CHAPTER 9

Ecological consequences of manipulative parasites

Kevin D. Lafferty and Armand M. Kuris

9. 1 Introduction

Parasitic "puppet masters", with their twisted, self-serving life history strategies and impressive evolutionary takeovers of host minds, capture the imagination of listeners—even those that might not normally find the topic of parasitism appealing (which includes most everyone). A favorite anecdote concerns the trematode *Leucochloridium paradoxum* migrating to the eyestalks of its intermediate host snail and pulsating its colored body, presumably to attract the predatory birds that are the final hosts for the worm. Identifying a parasite as "manipulative" infers that a change in host behavior or appearance is a direct consequence of the parasite's adaptive actions that, on average, will increase the fitness of the parasite. The list of parasites that manipulate their hosts is long and growing. Holmes and Bethel (1972) presented the earliest comprehensive review and brought the subject to mainstream ecologists. Over two decades ago, Andy Dobson (1988) listed seven cestodes, seven trematodes, ten acanthocephalans, and three nematodes that manipulated host behavior. Fifteen years later, Janice Moore (2002) filled a book with examples. The five infectious trophic strategies, typical parasites (macroparasites), pathogens, trophically transmitted parasites, parasitic castrators, and parasitoids (Kuris and Lafferty 2000; Lafferty and Kuris 2002, 2009) can modify host behavior, but the likelihood that a parasite manipulates behavior differs among strategies. The most studied infectious agents, non-trophically transmitted pathogens and macroparasites, have enormous public health, veterinary, and wildlife disease importance, yet few manipulate host behavior. The best-studied manipulative infectious agents are trophically transmitted parasites in their prey intermediate hosts. Parasitoids and parasitic castrators can also manipulate host behavior, but for different purposes and with different implications. Several studies of manipulative parasites conclude with phrases such as "may ultimately influence community structure" (Kiesecker and Blaustein 1999), yet few demonstrate ecological effects. Here, we consider the conditions under which manipulative parasites might have a substantial ecological effect in nature and highlight those for which evidence exists (see also Chapter 10).

Some changes in host behavior can result from pathological side effects that do not increase or can even decrease parasite fitness, or can result from an adaptive response (e.g., a defensive response) by the host to minimize the fitness cost of the infectious agent (Poulin 1995). For instance, the females of some species of phorid flies oviposit an egg behind the head of an ant. The fly larva penetrates the host cuticle and develops inside the head, soon causing the ant to decapitate itself. The phorid continues to feed on the tissues in the detached head, completes its development, pupates, and emerges as an adult through an opening at the base of the head. The presence of phorids disrupts worker ant activities, and a colony under attack engages in a frenzied, disoriented suite of behaviors, so much so that colonies of fire ants (*Solenopsis* spp.) fail to thrive in the presence of phorids (Feener and Brown 1995). Perhaps the best documented example of the ecological effect of defensive behaviors against infectious agents comes from research on cleaner

wrasses such as *Labroides dimidiatus* on coral reefs (Grutter et al. 2003). Infested fish visit cleaners several times a day, and the diversity of fishes decreases on patch reefs after removing cleaner wrasses. Many large predators and herbivores choose not to visit patch reefs lacking cleaners. Hence, fishes try to reduce ectoparasite abundance and this alters the structure of fish communities among reefs. Hosts can alter spatial patterns of foraging to avoid infection (e.g., leading to ungrazed "roughs" in pastures) and increase the time spent grooming, as opposed to other activities, such as watching for predators (Hart 1990). Such examples, though interesting in their own right, are not the subject of this review.

9.2 What makes a manipulator important ecologically?

Several factors can determine if a manipulative parasite will have ecological effects. (1) Changes to host individuals should scale with the strength of manipulation. (2) A high incidence of infection will have a greater effect on the host population. (3) Parasites that infect common or otherwise important hosts are more able to leave a mark on ecological communities. Unfortunately, we cannot yet evaluate how many parasites are manipulative or have strong effects, use common hosts, or have high incidence. Further, assessments of the "importance" of the ecological role of potential hosts are available for only a few communities.

Strong manipulations should benefit the parasite. In mathematical models, the probability that a parasite can invade a host population increases with the strength of manipulation (Dobson 1988). Strong manipulation also has consequences for host populations. For models of a trophically transmitted parasite, manipulation decreases the equilibrium abundance of prey, whereas the abundance of predators increases with manipulation (Lafferty 1992). This suggests that the ecological effects of manipulation will increase with the magnitude of the behavioral changes associated with parasitism. Limited access to physiological systems that influence host behavior, energetic costs of manipulation, and host counter-adaptations will constrain the strength of manipulation.

Several studies have measured the magnitude of manipulation by contrasting the behaviors or the susceptibility to predation of infected and uninfected hosts. A review of eight studies found that parasites of prey increased predation rates by a factor of 1.62 to 7.5 (Dobson 1988). These estimates are sensitive to sampling without replacement, suggesting such values might be underestimates (Lafferty and Morris 1996). A trematode metacercaria that encysts on the brain of killifish has perhaps the strongest effect documented in the literature. At average parasite intensities, infected killifish are 30 times more likely to be eaten by birds, a value much higher than the four-fold increase in the frequency of conspicuous behaviors observed in the aquarium (Lafferty and Morris 1996). In other words, a parasite-induced change in behavior can lead to an even greater change in transmission.

