appears that most parasites retain genetically deep phylogenetic signals of host or habitat exploitation that enable the parasites to cross potential host-species boundaries when ecological opportunities arise. Mutations or genetic modifications a priori *are not needed* as the underlying **symplesiomorphic** (meaning, shared ancestral) traits enable cross-species transmission to new hosts when they are available (that is, **syntopic**). These opportunities arise due to climate and geographic range-oscillations (the **oscillation hypothesis**; Brooks et al., 2019), **taxon pulses**, manifested by both multiplication and extinction of species (Erwin, 1985), and ecological fitting in sloppy fitness space (Janzen, 1980; Agosta, 2006; Agosta and Klemens, 2008; Agosta et al., 2010). Putting all of these together, Brooks and his colleagues (2019) have termed this the Stockholm Paradigm in honor of the researchers at the University of Stockholm in Sweden who first put these synthetic ideas into the literature stream.

Capacity

What is meant by capacity? As noted earlier, every species, including all parasites, have specific environmental resources they need in order to survive and reproduce. In the case of parasites, those resources are specific attributes of their hosts. For a given parasite species, if only 1 host species has the required resources, the parasite can survive only in association with that species, and its survival is tied to the survival of that species. But the vast majority of inherited attributes of all species are evolutionarily conservative, meaning they occur in more than 1 species of host.

All parasites live in association with a restricted number of hosts, and some not so restricted, as seen in *Toxoplasma*, and sometimes only 1 host species is infected. Sometimes parasites are restricted to a potential or actual species of host by limited **capacity** but mostly parasites are restricted by limited **opportunity**. And so, when the conditions change—say, as a result of climate change or intrusion of humans and their domestic animals into previously uncut forest—new opportunities are created and the parasites move into hosts they had the capacity to infect but never before had the opportunity to (this could be the result of trophic changes locally or of geographic dispersal into new areas).

Ecological Fitting

Ecological fitting (sensu Janzen, 1985) refers to cases when a parasite has the opportunity to encounter a new potential host that has the required resources for survival, the parasite will then be expected to add that species to its repertoire. This, by the way, eliminates the need for the right mutation to show up at the right time to allow or enable the parasite to jump into a new species of animal to make it a new host.

Fundamental Host Fitness Space

For any given parasite, the range of all hosts that have the required resources is called the **fundamental host fitness space** (in accordance with Hutchinson's notion of fundamental niche space; Hutchinson, 1959), which Agosta called fundamental fitness space in order to relate it directly to evolution (Agosta, 2006; Agosta et al., 2010). The actual hosts inhabited by the parasite at any given time represent the **realized host fitness space** (in accordance with Hutchinson's realized niche space and Agosta's use of the term *fitness* rather than *niche*). One of the keys to the evolutionary success of parasites is that the fewer species of animals used as actual hosts (that is, the smaller the realized fitness space), the more potential opportunities to inhabit new species of hosts exist. In other words, given the opportunity to come into contact with a suitable but previously unexposed (potential) host species, a parasite would add the new host to its host range and survive even if the original species of host went extinct. The fewer hosts actually used, the smaller the proportion of actual host fitness space compared to fundamental host fitness space and consequently the sloppier (meaning, more filled with potential opportunities) the host fitness space. At the same time, the more restricted the realized host fitness space, the more specialized the parasite is within that fitness space. Alternatively, the more species of potential hosts used, the larger the proportion of actual host fitness space compared to fundamental hosts space, the less sloppy the fitness space, the fewer new potential hosts, and the more generalized the parasite is in fitness space.

This insight, developed by Agosta (2006) and elaborated by Agosta et al. (2010) and Brooks and Agosta (2020), obviates the need to define or even discuss host specificity since it is basically impossible to look at host specificity in an evolutionary sense. Conversely, the idea of fitness space has a Darwinian evolutionary origin that can be tested in an evolutionary context.

Oscillation Hypothesis

Periods of climatic/environmental stability are usually associated with events of local geographic isolation, hence, specialization of parasites occurring in limited geographic areas and many potential hosts unexposed in other similar but separate geographic areas; periods of environmental perturbations are usually associated with increased or expanded species-level geographic distribution, hence, generalization may occur with fewer potential hosts. Parasites thus tend to oscillate between specializing and generalizing in host fitness space, depending on environmental conditions; this is called the **oscillation hypothesis** that was developed by Janz and Nylin (1998).

Taxon Pulse

All species of parasites and their actual and potential hosts alternate between geographic isolation (geographic contraction in space) and geographic expansion through space via dispersal. This is called the **taxon pulse** (Erwin, 1985).

