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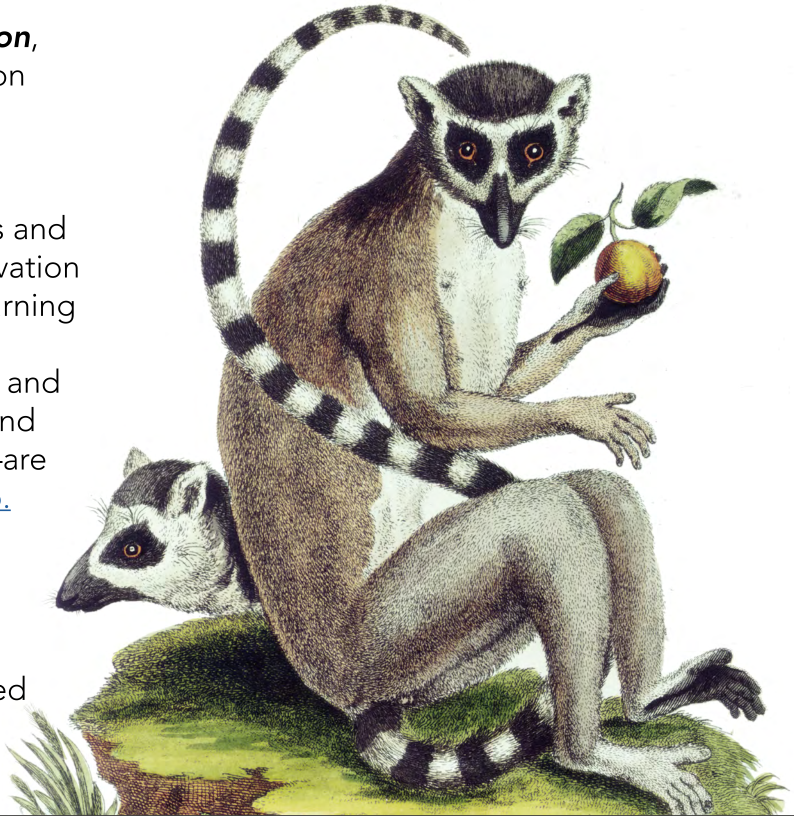

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Parasite Biodiversity

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ABSTRACT

A parasite is an organism that lives in an intimate and durable relationship with its host and imposes a cost on that host, in terms of its ability to survive, grow, and/or reproduce. Despite the fact that more than 40% of animal species are parasites, parasitism is rarely discussed in introductory biology courses. This may be because parasites are often hidden within their hosts—and therefore easy to ignore. But parasites have important roles to play in ecosystems and we ignore them at our own peril. In this module, students have the opportunity to discover the hidden world of parasites: they will come face to face with living parasites, learn about what differentiates parasites from free-living species, observe some common adaptations to a parasitic lifestyle, explore the ecological role of parasites in food webs, and assess how parasite abundance might change in a changing world. To accomplish these goals, this module includes an introductory PowerPoint presentation (including a video of parasite ecologist Dr. Chelsea L. Wood delivering this introductory lecture) and two exercises.* The first exercise is a wet lab that involves dissecting an easy (and disturbing) source of live parasite material: fresh fish from your local seafood market. The second exercise is a computer lab that will allow students to engage with real data to answer the question: how do human impacts on ecosystems change the abundance of parasites in wildlife? This module will introduce students to the basics of parasite ecology and provide an opportunity to practice their data analysis and interpretation skills.

INTRODUCTION: THE HIDDEN WORLD OF PARASITES

A parasite is an organism that lives in an intimate and durable relationship with its host[1], and imposes a fitness cost[2] on that host (Combes 2001). Parasites are everywhere, but they are often ignored due to their small size and cryptic[3] nature. Perhaps forty percent of all animal species are parasites (Dobson et al. 2008), and virtually all animals are infected by at least one species of parasite (Poulin and Morand 2000).

There are several types of close interactions that are similar to, but different from, parasitism. Parasites are different than symbiotic mutualists[4], or organisms that provide beneficial services for their host (Boucher et al. 1982; Thrall et al. 2007). For example, photosynthetic algae that live within corals and provide them with energy derived from the sun are engaged in a mutualistic, not parasitic, interaction with their host (Baker 2003). Parasites also differ from micropredators[5] and other free-living organisms[6], in that they must reside in association with their host for at least part of their life cycle. Micropredators (unlike parasites) do not live in intimate association with their prey, but rather feed in short bursts, interspersed with long periods of a free-living lifestyle. Examples of micropredators include mosquitos, bed bugs, and leeches. Micropredators take small, non-lethal meals from many hosts, whereas parasites exploit only one host per parasitic life stage (Poulin 2011a).

How many parasite species are there on the planet Earth? Considering that parasites are a diverse and complex group of animals, providing one accurate number of their species richness is nearly

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impossible. However, we can certainly put parasite diversity into perspective. For example, it is estimated that there are more than 70,000 species that attach externally to hosts (Poulin 2011b). The parasitic lifestyle is represented across nearly all taxa, and there are a reported 7,000 species of parasites known to infect crustaceans (Boxshall and Hayes 2019). In one of the most speciose ecosystems on the planet—the Great Barrier Reef—it was estimated that there are more than 20,000 parasites of fish (Rohde 1976); this number doesn't even account for parasites of invertebrates like corals and mollusks. Research is ongoing to identify and describe new parasite species and to refine these estimates of parasite biodiversity.

Two types of parasites—pathogens and macroparasites—are distinguished from one another by their mode of reproduction. Pathogens tend to be small, multiply within or on their host and to have very short generation times[7] in relation to their host (e.g., many parasitic bacteria, viruses, and fungi; Swinton et al. 2002). If a host is infected with a pathogen, it will ultimately succumb to the multiplying pathogen unless the host's immune defenses limit pathogen multiplication. In contrast, macroparasites do not multiply within their host and include some arthropod, flatworm, and nematode parasites (Poulin 2011a). Macroparasites can range in size from very small (invisible to the naked eye) to large (e.g., parasitic nematodes that inhabit sperm whale placentas can reach up to 8.4 meters long; Gubanov 1951). Macroparasites have longer generation times than pathogens and tend to accumulate slowly within a host because each individual requires an independent infection event. Although their growth rate and generation times are often different, both types of parasites can cause disease, which is defined as the fitness loss of a host due to parasitic infection. Macroparasites can be either endoparasites (i.e., parasites that live within the body of their host) or ectoparasites (i.e., parasites that live on the external surface of their host).

Humans have been aware of the existence of parasites for thousands of years. Both Hippocrates and Aristotle documented several parasites in their written works (Hoeppli 1956; Trompoukis et al. 2007) and parasites have also been discovered in ancient humans [e.g., Egyptian mummies (Gonçalves et al. 2003) and Ötzi the Ice Man (Dickson et al. 2000)]. Much of what we know about parasites is focused on parasites of humans and the diseases they cause. In fact, one of the first Nobel Prizes was awarded to Ronald Ross in 1902 for his research on the life cycle of the protozoan parasite, malaria. However, parasite ecology—the study of how parasites interact with other organisms and their environment—is a relatively new science. Despite the fact that humans have lived in association with parasites for millennia, there are still many important unanswered questions in parasite ecology and fundamental scientific discoveries yet to be made.

