# Parasites and Food Webs

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Every free-living species is host to a large diversity of parasitic species, the presence and influence of which have only recently received attention in studies of food webs. Initial studies of the St. Martin and Ythan food webs suggest that the consideration of parasites significantly changes the proportions of species at higher trophic levels; by definition the addition of parasites of top predators will lengthen the maximum lengths of food chains. However, until recently, the addition of parasites seems not to have had a major influence on levels of connectedness, nor on the scaling properties of food webs. Empirical long-term studies of the Serengeti illustrate the dramatic impact that a single pathogen may have on the long-term dynamics of food webs; ongoing comparative studies of salt marshes along the California coast illustrate that parasites may form a significant component of food-web biomass. Furthermore, parasites with complex (heteroxenic) life cycles have life-history stages that occupy a variety of different trophic positions in webs, these lead to complex long-loops in interactions between species that may

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considerably enhance the stability of food webs. We will conclude by examining how to include parasites into current theoretical models for food webs. In particular, we will examine whether the "niche model" may be scaled by metabolic rate, rather than body size, and examine how this affects our ability to organize species along a logical trophic-dynamic interaction spectrum.

## 1 INTRODUCTION

The world looks very different to a parasitologist or a pathologist (and not just because *Scientific American* listed parasitic worm research as the second worst career in science). The diversity of free-living organisms that compete with and consume each other is but a subset of biodiversity. To a parasitologist, free-living species represent a metapopulation of resource patches that exist for the benefit of an equal diversity of free-living species. Conceivably the diversity of parasitic species exceeds that of free-living species (Price 1980; Toft 1986). Thus, food webs that ignore parasites are seeing less than half of the species in an ecosystem; if parasites are as promiscuous in their interactions as free-living species, then at least three quarters of the links of the web are also missed. The main point of this chapter is to illustrate the major role that pathogens play in determining the structure and stability of food webs (Marcogliese and Cone 1997).

The last 20 years have seen a significant increase in our ecological understanding of the role that parasites and pathogens play in regulating host abundance, in modifying host behavior, and in mediating interactions between free-living species. In this chapter we discuss the role that parasites play in food webs. This discussion will be empirical, theoretical and speculative. Except for a few excellent exceptions, this field of study is wide open. If we take the recent significant increase in ecological understanding of pathogen ecology as an example (Grenfell and Dobson 1995; Hudson et al. 2002), there is clearly a huge potential for parasites to play a major role in structuring food webs. Yet given the diversity of parasites and pathogens, and our limited understanding of these taxa, then a full understanding of their ecological role is a long-term goal. We shall, therefore, focus on providing a handful of examples in which dramatic roles have been illustrated. We then review the current literature on the role of parasites in food webs, and conclude by examining how further consideration of parasites would influence current exciting discussions about the structure and dynamics of food webs.

Although there has been a historic absence of food web studies that contain information about parasites, a number of recent studies have reversed this. Long-term studies on the evolution of Anolis lizards on Carribean islands (Roughgarden 1995) included information on the gut and blood parasites of the lizards (Dobson et al. 1992; Schall 1992). When a food web for the island of St. Marten was constructed that included the helminth parasites of the lizards, it had two

main effects on the web: (1) it added species to the top trophic level; (2) it emphasized that a significant component of the web may be missing. Only lizards were examined for parasites, so there is likely a significant diversity of parasites in other animal and plant species that have been left out of the web. Of particular importance here will be parasites of the top carnivores; these pathogens will add a further trophic level to the food web.

The food webs developed for the Ythan estuary and Loch Leven in Scotland represent comprehensive efforts to include all of the parasitic helminths into the food webs for these two aquatic systems. Many of these species have complex (heteroxenic) life cycles that require them to sequentially utilize two or more hosts, each of which lives on a different trophic level. For example, the trematode, *Diplostomum spathaceum*, lives in the alimentary canals of fish-eating birds; this stage of its life cycle adds an additional trophic level above the fish-eating birds that would traditionally appear at the top of the food chain. The adult worms produce eggs that pass with the birds faeces into the water. On hatching, the miracidial stages actively search for snails which they penetrate and infect. This parasitic stage reproduces asexually, eventually taking over most of the reproductive tissue of the snail. Other digenetic trematodes are capable of both castrating their snail hosts and of prolonging their lives and increasing their body sizes. All of this increases the parasites' ability to produce the cercarial stages that are released from the snail back into the water, where they attempt to locate a fish to penetrate and parasitize. They then migrate to the eyes of the fish, where their presence causes the fish to view its world through increasingly opaque vision. This causes the fish to spend more time feeding in the better illuminated surface waters where they are more susceptible to predation by the birds that act as final hosts. Many trematodes, cestodes, nematodes, and acanthocephalans have life cycles of this complexity. Only the nematodes have species which can exhibit simple life cycles involving a single species of host.

