

Chapter 5

Biodiversity Loss and Infectious Diseases

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Abstract When conservation biologists think about infectious diseases, their thoughts are mostly negative. Infectious diseases have been associated with the extinction and endangerment of some species, though this is rare, and other factors like habitat loss and poorly regulated harvest still are the overwhelming drivers of endangerment. Parasites are pervasive and play important roles as natural enemies on par with top predators, from regulating population abundances to maintaining species diversity. Sometimes, parasites themselves can be endangered. However, it seems unlikely that humans will miss extinct parasites. Parasites are often sensitive to habitat loss and degradation, making them positive indicators of ecosystem “health”. Conservation biologists need to carefully consider infectious diseases when planning conservation actions. This can include minimizing the movement of domestic and invasive species, vaccination, and culling.

5.1 Introduction

We have all been sick from infectious diseases, and this predisposes us to view parasites with disdain. Here, I discuss the importance of infectious diseases (i.e., parasites and pathogens) for conservation. This is not a common topic. Nearly, half of conservation biology texts do not even mention infectious diseases (Nichols and Gómez 2011). Half of those texts that do mention infectious diseases only consider negative impacts of disease. But the story is much richer than this. Infectious diseases play important roles in ecosystems, hurting some species and favoring others. Under rare circumstances, they can cause their hosts to become

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endangered. Environmental change can favor or impair infectious diseases. Sometimes, parasites themselves can be endangered. For these reasons, parasite can give us interesting insight into environmental degradation, making them useful indicators. Furthermore, there are several actions that conservation biologists can take to protect species at risk from infectious disease.

5.2 The Role of Disease in Ecosystems

Parasites are pervasive. But due to their small size, parasites seem insignificant players at the ecosystem level. Do their numbers add up? Can they have effects even greater than their numbers would imply? What are their contributions to biodiversity and food webs? When do they control host populations?

Parasitism is a popular lifestyle, but exactly how popular is hard to tell because parasitologists have not yet looked at most animal species. What information exists about parasites is often only from one location and rarely for all parasite groups. Some authors have estimated the proportion of described species in various animal taxa that are parasitic. Poulin and Morand (2004) estimated that there were about 1.5 parasite species per vertebrate species. Several molecular genetic studies suggest that described parasite species are often suites of cryptic species that are simply difficult to distinguish morphologically (Miura et al 2005). If cryptic species are more common for parasites than for free-living species (highly possible given the lack of morphological characters in some parasite groups), there could be an even higher proportion of parasites on earth. An alternative approach is to go to a particular system and to estimate the richness of free-living and parasitic species. This has been done for estuarine systems where a third of the 314 species encountered are parasites, and this is probably a gross underestimate (Hechinger et al 2011b). It is unknown whether this percentage of parasitism is representative of other types of ecosystems, but parasites are unquestionably a large part of biodiversity.

Parasites are embedded in food webs, which track the flow of energy through ecosystems and are a fundamental theme of ecology. Even though many parasites are host specific, overall, parasites tend to have more hosts than predators have prey (Lafferty et al 2006). In part, this is due to complex life cycles, for which parasites can have one or more hosts per stage (Rudolf and Lafferty 2011). It is less commonly realized that consumers eat parasites, either when the parasites are larvae, or incidentally when parasites are inside prey (Johnson et al 2010). Inclusion of parasites in food webs greatly alters food-web structure, increasing measures like connectance and nestedness (Lafferty et al 2006). In addition, parasites make food webs less robust, because, as will be discussed below, parasites are more likely to suffer secondary extinctions than are free-living species (Lafferty and Kuris 2009; Rudolf and Lafferty 2011). So, from a food-web perspective, parasites appear to be important players in ecosystems (Lafferty et al 2008a).

One way to consider the role of a species in an ecosystem is to measure its biomass density. Although parasites are integral parts of food webs, for them to affect the flow of energy through a system, they must make up some biomass of that system. Parasites are small, so they might not be as important energetically as larger, free-living species. Kuris et al (2008) found that parasites make up 1–2 % of the living biomass in three estuaries. Although 1–2 % might not seem like much, it is exactly what is expected once one accounts for the upper trophic levels at which parasites operate (Hechinger et al 2011a). For instance, in three well-sampled estuaries, there was a greater biomass density of trematode parasites in snails than there was biomass density of birds (Kuris et al 2008). This means there is no reason to suspect that parasites have any less of a role in ecosystems than top predators.