An important part of parasite ecology is discovering, identifying, and naming new parasites. Early parasitology[8] focused on identifying and naming new parasites of humans. While our understanding of parasites has grown considerably in recent years (e.g., Smit et al. 2014), efforts to identify and name new parasites are an ongoing project. For example, a recent paper estimated that 85–95% of helminths (i.e., parasitic worms such as nematodes, flukes, and tapeworms) of vertebrates are unknown to science (Carlson et al. 2020). Today, scientists use a range of tools to visualize parasites, including dissecting microscopes, compound microscopes, and scanning electron microscopes (SEM). The names of new parasite species have also become more creative over time. In the past, parasites were primarily named for their appearance or the location of first discovery. For example, *Gnathia trimaculata* is named for having three spots ("tri" meaning three; Coetzee et al. 2009), *Gnathia masca* is named for have a face that appears to be wearing a mask (Farquharson et al. 2012a), and *Cymothoa sodwana* (a tongue-eating parasite) is named due to its prevalence[9] in Sodwana Bay, South Africa (Hadfield et al. 2013). Recently, a few parasite names have been dedicated to popular culture icons, such as musicians (e.g., Bob Marley, *Gnathia marleyi*; Farquharson et al. 2012b), politicians (e.g., President Obama, *Baracktrema obamai*; Roberts et al. 2016), and television characters (e.g., Xena, Warrior Princess, *Elthusa xena*; van der Wal et al. 2019). There is room for creativity and exploration in parasitology, as many currently undescribed species still await discovery.

Why are parasites rarely discussed? This is probably because parasites tend to be hidden within their hosts—and therefore easy to ignore. Although some parasites can cause disease, parasites as a whole are diverse and their contribution to ecosystem functioning is complex and often positive (Hudson et al. 2006; Kuris et al. 2008; Nichols and Gómez 2011). Despite their small size, parasites have important roles to play in ecosystems, and we ignore them at our own peril.

PARASITES IN YOUR LIFE

Where might you encounter parasites in your daily life? If you own pets or livestock, you might be familiar with the practice of "deworming" these animals. Antihelminthics are medications that treat infections of flatworms and roundworms, which animals can be exposed to in their environment. Parasitic worm infections in pets can vary in severity, from symptomless to severe; for example, heartworms can be fatal in dogs (Conboy 2011).

Humans can occasionally contract parasitic worm infections from their pets. One example is a single-celled parasite that is transmitted from cats to humans. *Toxoplasma gondii* is transmitted from cats through contact with cat feces, or from eating undercooked meat (especially pork, lamb, beef, and venison; Tenter et al. 2000; CDC 2010a). This parasite is found around the world, and an estimated 40 million people are infected with *Toxoplasma* in the United States alone (CDC 2010a). While toxoplasmosis (infection with *Toxoplasma gondii*) generally has mild flu-like symptoms which go unnoticed, this parasite can cause serious problems for pregnant women (who can transmit the parasite to their fetus) and immunocompromised individuals. This is why you may have heard that women should not clean litter boxes while they are pregnant.

Toxoplasma is a particularly fascinating parasite, due to its ability to manipulate the behavior of its host. In its lifecycle, *Toxoplasma* alternates between a host that it infects and uses temporarily (usually a small rodent, e.g., a rat), and its definitive (final) host[10], a cat (Beverley 1976; Dubey 2016). *Toxoplasma* manipulates its rodent host to become more vulnerable to predation by the definitive host (the cat). To do this, *Toxoplasma* changes neural pathways and activity in infected rodents, inhibiting their fear response and replacing it with sexual attraction to the smell of cat urine (Berdoy et al. 2000). These newly emboldened rodents are more likely to approach and be eaten by cats, transmitting *Toxoplasma* in the process. Humans are generally dead-end hosts[11] for *Toxoplasma* (in general, people are infrequently eaten by felines), but neurochemical processes similar to those in rats can affect infected humans as well (Webster 2001). Rather than causing sexual attraction to cat urine, however, *Toxoplasma* causes emboldened, sometimes reckless behavior due to an inhibited fear response. For example, *Toxoplasma* may influence the behavior of individuals in business and entrepreneurial settings (Houdek 2017). Researchers have found that college students infected with *Toxoplasma* are more likely to major in business, and in particular in "management and entrepreneurship" (Johnson et al. 2018). Furthermore, at an entrepreneurial event, individuals who were infected with *Toxoplasma* were 1.8 times more likely to have already started their own business than other attendees (Johnson et al. 2018). In addition to these specific instances, there is evidence that country-level patterns of *Toxoplasma* infection may even influence human culture (Lafferty 2006). This demonstrates how even a tiny, single-celled parasite can cause significant change at a global scale.

Another group of parasites you might encounter are seafood parasites. A variety of parasites infect fish, and a few of these parasites can be transmitted to humans, such as the broad fish tapeworm, *Diphyllobothrium latum*, (Figure 1; Scholz et al. 2009; Kuchta et al. 2013) and anisakid nematodes, *Anisakis* and *Pseudoterranova* spp. (Figure 2; Oshima 1987). The fish tapeworm is one of the largest tapeworms that can infect humans, growing up to 30 feet long (CDC 2010b). Human infection occurs when an individual eats raw or undercooked fish, although freezing fish thoroughly before eating or cooking the fish prevents the threat of infection (CDC 2010b). Anisakiasis (infection with anisakid nematodes) can also result from ingestion of raw or undercooked fish, and often is evidenced by symptoms that resemble food poisoning. Consequently, in the USA, the Food and Drug Administration mandates that all fish destined to become sushi (other than tuna) is thoroughly frozen before sale and consumption.