If manipulation is intensity-dependent (as it can be for typical parasites and trophically transmitted parasites), the behavior of the host depends on both the per-parasite manipulation and parasite intensity. In their mathematical models of macroparasite manipulators, Dobson and Keymer (1985) defined manipulation as α, a per-parasite multiplier of predation risk to final hosts such that, for no manipulation $\alpha = 1$, and, if a single parasite doubles the risk of predation, $\alpha = 2$. Intensity can make up for strength if manipulation is intensity dependent. The per-parasite effect translates to changes in behavior as a power function of intensity ($\alpha^{\text{Intensity}}$), meaning that parasites with small individual effects can, as a group, alter behavior if they reach high intensities. For instance, a weak manipulation of $\alpha = 1.0025$ by a single trematode metacercaria can lead to a thirty-fold increase in predation risk for killifish because infected hosts have a mean intensity of 1,400 metacercariae in the brain case (Lafferty and Morris 1996). Intensity-dependent manipulation can also lead to a high prevalence of the parasite in the intermediate host population because predators are not as likely to remove hosts with low intensity infections.

An indirect way to evaluate the strength of manipulation from field data is to examine the shape of the frequency distribution of parasites in the host population. Although most typical para-

sites have an "aggregated" or negative binomial distribution (Crofton 1971), the distribution of manipulative parasites in prey hosts appears less aggregated because the tail end of the distribution is truncated (e.g., Adjei et al. 1986; Shaw et al. 2010; Lafferty and Morris 1996; Crofton 1971; Joly and Messier 2004), suggesting that manipulation delivers the most infected prey to predators. For aggregated distributions fitted to a negative binomial distribution, the lower the k-value, the greater the degree of aggregation, with $k < 1$ considered highly aggregated (Shaw et al. 1998). Compiling data from Shaw et al. (1998), for 40 typical parasites and trophically transmitted parasites in their predator hosts, mean $k = 0.41$, whereas for 10 trophically transmitted parasites in their prey intermediate hosts known or prone to behavior modification, mean $k = 1.30$. Therefore, reduced aggregation appears to be a general feature of manipulative parasites.

The ecological role played by manipulative parasites should increase with the frequency that hosts become infected. For parasitoids, castrators, and predator hosts, parasite prevalence is a good measure of abundant manipulation. However, for manipulated prey hosts infected with trophically transmitted parasites, intense manipulation decreases prevalence because predators remove hosts soon after infection (Lafferty 1992). For example, larval acanthocephalans that cause terrestrial isopods to leave shelter are rare in the field because starlings eat infected isopods soon after the behavioral change (Moore 1984). Therefore, in many cases, it can be challenging to determine how abundant manipulation is just by looking at parasite prevalence. Incidence is a far better metric, but one that is harder to measure.

Indirect effects can result from a manipulative parasite if the host plays an important role in the ecosystem. Some hosts are too rare or do not have a disproportionate effect on the ecosystem. Other hosts do not interact much with other potential predators or competitors. However, abundant or interactive hosts can play important roles in ecosystems. For example, the effect of the strong manipulator, *Euhaplorchis californiensis*, is magnified in importance because its killifish host is often the most common fish in the estuarine systems of California and Baja California (Kuris et al. 2008). In three case studies below, we explore what happens when common parasites strongly manipulate hosts with important roles in ecosystems.

9.3 Parasitic castrators and parasitoids as host behavior manipulators

Parasitic castrators and parasitoids can take over the identity of their hosts. Once the parasite prevents reproduction of the host (and this often happens soon after infection), the genotype of the host no longer matters. If manipulation is weak or absent, parasites can compete with the uninfected host population (Lafferty 1993). The intensity of this competition depends on how similarly infected and uninfected hosts use resources. Manipulation can, therefore, reduce competition for castrators and parasitoids.

If parasitoid or castrator life histories differ from those of their hosts, host behaviors can change after infection. Such changes can cause the host to occupy a different niche where it might interact differently with its potential consumers, prey, and competitors. For instance, immigration of castrated snails adds a new phenotype to a community. As an example, when infected with a heterophyid trematode, the snail, *Batillaria cumingi*, moves lower in the intertidal habitat (Miura et al. 2006). Submergence seems adaptive for the parasite's life history because heterophyid cercariae shed from these snails seek to penetrate fishes. In another example, freshwater snails (*Physa acuta*) castrated by certain trematodes abandon their refuge under leaf litter and rise to the surface, perhaps improving the success of cercariae shed by these snails but also increasing their risk of predation by birds (Bernot 2003). In both cases, abundant infected snails occupy a new ecological niche.

Parasitic castrators can alter host-feeding rates with potential indirect effects on lower trophic levels. On rocky shores along the east coast of North America, the most common intertidal snail, *Littorina littorea*, has important impacts on algal communities and can be frequently parasitized by larval trematodes. Infected snails graze less, increasing colonization by ephemeral algae in areas where the

parasite is more prevalent (Wood et al. 2007). In contrast, *Physa acuta* infected with *Posthodiplostomum minimum* graze more than do uninfected snails, reducing periphyton biomass by 20% when the prevalence of infected snails exceeds 50% (Bernot and Lamberti 2008). This intensified grazing also alters the species composition of the periphyton community. These opposite effects of castrators on grazing rates illustrate how the ecological consequences of manipulation can vary among parasites.