Inclusion of parasitic helminthes instantly creates several problems when classifying their position in food webs; should we include *Diplostomum* as a single species, or should we include each of its lifecycle stages as a separate trophic species? If we choose the latter, then *Diplostomum* counts as five species, three parasitic, and the two free-living stages that make a substantial contribution to the benthos. The parasitized Ythan and Loch Leven webs include each parasitic helminth only as a single species—but this leads to more than a fifty percent increase in species numbers in the Ythan case and a doubling in the case of Loch Leven. These numbers would increase still further if we included each of the parasitic species' life history stages as different trophic species. Inclusion of the parasites also significantly increases the length of the food chains within the web and the average position of species in the web (fig. 2). Here we should note that these webs will still underestimate the net diversity of parasitic species; none of the microparasitic bacterial, viral, fungal or protoan parasites has been included. Studies of marine sediment from an estuarine habitat in southern California (which is broadly comparable to the Ythan estuary) have found over a thousand

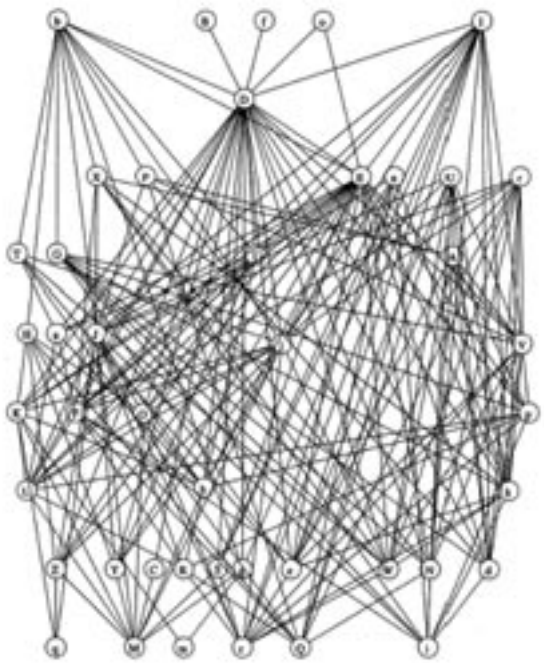

FIGURE 1 St. Martin food web—species b, f, and o are parasitic helminthes (after Goldwasser and Roughgarden 1993).

distinct viral genotypes, only 292 of which are currently represented in GenBank (Breitbart et al. 2004).

## 1.1 SILWOOD AND COSTA RICAN PARASITOID WEBS

A recent food web for an estuary in southern California (Carpinteria Salt Marsh) uses the concept of sub-webs to integrate parasites (Lafferty et al. in press). This reveals four sub-webs in the estuary. The predator-prey sub-web is what constitutes most published food webs and contains 81 species. The connectance of this sub-web is consistent with predictions of food-web theory. The addition of 39 parasite species provides a rich parasite-host web with many parallels to the Ythan and Loch Levan webs. The sub-web concept, when envisioned as a $2 \times 2$ matrix of parasites and free-living species, forced the authors to consider two previously unconceptualized sub webs. The first, predator-parasite, is the most richly linked of all. It includes all the parasites consumed when predators eat infected prey. This has dramatic evolutionary consequences as it indicates that parasites suffer great risks of predation. Many have adapted, and one third of the