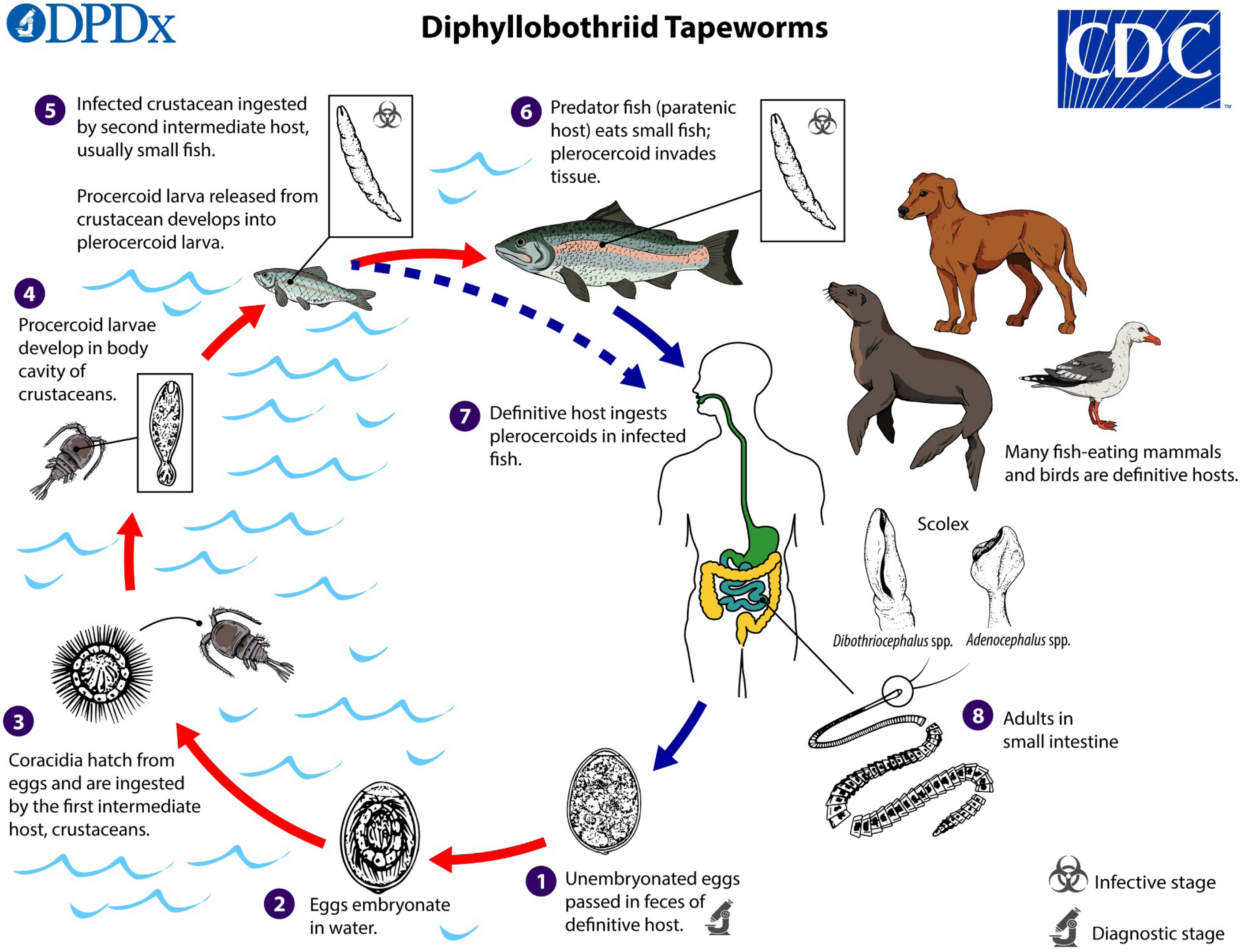

Figure 1. Life cycle of a parasitic cestode (*Diphyllobothrium* spp.). This group of tapeworms completes most of its life cycle in freshwater organisms (e.g., crustaceans and fish) before becoming mature in a human host, where they can cause the disease diphyllobothriasis. For a complete description of the *Diphyllobothrium* spp. life cycle, go to: https://www.cdc.gov/dpdx/diphyllobothriasis/index.html. (2002; CDC/Alexander J. da Silva, PhD; Melanie Moser). Image credit: DPDx/CDC (public domain).

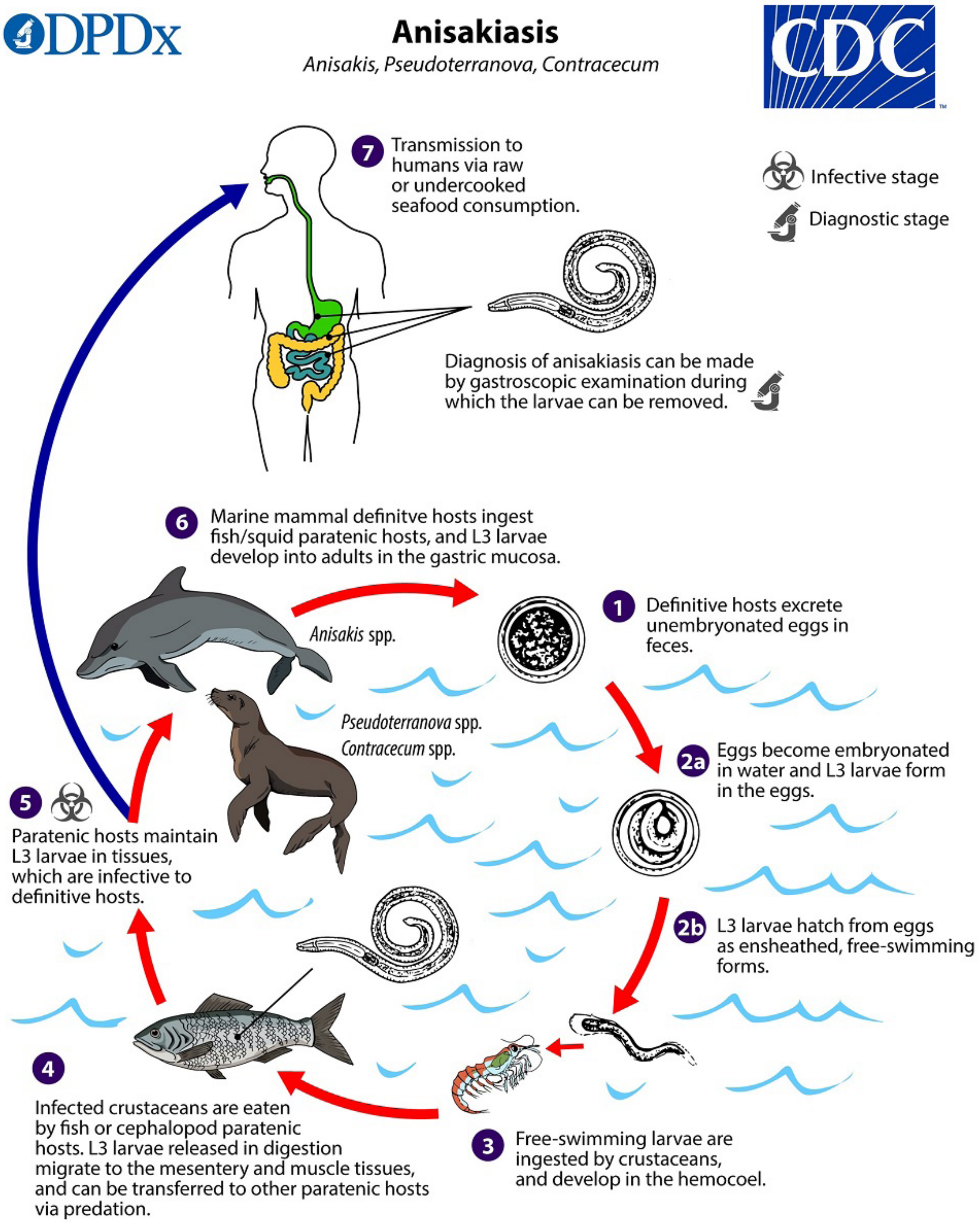

Figure 2. Life cycle of parasitic nematodes (*Anisakis*, *Pseudoterranova*, and *Contracecum*) which can cause anasakiasis in humans and marine mammals. For a complete description of the life cycle of *A. simplex* and *P. decipiens*, go to: https://www.cdc.gov/dpdx/anisakiasis/index.html. (2002; CDC/Alexander J. da Silva, PhD; Melanie Moser). Image credit: DPDx/CDC (public domain).

Toxoplasma gondii and the "sushi" parasites are only a small fraction of parasites that affect humans. For example, approximately one billion people are currently infected with the human roundworm, *Ascaris lumbricoides* (CDC 2010c). In this synthesis, we'll talk primarily about the broader diversity of parasites—not only those that affect humans but also the many parasites found across the animal kingdom.

