CHAPTER TEN

Is Infectious Disease Just Another Type
of Predator-Prey Interaction?

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SUMMARY

WHICH FACTORS FUNDAMENTALLY separate infectious disease from
other types of predator-prey interactions studied by community ecolo-
gists? Could parasitism and predation be combined into a unifying
model? After all, parasites and predators both convert energy and nutri-
ents contained in their resources (hosts or prey, respectively) into new
biomass and reproductive work. If these focal consumers perform simi-
lar roles, disease ecologists and community ecologists may essentially
study the same problems. Therefore, they should use the same concep-
tual toolkits. Given this important potential for more intellectual cross-
fertilization, we contemplate these questions by way of two arguments.
First, we consider the case that parasitism and predation are essentially
the same types of interactions, varying only quantitatively. This line of
argument highlights the many similar ways in which parasites and pred-
ators interact with their resources and other species at local and macro-
ecological scales. Perhaps, then, major differences between predators
and parasites vary only quantitatively, as a matter of body-size scaling.
Parasites are typically much smaller than their host, while predators are
similarly sized or exceed the size of their prey. The second case embraces
eight (or more) qualitative splits that separate different types of preda-
tors from different types of parasites (developed by Lafferty and Kuris
2002). These axes differentiate consumers that eat one versus more than
one resource individual per life stage, consumers that kill or do not kill
their resources, and so forth. Both lines of argument eventually lead to
the same challenge, however: Just how many qualitative models must
one consider to capture the range from predation to parasitism in na-
ture? The answer almost certainly depends on the focal question (impli-
cations for population dynamics, nutrient cycling, evolutionary change,
etc.) and the currency used to evaluate it.

INTRODUCTION

Nothing qualitatively distinguishes host-parasite interactions from other consumer-resource interactions. This statement provides a springboard for an interesting and challenging thought experiment contemplating fundamental similarities and differences between parasites and predators. No doubt, such a claim will immediately surprise, annoy, or enrage some students of parasitism and disease, particularly those who work to uncover the mechanistic underpinnings of disease biology in detail. After all, parasites exhibit an amazing diversity of strategies to infect their hosts, and some microbial parasites can even transfer genes horizontally (which predators cannot). Therefore, acceptance of such a claim could require much abstraction. Yet, for some questions, it might be possible and useful to aggregate predators and parasites into a single consumer strategy. Such a statement might make sense to ecologists who study interactions between free-living species (e.g., competition, predation), even if they, like many or most community and ecosystem ecologists, have not previously considered parasites in much detail. Indeed, this commonality claim, if true, might spur very useful interactions between community and disease ecologists, who already talk about similar phenomena in different languages (Mittelbach 2005). Perhaps many of the independently developed theories readily transfer among these largely separate subdisciplines.

In this chapter, we consider the question of parasites-as-predators from two viewpoints. First, we embrace a "parasites are just predators" line of reasoning to highlight the many geometric parallels between these two types of interactions (Anderson and May 1979; Earn et al. 1998; Holt et al. 2003; Morin 1999; Thomas et al. 2005). At some basic level, these geometries likely emerge because parasites, like predators, consume resources. Resources, be they humans or rabbits, contribute positively to the population growth of their consumers. Once acquired, consumers, be they the measles virus or foxes, convert some of the energy and materials concentrated in their resources into somatic and reproductive biomass and work, and dissipate the rest. Energy and materials flow through these interactions (Mitchell 2003; Polis and Strong 1996; see also Middelboe, chapter 11, and Eviner and Likens, chapter 12, this volume). Perhaps the important differences emerge, then, as a quantitative matter of scaling. The most obvious scaling dimension is variation in body size between consumers and resources: the ratio of consumer size to resource size varies greatly along a predation-parasitism gradient (Lafferty and Kuris 2002). Later we consider another, recently proposed scheme that assorts types of predators, parasites, and parasitoids along four qualitative axes (Lafferty and Kuris 2002). These axes focus on how many re-

source victims are attacked per life stage by the consumer, the implications of these attacks for victim fitness, whether the success of such attacks depends on attack intensity, and, in the case of parasites, whether hosts must die. Which perspective is most useful? Ultimately, the answer likely hinges on the particular question asked (e.g., concerning nutrient cycling, population growth rate and biomass, or evolutionary change) and the currency used to evaluate it.