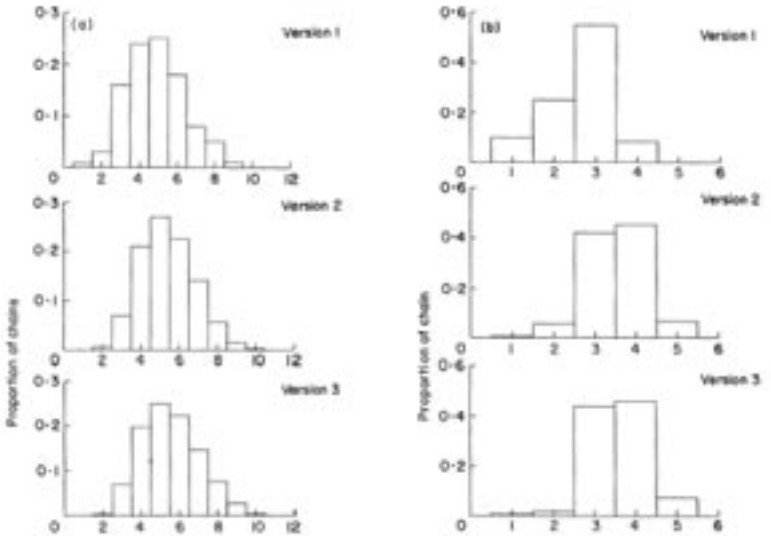


FIGURE 2 Ythan estuary and Loch Leven food webs; an increasing amount of information about parasites is included as we go from version 1, to 2, to 3. (After Huxham, Raffaelli, and Pike 1995).

TABLE 1 Nine parameters from four versions of the Ythan and Loch Leven webs. Version 4 of the Ythan web is exceptional in having tropho-, rather than biological, species.

| | Food-chain lengths | | | Species proportions | | | Omnivory | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mode | Mean | $(L/S)^d$ | % top | % middle | % basal | Degree | % | Species ($S$) |
| Ythan | | | | | | | | | |
| Ver. 1 | 5 | 5 · 00 | 4 · 42 | 0 · 28 | 0 · 68 | 0 · 04 | 7 · 65 | 33 · 7 | 94 |
| Ver. 2 | 5 | 5 · 38 | 3 · 82 | 0 · 45 | 0 · 53 | 0 · 02 | 3 · 90 | 35 · 0 | 135 |
| Ver. 3 | 5 | 5 · 54 | 4 · 37 | 0 · 45 | 0 · 53 | 0 · 02 | 5 · 06 | 43 · 0 | 135 |
| Ver. 4 | 5 | 5 · 54 | 3 · 51 | 0 · 56 | 0 · 42 | 0 · 02 | 2 · 12 | 18 · 5 | 168 |
| L. Levin | | | | | | | | | |
| Ver. 1 | 3 | 2 · 61 | 1 · 45 | 0 · 41 | 0 · 41 | 0 · 18 | 0 · 11 | 4 · 5 | 22 |
| Ver. 2 | 4 | 3 · 56 | 1 · 45 | 0 · 67 | 0 · 25 | 0 · 08 | 2 · 80 | 19 · 6 | 52 |
| Ver. 3 | 4 | 3 · 52 | 1 · 65 | 0 · 67 | 0 · 25 | 0 · 08 | 2 · 92 | 22 · 0 | 52 |
| Ver. 4 | 3 | 3 · 57 | 1 · 91 | 0 · 65 | 0 · 29 | 0 · 06 | 3 · 02 | 55 · 0 | 65 |

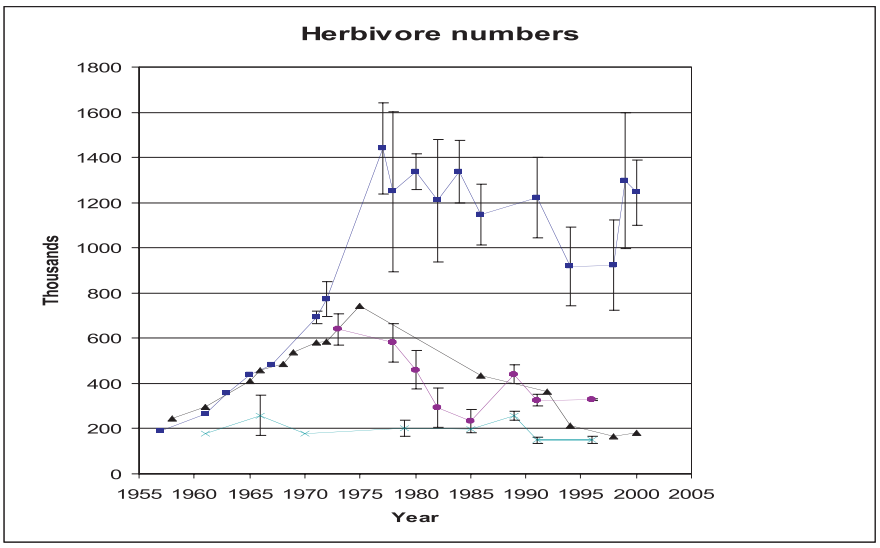


FIGURE 3 Abundance of different ungulate species in the Serengeti (data from Sinclair et al. 2005).