ADAPTATIONS TO A PARASITIC LIFESTYLE

With the advent and advancement of molecular techniques such as genome sequencing (Poulin and Randhawa 2015), new parasite species continue to be identified and described. Historically, species identification of parasites was based only on morphological differences, but we now pair morphological differences with genetic analyses to define parasite species (Nadler and De León

2011; Hoogendoorn et al. 2019; Lisitsyna et al. 2019). In doing so, scientists have realized there are many more species than was previously thought, and some are cryptic, meaning that two similar parasites may look nearly the same to the naked eye and under magnification but differ substantially in their DNA sequences (Soldánová et al. 2017; Welicky et al. 2017). New species of parasites are being found so frequently that they are regularly documented in parasitology journals (e.g., *Journal of Parasitology*, *International Journal for Parasitology*, *Parasitological Research*). However, identification is merely a first step in understanding parasite biology, and we must also know the life cycle of parasites. Unfortunately, this is challenging; for example, only 1% of the nearly 400 described trematode worm species from the Great Barrier Reef have fully described life cycles (Cribb et al. 2014, 2016; Huston et al. 2016).

Parasite life cycles can be difficult to describe because many parasites have multiple hosts during their lifetime and each parasite must be tracked through each host (e.g., Huston et al. 2016). Parasite life cycles may include direct transmission or complex lifestyles (Combes 2001). Parasites with direct life cycles are those in which a parasite infects a single host throughout its entire life span, whereas complex life cycles include several transitions between host species during the lifespan of a single parasite. We provide specific examples of these life cycle types below.

Direct Life Cycles

Parasites with direct transmission only infect one host species over the course of their life cycle. An example of a group of directly transmitted parasites are the strongyloid nematodes. This group of roundworms typically infect the gastrointestinal tract of mammals such as sheep (Figure 3), cattle, reindeer, and muskoxen. For example, *Ostertagia gruehneri* is a strongylid nematode that is found in reindeer (Hrabok 2006), and *Trichostrongylus axei* is found in sheep (Roeber et al. 2013). Both

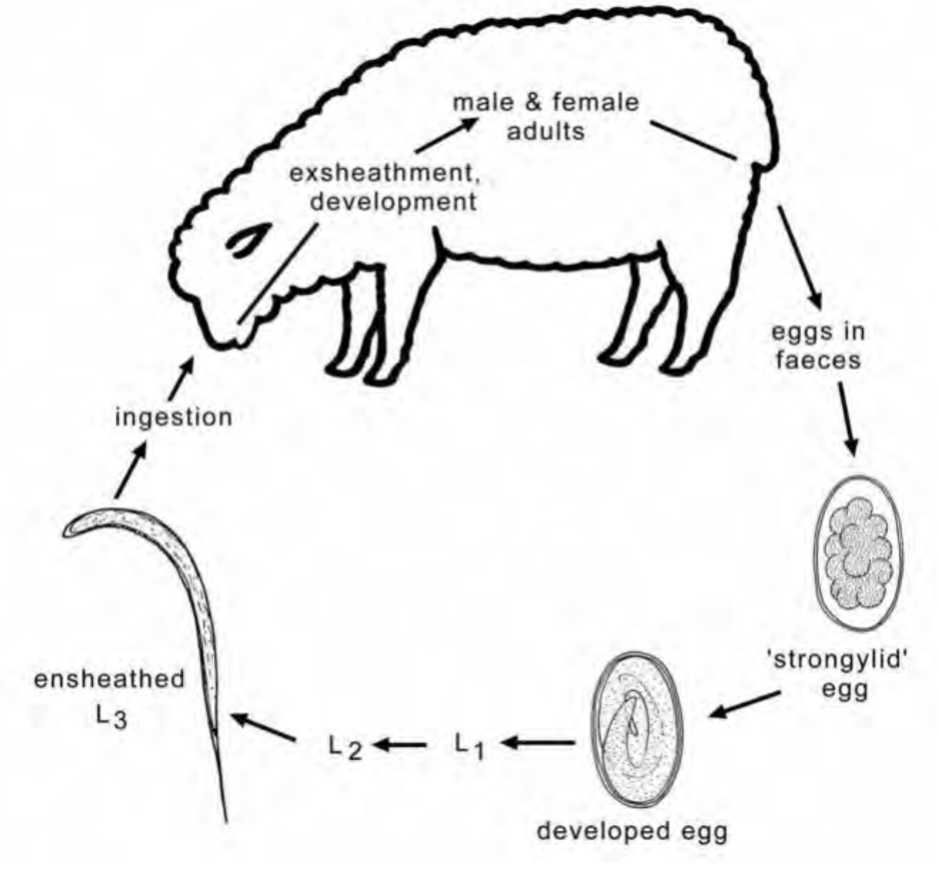

Figure 3. Life cycle of gastrointestinal nematodes (Order Strongylida) that infect sheep (Roeber et al. 2013). For most of their life cycle, these nematodes are free-living, with their first-, second-, and third-stage larvae (L1, L2, and L3, respectively) living in the environment. The L3 larvae are incidentally consumed by the sheep during grazing. Once inside the sheep, these parasites mature to the fourth larval (L4) stage and migrate to the gastrointestinal tract of the sheep where they become adults. Image credit: Roeber et al. 2013 (CC BY 2.0).

of these nematodes follow a similar life cycle. The nematodes mature and sexually reproduce in the gastrointestinal tract of their host, where they are passed onto the pasture in feces. Next, the nematode eggs undergo development in the "strongylid" phase before becoming a fully developed egg. After this, the egg hatches, and matures from the first larval stage to the second larval stage via molting. Then the larvae undergo a third developmental stage that is followed by incidental ingestion by the host. As the host grazes on the pasture, the parasite's life cycle is renewed.

Complex Life Cycles

Complex life cycles involve a transition between at least two hosts. These hosts are always different species and are often completely unrelated (e.g., a single parasite could inhabit a snail, a fish, and a bird during its life cycle). Intermediate hosts[12] are hosts infected with larval parasites, while definitive hosts (or final hosts) are hosts in which a parasite reaches adulthood and reproduces sexually. A parasite species may have more than one intermediate host in its life cycle (see Figure 4). An example of a parasite with a complex life cycle is the trematode, *Euhaplorchis californiensis* (Figure 4), which infects California horn snails (intermediate host), California killifish (intermediate host), and shorebirds (definitive host) during its life cycle (Lafferty and Morris 1996). This parasite also manipulates its second intermediate host. When *E. californiensis* infects the killifish, it migrates into the cranium, encysting on the surface of the brain (Martin 1950). It alters the behavior of the fish, changing brain chemistry (Shaw et al. 2009) and causing it to exhibit behavior easily seen by birds, such as jerking, flashing, and surfacing (Lafferty and Morris 1996). These behaviors cause an infected killifish to be 10–30 times more likely to be eaten by its definitive host, a shorebird (Lafferty and Morris 1996). Although this life cycle and apparent mind control may seem unique, these sorts of behavioral changes are common across many parasites with prey hosts that will be eaten by predator hosts. The ecological interactions among parasites, their hosts, and their environment are complex, and this next section will focus on how parasites can shape the ecosystems they inhabit.