9.3.1 Nematomorphs, endangered charr, and crickets in Japanese streams

Japanese fisheries biologists are making a dedicated effort to protect the Kirikuchi charr (a trout), *Salvelinus leucomaenis japonicas* (Fig. 9.1). Threatened by over-fishing and habitat destruction, the charr occurs in a few remaining watersheds (Sato 2007). To understand how to save the charr, biologists

track tagged fish, monitoring their diet and growth rate. Charr, like most stream-dwelling salmonids, feed on aquatic invertebrates as well as terrestrial insects that fall into the stream from the surrounding forest (Kawaguchi et al. 2003). This diet changes in the late summer and fall when fish start consuming terrestrial camel crickets (*Tachycines* spp.). Takuya Sato noticed that several of the crickets eaten by trout had once hosted nematomorph worms, *Gordionus chinensis*, in their abdomens (Sato et al. 2008).

Nematomorphs are parasitoids with a complex life cycle. Non-feeding nematomorph adults live in streams and produce larval worms that infect aquatic insects such as mayflies. Mayflies leave the stream and metamorphose into short-lived adults. However, the larval nematomorphs stay alive inside the mayfly carcasses that fall to the forest floor, infecting crickets that scavenge the infected carcasses. As it matures in the cricket, a growing nematomorph consumes almost all non-essential
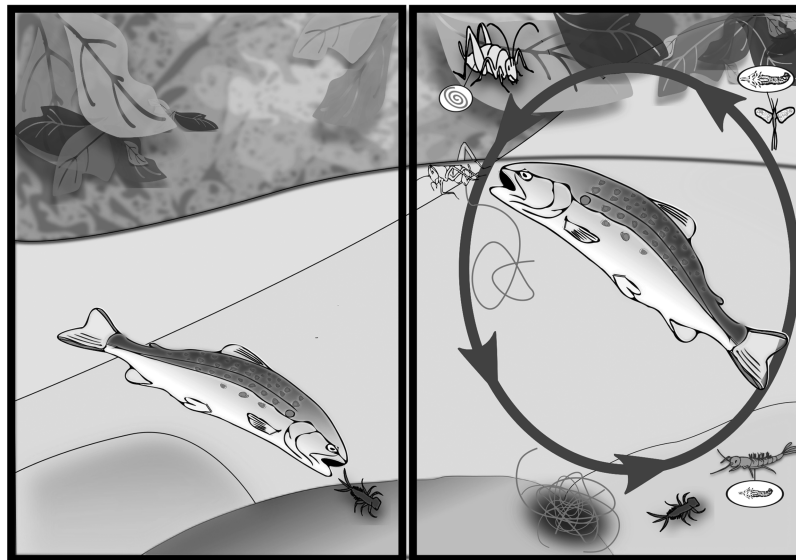

Figure 9.1 Hypothesized effects of a nematomorph worm on a Japanese stream ecosystem. In the left panel, the parasite is absent and charr forage on a sparse prey base of benthic arthropods. In the right panel, adult nematomorph worms mate in the stream. Their larvae infect larval insects and leave the stream as the insects mature and disperse into the forest. Crickets scavenging on dead insects ingest the larvae, and become the second host. As the worm matures in the cricket, it drives its host from the forest into the stream, attracting predation by charr. Such crickets provide 60% of the charr's energetic intake. Satiated by crickets, the charr eat fewer benthic insects, resulting in a higher production of adult insects that leave the stream for the forest. Artwork K. D. Lafferty. See also Plate 14.

fats and reproductive organs. Then comes a considerable challenge. Nematomorphs are aquatic as adults, yet crickets are terrestrial. A dramatic behavioral manipulation solves this problem; the worm causes the cricket to seek water (Thomas et al. 2002) (see also Chapter 2). Infected crickets jump into the stream, and the mature nematomorph worm explodes through the anus of the cricket. The parasitoid leaves its dying host twitching on the surface and swims away to find a mate. Charr attack insects falling into the stream and many consume the worm along with the cricket (Sato et al. 2008). This must have been a long-standing obstacle in the evolution of nematomorphs because the worms escape from the cricket's predators by squirming out through their gills, mouth, or anus (Ponton et al. 2006).

Realizing that nematomorphs were driving crickets into streams, Sato et al. (2011a) measured the contribution of manipulated crickets to the annual energy budget of the charr population. They pumped charr stomachs, divided the prey into several categories, and estimated the caloric content of the prey every month. The researchers set out baited traps in the forest for crickets and also measured the rate that insects fell into the stream. Crickets were common year round in the forest; however, infections with nematomorphs occurred in the summer and fall. Infected crickets were 20 times more likely to fall into streams than were uninfected crickets, confirming that the worm altered cricket behavior, and explaining the seasonal pulse of food for charr. Sato et al. (2011a) found that crickets delivered to the stream by nematomorphs contributed an amazing 60% of the charr's annual calories. This endangered fish might even depend on the nematomorph for its long-term persistence in Japan. Unfortunately for charr, the nematomorph is less prevalent in the conifer plantations that are increasingly replacing native forest (Sato et al. 2011b). There are other potential indirect effects of the nematomorph (Sato et al. 2011a). The nematomorph moves a substantial amount of energy from the forest to the stream. In return, satiated by crickets, charr consume fewer aquatic insects. This shifts energy from the stream back to the forest because many surviving aquatic insects, such as mayflies and damselflies, metamorphose into flying adults that move back to the forest

and become predators and prey for terrestrial animals (Sato et al. 2011a).