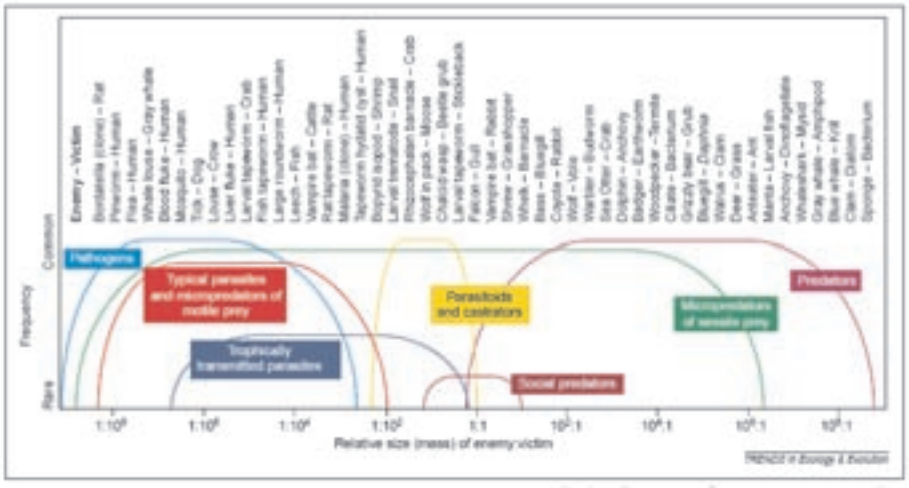


FIGURE 4 After Lafferty and Kuris, TREE.

predator-parasite links lead to host-parasite links. In other words, parasites frequently adapt to the predation of their hosts by parasitizing the host's predators. The final sub web in the Carpinteria web is a parasite-parasite web which, in this estuary, is dominated by intraguild predation among the larval trematodes that parasitize the first intermediate host snail (Sousa 1992; Esch and Fernandez 1994). The parasite sub webs add greatly to connectance, such that including parasites in the Carpinteria food web leads to a threefold increase in connectance, greater than expected from food web theory. Three quarters of the nearly 2000 links in this web involve parasites, even though the authors acknowledge that they have left out many parasitic species that are likely to be common.

Interestingly, the one other web that makes a comprehensive attempt to include parasites is the grassland web for Scotch Broom at Silwood Park (Memmott et al. 2000). Here the authors find that the inclusion of parasites and parasitoids again leads to an almost doubling of species: of the 154 taxa, 69 were parasitoids or pathogens (suggesting pathogens were undersampled!). In this web, resource species had a higher vulnerability to consumers than has been recorded in any other web. Each species was preyed upon by about 13 consumers, and around 50% of these were parasitoids. Similar features are also observed in the Carpinteria web, where the consumers at lower trophic levels are predominantly predators and are at higher trophic levels predominantly pathogens (Lafferty et al. in press). In the Scotch broom web, parasitoids were significantly more specific than predators. This is the opposite to what occurs in the Carpinteria, Loch Leven, and Ythan food webs, where the large numbers of parasitic helminthes utilize a diversity of host species, often at different trophic levels within the same life cycle. All of these webs that include parasites and parasitoids create problems for organizing principles that attempt to organize species along an axis based simply on body size: while predators are usually larger than the prey they consume (93% of species on Scotch broom), the parasitoids and pathogens are significantly smaller (79% on broom). We'll return to this point in the final discussion.

## 2 WHY PARASITES ARE IMPORTANT

We suspect that most food webs are like the one described for the Carpinteria salt marsh. Some will exhibit a lower diversity of parasites, (such as the communities of deep-sea vents that appear almost devoid of parasitic species (Kuris personal communication), but other communities will have higher parasite diversity. Here it's less easy to give an example, as only a few habitats have been extensively examined for parasites. As is often the case with protozoan and other invertebrates, the taxonomic capacity to undertake these studies is simply unavailable. Hopefully, developments in molecular taxonomy may allow us to obtain estimates of the parasitic diversity we are undersampling (Breitbart et al. 2004), but even this will be restricted to what we have already sampled. So we conclude

this section with a plea to other workers to extend their studies of other well documented webs to include parasites and pathogens in their collation of food web data.