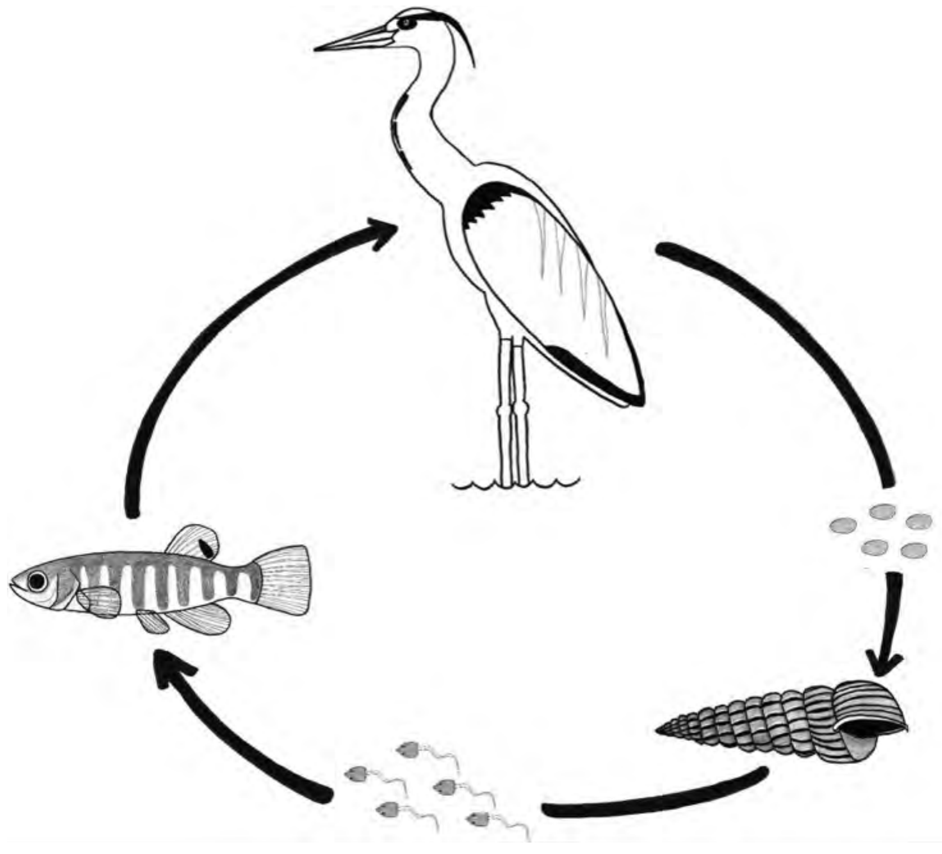

Figure 4. Life cycle of *Euhaplorchis californiensis*. The eggs of *E. californiensis* are shed in the feces of shorebirds (the definitive host), and then eaten by horn snails (the first intermediate host) where they undergo asexual reproduction. Next, the larvae of *E. californiensis* (cercariae) are shed from the snail into the water where they swim until they encounter a killifish (the second intermediate host). The infected killifish is eaten by a shorebird, and the cycle begins again. Image credit: Danielle Claar.

THE ECOLOGICAL ROLE OF PARASITES

Parasites have fundamental effects on ecosystem function, but this is seldom evident. They influence individual behavior, health, and distribution of their hosts, as well as the composition and diversity of ecological communities. These individual- and community-level effects can translate into changes in ecosystem function and the distribution of biodiversity, and they have shaped the evolution of life itself.

Parasite Effects on Individuals

As we have already seen in the examples of the brain cysts in the killifish and *Toxoplasma* in rats, parasites can influence the behavior of their hosts (Barnard and Behnke 1990; Barber et al. 2000; Hughes et al. 2012). Another well-researched example of behavioral manipulation is the interaction between the tapeworm *Schistocephalus solidus* and its second intermediate host, a three-spined stickleback (a small freshwater fish). When a stickleback is infected with *Schistocephalus* (Figure 5), the fish swims closer to the water's surface, is bolder, and is more likely to ignore overhead stimuli (e.g., they are less frightened of potential bird predators; Giles 1983). This is a clever behavioral manipulation by the parasite. By making the stickleback more visible in the water column, the parasite increases the likelihood that its intermediate host (the stickleback) will be eaten by its definitive host (a wading bird; Barber and Scharsack 2010). Once the stickleback and tapeworm are ingested by the bird, the parasite can continue its lifecycle and reproduce, shedding a new generation of tapeworm eggs into the environment (Figure 5).

