

# CONTENTS

## CHAPTER 1 AN INTRODUCTION TO PARASITISM

### 1.1 BUILDING AN UNDERSTANDING OF THE BASICS OF PARASITISM

Parasites live in or on their hosts and cause them harm

Opinions vary on how to define some of the key aspects of parasites and their biology

The residence time for a parasite in or on a host is highly variable

There are many additional ways to categorize parasites

### 1.2 HOSTS—ESSENTIAL LIFELINES FOR PARASITES

Hosts also fall into several different categories

### 1.3 APPRECIATING PARASITISM'S PLACE IN NATURE

Parasitism is one of several categories of symbiotic associations

Parasitoids straddle the boundary between predation and parasitism

Our understanding of parasitism is enhanced by an appreciation of its relationship to another ubiquitous type of symbiosis, mutualism

## REVIEW QUESTIONS

## REFERENCES

## CHAPTER 2 AN OVERVIEW OF PARASITE DIVERSITY

### 2.1 THE DIVERSITY OF PARASITE SPECIES

What constitutes a parasite species requires some explanation

Given these considerations, how many species of parasites inhabit the Earth?

Evolutionary trees are used to visualize evolutionary relationships and to display parasite diversity

Efforts are well underway to reveal the overall tree of life

1	Horizontal gene transfer (HGT) has been pervasive throughout the evolution of life	29
2	Many bacteria are parasites	29
2	Eukaryotes are a very diverse group that includes many different kinds of parasites	30
2	HGT has also played a role in the evolution of eukaryotic parasites	34
4	The Apicomplexa is a huge, important, nearly exclusive parasitic group of organisms	35
6	Many well-known parasites belong to familiar groups of multicellular organisms	37
6	<b>2.2 INSIGHTS INTO PARASITISM FROM THE STUDY OF DIVERSITY</b>	46
9	The phylogenetic affinities of enigmatic parasites can be revealed	46
12	Some groups of parasites remain “persistent problematica”	48
12	Studies of parasite diversity reveal how particular parasites came to infect humans	49
13	Studies of diversity can help reconstruct the historical biogeography of parasites	52
14	<b>2.3 THE ONGOING QUEST TO REVEAL AND UNDERSTAND PARASITE DIVERSITY</b>	53
18	DNA barcoding is one way to catalog parasite diversity	53
19	Some parasites exist in complexes of cryptic species	55
21	Whole lineages of unapparent parasites may escape our attention	57
21	Metagenomics provides a new way to reveal parasite diversity	57
23	Studies of parasite diversity help provide a better foundation for taxonomy	58
23	<b>2.4 OTHER WAYS TO CONSIDER PARASITE DIVERSITY</b>	59
24	Diversity within parasite species is extensive and important	60
26	Do parasites give rise to free-living organisms?	62
27	<b>REVIEW QUESTIONS</b>	64
27	<b>REFERENCES</b>	64

## CHAPTER 3 THE PARASITE'S WAY OF LIFE

### 3.1 A HISTORICAL PERSPECTIVE OF THE PARASITE LIFE CYCLE

Early medical and natural history studies gave rise to an understanding of parasite life cycles  
Mosquito transmission was first demonstrated for filarial worms  
Arthropod transmission for filarial worms suggested that other diseases may be similarly transmitted

### 3.2 AN OVERVIEW OF PARASITE LIFE CYCLES

Parasites with direct life cycles use only a single host  
Two or more hosts are necessary for those parasites with indirect life cycles

### 3.3 THE PARASITE'S TO DO LIST

Effective transmission is essential for all parasites  
High reproductive rates are common in many parasite life cycles  
Both sexual and asexual reproduction are used by apicomplexans such as *Toxoplasma gondii*  
Parasites may use strategies other than high fecundity to achieve transmission  
Many factors can complicate an understanding of parasite transmission  
Mathematical models provide a useful tool to predict transmission rates  
Many parasites must migrate to specific sites or tissues within the host  
The evolution of complex migration within a host is not always clear  
Parasites are adapted to maintain their position on or within the host  
Finding a mate is a requirement for many sexually reproducing parasites  
Parasite genomes reflect their adaptations to a parasitic lifestyle  
The relationship between parasitism and genome size is not always clear  
Propagules are released through a portal of exit  
Parasites undergo complex developmental changes in response to environmental cues  
Epigenetic phenomena and co-opting of host signaling molecules may be important in parasite development