Two Positions on Parasites as Predators

Position 1: "Parasites Are Just Predators"

At some level, disease ecologists and community ecologists have much more in common than they may realize (Mittelbach 2005). Students of both subdisciplines essentially study interspecific interactions among consumers, which attack other species to acquire their nutrients and energy, and resources, which defend or tolerate removal of acquired nutrients and energy by their attackers (Chase et al. 2000; Grover 1997). Furthermore, the net outcomes of these interactions in turn determine abundances of interactors and promote or degrade opportunities for coexistence (see chapter 7, this volume). Yet attempts to fully map webs of interactions among these consumers and resources quickly run into a "curse of dimensionality" problem. The number of links between consumers and resources explodes into temporal and spatial intractability (Raffaelli and Hall 1996; Warren 1989; Yodzis 1996). Although one might abstract properties of these complex webs using a variety of indices (Cohen 1978; Lawton and Warren 1988), we consider two more mechanistic approaches here. First, both disease and community ecologists have focused on very similar subsets of interaction "modules," starting with two species and then building up direct and indirect interactions among three to four species (Holt 1977; Holt and Pickering 1985; Holt et al. 2003; see also Lafferty, chapter 9, and Holt, chapter 15, this volume). Here we consider a few of these modules to illustrate this point. Second, many similar patterns emerge from a macroscopic look at these interactions in both disease and community ecology (Gaston and Blackburn 2000; Guégan et al. 2005). These similar patterns include diversity-latitude and diversity-area relationships and local versus regional diversity curves.

QUALITATIVE PARALLELS SEEN THROUGH THE MODULE APPROACH.

The module approach emphasizes how similar subsets of interactions arise in both predator-prey and parasite-host dynamics. The simplest module involves a binary interaction in which a consumer species, be it a

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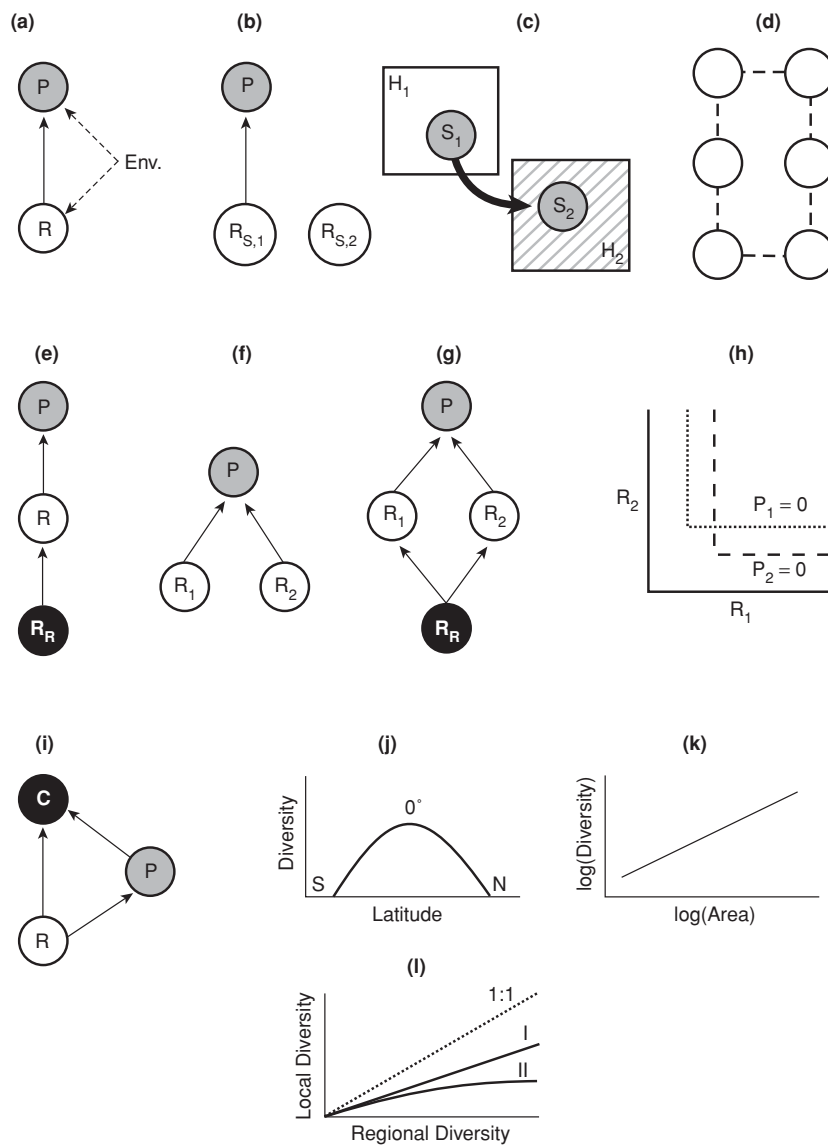
Figure 10.1 Parallel interaction geometries, life cycle complexities, spatial dependencies, and macroecological patterns between parasite-host and predator-prey interactions. (a) Environment (Env.)-dependent binary predator/parasite (*P*)-resource (*R*) interactions which can incorporate (b) differences in vulnerability of *R* to *P* with changes in stage, *S* (e.g., from S_1 to S_2), (c) stage-dependent shifts between habitats, *H*, (d) movements in space (where circles represent local populations of *R* and *P* linked by dispersal via dotted lines), and (e) cascading