Parasites might reduce or regulate the abundance of their hosts (Tompkins and Begon 1999). To reduce host abundance, exposure to parasites needs to be common, and parasites need to negatively affect infected hosts. For instance, adding tapeworm eggs to beetle colonies depresses the density of the beetle host because infected beetles have decreased fecundity and survivorship (Keymer 1982). To regulate the host population, however, means to reduce host density when hosts are abundant, but not when hosts are rare. Host population regulation is a key assumption that affects how we hypothesize the role infectious diseases in conservation biology. Modeling has helped determine the criteria under which pathogens and parasites can regulate host populations (Anderson and May 1978; May and Anderson 1978). The basic premise behind regulation for pathogens is density-dependent transmission. Such pathogens only invade dense host populations and fade out when the density of susceptible hosts declines (Lloyd-Smith et al 2005). However, for typical parasites, hosts can be re-infected, but density-dependent effects (e.g., crowding or increased mortality for heavily infected hosts) will limit parasite abundance. Additional complexities such as refuges from parasitism or invulnerable stages can theoretically allow the host to persist when the infectious agent becomes common. In a classic experiment on parasite regulation of host abundance, a nematode parasite was able to depress the population of laboratory mice to 10 % of control densities (Scott 1987). Examples of regulation (or failed regulation) from the field include the whole of biological control literature. The dramatic effect of myxomatosis virus on rabbits in Australia is a textbook example (Fenner and Ratcliffe 1965). Whereas myxomatosis caused mass mortalities of rabbits, a nematode parasite that reduces the fecundity of reindeer appears to reduce host densities to a relatively stable equilibrium (Albon et al 2002). A potential consequence of regulation by infectious diseases is the promotion of biodiversity. If infectious diseases prevent some species from out-competing others, coexistence among competitors becomes more likely (Clay et al 2008). Whether or not parasites "control" host populations, most host populations would be more abundant if they did not suffer from infectious diseases.

Some parasites manipulate their hosts, with consequences for conservation. Parasites can increase the susceptibility of their intermediate hosts to predation

by final hosts (Lafferty 1999), and this can alter predator-prey dynamics (Dobson 1988; Lafferty 1992). For instance, mathematical models suggest that a tapeworm that debilitates moose might allow endangered wolves to persist in some locations (Haderler and Freedman 1989). A recent example indicates how a manipulative parasite can have a positive indirect benefit for conservation. The manipulating parasite is a nematomorph worm that causes its cricket host to jump into streams where the worm reproduces (Thomas et al 2002). In Japan, these manipulated crickets form the bulk of the diet for an endangered trout (Sato et al 2011). Without the parasite, these trout might become extinct. In these and other examples, the parasite benefits predators and impacts prey populations. It would be useful to know whether other endangered predators receive indirect benefits from parasites and how this might be used in management programs.

Parasites make up much of biodiversity, and they appear to play important roles. They are common parts of food webs with many connections to free-living species. Though small, when combined, they have as much mass as predator populations. Parasites have the potential to affect species of concern, because they can depress host populations. However, due to density-dependent transmission, the effect of parasites will tend to wane as hosts become rare. This can lead parasites to handicap competitive dominants, facilitating biodiversity and coexistence. Although the direct effects of parasites are bad for host individuals, indirect effects might be positive, particularly for predators that feed on prey manipulated by parasites. Biologists have been wrong to ignore the role of parasites in natural systems, but this is changing for the better.

5.3 Diseases as Agents of Endangerment

Some parasites can kill or seriously affect the health of their hosts, and a few can have noticeable effects on host populations. Anthrax, plague, influenza, HIV, smallpox, malaria, hookworm, river blindness, and dysentery are examples of infectious diseases that have shaped human history. When might an infectious disease endanger its host, or cause its extinction? Which types of infectious diseases are more commonly associated with conservation impacts?