### REVIEW QUESTIONS

### REFERENCES

## CHAPTER 4 HOST DEFENSE AND PARASITE EVASION

<b>CHAPTER 3 THE PARASITE'S WAY OF LIFE</b>	<b>67</b>	<b>CHAPTER 4 HOST DEFENSE AND PARASITE EVASION</b>	<b>111</b>
<b>3.1 A HISTORICAL PERSPECTIVE OF THE PARASITE LIFE CYCLE</b>	<b>68</b>	<b>4.1 AN EVOLUTIONARY PERSPECTIVE ON ANTI-PARASITIC IMMUNE RESPONSES</b>	<b>112</b>
Early medical and natural history studies gave rise to an understanding of parasite life cycles	68	Prokaryotes have developed remarkable immune innovations during their billions of years encountering parasites	112
Mosquito transmission was first demonstrated for filarial worms	69	Many kinds of parasites compromise the health of plants so it is important to know how plants defend themselves	113
Arthropod transmission for filarial worms suggested that other diseases may be similarly transmitted	71	Although plants lack specialized immune cells, they still can mount effective, long-term responses to parasites	115
<b>3.2 AN OVERVIEW OF PARASITE LIFE CYCLES</b>	<b>72</b>	Many nematode species are specialized to parasitize plants	116
Parasites with direct life cycles use only a single host	73	Invertebrates have distinctive and diverse innate immune systems	117
Two or more hosts are necessary for those parasites with indirect life cycles	73	Invertebrates, including vectors and intermediate hosts, mount immune responses to contend with their parasites	118
<b>3.3 THE PARASITE'S TO DO LIST</b>	<b>77</b>	Invertebrates also adopt distinctive behaviors to supplement their anti-parasite immune responses	120
Effective transmission is essential for all parasites	77	Parasites suppress, manipulate, and destroy invertebrate defense responses	122
High reproductive rates are common in many parasite life cycles	85	Some parasites rely on symbiotic partners to subvert the immune responses of their invertebrate hosts	123
Both sexual and asexual reproduction are used by apicomplexans such as <i>Toxoplasma gondii</i>	88	Some invertebrates enlist symbionts to aid in their defense	124
Parasites may use strategies other than high fecundity to achieve transmission	90	Researchers hope to manipulate invertebrate immune systems to achieve parasite control	125
Many factors can complicate an understanding of parasite transmission	90	<b>4.2 AN OVERVIEW OF VERTEBRATE DEFENSE</b>	<b>127</b>
Mathematical models provide a useful tool to predict transmission rates	92	<b>4.3 IMMUNE RESPONSES TO EUKARYOTIC PARASITES</b>	<b>129</b>
Many parasites must migrate to specific sites or tissues within the host	93	Recognition of PAMPs initiates the immune response to protozoa	129
The evolution of complex migration within a host is not always clear	96	Immune responses to protozoa include both humoral and cell mediated components	131
Parasites are adapted to maintain their position on or within the host	97	Protective immunity to malaria develops as a consequence of repeated exposure	133
Finding a mate is a requirement for many sexually reproducing parasites	98	Immune responses are generated against each stage in the <i>Plasmodium</i> life cycle	134
Parasite genomes reflect their adaptations to a parasitic lifestyle	99	Helminth parasites provoke a strong Th-2 response	137
The relationship between parasitism and genome size is not always clear	101	Extensive changes to the intestinal epithelium occur in response to intestinal helminths	140
Propagules are released through a portal of exit	101	Immunocompromised hosts are more vulnerable to parasitic infection and increased pathology	141
Parasites undergo complex developmental changes in response to environmental cues	105		
Epigenetic phenomena and co-opting of host signaling molecules may be important in parasite development	106		
	107		

## 4.4 PARASITE EVASION OF HOST DEFENSES

Many parasites are able to evade complement-mediated innate immune responses

Intracellular parasites have evolved mechanisms to avoid destruction by host cells

Parasites may interfere with intracellular signaling pathways

Some parasites interfere with antigen presentation, resulting in an impaired immune response

Some parasites regularly change their surface antigens to avoid immune responses

Parasites frequently suppress or alter host immune responses by interfering with cell communication

Some parasites render themselves invisible to immune detection

Various parasites are able to undermine the effector functions of antibodies

## REVIEW QUESTIONS

## REFERENCES

# CHAPTER 5 PARASITE VERSUS HOST: PATHOLOGY AND DISEASE

## 5.1 PATHOLOGY RESULTING FROM PARASITIC INFECTIONS

Parasites can induce pathogenesis in various ways

Pathology can be categorized as one of several general types

Parasites can cause direct trauma to host cells, tissues, and organs

Mechanisms underlying the pathogenicity of *Entamoeba histolytica* remain obscure