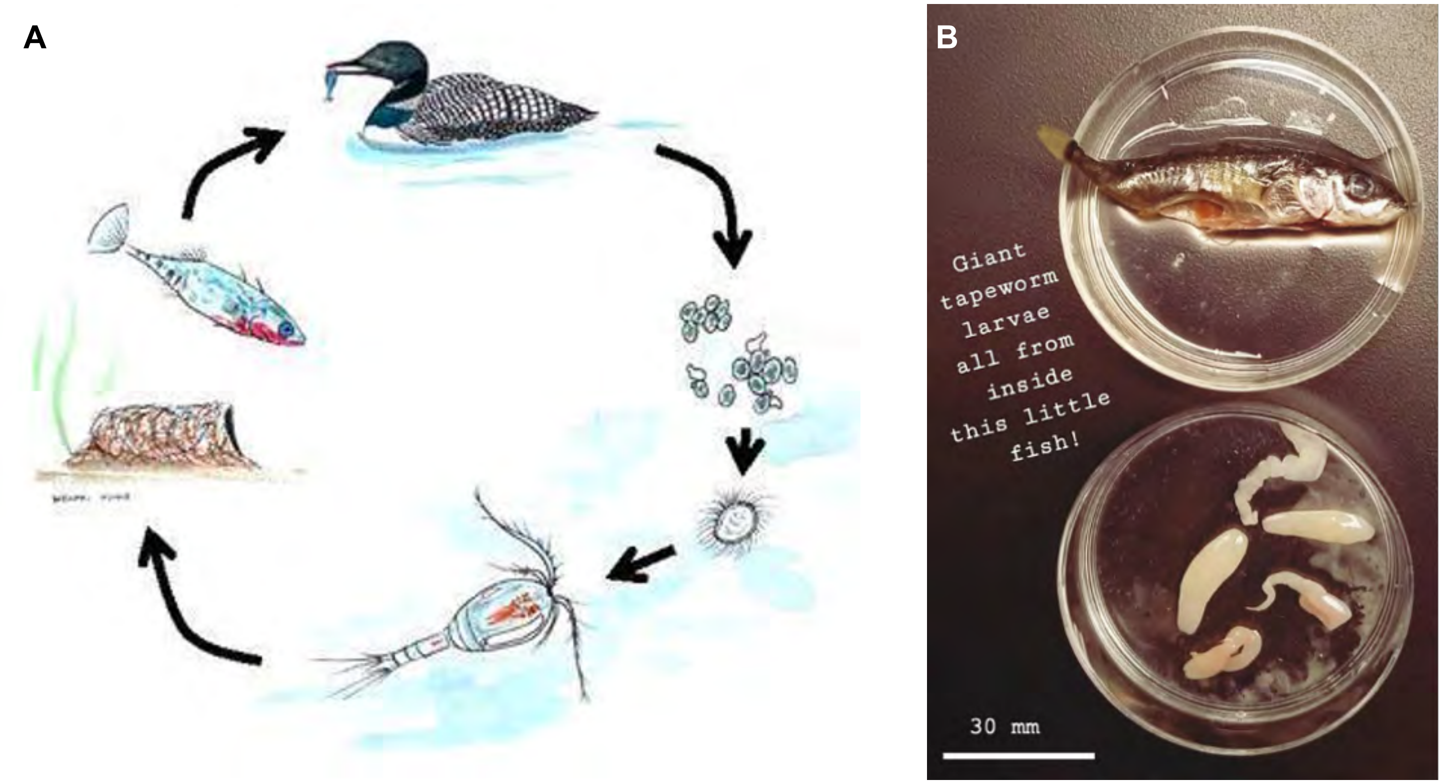

Figure 5. (A) Life cycle of *Schistocephalus solidus*. *Schistocephalus* eggs are excreted in the feces of water birds. These eggs hatch and become coracidia (the first larval stage). Coracidia are ingested by a copepod (the first intermediate host) where they continue to develop as the second larval stage (procercoids). Next, the copepod is eaten by a stickleback fish, and the plerocercoid (third larval stage) of *Schistocephalus* continues to develop in the abdomen of the fish until the fish is consumed by a wading bird and the cycle continues (Weber et al. 2017) (B) Photo of stickleback dissection. All *Schistocephalus solidus* tapeworm plerocercoids in the bottom petri dish came from this one stickleback. Image credits (L-R): Weber et al. 2017; Katie L. Leslie.

Parasites also affect individuals by affecting host reproduction. If hosts spend enough energy fighting against or accommodating their parasites, their reproductive output (i.e., the number of offspring they can produce) can be decreased. Additionally, some parasites purposefully castrate or sterilize their host, so the host is completely unable to reproduce (Kuris 1974). This strategy is fairly common in the marine realm, where, for example, many types of larval trematodes can castrate snails, and parasitic isopod and barnacle species can castrate their host crustaceans (Lafferty and Kuris 2009a). Even some vertebrate hosts can be parasitically castrated, such as the five-lined cardinalfish (Fogelman and Grutter 2008). As "body snatchers," parasitic castrators usually block host reproduction for the remaining life of the host.

Finally, and perhaps most obviously, parasitic infection can cause loss of fitness and even death. Depending on their parasite load, a host might have mild to moderate disease symptoms, which may remain relatively stable over the lifetime of the host, or they may progress to severe disease symptoms and ultimately die as a result of their infection. The impact of macroparasites on hosts is dependent on the number of parasites that a host is exposed to and the relative disease potential of those parasites (Anderson and May 1978). So, if a human is infected by only one hookworm, they may display no noticeable disease symptoms, but if it is exposed to 100 hookworms, they may become severely anemic. Conversely, the impact of pathogens is less dependent on the number of parasites to which a host is initially exposed (Anderson and May 1979). This is because pathogens reproduce within the host. Causing the death of their host is not an ideal situation for most parasites. The host provides habitat and nutrition for a parasite, so it is against the interest of the parasite for its host to die. One exception is diseases that are spread from carcasses to living hosts via contact transmission (e.g., anthrax, Ebola). Another obvious and common exception, discussed earlier in the context of *Toxoplasma* and *Schistocephalus* infections, is trophic transmission, or when the parasite has a complex life cycle that necessitates their intermediate prey host (in these cases a rat and a stickleback fish) to be eaten by a predator definitive host (respectively a cat and a wading bird).

Parasite Effects on Populations

The effects of parasites on individual hosts can lead to broader impacts on host populations (Wood and Johnson 2015). Crustacean parasites can reduce growth, reproduction, and survivorship of reef fishes[13], which leads to population regulation and strengthens density-dependent interactions. A study of the bridled goby (*Coryphopterus glaucofraenum*) infected with the copepod gill parasite *Pharodes tortugensis* showed that parasitic infection prevalence increased the negative effects of high host density on host survival (i.e., a high density of gobies was associated with increased mortality in such populations). This effect was disproportionately worse for infected compared to uninfected gobies (Forrester and Finley 2006). Parasitism may also influence host populations by inducing boom-and-bust cycles in host population size (Hudson et al. 1998). For example, red grouse populations (a valuable game bird in the United Kingdom) typically experience boom-and-bust cycles (i.e., high population density followed by crashes to low population density). When these grouse populations were treated with an antihelminthic to clear parasitic nematode (*Trichostrongylus tenuis*) infections, these cycles were dampened, causing a more consistent population density of grouse over time (Hudson et al. 1998). This suggests that parasitism drives cyclical population sizes in red grouse and may influence other parasitized populations in a similar way. Finally, parasitic castration (discussed above) can also influence host populations. Although castration is an individual effect, it directly influences reproduction. Therefore, the intensity of infection by parasitic castrators can drive host population size (Kuris 1974; Blower and Roughgarden 1987). These types of effects on host populations can link individual effects of parasitism to community- and ecosystem-wide effects.

Parasite Effects on Communities

Another important ecological role played by parasites is regulating host community structure and biodiversity. By regulating host populations, some parasites can influence the outcome of competition of hosts in the environment (Mordecai 2011). Specifically, this occurs when parasites limit the population size of the numerically dominant host, allowing rarer hosts to persist and even thrive. Specialist parasites may facilitate species coexistence by keeping a singular dominant species in check while allowing rare species to persist (Fenton and Brockhurst 2008; Grewell 2008). Generalist and specialist parasites can also regulate community composition on a diel (daily) cycle. For example, parasites can influence the timing of host foraging and cleaning activity patterns (Sikkel et al. 2004; Sikkel et al. 2006) and when hosts leave and return to their daytime and nighttime habitats, such as the daily migration of French grunts (a Caribbean fish) between reef and seagrass habitats (Welicky and Sikkel 2015; Sikkel et al. 2017). Parasitism may also influence niche partitioning; for example, parasitism by a fungus alters competition among two species of tropical spider, allowing one species to live adjacent to riverbanks but excluding the other and limiting its distribution to further away from the river margin (Cardoso et al. 2018). Finally, parasites can increase biodiversity and alter community structure concurrently by introducing new diseases, bacteria, and viruses to hosts which in turn reduces host abundance by decreasing their survival rate and fitness (reviewed in Hadfield and Smit 2019). While several such examples of parasite influence on community ecology have been documented, it is likely that many more exist, waiting to be discovered.

Parasite Effects on Food Webs

Parasites can influence not only individuals and communities but can also cause changes that cascade throughout ecosystems (Figure 6; Buck and Ripple 2017). For example, rinderpest, a morbillivirus related to measles in humans and distemper in canines, caused an ecosystem cascade when it underwent a series of outbreaks in Africa (Holdo et al. 2009). Rinderpest outbreaks decimated ungulate (e.g., wildebeest and buffalo) populations. This caused cascading effects on both vegetation and tree communities which are shaped by ungulate grazing, as well as predator populations (e.g., lions and hyenas) that consume ungulates (Dobson et al. 2006). Widespread extermination of rinderpest after the development of a vaccine caused another cascade that allowed savannah ecosystems to rebound towards a pre-outbreak baseline ecosystem structure (Dobson et al. 2006).