Exceptions to basic epidemiological theory must occur for an infectious disease to extirpate a host (de Castro and Bolker 2005; Lafferty and Gerber 2002). Under typical density-dependent transmission, as disease drives host populations down, it crosses a threshold density, below which the parasite can no longer transmit fast enough to persist in the host population. Nevertheless, some circumstances can prevent disease from fading out. For instance, captive breeding programs maintain animals at high densities in association with other species. In a notable example, a captive colony of black-footed ferrets was nearly extirpated when the group was accidentally exposed to canine distemper virus (CDV) (Williams et al 1988). Similarly, the last known *Partula turgida* land snails from Tahiti (Cunningham and Daszak 1998) were extirpated from the London Zoo after a microsporidian

pathogen contaminated the cultures. Although this is the first documented extinction caused by a parasite, the snail's earlier extinction in the wild was caused by the introduction of a predatory snail. In nature, an infectious disease can extirpate a host if it has a second, more tolerant, host species. American gray squirrels have replaced British red squirrels, in part due to a shared parapox virus introduced with the tolerant gray squirrel (Tompkins et al 2002). Likewise, canine distemper from domestic dogs can spillover to endangered wolves, lynxes, wild dogs, foxes, and lions, causing heavy mortality (Cleaveland 2009). Alternatively, if the disease agent can live outside the host, it will be able to survive periods of low host abundance, and not fade out. For instance, the chytrid fungus that causes mass mortalities in some species of amphibians can grow saprophytically without amphibians (Longcore et al 1999). Other examples are more complicated. For instance, a long time lag between infection and pathology can allow an infectious disease to reach a high prevalence before driving host numbers down (Lloyd-Smith et al 2005). In California, endangered intertidal black abalone are susceptible to a bacterial pathogen, but do not normally exhibit mortality, allowing all abalone to become infected in a local population; however, when water temperatures become warm, infected animals die, leading to mass mortalities (Ben-Horin et al 2013). Knowing the special circumstances under which infectious diseases can drive hosts to low abundances is essential when trying to manage endangered species.

Although infectious disease is listed as one of the five main causes of extinction (Wilcove et al 1998), links between disease and endangerment are not common (Smith et al 2006). In a summary of the IUCN Red List of Threatened and endangered species, Smith et al (2006) found that infectious disease was a contributing factor in <4 % of the 833 plants and animals documented to have gone extinct in modern times and <8 % of the 2,852 critically endangered species. These numbers relegate infectious disease to a relatively minor threat to species in contrast with habitat destruction and hunting. It seems likely, therefore, that the special cases that cause infectious diseases to seriously affect populations of their host species are not pervasive in nature. Still, they are numerous enough to take seriously.

Some types of infectious diseases repeatedly affect host species of concern. For initially common host species, the most common problems are introduced fungal, viral, and protozoal pathogens (e.g., chytrid fungus, avian malaria); for already endangered species, viruses that spillover from domestic animals (e.g., rabies, CDV), most commonly dogs, are the greatest concern (Lafferty and Gerber 2002; Smith et al 2006). Fungal diseases are particularly vexing because they are not well understood even though they have been an issue for conservation biologists for a long time. Chestnut blight was one of the first infectious diseases of conservation concern, whereas white-nose syndrome is a recent fungus (*Geomyces destructans*) to North America thought to be driving bat species toward extinction in the USA but not in Europe. Despite the preponderance of viruses and fungi, several other parasitic groups are of concern to conservation biologists.

Parasites are not common sources of endangerment and are even more rarely associated with extinctions. This is due to the importance of density-dependent transmission, which causes many infectious diseases to fade out before they drive

their host populations to low densities. However, when an introduced or domestic species supports a pathogenic infectious disease, a spillover into wildlife or captive populations can lead to serious threats.

5.4 The Response of Infectious Diseases to Environmental Degradation

The world is changing. Human actions that endanger species and degrade the environment can also affect infectious diseases. Conservation biologists are most concerned with situations where environmental impacts also increase infectious diseases. However, infectious diseases might also suffer from impacts. The outcome at the population level should depend on how stressors interact with the vital rates of hosts and infectious diseases. Pollution, biodiversity loss, hunting/fishing, and climate change might favor some infectious diseases but impair others. Have there been changes to infectious diseases over time associated with environmental degradation?