## 3 TWO EMPIRICAL EXAMPLES

Do parasites play any significant role in food web structure? There is a handful of examples that suggest their introduction, or removal, may have very dramatic effects. The two examples described below show how parasites cause ecosystem-wide cascading effects on the abundance of nearly all the free-living species in two well-studied communities at very different spatial scales. Anecdotal evidence exists for other similar ecosystem-wide outbreaks, for example, pathogen-driven die-offs of Diadema urchins in the Caribbean (Lessios et al. 1984; Lessios 1988). Around California's Channel Islands, food webs affect disease and disease, in turn, affects food webs. Fishing for lobsters leads to increases in the density of sea urchin populations and at high densities, bacterial epidemics are more common (Lafferty 2004). Reductions in sea urchin populations following an epidemic lead to a shift in the state of the rocky reef community from sea urchin barrens to kelp forests (Berhens and Lafferty 2004). It would be interesting to know if there are other examples. Disease outbreaks certainly occur and disrupt long-term studies, but these are too often dismissed as unfortunate accidents, rather than accepted as natural events.

### 3.1 RINDERPEST IN THE SERENGETI

Perhaps the best example of a pathogen completely modifying the structure of a food web would be the introduction of the rinderpest virus into sub-Saharan Africa in the 1890s. Rinderpest is a morbillivirus that infects hoofed animals: cattle, wild buffalo, wildebeest, giraffe, and other large antelope. It is closely related to both canine distemper (CDV) and measles, two of the commonest diseases of humans and their domestic dogs. The recent evolution of these three pathogens is intimately entwined with the domestication of dogs and cattle, which created the opportunities for the pathogen to establish itself in new host species, where a few mutations allowed it to differentiate itself from rinderpest which the ancestral main trunk of the morbillivirus tree (Norrby et al. 1985; Barrett 1987). The split between the three pathogens is so recent (<5000 years) that there is still strong cross immunity between them; inoculation of dogs with rinderpest vaccine will protect them against distemper. This again raises interesting questions about how we classify pathogens in food webs where they may fail to establish a dependence upon a host, but stimulate an immunological response which allows the host to protect itself against invasion by a potentially lethal natural enemy.

Rinderpest caused one of the largest pandemics in recorded history. It took ten years to spread from the Horn of Africa to the Cape of Good Hope, during

which time it reduced the abundance of many ungulate/artiodactyl species by as much as 80% (Branagan and Hammond 1965). This, in turn, produced a temporary glut of food for decomposers and scavengers, such as vultures and jackals. However, this quickly led to a massive reduction in food supply for the predators that relied on wildebeest and other game for food. The removal of the ungulates changed the grazing intensity on both shrubs and grasses. This seems to have allowed some tree species to undergo a pulse of recruitment; thus, many of the individual fever trees that create woodlands in damper areas of the savanna are now just over a hundred years old. In contrast, reduced levels of grass grazing led to an increased fire frequency, which prevented the reestablishment of Miombo bushland that had previously covered the savanna. This, in turn, modified the habitat for many of the predators that require thicker bush coverage to successfully attack their prey.