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predator or parasite, can potentially regulate the abundance and dynamics of its resource species (figure 10.1a). There are many examples of consumers exerting strong controls on their resources in community ecology (Morin 1999; Murdoch et al. 2003). Classic examples include predation on large zooplankton by size-selective fishes (Brooks and Dodson 1965), and the elimination of small-bodied minnows by piscivorous fishes (Mittelbach et al. 1995). Parasites can also regulate their hosts, as shown in the lab (Scott 1987; Scott and Anderson 1984) and in the field (grouse: Dobson and Hudson 1992; Hudson et al. 1992, 1998; old field grasses: Mitchell 2003; urchins: Lafferty 2004). Predators and parasites can also destabilize consumer-resource interactions (e.g., *Daphnia*-algae oscillations: McCauley et al. 1999; nematode-grouse oscillations: Hudson et al. 1998) and modify the behavior of their resource (Abrams 2004; Abrams et al. 1996; Moore 2002; Poulin 1994; Werner and Peacor 2003). Furthermore, both types of consumer-resource interactions can be strongly influenced, even synchronized, by environmental variability (Earn et al. 1998; Pascual et al. 2000; Post and Forschhammer 2002; Ranta et al. 1997; Rodó et al. 2002; Rohani et al. 1999; see also chapter 3, this volume).

These parallels suggest that two-species parasite-host and predator-prey interactions could be captured with a common, low-dimensional model (see figure 10.1a). Assuming continuous reproduction, this model might take the form

$$dP/dt = f(P, R, E) \tag{1.a}$$
$$dR/dt = g(P, R, E), \tag{1.b}$$

where P is predator density—or a surrogate for parasite density, using density of infected hosts to track parasites; R is resource density; and E represents environmental variability. Functions f and g capture the density-dependent and/or density-independent interplay between P, R, and E, where traits of P and R themselves may also depend on the other state variables. With work, one could specify general functional

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indirect effects upon the resource's own resource, $R_{R.}$ (f) Multiple resources, R_1 and R_2, interact with the consumer through apparent competition or (g) through a diamond arrangement. (h) Interactions among multiple consumers and resources may depend on resource ratios and stoichiometry, where nullclines of the classic resource-ratio model are shown. (i) Predators at higher trophic levels, C, may eat both P and R. Several macroecological parallels include (j) diversity peaks near the equator, (k) area-diversity relationships, and (l) proportional (type I) or saturating (type II) relationships between regional and local species richness, where the dotted line represents a 1:1 comparison.