Stress can have different effects on host populations than on individuals (Lafferty and Holt 2003). Although a stressed individual is more likely to become infected with a parasite, it is also more likely to die, thereby reducing the abundance of infected hosts and increasing the mortality rate of parasites within hosts. For this reason, the net effect of stress on a parasite population is difficult to predict and can, counter-intuitively, lead to decreases in parasitism.

Pollution can increase host susceptibility to infection, but it can also be toxic for parasites (Lafferty 1997). Many free-living parasite stages (e.g., eggs, larvae) have shorter life spans when exposed to toxic substances. Furthermore, parasites can be more susceptible to contaminants than their hosts are (this is the premise behind using drugs to treat infectious diseases). As a result, helminths tend to decline with hydrocarbon or heavy metal exposure, whereas some protozoans and monogeneans increase in polluted areas. Most parasites increase in prevalence with eutrophication, because nutrients increase the productivity of host populations. The response of parasites to pollution, therefore, depends on the type of pollution and the type of parasite.

The addition of “non-competent” species to a habitat can theoretically reduce the transmission of some types of infectious diseases via the dilution effect (Keesing et al 2006). The dilution effect is mostly likely to occur for vector-transmitted diseases, in which transmission is frequency dependent. This means that bite rates of vectors are not usually limited by host availability. In such cases, vectors can bite several different types of hosts. If a vector carrying a host-specific pathogen bites a non-competent host, the disease will not transmit. Some assumptions are needed for the dilution effect to occur: Non-competent hosts are lost from communities before competent hosts, and non-competent hosts do not magnify vector populations. The dilution effect has been touted as a win-win situation for biodiversity and human health if the addition of non-competent species is associated with increases in biodiversity (Keesing et al 2010). Despite its popularity

among conservation biologists, it is not clear how often the dilution effect occurs in nature and whether dilution is positively associated with biodiversity (Salkeld et al 2013).

Although the dilution effect is a theoretical possibility, biodiversity loss can lead to the decline of some types of infectious diseases. This is particularly true when parasites are host specific and have complex life cycles. For generalist parasites, the loss of a single host species will not eliminate the parasite from the system. Parasites with complex life cycles, however, require at least one species from each obligate host category (Lafferty and Kuris 2009; Rudolf and Lafferty 2011). Such parasites can be sensitive to biodiversity loss. If biodiversity loss leads to a few abundant species, one might expect to find a few prevalent parasite species. In general, parasite diversity and abundance should follow host diversity and abundance (Hechinger and Lafferty 2005; Lafferty 2012).

Hunting and fishing are types of biodiversity loss that can reduce host abundance and thus alter disease dynamics (Dobson and May 1987; Wood et al 2010). As fishing drives target species below a threshold level for transmission, parasite species will not be able to complete their life cycles. In addition, sport fishing and certain commercial gear targets the larger, older individuals that also have the most parasites. Reports of parasites of marine mammals have increased since these animals were released from hunting pressure, whereas reports of parasites of fishes have decreased as many fish stocks crashed (Ward and Lafferty 2004). Experimental fishing drives parasites to low levels (Amundsen and Kristoffersen 1990), confirming a causal link between fishing and parasite loss. This can have community-level implications. For instance, parasite communities are more diverse in coral reef fishes at unfished sites than at fished sites (Lafferty et al 2008b). Sometimes, fishing can have indirect, positive effects on parasites. When fishing top predators releases prey populations from predation pressure, parasites of prey will benefit (Behrens and Lafferty 2004; Lafferty 2004; Packer et al 2003; Sonnenholzner et al 2011). For these reasons, it can be difficult to predict the net effect of fishing on the diseases of an ecosystem.

Climate change has the potential to alter the distribution of infectious diseases. Although disease expansion in higher latitudes gets the most attention, areas near the equator might become too warm for parasites (Lafferty 2009). As a result, some locations will see more infectious diseases, while other locations will see decreases. The biggest changes are likely to occur at high latitudes where climate is changing most rapidly and where tropical diseases can expand (Kutz et al 2005). Extreme weather events can affect hosts and parasites. For instance, a hurricane that devastated the Yucatan Peninsula, Mexico, in 2007 impacted free-living species, but it was the parasites that took the longest to recover (Aguirre-Macedo et al 2011). Overall, climate change should create similar challenges for hosts and parasite alike.