The development of a vaccine for rinderpest in the 1950s allowed these processes to be reversed. There is an instructive irony here: the presence of rinderpest in wildlife was blamed as the major reason why it had proved almost impossible to establish large-scale cattle ranches in East Africa. The rinderpest vaccine was largely developed to help the cattle industry, and although it was only ever applied to cattle, this, in turn, led to its disappearance from wildlife. Thus, cattle had been the reservoir and the repeated epidemics observed in wildlife were in response to constant spillovers from cattle (Plowright 1982). Rinderpest vaccination has successfully eradicated the disease from most parts of Africa, except in times of civil unrest, when declines in vaccination coverage allow it to resurge. The impact on wildlife has been spectacular. In the Serengeti, wildebeest numbers have grown from around 250,000 to over 1.5 million, buffalo have appeared in areas where they were previously unrecorded, and lion and hyena numbers have increased dramatically in response to the enhanced food supply (Sinclair 1979; Sinclair and Arcese 1995). Ironically, this strengthens our contention that predators are less effective than pathogens in regulating host abundance. The numbers of some species have declined; for example, there are fewer Thompson's gazelles, perhaps because of more competition for grassland forage, but more likely because of increased predation pressure from the more numerous hyenas (Sinclair et al. 1985; Dublin et al. 1990). African hunting dogs have also declined, since wide-scale rinderpest vaccination allowed their prey to increase in abundance, this is at first surprising. However, the decline may be due primarily to increase competition with more abundant hyenas (Creel and Creel 1996). There may also be increased risk of infectious disease, particularly distemper. In the absence of rinderpest, it may be that hunting dogs (and other carnivores such as lions), no longer acquire cross-immunity to distemper. This pathogens may have caused CDV outbreaks that led to the extinction of several wild dog packs and a 30% decline in lion abundance. The increased wildebeest abundance has in turn reduced the excess of dried grass during the dry season, this has, in turn, led to a reduction in fire frequency, which has allowed the miombo bushland to return to some areas of the Serengeti (Sinclair et al., in review).

The key point here is that while the biomass of the rinderpest virus in the Serengeti was always less than 10kg, the virus had an impact on the abundance and dynamics of nearly all of the dominant plant and animal species in the system—even on those which it did not infect. It strengthens the notion that indirect effects may be as important in shaping species abundance and web linkages as are direct interactions. It also reinforces the earlier comments that pathogens may be as powerful as predators in regulating abundance and distribution.

## 3.2 PARASITIC EYE-FLUKES IN SLAPTON LEY, DORSET

A second empirical example comes from a long-term study of a small lake adjacent to the south coast of the United Kingdom. Clive Kennedy has been studying the fish and parasites of Slapton Ley since the early 1970s (Kennedy 1981; Kennedy and Burroughs 1981; Kennedy 1987; Kennedy et al. 1994). Although no detailed data are available on the invertebrates that form the major component of the diet of the fish, long-term data are available on the relative abundance of the main fish species, their principle parasitic helminthes, and the birds that act as definitive hosts for several key species of trematodes that exhibit the complex (multi-host) life cycles described above. In the early years of the study, the fish populations and their parasites appeared relatively constant. However, nutrient runoff from neighboring agricultural land was leading to increased eutrophication. This favored one species of fish over its two potential competitors. By the late 1970s, rudd completely dominated the fishery and the high densities of this species meant that most individuals were stunted and reached reproductive maturity at late age and small body size. Sometime in the early 1980s, the lake was colonized by Great Crested Grebes (*Podiceps major*). This bird acts as the definitive host for two helminth species, the cestode *Ligula intestinalis*, and the digenetic trematode, *Tylodelphys clavata*. Both of these parasite species were introduced into the fish community when the birds recolonized, they both have complex life cycles which sequentially involve crustacea, fish, and birds in the case of the cestode, and snails, fish and birds in the case of the trematode. Both species have dramatic impacts on their fish hosts: the trematode lives in the eyes of the fish, occluding its vision and increasing its susceptibility to predation by the birds that act as the final host; the cestode lives in the body cavity of the fish and can grow to a body size that may exceed that of an uninfected fish. This significantly increases the energetic demands of the fish, which in turn causes its host to grow to a significantly bloated size, increasing its susceptibility to predation by the piscivorous birds that act as predators on the fish and final hosts for the parasite. The introduction of the two parasite species quickly had a dramatic impact on the rudd population, whose numbers rapidly declined over the following few years. While this reduced the level of intraspecific competition and alleviated the stunting (Burroughs and Kennedy 1979), the intensity of interspecific competition increased as the numbers of roach increased. A final twist to the complexity of the system is provided by the continued presence of a

second species of trematode, which also parasitizes the eyes of fish. This species competes directly with the introduced trematode as both use exactly the same niche for the same part of their life cycle. The increase in the abundance of the introduced eye-fluke was matched by a significant decline in the abundance of the original eye-fluke. After a time, a third species of eye-fluke colonized the lake. This also competes with the other two species of eye-fluke. The important point here is that the direct impact of the piscivorous bird species was relatively minor, their abundance was always restricted to one or two breeding pairs and their young. However, the presence of the birds has a profound indirect effect on the fish species in the system because of their ability to complete the life cycle of the parasites that impact nearly every fish in the lake.