Environmental perturbations drive taxon pulses, which drive host range oscillations, which drive parasite diversification by ecological fitting in sloppy fitness space, reinforced by natural selection (Agosta et al., 2010). Well worked-out examples that show these various parts of the Stockholm Paradigm include those presented in Brooks et al. (2006; 2015; 2019) and Malicka et al. (2015).

Ecological Fitting Example

Surveys and inventories are the primary ways that large scale and complete collections of parasites and their actual and potential hosts are accumulated over large geographic scales in short periods of time (Gardner, 1996; Gardner and Jiménez-Ruiz, 2009; Gardner et al., 2012; Galbreath et al., 2019). A final example of ecological fitting presented here stems from survey and inventory work on mammals and their parasites funded by the National Science Foundation (grant numbers BSR-9024816 and DEB-9496263), from a collection locality labeled 7 km S, 4 km E Cruce Ventilla in the Department of Oruro, Bolivia (read as "7 kilometers south and 4 kilometers east of Cruce Ventilla in the Department of Oruro, Bolivia"). The specific locality, referred to here as near Cruce Ventilla, was visited by a field team from the Museum of Southwestern Biology (Albuquerque, New Mexico, United States) and the American Museum of Natural History (New York, New York, United States), September 29–30, 1986 (Anderson, 1997).

Several species of mammals and their parasites were obtained at this locality. Of particular interest, 3 of the species of mammals were collected from the same burrow systems that had been constructed and were being actively used and maintained by subterranean rodents called highland tuco-tucos; species name *Ctenomys opimus* (Wagner). At this locality, several specimens of *C. opimus* were collected from the burrows, as well as several individuals of yellow-toothed cavy, species name *Galea musteloides* Meyen, and many individuals of 1 species of leaf eared mice, species name *Auliscomys boliviensis* (Waterhouse, 1846). Specimens of the mammals were collected sequentially or simultaneously, and all of the mammals were recorded as using the same burrow systems using the same entrances and exits. Great care was taken in performing the collections and necropsy on the specimens at this site because it appeared to be an opportune chance to identify any parasites that potentially could be shared among the 3 syntopic species of rodents that were occurring in the same micro-geographic space, using the same ecological space, and using the same resources (Rivas, 1964).

After collections were made using standard methods and necropsies performed (see Gardner and Jiménez-Ruiz, 2009; Galbreath et al., 2019), it was immediately evident that a single species of parasite was shared among 2 of the species of rodents but not all 3. The metacestodes were found only in *Ctenomys* and *Auliscomys*. This cestode was identified later as the larval form of *Taenia talicei* Dollfus, 1960, a polycephalic (meaning, having many scolexes) taeniid (order Cyclophyllidea: family Taeniidae: genus *Taenia*) identified by the morphology of the hooks and the multi-strobilate (many strobila associated with a single infection) nature of the larvae. Pinworms of the genus *Helminthoxys* were found in the cecum of the *Galea* but not in the cecum of individuals of *C. opimus*. However, many individuals of *C. opimus* were infected with a species of *Paraspidodera* that occurred in their cecae and large intestines. The individuals of *A. boliviensis* that were examined were shown to be infected with trichostrongylid nematodes (phylum Nemata: superfamily Trichostrongyloidea) in the small intestine and pinworms of the genus *Syphacia* (phylum Nemata: order Oxyurata) in the cecum. Current investigations are under way on both the endoparasites and the ectoparasites of this same host assemblage near Cruce Ventilla, Bolivia. This sharing of metacestodes among several species of rodents of widely divergent phylogenetic lineages illustrates the phenomenon of **ecological fitting** and the fact that metacestodes of *Taenia talicei* have broad host-range tolerances while the adults probably are more restricted (although no carnivores were collected and examined at or near this locality). It is generally observed that adult cestodes in the genus *Taenia* show host range use that is somewhat narrow, and this may partly be due to the effects of sympatric or syntopic species of intermediate hosts.

Economic and Hygienic Importance of Parasites

Some of the most important tropical diseases of humans are caused by parasites, such as schistosomiasis (bilharziasis) (caused by the blood fluke *Schistosoma*), filariasis (caused by several different species of filarioid nematodes), amebic dysentery (the protozoan *Entamoeba histolytica* is the causative agent of this one), and, in particular, malaria (at least 5 species of the protozoan *Plasmodium*). Annually, more than 247 million people are infected with various species of *Plasmodium*, the causative agent of malaria, and around 619,000 people die from it every year worldwide, particularly children in sub-Saharan Africa. The webpages of the World Health Organization (WHO), Division of Tropical Diseases and of the United States Centers for Disease Control and Prevention (CDC) contain information about the current status of the important parasitic diseases, which is continually updated. Information on prevalences of infection with various parasites and their geographical distribution are available at the CDC web site (https://cdc.gov) and at the WHO site (https://platform.

who.int/mortality/themes/theme-details/topics/topic-details/MDB/infectious-and-parasitic-diseases).