9.4 Trophically transmitted parasites as host behavior manipulators

Trophic transmission is a common life history strategy for parasites and seems to select for manipulation. For most parasites, a common cause of death is probably predation of the host (Johnson et al. 2010). However, some parasites have adaptations to survive predation and use the predator as the next host in the life cycle. At worst, parasitizing a predator makes the best of a bad situation. However, if the predator is large and long-lived, the parasite can extend its lifespan and have increased access to food (Lafferty 1999). Alternatively, parasites of predatory hosts might find it advantageous to add prey hosts to their life cycle (Choisy et al. 2003). Prey are more abundant than their predators and are therefore more likely to contact a free-living infectious stage of the parasite. The predator host then unintentionally contacts the parasite as it hunts for prey. For either evolutionary pathway, a trophically transmitted parasite will benefit from increasing predation rates on infected prey so long as the parasite delays manipulation until its maturation and can focus increased predation on suitable predatory hosts. Next, we provide two examples of how manipulation by trophically transmitted parasites might have ecological effects.

9.4.1 Tapeworms, wolves, moose, and forests on Isle Royale

Moose (*Alces alces*) probably first crossed the 30 kilometers to Isle Royale, in Lake Superior from the mainland around 1900, increasing in number due to an abundance of food and absence of wolves (*Canis lupus*) (Fig. 9.2). Population explosions led to periods of over-grazing and mass starvation. In 1949, wolves colonized the island over a rare ice bridge and began to reduce the number of moose. Since 1958, ecologists such as David Mech and Rolf Peterson have studied this 540 square-kilometer outdoor laboratory (see the comprehensive book by Peterson 1995). They have found that many outside
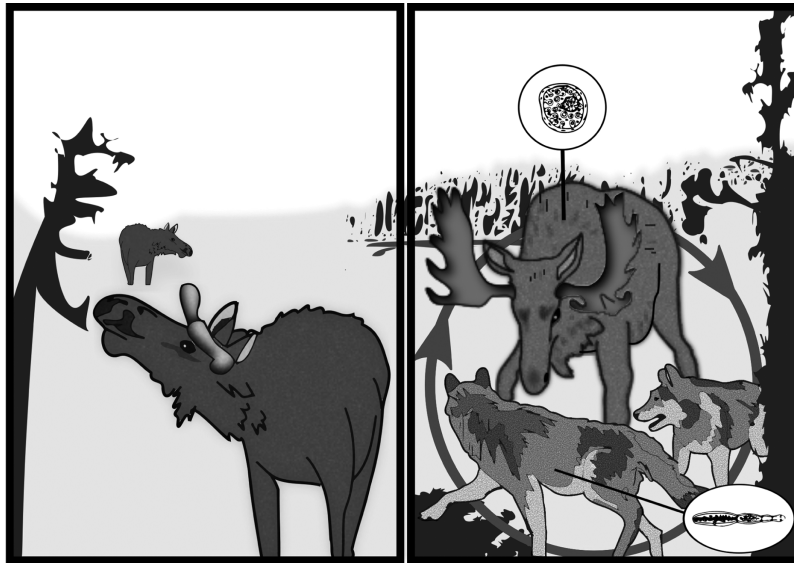
Figure 9.2 Hypothesized effects of a tapeworm on the Isle of Royale ecosystem. In the left panel, the parasite is absent, and wolves have a hard time persisting on moose. Moose, unchecked by predators, over-graze the forest. Right panel, the adult worms of *Echinococcus granulosus* live in the intestines of wolves where they cause little pathology. Tapeworm eggs contaminate the soil and are incidentally ingested by moose. Larval tapeworms form hydatid cysts in the lungs of moose. Wolves can more easily prey on infected moose, reducing the abundance of the moose population and allowing re-vegetation of the island. Artwork K. D. Lafferty. See also Plate 15.

forces affect the success of wolves and moose. For instance, an increase in moose density followed an epidemic of canine parvovirus that almost extirpated wolves in the 1990s. The moose over-grazed the forests and again began to starve. In poor condition, the moose suffered from an outbreak of ticks, and extreme cold weakened their health even more. At the same time, the wolf population began to rebound. This back and forth pattern results in cycles of wolves tracking the abundance of moose, offset by about a decade.

On Isle Royale, the tapeworm, *Echinococcus granulosus*, uses moose as the intermediate host and wolves as the final host. Moose ingest tapeworm eggs from soil and water contaminated with wolf feces. Larval tapeworms form large, debilitating hydatid cysts in the lungs, braincase, liver, and other organs of the intermediate host. Wolves acquire the tapeworms when they eat an infected moose. In the wolf, the small adult tapeworms live in the intestine and cause no measurable harm. Throughout its range, prevalence of

E. granulosus in wolves ranges from 14–72% (Rausch 1995).

The debilitating effects of hydatid cysts likely make it easier for wolves to kill moose. Evidence for this is indirect. Hunters shoot more infected moose earlier in the hunting season (Rau and Caron 1979), and heavily infected moose are less common than expected (Joly and Messier 2004), suggesting hunters or predators remove infected individuals from herds.