## 4 THEORETICAL IMPLICATIONS

Consideration of the two examples provided above and the brief historical review of food web studies that incorporate parasites suggests a number of important insights that point to new directions for future studies of parasites, food webs, and ecosystem function. First, the inclusion of parasites and pathogens significantly increases the diversity of species in food webs. In its simplest form, diversity is increased because most free-living species harbor "several specific pathogens" that are specialized to use only one host species. This will always lead to somewhere between a doubling and a quadrupling of the number of species in the web, depending on how accurately we can quantify "several species of specific pathogens." An important consideration here is that these pathogens may play a key role in regulating the abundance of individual host species, which will magnify the regulatory action of other intraspecific regulatory factors and thus help maintain the stability of the web as a whole. Where direct life-cycle pathogens are shared between species, such as occurs with rinderpest in the Serengeti, then pathogens can again play an important role in allowing species with similar resource requirements to coexist stably (Hudson and Greenman 1998; Dobson 2004). This occurs due to the strong frequency-dependent regulation of species abundance when rates of within-species pathogen transmission exceed those of between-host species transmission; this effectively prevents any one competitor from becoming too common as it then receives the majority of the impact of the pathogen. Such asymmetries in transmission are likely to arise when hosts are aggregated into conspecific herds or groups, or when small degrees of spatial niche separation ensure that opportunities for transmission occur more often within than between species. In contrast, where asymmetries occur in either the hosts' susceptibility to infection, or in the duration of time for which they are infectious, then this may allow one species to reverse a competitive disadvantage with a more susceptible species and potentially drive it extinct.

Thus, a healthy ecosystem (or food web) is not one that is devoid of parasites and pathogens (Lafferty 1997; Huspeni and Lafferty 2004), on the contrary,

the absence of these species may allow one or two species to significantly increase in abundance and outcompete species that may have to battle both their own parasites and an increased intensity of competition from a released competitor. This situation may occur frequently when alien species are introduced into an area through accidental or deliberate anthropogenic introduction. Surveys that compare the parasite burdens of host species in their native ranges with those of species in areas where they been introduced and have successfully established show less than half of the parasite species diversity in the introduced area (Mitchell and Power 2003; Torchin et al. 2003)

## 4.1 COMPLEX LIFE CYCLES CREATE LONG LOOPS

The second major impact of parasites on food webs relates to recent work on the potential stabilizing role of species that introduce weak interactions into long loops (Neutel et al. 2002). In the absence of such weak links, long loops would be destablizing. Many of the parasitic helminthes with complex life cycles fulfill these criteria. Although they may have strong impacts on some species in their life cycle (witness the worms that impact the fish at Slapton Ley), these species are less specific in their "choice" of birds that act as definitive hosts, and have only a weak, and experimentally non-detectable impact on the fitness of their avian hosts. When they parasitize the snails in their life cycle, they often only infect a small proportion of the snail population (<1–10%), their impact on these hosts is usually in the form of castration, which maintains the host within the same functional role in the food web. Castration of the snail by the worm may considerably increase snail body mass and its survival, which is considerably advantageous to the parasite, as most of the snail's tissue is producing parasite infective stages. Although only a small proportion of these will successfully locate and infect fish, the rest are likely to form an important addition to the food supply of freshwater invertebrates and even the fish species they are attempting to parasitize. The impact of this on overall web dynamics requires further exploration; in particular, food web studies need to more sharply consider interactions between species, where the interaction between the species has impacts on the fecundity component of fitness, rather than the survival term. However, the net effect of including complex life cycle parasites into food webs is that we have added a significant number of species which have complex, but relatively weak, links with a significant number of free-living species on two or three different trophic levels. This again could theoretically have an important stabilizing impact on food structure and long-term persistence.