forms of *f* and *g* that more specifically characterize this interplay. Then, to this specified model, one could also add several phenomena common to both host-parasite and predator-prey interactions, including (1) stage-specific vulnerability of the resource (e.g., size refuges: Chase 1999; recovery/immunity of infected hosts: Anderson and May 1979; figure 10.1b); (2) stage-specific (ontogenetic) switches in habitat use for consumer or resource (where multiple host species provide different habitats for various stages of a parasite's life cycle: Werner and Gilliam 1984; figure 10.1c); (3) spatially segregated populations linked by dispersal (metapopulations), where parasites disperse on at least two scales (from host to host and among host populations: Grenfell and Harwood 1997; Grenfell et al. 2001; Guégan et al. 2005; Rohani et al. 1999; figure 10.1d); and (4) "cascading" indirect effects on the prey's own resource (Carpenter and Kitchell 1993; Lafferty 2004; Power et al. 1985; figure 10.1e). Finally, such a model provides a foundation on which to add interactions of other species with both consumer and resource (see Lafferty, chapter 9, and Holt, chapter 15, this volume).

This flexibility to incorporate other species becomes particularly important for two obvious, parallel classes of interactions. The first is apparent competition (Holt 1977; Holt and Lawton 1994; Holt and Pickering 1985), in which two otherwise noninteracting resource species share a common consumer (figure 10.1f). This consumer can degrade diversity of resource species by reducing the abundance of or eliminating its competitors. In situations in which resources compete interspecifically (Grover 1997; Holt et al. 1994; Leibold 1996), these consumers can also preserve diversity by slowing or eliminating competitive exclusion (figure 10.1g; see Clay et al., chapter 7, this volume). Examples of these consumer-mediated interactions certainly occur in host-parasite systems (Holt et al. 2003; Hudson and Greenman 1998; Jaenike 1995; Tompkins et al. 2003; Yan et al. 1998) and are sometimes called "spillover" (Power and Mitchell 2004). In this case, the basic model expands to include a second resource species:

$$dP/dt = f(P, R_1, R_2, E) \tag{2.a}$$
$$dR_1/dt = g_1(P, R_1, R_2, E) \tag{2.b}$$
$$dR_2/dt = g_2(P, R_1, R_2, E), \tag{2.c}$$

where the interaction between resource species R_1 and R_2 could be mediated indirectly through a shared resource of their own. With this type of model structure, one can also flip the question around: How do multiple resources, be they two separate species of hosts/prey resource

(Grover 1995; Holt et al. 2003; Begon, chapter 1, this volume) or multiple nutrients provided within the tissues of a host/prey resource (Smith and Holt 1996; Sterner and Elser 2002), influence the ability of the parasite or predator to persist? In the separate-resource case, different resource species may vary in their vulnerability to the consumer, may interfere with capture of more profitable resources, or may be completely invulnerable (Grover 1995, 1997; Holt et al. 2003; Schmidt and Ostfeld 2001; Begon, chapter 1, this volume). In this multiple nutrient–one resource species case (figure 10.1h), resources may stoichiometrically constrain their consumers (Sterner and Elser 2002), either incidentally (e.g., variable nutrient storage by plants; Hall 2004) or as part of active defense from parasites (e.g., iron withholding by hosts; Smith and Holt 1996). Amazingly, this interface between parasites, hosts, and resources of the host remains largely unexplored, despite the tremendous attention that analogous systems have garnered in community ecology.