Another example of a parasite-induced cascade was the epidemic mortality of the Caribbean black-spined sea urchin (*Diadema antillarum*; Figure 6; Lessios 1988). This urchin was a keystone herbivore in the Caribbean until the 1980s when a host-specific bacterial pathogen wiped out approximately 98% of the urchin population (Lessios 1988). The urchins were a keystone species because they were keeping macroalgae communities in check via grazing. When the urchin population was decimated, the keystone was metaphorically removed and the rest of the community shifted and macroalgae overgrew the reef—transitioning the system from being coral-dominated to algae-dominated (Hughes 1994).

Furthermore, parasites may strengthen trophic interactions and maintain a "cohesive matrix" of food web interactions (Lafferty et al. 2006). Specifically, parasites may affect food web stability and structure by altering the interactions that are represented in a typical food web model (Lafferty et al. 2008). Specifically, the presence of parasites increases the number of links (i.e., interactions between two organisms) in a food web, which can help stabilize food web structure, even under external stressors. However, the incorporation of parasites into food web models is still in its infancy, and more research is needed in order to build, understand, and analyze how food web dynamics change when parasites are included.

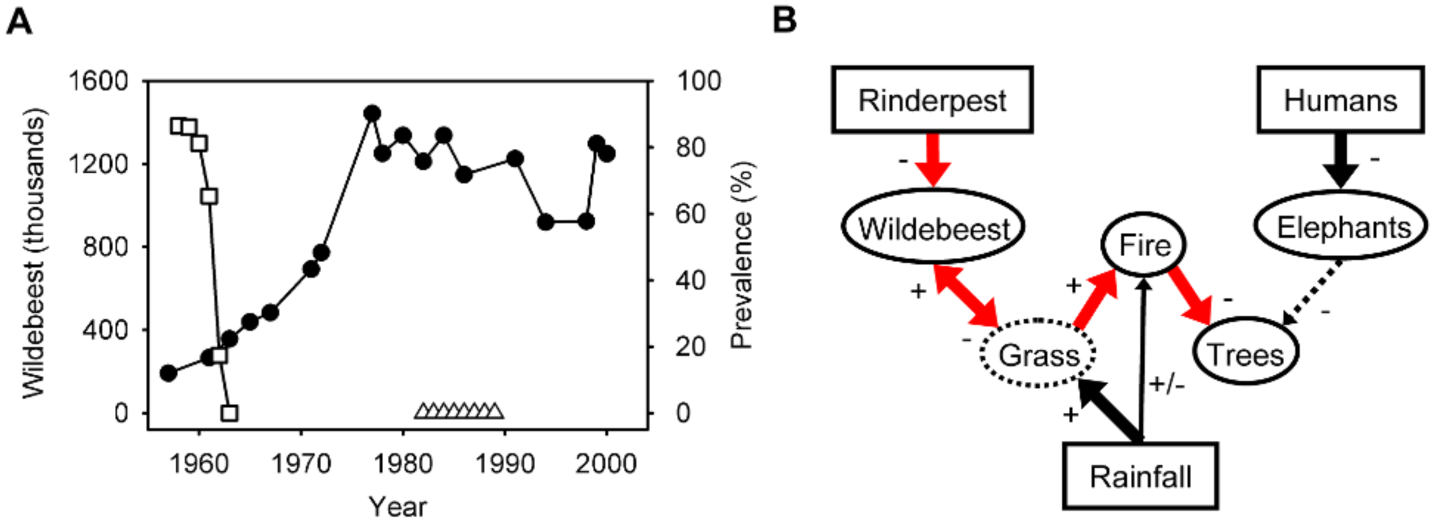

Figure 6. Rinderpest-mediated regulation of ecosystem dynamics (Holdo et al. 2009). (A) Serengeti wildebeest population (filled circle) and rinderpest seroprevalence reported for the periods 1958–1963. (B) Inferred causal relationships driving tree population dynamics in the Serengeti. The dominant effects are shown with thick arrows. Highlighted in red is a four-step pathway of causality linking rinderpest with tree population dynamics. Rinderpest decreases wildebeest populations, which in turn consume less grass. The increase in grasses also increases the risk for fire, which also burns down trees. This leads to multiple pressures on elephant populations, both from direct human impacts and from altered tree popullations. The grass compartment, as an unobserved variable, is shown in dotted outline. Image credits: Holdo et al. 2009 (CC BY).

Parasite Effects on Evolution

Parasitism can drive the evolution of species, both parasite and host, in a number of ways. First, parasitism can induce an evolutionary arms race between a parasite and its host (Medel et al. 2010). This occurs when the parasite damages the host (i.e., causes decreased fitness of the host), and the host responds by improving their defenses against that parasite. In turn, as long as these defenses do not completely clear the parasitic infection, the parasite may evolve novel strategies to circumvent host defenses. This can become an ongoing cycle: host improves defenses, parasite circumvents defenses, host reinforces defenses, and so on. This cycle is termed the "Red Queen hypothesis," a name inspired by a quote from the Red Queen in Lewis Carroll's *Through the Looking-Glass*: "Now, here, you see, it takes all the running you can do, to keep in the same place" (Van Valen 1973, 1977). This type of arms race or competition has enabled the development of several amazing adaptations and may have even been responsible for the evolution of sex (Hamilton 1980; Lively 2010). This is because asexual populations are clonal (i.e., genetically identical), while sexual populations allow for selection of traits that can defend them against parasites. Co-evolution can either be driven by the Red Queen effect (i.e., the evolution of host defenses and parasite virulence[14]) or by evolution of both the parasite and the host to their environment.

Parasitism may also drive the evolution of sexual selection in some species (Clayton 1991). For example, the eyebrow coloration of red grouse (mentioned above) is driven by their interactions with parasites (Hamilton and Zuk 1982). The eyebrows of male grouse are red, and some individuals have a drab, rust colored red while others have brilliantly red eyebrows. Research has shown that the redness of these feathers is an "honest signal" of the male's resistance to parasitism by the gut nematode *Trichostrongylus tenuis* (Hamilton and Zuk 1982). This is because production of the carotenoid pigments that make male grouse feathers bright red is energetically costly. Infected males must invest a disproportionate amount of energy responding to parasitism by *T. tenuis*. This depletes energy reserves which might otherwise have been used for coloration. During mating, females tend to select for showier, more brightly colored males, which increases their fitness by producing offspring that are more likely to inherit resistance to *T. tenuis*. Carotenoid production (and associated red coloration) is also associated with exposure to, and resistance from, parasites in fishes such as the three-spined stickleback (Folkstad et al. 1994). These are just a couple of examples of how parasitism can influence evolution and sexual selection, but many more examples exist across the animal kingdom.

PARASITES IN A CHANGING WORLD

Links between host–parasite interactions and the surrounding environment are complex and highly variable (Wolinska and King 2009; Mostowy and Engelstädter 2011). Parasitism may be affected by a number of environmental factors, such as climate change (Marcogliese 2001), fishing or harvest of host species (Wood et al. 2010), pollution (Sures 2008), and habitat loss (Mbora and McPeek 2009). The effect of environmental changes on parasite survival and reproduction can be non-linear (i.e., context dependent; Kutz et al. 2014), therefore, it is often difficult to predict how climate change and other human-caused changes to the environment will alter parasitism. Climate change and other stressors will most likely instigate increased abundance of some parasites, while decreasing the abundance of others. Since parasites are strictly dependent on their hosts, changes to host populations may cause the decline, or even loss, of parasite species. As Lafferty (2013) commented, "Parasites, due to their strict dependency on hosts, are sensitive members of communities. They are likely to disappear before their hosts and therefore can make good indicators of ecosystem complexity, decreasing with degradation." Parasites may be our "canaries" in the global climate "coal mine."