## 4.2 PARASITES AND THE CASCADE MODEL

The third theoretical area in which the inclusion of parasites may be important is in consideration of their role in modifying the cascade and niche models which have recently deepened our understanding of the ways food webs are or-

ganized. These models are discussed in more detail elsewhere in this volume (Dunne Chapter 2; Cohen et al. 2003). Here, we will simply note that they seek to arrange species along an axis in a way that reflects a cascade of energy up the food chain. At first it is hard to imagine how parasites might fit into this framework. In particular, species with complex life cycles may need to be split into "meta-morpho-species," which appear at multiple positions along the trophic cascade. Obviously, we would also have this problem with aphids, mosquitoes, and other insects that occupy less dramatically different trophic locations at different points in their complex life cycles. Alternatively, consideration of parasites may allow us to consider the major ecological determinants of the species we wish to organize in a trophic cascade along a niche axis. While initial attention has focused on body size as a way of organizing the niche/cascade model, the small size of parasites and their position at the top of the trophic pyramid almost completely falsifies the notion of organizing trophic species along lines of body size. However, the limited amount of physiological evidence available suggests that parasites (and insect parasitoids) are highly efficient at energy assimilation and have relatively high metabolic rates for their body sizes (Bailey 1975; Calow 1979, 1983). This raises the intriguing prospect that perhaps the niche/cascade models reflect an underlying organization along an axis that is driven by either assimilation efficiency, or by basal metabolic rate. There is a certain "poetic justice" to this as it would shift food web studies closer to their origins in the work of Lindeman (1942). Simultaneously, it could allow us to bring many of the developments in food web ecology closer to work on ecosystem function; an exciting goal for the future of ecology.

## 5 CONCLUSIONS

Developing a deeper understanding of the role that parasites and pathogens play in food webs is perhaps the greatest empirical challenge in food web biology. As we mentioned at the outset, they may double the number of species in some systems and quadruple the number of links (Lafferty et al. in press). A variety of theoretical studies suggest that parasites have properties that will allow them to play major roles in stabilizing the long-term dynamics of food webs. Particularly important here is the strong potential that specific, directly transmitted pathogens have to regulate the abundance of their hosts. Complementary to this are the properties of parasites with complex life cycles which may also be stabilizing through the long loops of weak interactions they create with many hosts species on two or more trophic levels. In both these respects, parasites are likely to be as important, if not more important, than the predator-prey links that form most of the structure of food webs. Here it is important to recognize that simply dividing natural enemies into predators and parasites is perhaps too great a simplification. Lafferty and Kuris (2001) and Dobson and Hudson (1986) have proposed a more comprehensive classification of resource consumer interactions

TABLE 2 Predators versus Pathogens

| Predators | Pathogens |
|---|---|
| Usually same size as victim | Much smaller than victims |
| Similar, or slower, rate of population increase | Much faster rate of population increase |
| Tend to satiate | Insatiable, unless vectored, or STD's |
| Indirect impact when change victim's behavior | Subtle changes of host behavior |
| Energetically fairly efficient | Energetically very efficient |

based on the ratio of the body mass of the consumer to its resources (fig. 5). The ratios span at least 16 orders of magnitude, with microbial pathogens of vertebrates covering several orders of magnitude at one end of the spectrum, and vertebrate herbivores and their prey at the other. All other forms of resource consumer relationship occupy overlapping ranges at other points along this spectrum. In many ways this attempt to classify the major form of interactions between species in food webs takes up a challenge first proposed by T. R. E. Southwood in his Presidential Address to the British Ecological Society (Southwood 1977); it provides a way of organizing species interactions to form one potential axis of a Periodic Table of Ecological Interactions, distantly equivalent to the table that appears on the walls of chemistry and science laboratories in schools. Ultimately, studies of food webs will need a similar organizing principle and some form of this body-size-dependent classification of interactions between species and their natural enemies is likely to be one major organizing axis.

These ideas echo one of the major organizing principles in current studies of food web organization, the cascade model and the niche model (Cohen et al. 1990; Williams and Martinez 2000). These models provide a framework for describing the properties of interactions between species in a food web when parasites are ignored. Species are organized along an axis for which a potential explanation is body size. However, once parasites, parasitoids, and pathogens are included in this classification, the system would begin to break down, mainly because these natural enemies are often significantly smaller than those of the species they exploit.

When the food web is organized as a matrix of interactions, the inclusion of parasites and pathogens creates significant numbers of interactions below as well as above the diagonal—this will initially violate the cascade model assumptions. Nevertheless, this should only be seen as a challenge for food web ecologists to search for a modified organizing principle. It may be that species are actually ordered based on energetic efficiency or nitrogen assimilation rates rather than on body size. This would recapture many of the properties observed when the

cascade model and niche models are applied to webs that ignore parasites. Ultimately, parasites and pathogens present a variety of challenges to food web ecologists, none are unassailable, and many may provide important new insights into the complex properties of ecological webs.

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