As humans degrade the environment, biodiversity will decline, both for parasites and free-living species. Those few cases where free-living species will decline, but parasites will increase, will create a special challenge to conservation biology. In particular, if climate change introduces new pathogens to naive hosts,

impacts could occur. Nevertheless, overall, pollution, fishing, and climate change seem as likely to harm parasites as to benefit parasites.

5.5 Endangered Parasites

Parasites are sensitive to environmental change, and some have suggested that they could make up the unseen majority of species extinctions (Dobson et al 2008; Dunn et al 2009; Koh et al 2004; Poulin and Morand 1997; Sprent 1992). The success of vector control in suppressing human diseases underscores how removing a host (e.g., a mosquito) can lead to parasite loss (e.g., malaria). Parasite endangerment should relate to host endangerment, host specificity, and life cycle complexity.

When all hosts are gone, no parasites can remain. For instance, the trematode *Pleurogonius malaclemys* only infects snails in the presence of the endangered diamondback terrapin (*Malaclemys terrapin*), the sole final host for the trematode (Byers et al 2011). When a diamondback terrapin population is extirpated, it takes its host-specific parasites with it. This is consistent with the observation that extinction of the snail *Cerithidea californica* is linked to the loss of several parasite species of birds that require the snail as a first intermediate host (Torchin et al 2005). The pygmy hog-sucking louse (*Haematopinus oliveri*) is specific to an endangered pig, leading it to be the only parasite listed on the IUCN Red List (Whiteman and Parker 2005). However, to my knowledge, there is no documentation of an accidental parasite extinction. An example of parasite extinction that has since been proven false is feather lice (genus *Columbicola*) from the extinct passenger pigeon. These lice were less host specific than initially thought and have been found on other species (Dunn 2002). Still, endangered species have parasites, and, if these parasites are host specific, the parasites are arguably more endangered than their hosts. Parasites can go extinct well before their hosts, because some parasites occur only in part of the range of their hosts and, for parasites with density-dependent transmission, the host only need drop below a threshold density for the parasite to go extinct. Many endangered species might have already dropped below that threshold for some of their parasites. Perhaps as a result, endangered primates have fewer parasites than primate species that are not threatened (Altizer et al 2007). Alternatively, such a pattern could occur if the factors that lead to host endangerment (insular, isolated populations) also limit parasite communities. In other words, if hosts with high extinction risk have fewer parasites to start with, then fewer parasites will be found in endangered species. For instance, parasites are less diverse in hosts with narrow diets (Chen et al 2008; Vitone et al 2004), and specialists should be more prone to extinction (Purvis et al 2000). On the other hand, large species, which are more likely to be threatened by habitat loss and overharvest (Purvis et al 2000), tend to host more parasite species (Vitone et al 2004). Similarly, top predators are more likely to go extinct, and parasite diversity increases with host trophic level (Lafferty et al 2006). Unfortunately, due to

a lack of historical information on parasites before the biodiversity crisis, it is difficult to know which parasites have already gone extinct. No matter the association between parasite richness and host propensity of endangerment, it remains that the most endangered species are parasites of currently endangered species (Dunn et al 2009).

Host specificity makes parasites more susceptible to endangerment. One way to understand this effect is to take a set of host species and their parasites and then plot how the proportion of extant parasites would change as host species were removed from the system. The endpoints of this relationship are obvious. When all hosts are present, all parasite species are present and when no host species are present, no parasites will be present. If parasites are strictly host specific, the relationship should be linear. However, the more general the parasites are, the less sensitive they will be to biodiversity loss of hosts, leading to an initially slow parasite loss rate as hosts are removed (Koh et al 2004; Lafferty 2012). This is because generalist parasite species should be able to persist even if only a single host species remains. Some parasite taxa are more specific than others, suggesting that patterns of parasite extinction will vary from group to group. For instance, using data for North American carnivores, lice are much more host specific and, therefore, much more prone to extinction, than are viruses (Dunn et al 2009).