How might manipulation by this tapeworm alter the Isle Royale ecosystem? Simple mathematical models hypothesize that there could be situations where wolves could not persist on moose as prey without the assistance of the debilitating parasite (Hadeler and Freedman 1989). More recent models have suggested that manipulative parasites do not affect the invasion criteria for a predator population. This is because at the moment of first contact between a predator and prey population, the prey population is uninfected and unmanipulated (Fenton and Rands 2006). In other words, for wolves to benefit from infected moose, the wolves must

first bring the parasite with them and establish the life cycle. On Isle Royale, the initial pack of wolves encountered an uninfected moose population and wolves established without the initial help of the parasite. However, it is probable that the presence of the tapeworm enables wolves to drive the moose population to lower levels than would be possible without the tapeworm in the system. Consequently, the tapeworm might indirectly favor forests on Isle Royale. A further theoretical effect of a parasite that increases susceptibility to predation is an increase in oscillations between predator and prey (Fenton and Rands 2006), suggesting that the tapeworm could influence the period and amplitude of the moose–wolf cycle seen on Isle Royale.

9.4.2 Trematodes, cockles, limpets, and anemones in New Zealand mudflats

On the mudflats of New Zealand, the most noticeable inhabitant is the "cockle", *Austrovenus stutchburyi* (Stewart and Creese 2002) (Fig. 9.3). This little neck clam reaches 6 cm in width and can attain densities of thousands per square meter, supporting a recreational and commercial harvest (Hartill et al. 2005). As the most abundant component of the biomass on these flats, cockles are also a common resource for birds, fishes, and crabs (Thompson et al. 2005).

Cockle shells can protrude from the sediment, creating a habitat for several epibionts, including an anemone (*Anthopleura aureoradiata*), chitons, the estuarine barnacle *Elminius modestus*, tubicolous amphipods, and serpulid worms (Thomas et al. 1998). Exposed shells also are substrates for algae that support a small limpet, *Notoacmea helmsi*. In the bays of New Zealand, there are few alternative natural substrates for this rich and distinctive epibiont community, and the provision of novel habitat makes *A. stutchburyi* an "ecosystem engineer" (Thomas et al. 1998).

Pied oystercatchers (*Haematopus ostralegus finschi*) foraging on the mudflats carry adult trematode worms in their intestines. For many trematode species in New Zealand mudflats, the first intermediate host snails are either
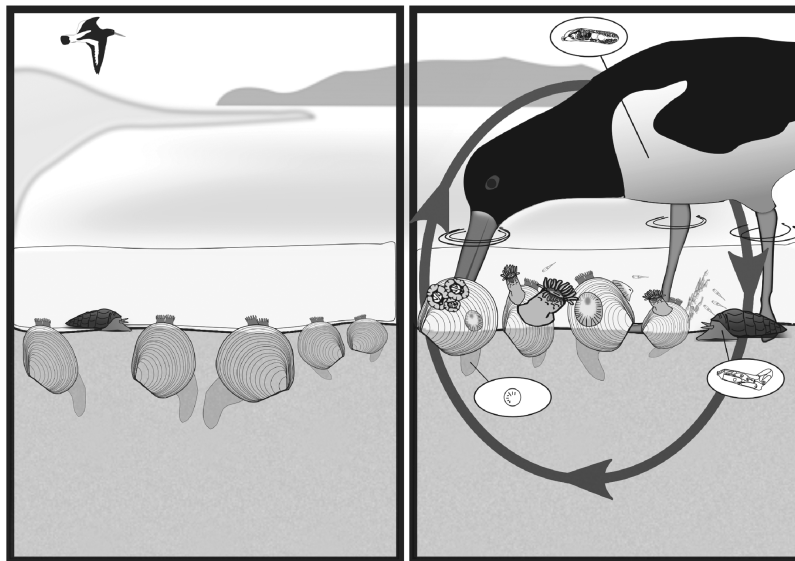

Figure 9.3 Hypothesized effects of a trematode on a New Zealand mudflat ecosystem. In the left panel, cockles burrow into the sediment with only their siphons protruding. In the right panel, adult trematodes live in the intestine of shorebirds. Birds defecate trematode eggs onto the mudflat where they infect an estuarine snail as the first intermediate host. Trematode cercariae emerge from the snail and then seek out a cockle as a second intermediate host, forming a cyst in the foot. Infected cockles have impaired digging abilities, making them easier prey for birds. Raised above the mud surface, the cockles provide hard substrate for a community of invertebrates and algae. Artwork K. D. Lafferty. See also Plate 16.

Zeacumantus subcarinatus or *Cominella glandiformis*. Trematode cercariae emerge from the infected snail and then encyst in a second intermediate host (which varies among trematode species), and the life cycle is completed when an oystercatcher eats an infected second intermediate host. Two trematode genera (*Curtuteria* and *Acanthoparyphium*) with six cryptic species use the cockle as a second intermediate host, encysting in the tip of the foot (Babirat et al. 2004).

Key to the understanding of this system was the discovery that the trematodes, by encysting in the foot, reduce the burrowing ability of the cockles, thereby stranding them on the surface where they become easy prey for oystercatchers (Thomas and Poulin 1998). The trematodes, therefore, are the mechanism by which the cockles increase the available substrate for epibionts to colonize. In addition, by digging less, infected cockles modify properties of the sediment, which alters infaunal communities (Mouritsen and Poulin 2005). Two types of evidence show a clear cause-effect relationship between the trematode and changes to the ecosystem. Experimentally increasing or decreasing the number of stranded cockles alters the mudflat community (Mouritsen and Poulin 2005). Also, by comparing 17 sheltered bays around Otago Harbour, Mouritsen and Poulin (2010) showed that spatial variation in trematode infections was associated with corresponding variation in the intertidal community. It appears that New Zealand mudflats would have less biodiversity without these manipulative parasites.