Global warming will lead to a spread of parasitic infections into some countries and increase prevalences of parasites in others that already have high parasite loads in their populations, especially in tropical and subtropical regions that will continue to warm over the next few hundred years (Brooks et al., 2019).

Parting Thought

The rest of this book provides an in-depth overview of many species of parasites, how they are related to one another, their adaptations, effects on hosts, and their importance as fellow inhabitants on Earth.

This introduction is fittingly ended with a quote from Harold W. Manter (Figure 2), one of the leaders in parasitology from the late 1920s through 1970 and the namesake of the Harold W. Manter Laboratory of Parasitology, one of the world's leading laboratories of systematic parasitology. Manter was an early proponent of the mutability of continents and plate tectonics and worked to provide evidence of continental movement with data from parasites and their hosts. From this work, he proposed the idea of **parascript** (Brooks and McLennan, 1993). Extracted from the book Host-Parasite Relationships (McCauley, 1966), Manter stated:

> Thus, parasites reflect both current environmental conditions and also the influences of ancient times—both ecology and phylogeny … Parasites of fishes, particularly such an abundant and diverse group as the Trematoda, furnish information about present-day habits and ecology of their individual hosts. These same parasites also hold promise of telling us something about host and geographical connections of long ago. They are simultaneously the product of an immediate environment and of a long ancestry reflecting associations of millions of years. The messages they carry are thus always bilingual and usually garbled. Today, we know only a few selected pieces of the code. As our knowledge grows, studies based on adequate collections, correctly classified and correlated with knowledge of the hosts and life cycles involved should lead to a deciphering of the messages now so obscure. Eventually there may be enough pieces to form a meaningful language which could be called ***PARASCRIPT: The language of parasites which tells of themselves and their hosts both of today and yesteryear***.

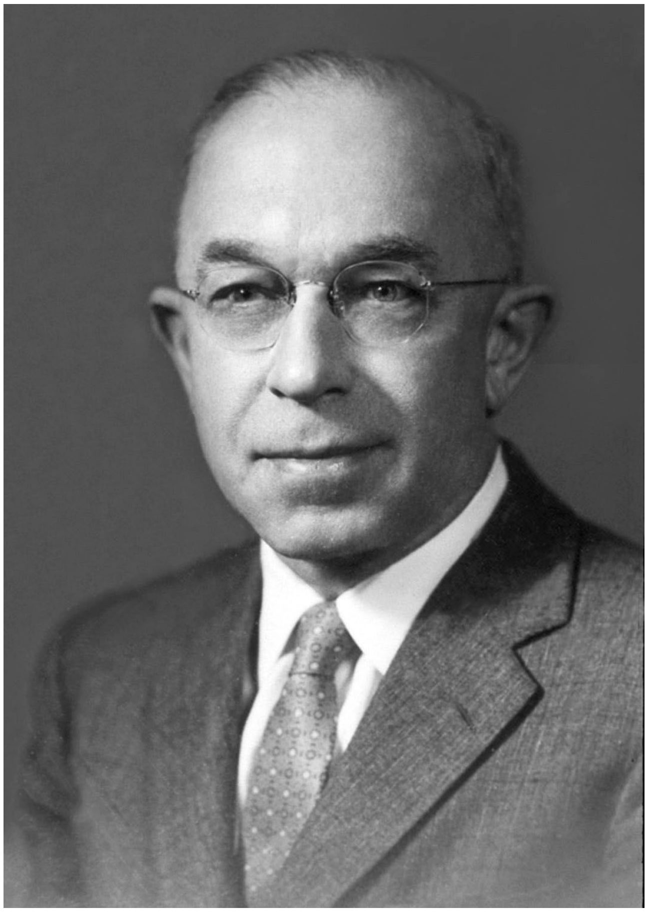

Figure 2. Harold Winfred Manter (1898–1971), circa 1960. Manter was a professor in the Department of Zoology, University of Nebraska (Lincoln campus; Lincoln, Nebraska, United States) from 1925 to 1971. He worked on systematics and biogeography of parasites of fishes, although during his tenure at Nebraska, he trained dozens of students in other areas of parasitology. The Harold W. Manter Laboratory of Parasitology (HWML) was named after him, having been established after his death in 1971 by Curator of the Parasitology Division of the University of Nebraska State Museum, Mary Lou Hanson Pritchard. Source: HWML. License: CC BY.

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