A second type of interaction incorporates a top consumer predator that feeds on both a consumer and a resource (figure 10.1i). One label for this type of interaction is intraguild predation, a type of omnivory (Holt and Polis 1997; Polis et al. 1989; Holt, chapter 15, this volume). Notably, models of this interaction predict that the top predator (the "intraguild predator") can eliminate the consumer ("intraguild prey"), particularly at high productivity (Holt and Polis 1997). A similar interaction occurs in host-parasite systems when predators, acting as the intraguild predator, preferentially cull infected hosts (where the parasite is the intraguild prey; Ostfeld and Holt 2004; Packer et al. 2003; Holt, chapter 15, this volume). Examples include predation upon grouse infected with nematodes (Hudson et al. 1992) and predation on infected zooplankton by fishes (Duffy et al. 2005). These selective predators can potentially reduce or eliminate disease within an ecosystem, possibly through dramatic extinctions of the parasite (Duffy et al. 2005; Hall et al. 2005; Packer et al. 2003; see also Holt, chapter 15, this volume). However, it is also possible that parasites require predators to eat infected hosts in order to continue their life-cycle (Lafferty 1999). One could readily capture both scenarios by adding a top predator to the base consumer-resource model (equation 1) to create a third major food web module with blurred trophic relationships:

$$dC/dt = h(P, R, C, E) \qquad (3.a)$$
$$dP/dt = f(P, R, C, E) \qquad (3.b)$$
$$dR/dt = g(P, R, C, E), \qquad (3.c)$$

where now the density of a top consumer (C) can shape interactions between predator and prey.

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PARALLELS SEEN THROUGH A MACROECOLOGICAL APPROACH

Evidence from macroecology supports the hypothesis that host-parasite and predator-prey interactions are essentially similar. Macroecology (Brown 1995; Gaston and Blackburn 2000) has yielded several interrelated, large-scale patterns that apply to both sets of interactions. These patterns include relationships between latitude and diversity, area sampled and diversity, and diversity at regional versus local scales. Each of these patterns ultimately depends on how finite living material supported in a region becomes partitioned among individuals and species. First, ecologists have documented examples of diversity peaks of parasites and predators at equatorial regions (figure 10.1j; Calvete et al. 2003; Gaston and Blackburn 2000; Guernier et al. 2004). Second, species-area relationships predict a positive but decelerating accrual of species as area of habitat increases (figure 10.1k; Gaston and Blackburn 2000; Rosenzweig 1995). Although commonly observed for a variety of species (e.g., birds: Reed 1981; Wright 1981), these relationships hold for parasites on two relevant scales (Guégan et al. 2005). The morphology of a host species provides the first scale (Guéguan and Hugueny 1994; Guéguan et al. 1992). Here, richness of parasites increases with increases in body size of host species. Habitat use by host species (Brändle and Brandl 2003; Calvete et al. 2004; Goüy de Bellocq et al. 2003; Marcogliese and Cone 1991) provides a second relevant scale. As true for the area-diversity relationships for predators (Gaston and Blackburn 2000; Rosenzweig 1995), the mechanisms driving these patterns for parasites remain a subject of debate. Viable hypotheses for both consumer types include mechanisms by which predators and parasites partition habitat and resources (Gaston and Blackburn 2000; Guégan et al. 2005).

Third, some local-to-regional diversity patterns imply a role for species interactions in both predator-prey and parasite-host systems. The diversity of species at a local site commonly scales with diversity in the region containing the site (Cornell and Lawton 1992; Gaston and Blackburn 2000; Srivistava 1999). Diversity at a local site can either increase proportionately with regional diversity (type I), or it can saturate as regional diversity becomes more rich (type II; figure 10.1l). All else being equal among locations, type I relationships typically arise if species do not interact, while type II patterns provide a signature of strong interactions at high levels of regional diversity. Most assemblages of predators and parasites show proportional increases (free-living examples: Shurin et al. 2000; Srivistava 1999; parasite examples: Calvete et al. 2003; Guégan and Kennedy 1993). This result has important implications for the management of invasive species because it suggests that local communities of newly established pest species remain undersaturated with

parasites (Elton 1958; Keane and Crawley 2002; Mitchell and Power 2003; Torchin et al. 2003; see also, Perkins et al., chapter 8, and Lafferty, chapter 9, this volume). However, saturating patterns do arise in both predator and parasite systems (Calvete et al. 2004; Kennedy and Guégan 1994; Shurin 2000). If coupled with supplementary, mechanistic evidence, these patterns could signal that strong interactions may constrain membership in certain parasite and predator communities.