Life cycle complexity makes parasites more susceptible to endangerment because there are more weak links in the chain. In other words, if even one stage in the life cycle cannot find a host, the parasite cannot persist. When trying to estimate extinction risk it is, therefore, important to distinguish between a parasite that can use many hosts from a parasite that must use many different hosts (Lafferty and Kuris 2009; Rudolf and Lafferty 2011). Most parasite species require more than one host, and incorporating this into plots of parasite and host extinction opens up the possibility that proportional rates of parasite extinction can exceed proportional rates of host extinction (Lafferty 2012). In other words, the loss of parasite diversity could exceed rates of free-living extinctions, and this loss would be especially high for parasites with complex life cycles.

It seems probable that many parasites have gone extinct and multitudes more are endangered. Host-specific parasites, particularly those with complex life cycles, are most at risk. Although few will shed a tear at the extinction of a parasite, there are two reasons one might miss these parasites. As indicated above, parasites are important players in natural ecosystems, and losing a parasite could have just as big an ecological consequence as losing a top predator. Second, many parasites are as inherently interesting as the charismatic megafauna whose photos adorn the brochures of conservation organizations. Most people would agree we have an obligation to preserve the sperm whale (*Physeter macrocephalus*) if only because it is charismatic, large, and fierce. However, consider *Placentonema gigantissima*, a parasite of sperm whales. This species is even more endangered than the sperm whale. The worm is also fascinating in its own right, reaching over 10 m. Fortunately, saving endangered parasites takes little additional effort because conserving endangered hosts is the best way to conserve parasites. Perhaps the more relevant question is whether we should place more emphasis on

protecting hosts with many host-specific parasites than hosts with none. After all, hosts with many parasites represent a trove of biodiversity.

5.6 Parasites as Indicators of Environmental Quality

Parasites can indicate impacts to the environment. A community of parasites reveals something about the community of hosts present in the environment, and knowing what parasites increase or decrease with environmental change helps make it possible to understand how the environment is changing for hosts in the system. What types of parasites make proverbial canaries in a coal mine? Ideal parasite indicators are species with complex life cycles for which one of the hosts is easy to sample. Parasites of fishes and snails show particular promise as indicators (Lafferty 1997).

Indicator species should be easy to sample and yield information about processes that are otherwise hard to come by. If you wanted to know whether a species was in decline, it might be useful to look at its parasites. This is because fewer parasites might indicate that the density of the host has dipped below the level where transmission is efficient. However, sampling endangered hosts to look for their parasites is both difficult and defeats the purpose of conserving them. Instead, one could sample an intermediate host that shares parasites with the endangered host. For this reason, parasites with complex life cycles can make good indicators of a target host if one of the other hosts in the life cycle is easy to sample (Huspeni et al 2005).

Parasites of fishes can increase or decrease with pollution, providing a biologically meaningful indicator of water quality (Marcogliese 2005). They can also indicate food-web links (Valtonen et al 2010). For instance, sharks are hard to sample and in decline. They have tapeworms with complex life cycles that use reef fishes as intermediate hosts. In areas with many sharks, the reef fishes are commonly infected with tapeworm larvae, suggesting that by sampling tapeworm larvae in small fish that are easy to collect, one could track the abundance of sharks in time and space (Lafferty et al 2008b). Many fishes are relatively easy to sample, and they have communities of parasites that reflect the food webs they live in, give information about fish density, and also indicate aspects of the physical environment.

Communities of trematode parasites in snails are another system with broad application as indicators. The final hosts of these parasites are vertebrates such as birds. Areas with a high abundance and richness of birds have a high abundance and richness of trematodes infecting local snail populations (Hechinger and Lafferty 2005). Snails from degraded portions of estuaries are less parasitized, and parasitism increases after habitat restoration, presumably because restoration makes conditions more attractive for birds that then spread trematodes to snails (Huspeni and Lafferty 2004). Trematodes and snails are broadly distributed in aquatic habitats and could be used as indicators in many locations (Huspeni et al 2005).