9.5 The ecological reach of host behavior manipulators

Where might we find other cases where manipulative parasites have ecological effects? Some widespread infectious wildlife diseases with major human public health concerns can manipulate the behavior of their prey hosts. The most notable of these are *Toxoplasma gondii* and other two-host coccidians, taeniid tapeworms such as *Taenia solium*, *T. multiceps*, and *Echinococcus* spp., the raccoon roundworm, *Baylisascaris procyonis*, and *Trichinella* species. These parasites often have low host specificity for the prey hosts. In prey hosts, all are either neurotropic (e.g., *T. gondii*, *B. procyonis*), or infect the lungs, diaphragm, or other key organs needed for stamina (e.g., *Echinococcus* spp. *T. solium*, *Trichinella* spp.). Their ability to modify host behavior, either through involvement with brain chemistry or muscle physiology, probably makes hosts less wary or more risk tolerant, or impairs escape responses (see Chapter 3). A combination of negligible host specificity and increased susceptibility to predators enables these parasites to be widespread. For instance, *T. gondii* infects any warm-blooded vertebrate (terrestrial or aquatic) as an intermediate host on every continent (Tenter et al. 2000). Infections with *T. gondii* can be prevalent, sometimes with substantial pathology (Dubey and Beattie 1988). Such a common and sizeable manipulation suggests *T. gondii* has the potential for large-scale ecological effects. Similarly, *Baylisascaris procyonis* infects more than 100 species of potential prey for raccoons and is common in North America and Europe (Kazacos 2001). *Echinococcus multilocularis* occurs throughout arctic ecosystems (Rausch 1995) and *Trichinella* spp. infections build through the food chain via carnivory and carrion feeding (Pozio et al. 1992). These parasites meet the criteria for having strong ecological effects.

9.6 Testing for the ecological effects of manipulative parasites

A research program on the ecological effects of manipulative parasites will require collaboration between ecologists and parasitologists. Ecologists identify free-living species that play important roles in ecosystems. Parasitologists can then search these important hosts for parasites that are abundant and have the ability to manipulate host behavior. Together, ecologists and parasitologists could conduct studies that link behavioral changes to ecological effects.

The hypothesized ecological role of *Echinococcus granulosus* indicates the importance of working in systems like Isle Royale where indirect effects cascade through the food web. The prediction that the tapeworm could indirectly affect forest growth comes from substantial observational work on the

prevalence of the tapeworm in moose and wolves, the potential effect of the parasite on moose, the effect of moose on vegetation, and the effect of wolves on moose. This system is simple enough to explore with mathematical models, which can reveal additional predictions (e.g., about increased cycling). Carnivore reintroduction programs manipulate the presence of wolves and parasites and might lend insight into the effect of *E. ganulosus* at other locations. Wolves and other large carnivores have been extirpated from large areas of their former ranges and are sometimes reintroduced (such as into Yellowstone National Park in 1995). Before initiating such programs, it should be possible to determine if parasites such as *E. granulosus* are circulating in the ecosystem. Because hydatid disease has severe human health consequences, veterinarians involved in relocations treat wolves at least twice with antihelminth drugs to eliminate tapeworms. Reintroductions, therefore, are an opportunity to observe wolf–prey dynamics without *E. granulosus*. Specifically, comparing dynamics in worm-free areas with source areas where the worm occurs could indicate how this tapeworm affects forest ecosystems. Other species might be more tractable for studying the ecological effects of manipulative tapeworms. *E. multilocularis*, for instance, uses smaller carnivores like foxes and coyotes as final hosts and rodents as intermediate hosts. One could explore how the presence or absence of this tapeworm across island habitats affects predator–prey dynamics.

Research on the New Zealand cockle required a variety of approaches. Observations of stranded, fouled cockles combined with parasitological investigations led to the hypothesis that the parasite manipulated the cockle in a way that altered the ecosystem. Researchers also studied across many sites, permitting an understanding of how variation in parasitism drove changes to the ecosystem. This system was amenable to experimentation because the behavioral manipulation could be mimicked in the laboratory and field, as could parasitization rates (by manipulating snail densities). Finally, by creating a food web for the system (Thompson et al. 2005), researchers had a model for various direct and indirect relationships among

species potentially connected to the stranding of parasitized cockles on the mudflat surfaces. These efforts have resulted in this system being the most cited example of how parasites can affect ecosystems.

The Japanese nematomorph study indicates how non-parasitologists can reveal effects of parasites. Through careful and repeated quantification of charr stomach contents, anomalies were discovered that pointed to the role of the nematomorphs. These biologists were focused on the flow of energy among ecosystems, and were thus able to discover the dramatic contribution of parasitized crickets to the diet of endangered charr.

9.7 Conclusions

Numerous studies have shown that the direct effects of parasitism significantly affect populations, community structure, and ecosystem energetics (e.g., Hudson et al. 1998; Waldie et al. 2011; Lafferty et al. 2006; Kuris et al. 2008; Hechinger et al. 2011). In addition, manipulative parasites are more than just entertaining cocktail party anecdotes. They can exert effects across hierarchical ecological levels. Those that have strong manipulative effects on their hosts can alter aspects of the distribution and abundance of their host populations. If parasitism is common, effects on the host population can be strong. If the host is common or interacts with other species in the system, indirect effects on the food web could occur through the alteration of trophic cascades, creation of new habitats, or new niches, or by altering the flow of energy among habitats. It will be a while before we have a systematic understanding of the importance of manipulative parasites at the ecosystem level. Further insight into the effects of manipulative parasites will require challenging experiments and observations, ideally with strong collaboration among parasitologists and ecologists.