THE DIFFERENCES HINGE ON SCALING, AND THE CHALLENGE

Suppose that we accept the argument suggested by these parallel community and macroecological patterns, namely, the parasite-host interactions are qualitatively similar to predator-prey interactions. Perhaps, then, the main quantitative difference among them revolves around scale in general and body size in particular. The ratios in body size between consumer and resources differ over sixteen orders of magnitude (Lafferty and Kuris 2002; figure 10.2). In general, parasites are much smaller than their hosts, parasitoids and social predators are relatively similar in size to their resources, and traditional predators are larger than their prey (figure 10.2). Given these huge differences in size, small parasites and large predators perceive their environments and their resources at very different grain sizes (Gaston and Blackburn 2000). Perhaps more important these differences in size can drive wide variation in the dynamics of consumer-resource interactions, particularly in terms of the size of oscillations (Yodzis and Innes 1992). They can have large implications for the speed of turnover and recycling of materials and energy
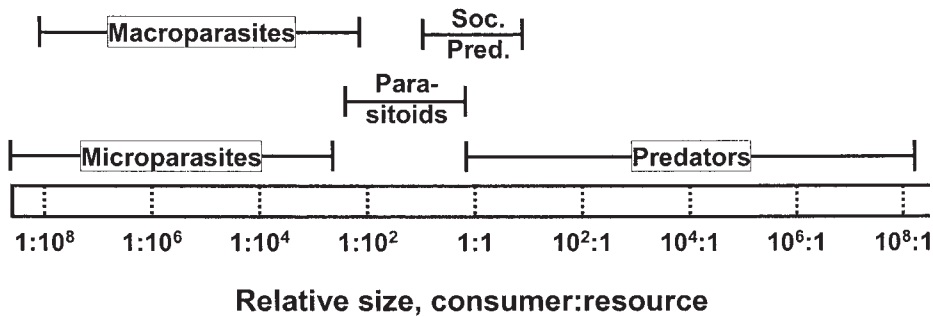

Figure 10.2. Body-size scaling in predator-prey and parasite-host interactions, drawn conceptually. Consumer-resource interactions, including those between host and parasite, scale over many orders of magnitude in relative body size between consumer and resource. Parasites tend to be smaller than their resources, parasitoids and social predators are roughly similarly sized, while predators are typically larger then their prey. (Modified from Lafferty and Kuris 2002.)

(Cyr and Pace 1993). For instance, whether they constitute small amounts of biomass in ecosystems to amounts comparable to that occupied by top predators, parasites can vastly alter biomass and nutrient flow (Polis and Strong 1996; Mitchell 2003; Sukdheo and Hernandez 2005; chapters 11 and 12, this volume).

Nonetheless, if parasite-host and predator-prey interactions mainly vary along gradients of body size, we can potentially take advantage of scaling relationships to create a unifying, overarching consumer-resource model. Several important relationships have recently emerged as functions of body size. Across many taxa, body size scales as a one-quarter or three-quarter power with basal metabolic rate, development time, and maximal population growth rates (Brown et al. 2002). Ideally, these scaling relationships can be used to predict ecological phenomena such as population density and growth rates of predators and parasites. Recent work with forest stands reveals the potential of this approach (Enquist et al. 1998, 1999). Once one controls for body size, variation in temperature (figure 10.2b) and phosphorus content might also explain variation in metabolic rates among predators and parasites (Gillooly et al. 2001, 2002). However, a comprehensive metabolic theory of ecology remains in its infancy (see Savage et al. 2004 for a recent step forward). Such a theory would connect metabolic processes at the level of the individual parasite or predator to their influence on the rate and magnitude of ecosystem-level fluxes of energy and materials. Until this theory is developed, the potential for metabolic theory to unify predator-prey and parasite-host interactions will remain unrealized.