Parasitic infection can alter host-cell growth patterns

Many parasites adversely affect host nutrition

*Plasmodium* infections can result in host iron deficiency

Toxins are a less frequent component of parasite pathology

Pathology often results from immune-mediated damage to host cells and tissues

Immunopathology is an important component of the pathology observed in malaria

Granulomas formed in response to parasite antigen are both protective and pathological

Parasites may serve as a trigger for autoimmunity

143	Toxoplasma gondii may both contribute to and help to prevent atherosclerosis	180
143	<b>5.2 PARASITES AND HOST BEHAVIOR</b>	<b>180</b>
144	Some parasites may modify host behavior to facilitate transmission	180
145	The mechanisms that parasites use to alter host behavior are obscure	182
146	Infected hosts may display unusual neurotransmitter profiles in their central nervous systems	183
147	<b>5.3 PARASITE-MEDIATED AMELIORATION OF PATHOLOGY</b>	<b>185</b>
150	Parasitic infection may be required for proper immune system development	186
151	Certain intestinal helminths may reduce the host inflammatory response	187
152	Intestinal helminth infection results in activation of regulatory T cells	188
153	Intestinal helminths can be administered therapeutically	188
154	<b>REVIEW QUESTIONS</b>	<b>189</b>
	<b>REFERENCES</b>	<b>190</b>

# CHAPTER 6 THE ECOLOGY OF PARASITISM

## 6.1 DEFINING THE HABITATS OF PARASITES

159

160

161

162

163

164

165

166

167

168

169

170

171

172

173

174

175

176

177

178

179

Parasites occupy multiple habitats in succession

Parasites have microhabitat preferences and occupy specific sites within their hosts

Host specificity is one of parasitism's most distinctive properties

Encounter and compatibility filters determine the range of host species used by a parasite

The origins and consequences of host specificity are debated

Underlying mechanisms dictating specificity are also often not known

## 6.2 PARASITE POPULATION BIOLOGY

Parasite populations are complex

Parasites often show aggregated (overdispersed) distributions in their hosts

Both density-independent and density-dependent factors influence parasite population size

Intraspecific competition can regulate parasite populations in different ways

---

Parasite population studies often require a long-term perspective and detailed sampling	210	Models for parasites with complex life cycles involving vectors become more complex	248
<b>6.3 PARASITE COMMUNITIES</b>	<b>210</b>	New models open the black box and estimate microparasite populations within hosts and the influences on them	249
The richness of parasite communities varies among host species for reasons that are still debated	212	Models need to take spatial and temporal factors into account	250
Most studies suggest parasite communities are stochastic in nature	213	Some individual hosts may serve as superspreaders	251
Parasite species within infracommunities engage in negative and positive interactions with one another	217	<b>REVIEW QUESTIONS</b>	253
Generalizable patterns are also elusive in component communities of parasites	218	<b>REFERENCES</b>	254
Human parasites have a distinctive community ecology	219	<b>CHAPTER 7 EVOLUTIONARY BIOLOGY OF PARASITISM</b>	259
<b>6.4 THE ROLE OF PARASITES IN FOOD WEBS AND ECOSYSTEMS</b>	<b>221</b>	<b>7.1 MICROEVOLUTION IN PARASITES</b>	260
Parasites can be a food source for other organisms	224	The subdivided nature of their populations influences the evolution of parasites	261
<b>6.5 GLOBAL PATTERNS IN PARASITE DIVERSITY</b>	<b>225</b>	The effective population size, $N_e$ , influences parasite evolution	261
Hosts try both to avoid infection and to actively remove parasites if they do become infected	225	The mode of parasite reproduction affects microevolutionary change	262
Hosts also change their diets and engage in self-medication when infected	228	Stability of the host environment influences parasite microevolution	265
Parasites influence host migratory behavior	229	The mobility of parasites impacts their evolution, as exemplified by bird lice	265
Parasites can regulate host populations, but examples are few	230	Parasite microevolutionary change is strongly impacted by host mobility	267
Parasites influence competitive interactions among hosts	233	A parasite's life cycle also affects the potential for evolutionary change	267
Parasites can manipulate their hosts to affect the likelihood of predation	234	<b>7.2 COEVOLUTION OF PARASITE–HOST INTERACTIONS</b>	269
<b>6.7 ECOLOGICAL IMMUNOLOGY</b>	<b>238</b>	Parasites and hosts reciprocally affect each other's evolution	269
<b>6.8 THE METABOLIC THEORY OF ECOLOGY AND PARASITES</b>	<b>241</b>	Parasites and hosts engage in arms races	271
<b>6.9 EPIDEMIOLOGY AND ITS RELATIONSHIPS WITH ECOLOGY</b>	<b>242</b>	In parasite–host relationships, there can be an advantage to being rare	273
Modeling is an invaluable approach to the study of infectious diseases	243	Parasites and hosts can be locally adapted, or maladapted, to one another	273
Microparasites exemplify basic modeling approaches that estimate population size and clarify transmission	244	Some factors conspire to limit strong coevolutionary dynamics between parasites and hosts	274
Models of macroparasite populations and transmission involve keeping track of individual parasites	246	<b>7.3 THE EVOLUTION OF VIRULENCE</b>	274
		Virulence and transmission biology of parasites are linked	275
		The trade-off hypothesis requires a nuanced approach	276
		The mode of transmission influences virulence	278