Acknowledgements

References

Adjei, E. L., Barnes, A., and Lester, R. J. G. (1986). A method for estimating possible parasite-related host mortality, illustrated using data from *Callitetrarhynchus gracilis* (Cestoda, Trypanorhyncha) in lizardfish (*Saurida* spp). *Parasitology* **92**, 227–243.

Babirat, C., Mouritsen, K. N., and Poulin, R. (2004). Equal partnership: two trematode species, not one, manipulate the burrowing behaviour of the New Zealand cockle, *Austrovenus stutchburyi. Journal of Helminthology* **78**, 195–199.

Bernot, R. J. (2003). Trematode infection alters the antipredator behavior of a pulmonate snail. *Journal of the North American Benthological Society* **22**, 241–248.

Bernot, R. J. and Lamberti, G. A. (2008). Indirect effects of a parasite on a benthic community: an experiment with trematodes, snails and periphyton. *Freshwater Biology* **53**, 322–329.

Choisy, M., Brown, S., Lafferty, K. D., and Thomas, F. (2003). Evolution of trophic transmission in parasites: why add intermediate hosts? *American Naturalist* **162**, 172–181.

Crofton, H. D. (1971). A quantitative approach to parasitism. *Parasitology* **62**, 179–193.

Dobson, A. P. (1988). The population biology of parasite-induced changes in host behavior. *Quarterly Review of Biology* **63**, 139–165.

Dobson, A. P. and Keymer, A. E. (1985) Life history models. In: *Acanthocephalan Biology* (eds Crompton, D. and Nickol, B.) Cambridge University Press, Cambridge.

Dubey, J. P. and Beattie, C. P. (1988) *Toxoplasmosis of Animals and Man.* CRC Press, Boca Raton, Florida.

Feener, D. H. and Brown, B. V. (1995). Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Annals of the Entomological Society of America* **85**, 80–84.

Fenton, A. and Rands, S. A. (2006). The impact of parasite manipulation and predator foraging behavior on predator-prey communities. *Ecology* **87**, 2832–2841.

Grutter, A. S., Murphy, J., and Choat, H. (2003). Cleaner fish drives local fish diversity on coral reefs. *Current Biology* **13**, 64–67.

Hadeler, K. P. and Freedman, H. I. (1989). Predator-prey populations with parasitic infection. *Journal of Mathematical Biology* **27**, 609–631.

Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: five strategies. *Neuroscience and Biobehavioral Review* **14**, 273–294.

Hartill, B. W., Cryer, M., and Morrison, M. A. (2005). Estimates of biomass, sustainable yield, and harvest: neither necessary nor sufficient for the management of non-commercial urban intertidal shellfish fisheries. *Fisheries Research* **71**, 209–222.

Hechinger, R. F., Lafferty, K. D., Dobson, A. P., Brown, J. H., and Kuris, A. M. (2011). A common scaling rule for abundance, energetics and production of parasitic and free-living species. *Science*, **333**, 445–448.

Holmes, J. C. and Bethel, W. M. (1972) Modifi cation of intermediate host behavior by parasites. In: *Behavioural Aspects of Parasite Transmission* (eds Canning, E. U. and Right, C. A.) Zoological Journal of the Linnean Society, London.

Hudson, P. J., Dobson, A. P., and Newborn, D. (1998). Prevention of population cycles by parasite removal. *Science* **282**, 2256–2258.

Johnson, P. T. J., Dobson, A., Lafferty, K. D., Marcogliese, D. J., Memmott, J., Orlofske, S. A., Poulin, R., and Thieltges, D. W. (2010). When parasites become prey: ecological and epidemiological significance of eating parasites. *Trends in Ecology and Evolution* **25**, 362–371.

Joly, D. O., and Messier, F. (2004). The distribution of *Echinococcus granulosus* in moose: evidence for parasite-induced vulnerability to predation by wolves? *Oecologia* **140**, 586–590.

Kawaguchi, Y., Nakano, S., and Taniguch, I. Y. (2003). Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology* **84**, 701–708.

Kazacos, K. R. (2001) *Baylisascaris procyonis* and related species. In: *Parasitic Diseases of Wild Mammals*, 2nd edn. (eds Samuel, W. M., Pybus, M. J., and Kocan, A. A) Iowa State University Press, Ames.

Kiesecker, J. M. and Blaustein, A. R. (1999). Pathogen reverses competition between larval anurans. *Ecology* **80**, 2142–2148.

Kuris, A. M., Hechinger, R. F., Shaw, J. C., Whitney, K. L., Aguirre-Macedo, L., Boch, C. A., Dobson, A. P., Dunham, E. J., Fredensborg, B. L., Huspeni, T. C., Lorda, J., Mababa, L., Mancini, F., Mora, A. B., Pickering, M., Talhouk, N. L., Torchin, M. E., and Lafferty, K. D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 515–518.

Kuris, A. M. and Lafferty, K. D. (2000) Parasite-host modeling meets reality: adaptive peaks and their ecological attributes. In: *Evolutionary Biology of Host-Parasite Relationships: Theory Meets Reality* (eds Poulin, R., Morand, S., and Skorping, A.) Elsevier, Amsterdam.