Parasites, Biodiversity Decline, and Co-Extinction

Parasites are particularly susceptible to declining host biodiversity (Lafferty 2012). Biodiversity decline occurs when environmental and human-caused stressors cause the extirpation[15] or extinction[16] of one or more species in an ecosystem. Biodiversity decline can happen as a result of a number of influences, including exploitation (e.g., overharvest, overfishing), habitat degradation, loss, and fragmentation. Since many parasites rely upon multiple hosts to complete their life cycle, the loss of only one host could cause the extirpation of a parasite from an ecosystem (Lafferty and Kuris 2009b; Byers et al. 2011). Further, many parasites are host-specific (i.e., they can only associate with one host species during each life stage). If a host species is lost from an ecosystem, all its host-specific parasites are lost as well (Lafferty 2012).

One of the biggest threats to parasite biodiversity is co-extinction. Co-extinction occurs when the extinction of a host species causes the extinction of all of its associated parasite species (Dunn et al. 2009). For example, recent research has used coprolites (fossilized dung) from extinct moa birds in New Zealand to demonstrate that the extinction of these bird hosts caused the co-extinction of multiple gut parasites (Boast et al. 2018). Co-extinction may be caused by habitat loss, overharvest of hosts, ecosystem degradation, or a number of other human-caused factors. Since most hosts contain multiple parasite species, many of which remain undescribed, it is likely that many co-extinctions happen quietly and that many parasite species are lost before they are even discovered (Strona 2015).

Parasites and Climate Change

Climate change can alter parasitism, either by increasing or decreasing parasite transmission (Marcogliese 2008; Pickles et al. 2013). Gradual climate warming can change both host and parasite distributions (Dobson and Carper 1992; Marcogliese 2001; Polley and Thompson 2009). These changes in distributions can cause the introduction of hosts and/or their parasites to new geographic regions, and therefore may expand a parasite's range (Epstein 2010). Two examples are the oyster parasite, *Perkinsus marinus*, on the east coast of the United States (Ford and Smolowitz 2007) and bird parasites along elevation gradients (Zamora-Vilchis et al. 2012). Alternatively, warming may lead some geographic regions a parasite had previously inhabited to become uninhabitable. This can cause the parasite's range to either contract (i.e., get smaller) or to shift (i.e., stay the same size but move towards areas with suitable temperatures; Epstein 2010). Warming may also speed up a parasite's life cycle (e.g., Macnab and Barber 2012). In the Arctic, rapid warming has increased the number of times parasites can reproduce during each summer, which has led to an increase in parasitic nematode infections in reindeer and musk ox populations (Kutz et al. 2005).

Parasitism can also be affected by climate oscillations, such as El Niño, which can cause both short-term warming as well as changes to rainfall patterns (Mouritsen and Poulin 2002; Claar and Wood 2020). Climate oscillations can cause outbreaks in human pathogenic diseases such as chikungunya, hantavirus, Rift Valley fever, cholera, plague, and Zika (Anyamba et al. 2019). Although climate oscillations may limit the range of some parasites, they can also cause outbreaks in marine and wildlife diseases (Harvell et al. 2002; Mouritsen and Poulin 2002). These outbreaks can significantly impact conservation efforts by rapidly altering the balance between hosts and parasites.

CALL FOR PARASITE RESEARCH

Parasite research is a growing field, but there are many things that we still do not know. Many questions remain including: how does parasite burden change with increasing sea water temperature? How does parasite intensity vary between invasive and native species? And how can parasite ecology inform public health? Whether you are interested in behavior or ecology or history or physiology or biodiversity or climate change, there's a world of fascinating parasite research just waiting to be explored.

SUGGESTED SUPPLEMENTARY READING

RESEARCH AND SYNTHESIS ARTICLES

- Lafferty, K.D. 2013. Parasites in marine food webs. Bulletin of Marine Science 89(1):123–134.
- Medel, R., M.A. Mendez, C.G. Ossa, and C. Botto-Mahan. 2010. Arms race coevolution: the local and geographical structure of a host–parasite interaction. Evolution: Education and Outreach 3(1):26–31.
- Kuris, A.M. et al. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454(7203):515–518.
- Lafferty K.D., G. DeLeo, C.J. Briggs, A.P. Dobson, T. Gross, and A.M. Kuris. 2015. A general consumer-resource population model. Science 349(6250):854–857.

POPULAR SCIENCE

- Frazer, J. 2013. Nematode roundworms own this place. Scientific American Blog. https://blogs.scientificamerican.com/artful-amoeba/parasitic-roundworms-own-this-place/?redirect=1
- McAuliffe, K. 2012. How your cat is making you crazy. The Atlantic. https://www.theatlantic.com/magazine/archive/2012/03/how-your-cat-is-making-you-crazy/308873/
- Cohen, J. 2017. Reciprocal effects: new paradigm for describing trophic cascades caused by infectious agents. University of California – Santa Barbara. Science Direct. https://www.sciencedaily.com/releases/2017/07/170720133058.htm

TEACHING RESOURCES

- Primer on disease ecology: https://www.nature.com/scitable/knowledge/library/disease-ecology-15947677
- Teaching resource (includes field labs): https://www.researchgate.net/profile/Gregory_Sandland/publication/228796011_Understanding_Ecological_Principles_through_Parasitological_Pedagogy/links/09e4150a39c464e495000000/Understanding-Ecological-Principles-through-Parasitological-Pedagogy.pdf

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GLOSSARY

1. **Host:** an organism that provides a resource (i.e., nutrition, mobility) for the parasite(s) that infests/infects it, and experiences a fitness cost as a result of infection
2. **Fitness cost:** a reduction of an organism's ability to survive, grow, and/or reproduce
3. **Cryptic:** hidden and hard to see
4. **Symbiotic mutualists:** an organism that lives in an intimate and durable relationship with its host, and provides a fitness benefit to that host (i.e., an increase in an organism's ability to survive, grow, and/or reproduce; Douglas 2010)
5. **Micropredator:** organisms that take small meals during a short interaction time, but do not live in a persistent interaction with a host
6. **Free-living organism:** an organism that does not live in or on another organism; most free-living organisms are host to parasites and/or symbionts
7. **Generation time:** time between two consecutive generations within a population; the average time between birth and reproduction
8. **Parasitology:** the study of parasites
9. **Prevalence:** the total proportion of infected hosts within the host population
10. **Definitive host:** the host in which a parasite reaches sexual maturity and reproduces
11. **Dead-end host:** a host that a parasite can infect, but from which the parasite cannot continue its life cycle
12. **Intermediate host:** a host in which a parasite undergoes development and growth
13. **Fishes:** a group of multiple fish from multiple species. In contrast to the plural fish, which references multiple fish from one species

14. **Virulence:** a parasite’s ability to infect or damage its host
15. **Extirpation:** complete loss of a species from part of its range; the species may be gone from an ecosystem or region, but still persists in other areas
16. **Extinction:** complete loss of a species from its entire range; no individuals of the species remain