With or without such a comprehensive metabolic theory, the ultimate challenge posed by this position ("parasites are just predators") is to write a model that captures the essence of both types of consumer-resource interactions. In other words, one must specify equation (1) to some useful degree of detail. Because size and metabolism closely associate, scaling relationships could help to solve the "plague of parameters" problem inherent in such an ambitious endeavor (Yodzis and Innes 1992). But is it possible to write such a model? If so, would the resulting structure necessarily remain so general as to offer little practical utility?

Position 2: "Predators and Parasites Differ Fundamentally"

Some might argue that well-intentioned efforts to compose such a "unifying model of consumer-resource interactions" will ultimately fail. After all, they might say, host-parasite interactions qualitatively differ among themselves (parasite, parasitoid, etc.) and from predator-prey interactions in many ways. The danger of this line of argument lies in its potential overemphasis on differences rather similarities. Are consumer-

resource interactions just collections of many strategies to acquire resources? The challenge for proponents of the "predators and parasites differ fundamentally" argument is to find an intellectual middle ground. This middle ground should hinge on simple but meaningful categorization of these differences using only a few axes of separation.

A recent analysis, based on the concept of adaptive peaks, provides a very useful starting point for such an endeavor. Lafferty and Kuris (2002) outline key differences between "predators" and "parasites" and among classes of parasites (see figure 10.2). A first dichotomy immediately splits predators from parasites: how many resource victims are attacked in a life stage? Predators attack more than one individual, while parasites attack only one victim per life stage. A second axis separates parasitoids and parasitic castrators from other types of parasites: does the consumer reduce the fitness of its resource to zero? The former classes do reduce it to zero, while typical parasites do not. A third difference splits the two main categories of parasites into four. Some parasites (microparasites, macroparasites, and parasitic castrators) do not necessarily have to kill their hosts, while others (trophically transmitted parasites [Lafferty 1999] and parasitoids) require the host to die to compete their life cycle. Finally, a fourth axis can further separate some of the groups: does the effect of attacks by consumers depend on intensity (i.e., the number or density of parasites per host)? Lafferty and Kuris (2002) use this fourth axis to split the six groups forged by the first three dichotomies into ten useful ones; these ten are presently occupied by extant consumer-resource types. Here we use it to split these six into the eight classes, which are likely obvious to most readers. First, as pointed out years ago (Anderson and May 1979; May and Anderson 1979), intensity dependence cleaves macroparasitism from microparsitism because intensity and aggregation of infection by the former (but not the latter) determines pathology. This split also meaningfully divides predators into solitary and social predators. Social predators rely on other members of a group to attack relatively large-bodied resources (figure 10.3). As a result of this strategy, they can suffer Allee effects (inverse density dependence) at small population sizes (Case 1999).

While intuitively appealing, this classification scheme does not fully resolve the overarching question of this essay. For instance, it is unclear whether these eight (presented here) or ten categories (presented in Lafferty and Kuris 2002) include the essential—but not superfluous—axes on which one can array predators and parasites. Although distinct mathematical models have been written for most of these categories, do we really need eight to ten different models to characterize the array of predator-prey and parasite-host interactions? A safe answer to broad, difficult questions like this one is "it depends": the answer likely depends