Lafferty, K. D. (1992). Foraging on prey that are modified by parasites. *American Naturalist* **140**, 854–867.

Lafferty, K. D. (1993). Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica. Marine Ecology Progress Series* **96**, 229–237.

Lafferty, K. D. (1999). The evolution of trophic transmission. *Parasitology Today* **15**, 111–115.

Lafferty, K. D. and Kuris, A. M. (2002). Trophic strategies, animal diversity and body size. *Trends in Ecology & Evolution* **17**, 507–513.

Lafferty, K. D. and Kuris, A. M. (2009). Parasitic castration: the evolution and ecology of body snatchers. *Trends in Parasitology* **25**, 564–572.

Lafferty, K. D. and Morris, A. K. (1996). Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397.

Miura, O., Kuris, A. M., Torchin, M. E., Hechinger, R. F., and Chiba, S. (2006). Parasites alter host phenotype and may create a new ecological niche for snail hosts. *Proceedings of the Royal Society B-Biological Sciences* **273**, 1323–1328.

Moore, J. (1984). Altered behavioral responses in intermediate hosts: an acanthocephalan parasite strategy. *American Naturalist* **123**, 572–577.

Moore, J. (2002) *Parasites and the Behavior of Animals*, Oxford University Press, Oxford.

Mouritsen, K. N. and Poulin, R. (2005). Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects. *Oikos* **108**, 344–350.

Mouritsen, K. N. and Poulin, R. (2010). Parasitism as a determinant of community structure on intertidal flats. *Marine Biology* **157** 201–207.

Peterson, R. O. (1995) *The Wolves of Isle Royale: A Broken Balance.* Willow Creek Press, Minocqua WI.

Ponton, F., Lebarbenchon, C., Lefèvre, T., Biron, D. G., Duneau, D., Hughes, D. P., and Thomas, F. (2006). Parasitology: parasite survives predation on its host. *Nature* **440**, 756.

Poulin, R. (1995). "Adaptive" changes in the behaviour of parasitized animals: A critical review. *International Journal for Parasitology* **25**, 1371–1383.

Pozio, E., La Rosa, G., Rossi, P., and Murrell, K. D. (1992). Biological characterization of *Trichinella* isolates from various host species and geographical regions. *Journal of Parasitology* **78**, 647–653.

Rau, M. E., and Caron, F. R. (1979). Parasite-induced susceptibility of moose to hunting. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **57**, 2466–2468.

Rausch, R. L., (1995) Life cycle patterns and geographic distribution of *Echinococcus* species. In: *Echinococcus and Hydatid Disease.* (eds Thompson, R. C. C., and Lymbery, A. J.) CAB International, Wallingford, Oxon.

Sato, T. (2007). Threatened fishes of the world: Kirikuchi charr, *Salvelinus leucomaenis japonicus* Oshima, 1961 (Salmonidae). *Environmental Biology of Fishes* **78**, 217–218.

Sato, T., Arizono, M., Sone, R., and Harada, Y. (2008). Parasite-mediated allochthonous input: do hairworms enhance subsidised predation of stream salmonids on crickets? *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **86**, 231–235.

Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y., and Lafferty, K. D. (2011a). Nematomorph parasites drive energy flow through a riparian ecosystem. *Ecology* **91**, 201–207.

Sato, T., Watanabe, K., Tokuchi, N., Kamauchi, H., Harada, Y., and Lafferty, K. D. (2011b). A nematomorph parasite explains variation in terrestrial subsidies to trout streams in Japan. *Oikos* **120**, 1596–1599.

Shaw, D. J., Grenfell, B. T., and Dobson, A. P. (1998). Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* **117**, 597–610.

Shaw, J. C., Lafferty, K. D., Hechinger, R. F., and Kuris, A. M. (2010). Ecology of the brain trematode *Euhaplorchis californiensis* and its host, the California killifish (*Fundulus parvipinnis*). *Journal of Parasitology* **96**, 482–490.

Stewart, M. J. and Creese, R. G. (2002). Transplants of intertidal shellfish for enhancement of depleted populations: preliminary trials with the New Zealand little neck clam. *Journal of Shellfish Research* **21**, 21–27.

Tenter, A. M., Heckeroth, A. R., and Weiss, L. M. (2000). *Toxoplasma gondii*: from animals to humans. *International Journal for Parasitology* **30**, 1217–1258.

Thomas, F. and Poulin, R. (1998). Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? *Parasitology* **116**, 431–436.

Thomas, F., Renaud, F., De Meeüs, T., and Poulin, R. B. (1998). Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone? *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1091–1096.

Thomas, F., Schmidt-Rhaesa, A., Martin, G., Manu, C., Durand, P., and Renaud, F. (2002). Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts? *Journal of Evolutionary Biology* **15**, 356–361.

Thompson, R. M., Mouritsen, K. N., and Poulin, R. (2005). Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *Journal of Animal Ecology* **74**, 77–85.

Waldie, P. A., Blomberg, S. P., Cheney, K. L., Goldizen, A. W., and Grutter, A. S. (2011). Long- term effects of the cleaner fish *Labroides dimidiatus* on coral reef fish communities. *PLoS ONE,* **6**, e21201.

Wood, C. L., Byers, J. E., Cottingham, K. L., Altman, I., Donahue, M. J., and Blakeslee, A. M. H. (2007). Parasites alter community structure. *Proceedings of the National Academy of Sciences of the United States* **104**, 9335–9339.