The use of parasites as indicators is in its infancy. It is counter-intuitive that parasites indicate good environmental conditions. Although current examples are from aquatic systems, parasites of terrestrial animals might also make good indicators. Despite the considerable evidence, it is still difficult to convince people that a healthy system is one with many parasites (Hudson et al 2006).

5.7 Conservation Strategies in a World Full of Parasites

Conservation biologists need to be aware of infectious diseases when managing threatened species (Gerber et al 2005; Lafferty and Gerber 2002). For instance, nature reserves should be designed with attention to maintaining natural infectious processes, and wildlife should be assessed for background parasites so that new diseases are easier to detect. Species invasions should be minimized to reduce the threat of novel diseases. Vaccinations and culling can be used to break the cycle of transmission. Population viability analysis (PVA) models should include infectious processes. In addition, captive rearing programs should take care to avoid exposing threatened species to disease.

Parasites are part of natural systems, and it makes sense to include them in the design of reserves, reintroductions, and conservation programs. This is not current practice. A common precaution for reintroduction programs is to treat animals for parasites before they are released. Although there is an obvious benefit to release healthy individuals, it might be worth considering whether some infectious diseases should be simultaneously reintroduced to a system with their hosts. For instance, wolves are sometimes reintroduced to help them re-establish parts of their former range where they were extirpated by hunting. Reintroduced wolves are dewormed before release (such as into Yellowstone National Park in 1995). The wolves then enter a habitat potentially free from the tapeworm that debilitates their prey. Might the wolf's reintroduction be more successful with the tapeworm than without it? An important consideration for this example is that the tapeworm is not specific to wolves and, furthermore, can be pathogenic to livestock and humans, which can be accidental hosts. Another consideration is whether to have corridors between reserves (to maintain gene flow and metapopulation dynamics), because this will also allow the spread of infectious diseases among reserves (Hess 1994). If native infectious diseases are a natural part of ecosystems, conservation biologists should not try to exclude them. On the other hand, if introduced diseases are a known threat, isolation and prevention might be a valuable strategy.

Usually, the threats from infectious disease derive from human encroachment into natural habitats (Cleaveland 2009). Prohibiting the arrival of new diseases might be the best way to minimize the effect of infectious diseases on species of concern. However, this is not easy. Lessons from introduced avian malaria in Hawaii did not prevent the arrival of malaria vectors in the Galápagos (Wikelski et al 2004) and the subsequent exposure of Galápagos penguins (*Spheniscus mendiculus*) to malaria (Levin et al 2009). People move animals intentionally all the

time and the legal and illegal pet trade ship a baffling number of wild caught animals, including their infectious diseases, to every potential market on earth (Rosen and Smith 2010). Dogs and cats are popular pets, including for people living in and near nature reserves. In poor countries, veterinary care is a low priority, leading to a high prevalence of disease in pets, which are often loose and intermix with wildlife. Even in wealthy countries, pets have several infectious diseases that can be transmitted to wildlife. Though veterinary services are available and laws might prohibit movement of pets, pet owners are often reluctant to follow protocols if it inconveniences them. For instance, on Catalina Island in Los Angeles County, California, pets have exposed the endemic island fox (*Urocyon littoralis*) to canine distemper virus (among other pet-transmitted diseases) (Clifford et al 2006), leading to a near extirpation. Therefore, although quarantines and importation bans are essential tools for protecting wildlife, they are difficult to enact and enforce.

If an epizootic occurs or seems pending, reducing the abundance of susceptible hosts will decrease the chance of disease spread. Vaccination and culling are two ways to reduce the density of susceptible hosts. Vaccination is preferred for endangered species because it protects existing populations and decreases the relative as well as the absolute abundance of susceptible hosts, making it effective against density-dependent and frequency-dependent transmission. The existence of vaccinations for diseases of humans and domestic animals makes it possible to vaccinate endangered wildlife against common viral pathogens. One of the earliest interventions to protect endangered species against infectious diseases was the vaccination of chimps in Gombe against polio (Van-Lawick-Goodall 1971). Vaccination campaigns for several endangered species have been mounted against canine distemper virus and feline leukemia virus, though it is difficult to evaluate success, particularly without unvaccinated control populations (Cleaveland 2009). Vaccination programs can be controversial. The campaigns are expensive and require capturing a large proportion of the target population, with attendant risks to animals during handling. Culling is sometimes suggested as a potential option when no vaccine is available. However, to be effective in eradicating an infectious disease, culling often must be severe and persistent. This might be acceptable when the host is a domestic or otherwise common animal (Ferguson et al 2001), but culling a threatened species might put it at greater risk of extinction. Moderate levels of culling were not able to stop the spread of Tasmanian devil facial tumor disease, and models indicated that the level of culling need to eliminate the disease would place the species in substantial risk of extinction (Beeton and McCallum 2011). Culling or vaccinating threatened species are likely to be used only in desperate situations where managers also have substantial resources and access to the threatened species. Nonetheless, given how frequently viruses from domestic animals threaten wild species, this last option might often be worth the cost.