## 7.4 MACROEVOLUTIONARY PARASITOLOGY

New parasite species are potentially formed in at least three different ways

Different outcomes can be expected when parasites or their hosts diversify

What does the evidence suggest about how parasites have speciated?

Does sympatric speciation occur in parasites?

Host switches can enable radiations in parasites

Parasites go extinct, sometimes along with their hosts

Macroevolutionary patterns among parasites are not yet very clear

## 7.5 SOME DISTINCTIVE ASPECTS OF PARASITE EVOLUTION

Organisms have repeatedly adopted parasitism by more than one route

Some parasites are derived from their hosts

Selection can favor the evolution of complex parasite life cycles

Sometimes complex life cycles are simplified secondarily

Parasites often have simplified bodies or genomes but also have other talents not seen in free-living organisms

## 7.6 PARASITE EFFECTS ON HOST EVOLUTION

Parasites select for genetic changes and genetic diversity in their hosts

Parasites affect the evolution of host MHC genes

Parasites play a role in host selection of mates

Host speciation may be facilitated by parasites

Can infection directly cause speciation?

Parasites are believed to favor the evolution of sexual reproduction in their hosts

Parasites can cause extinction of host species

## REVIEW QUESTIONS

## REFERENCES

## CHAPTER 8 PARASITES AND CONSERVATION BIOLOGY

### 8.1 SOME THEORY ABOUT PARASITES AND CONSERVATION BIOLOGY

Theory often predicts parasites will not extirpate their hosts, but by no means always

Persistent parasite infectious stages may also favor demise of host populations

279	The presence of a parasite-tolerant host species may endanger a susceptible one	321
279		
284	<b>8.2 PARASITES INFLUENCE EFFORTS TO PRESERVE HOSTS</b>	322
284	Parasites can cause extinction of host species	322
285	Parasites work in concert with other stressors to affect hosts	323
287	The impact of parasitism is influenced when hosts occur in small or fragmented populations.	324
289	Parasites can strongly affect hosts with reduced genetic variation	326
290	Captive host populations are often very vulnerable to parasites	328
293		
296	Parasites are frequently transferred from abundant host species to rare relatives, including from humans to our great ape cousins	328
296		
297	Farming can pose parasite problems for wild host species	329
298	Parasites of an iconic symbol—the giant panda—point out our need to know more	330
299		
300	<b>8.3 DANGERS RESULTING FROM SPECIES INTRODUCTIONS</b>	331
300	Parasites can be introduced with their hosts and have spillover effects	332
301	Introduced hosts can favor indigenous parasites and cause spillback effects	333
301		
303	Sometimes introduced nonhost organisms can influence indigenous parasite transmission	335
303		
304	Invading hosts can benefit by leaving their natural enemies, such as parasites, behind	336
304		
307	Invasive hosts can potentially be controlled by parasites from their original range	337
307		
309	Introductions of parasites or hosts often fail	338
309		
311	Translocations of endangered host species can have unforeseen consequences	338
311		
312	Can invasional meltdown occur?	339
312		
313	<b>8.4 PARASITES AS INDICATORS OF ENVIRONMENTAL HEALTH</b>	339
314	Parasites can help us monitor ecosystem integrity	339
314		
317	<b>8.5 PARASITES AS INFERENTIAL TOOLS TO PRESERVE HOST BIODIVERSITY</b>	342
317	Parasites can provide information useful to preserving their hosts	342
319	<b>8.6 THE NEED TO PRESERVE PARASITE DIVERSITY</b>	344
319	Parasites play key roles in maintaining ecosystem health	344
320	Parasites are drivers of biodiversity	345
320		