More and more species now only exist in captivity. In the case where a species is being managed with captive breeding, managers should take extra precautions to prevent disease. Animals should be held in at least two separate locations to provide an insurance against contamination of a facility. Workers should observe high standards of hygiene and try to limit actions that would spread infections

among individuals. In addition, animals should be housed away from other organisms that could be a source of infectious diseases. Once animals are ready for reintroduction, veterinarians should check for any infections acquired in captivity before release into the wild. This will help reduce the risk of releasing sick animals, which will have a lower probability of surviving and could be a source of infectious disease that could affect other individuals. Due to past catastrophes, it is now more common for veterinarians to be involved in captive breeding programs. While this is standard practice, it can have unintended consequences. When the last remaining California condors were caught for captive breeding, veterinarians treated them for a host-specific louse. The California Condor is recovering in the wild, but the condor louse is now gone—the only known example of conservation biologists intentionally causing an extinction.

In many countries, a PVA is a legal requirement of threatened and endangered species recovery plans. PVAs are useful for determining the prospects of endangered species, but ignoring disease can decrease their accuracy. PVAs are stochastic models that use measures of vital rates (birth, death) and their variance to estimate the expected time until a population will go extinct. For instance, eventually a run of bad years in computer simulation will drive birth rates below replacement, leading to extirpation. Management then tries to identify which vital rates can be improved to try to extend the expected time to extinction to the distant future. Measured rates of death and reproduction include the effects of infectious diseases, but PVAs assume that these rates are inherent to the species. If infectious diseases are important drivers of vital rates, but PVAs do not treat them as density-dependent processes, the results will give overly optimistic estimates of extinction times (Gerber et al 2005). Therefore, managers should carefully consider how important infectious diseases are in their systems before interpreting recommendations from PVAs.

Little effort has gone into planning conservation around infectious disease. This is in part because conservation biology does not often consider infectious diseases at the population level. It is also because managing infectious diseases is difficult. On the other hand, humans have been attempting and sometimes succeeding in managing infectious diseases in human and livestock populations, suggesting that conservation biologists have good models to follow, vaccination programs being the most obvious. Still, if infectious diseases are natural components of ecosystems, these processes should be allowed to play out, though there might be associated risks to human and livestock health that need to be considered and mitigated.

5.8 Conclusion

Conservation biologists do often not think about parasites, and if they do, they tend not to like them. This abhorrence makes sense because infectious diseases have been associated with the extinction and endangerment of some species. However, for conservation biologists to deal with infectious diseases, it is first necessary to

understand other factors, for example, habitat loss and overharvest, that are the overwhelming drivers of endangerment. Furthermore, parasites are pervasive and integral components of all ecosystems. They play important roles as natural enemies on par with top predators. Many of these roles are considered positive from a conservation perspective, from regulating population abundances to maintaining species diversity. A world without parasites would be different, and perhaps not better. Parasites can themselves become endangered along with their hosts. However, it seems unlikely that humans will act to protect parasites from extinction. Parasites are sensitive to environmental changes. It is a surprise to most people that parasites are often sensitive to habitat loss and degradation. Ironically, this makes some parasites positive indicators of ecosystem “health”. Though I argue it is important for conservation biologists to think about parasites, there are not many management options for dealing with them, apart from minimizing the movement of domestic and invasive species. I hope that with increasing research on the ecology of parasites, we will have more options for managing them in the future.

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