Parasites are a source of pharmacological and therapeutic novelties	345	Drug resistance can be prevented or reversed	382
Slip sliding away—parasite diversity is being lost	346	Concerns about resistance highlight the need for new anti-parasitic drugs	385
<b>REVIEW QUESTIONS</b>	<b>351</b>	New drugs are also needed to replace older more toxic medications	387
<b>REFERENCES</b>	<b>352</b>	The manner in which new drugs are discovered has changed considerably	387
		Potentially effective drugs usually require chemical modification prior to their use	388
	<b>355</b>	Economic issues often affect the rate at which new drugs are developed	389
<b>CHAPTER 9 THE CHALLENGE OF PARASITE CONTROL</b>			
<b>9.1 STRATEGIES TO REDUCE PARASITE TRANSMISSION</b>	<b>356</b>	<b>9.3 VACCINES</b>	<b>390</b>
Parasite transmission may be reduced in various ways	356	Vaccines must be safe and inexpensive, while inducing long-term immunity	392
Parasites using trophic transmission can be controlled by insuring food safety	357	Vaccines against eukaryotic parasites are particularly problematic	393
Proper sanitation is the key to controlling parasites transmitted via the fecal-oral route	358	Vaccines can be categorized into several types	394
Various other factors influence the success of control efforts	360	An effective malaria vaccine has been the object of intensive investigation	396
The control of vector-borne diseases focuses on reducing human–vector contact	362	Vaccines against different life-cycle stages offer different potential benefits	396
The discovery of DDT radically altered vector control efforts	363	Recent candidate vaccines may be used clinically in the near future	398
Newer insecticides provide alternatives to DDT	364	A few anti-eukaryote vaccines are available for veterinary use	398
Transmission of vector-borne parasites can be reduced through environmental manipulation		Vaccines against helminth parasites are being investigated	399
Biological control offers the possibility of low-cost, sustainable control			
The production of transgenic vectors provides hope as a means to reduce vector capacity	369	<b>REVIEW QUESTIONS</b>	<b>401</b>
		<b>REFERENCES</b>	<b>402</b>
<b>9.2 ANTI-PARASITIC DRUGS</b>	<b>372</b>	<b>CHAPTER 10 THE FUTURE OF PARASITOLOGY</b>	<b>405</b>
Various factors influence the selection of the best anti-parasitic drug in different situations	373	<b>10.1 OUR FUTURE WORLD</b>	<b>405</b>
Different drugs may be appropriate for treatment and for prophylaxis	374	<b>10.2 SOME FUTURE CHALLENGES FOR PARASITOLOGISTS</b>	<b>407</b>
Drugs may be used to either treat or protect individuals or to protect a population	374	There is always something new to be found under the parasitological sun	407
Certain drugs are active only against specific parasite life-cycle stages	375	We need to better understand the ecological and evolutionary roles of parasites	408
Drug use may affect the immune status of the population	377	Revealing how parasite and host molecules interact is needed to clarify many fundamental aspects of parasitism	411
The use of anti-parasitic drugs can lead to resistance	378	Climate change will affect parasites, but we know little about how	412
Genetic alterations can cause resistance in diverse ways	379		
Resistance poses a considerable problem for disease control programs	381		

---

<b>10.3 CONTROLLING PARASITES IN THE FUTURE</b>	<b>417</b>
Improved understanding of immunity should enable development of new anti-parasite vaccines, but so far the parasites are winning	417
Chemotherapy-based control is an arms race between human ingenuity and parasite evolvability	418
Integrated control may provide the best prospects for sustainable parasite control and is built on a thorough knowledge of parasite biology	420
Major programs are underway to eliminate many parasites as public health problems	422
We will need improved methods to detect low levels of parasite infection and transmission in the future	424
Provision of improved living conditions, including education, will further discourage parasite transmission	425
<b>REVIEW QUESTIONS</b>	<b>426</b>
<b>REFERENCES</b>	<b>427</b>
<b>ROGUES' GALLERY OF PARASITES</b>	<b>429</b>
<b>THE PROTOZOA</b>	<b>430</b>
<b>PHYLUM PLATYHELMINTHES</b>	<b>458</b>
<b>PHYLUM NEMATODA</b>	<b>479</b>
<b>THE ARTHROPODS</b>	<b>496</b>
<b>OTHERS</b>	<b>518</b>
<b>GLOSSARY</b>	<b>527</b>
<b>INDEX</b>	<b>539</b>