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(1) Number of victims attacked
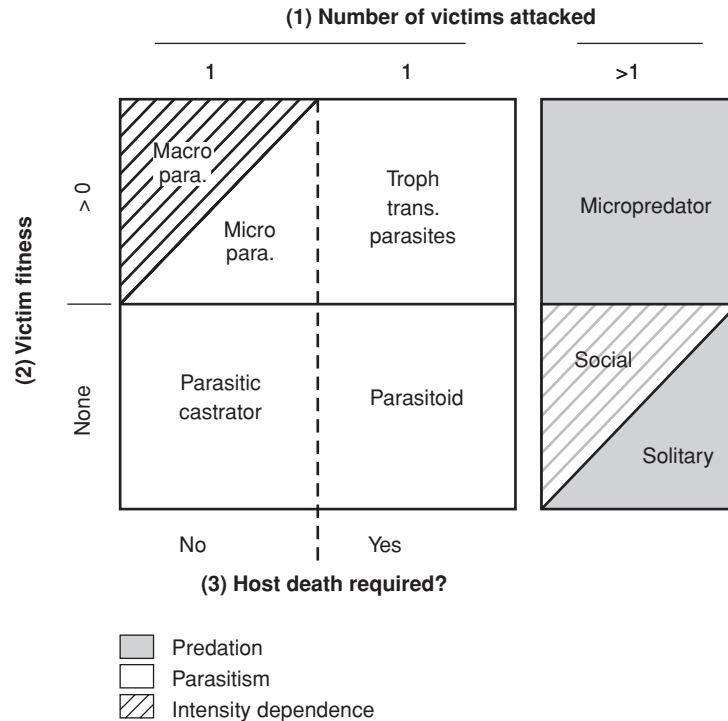
Figure 10.3. A scheme developed to qualitatively distinguish predation and parasitism (modified from Lafferty and Kuris 2002). The number of victims attacked in a lifetime (1) splits predation (right) from parasitism (left), while effects on victim fitness (2) split parasitoids and parasitic castrators (bottom) from macroparasites and trophically transferred parasites (top). This axis also splits micropredators from more typical predators. Among parasites, obligate host mortality (3) further differentiates parasitoids from parasitic castrators (bottom) and more typical parasites from trophically transmitted parasites (i.e., those requiring that their host be eaten by a predator to complete a life cycle). Finally, each of the six boxes created by 1–3 could be split again along an intensity-dependence (upper hatched triangle) or intensity independence (lower triangle) axis. Here the split is shown only to differentiate macroparasites from microparasites and social from solitary (typical) predators.

on the question examined and the currency used to address it. For instance, these characterizations outlined by Lafferty and Kuris (2002) may represent distinct, size-dependent (figure 10.2a) evolutionary strategies, or adaptive peaks, along a continuum of consumer-resource strategies. Such a hypothesis could be explored by studying trajectories of evolutionary models that use size-based scaling laws or by empirically

observing consumers that are forced to switch feeding strategies. Furthermore, this classification scheme was developed based on interactions of individuals. From the perspective of individuals, these differences in behavior of consumers may matter greatly for individual fitness, and therefore they may greatly influence (co)evolutionary dynamics. However, these strategies may or may not yield different outcomes for dynamics and stability of populations or energy and material flows through food webs in ecosystems. Furthermore, they may or may not yield different outcomes for diversity maintenance or degradation when inserted into common interaction modules, such as apparent competition and intraguild predation. Definitive answers to these questions, then, likely first require specification of a currency (R_0, dynamics of populations, flow rate of energy, rate of evolutionary change, etc.) followed by systematic assessment of each of the eight to ten consumer-resource models. Perhaps some of Lafferty and Kuris's (2002) consumer-resource types can be collapsed into a subset for certain questions or currencies but not for others. Such an ambitious task presents a potentially rewarding challenge for theoretical population biologists.

Discussion

This essay approaches a difficult but fundamental question: Are parasites qualitatively different from predators? Such a pursuit presents a challenge, and we consider this essay only a start toward answering this question. In many ways, this thought experiment prompted more questions than it answered, a result that largely reflects the current stage reached in the evolution of disease ecology as a discipline. The first argument ("parasites are just predators"), even if ultimately wrong, does stress the tremendous similarities between disease ecology and more traditional community and macroecology. For whatever reason, these epidemiological and mainstream ecological subdisciplines have largely evolved separately (at least until fairly recently). This separation existed despite the fact that these subdisciplines fundamentally face very similar issues (such as introduction of exotic species, enemy release, and maintenance or degradation of diversity) even when considered with different aims in mind (eradication of parasites vs. promotion or erosion of diversity by predators). Solutions to these problems might benefit greatly from a healthy dose of conceptual cross-fertilization.

The second argument, following Lafferty and Kuris's (2002) categorization, provides a pathway to pursue a "predators and parasites differ fundamentally" position. If one posits that parasites fundamentally differ from predators, some questions still remain, however. Just how many consumer-resource types are required to satisfyingly capture the range of

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interactions along the parasitism-predation gradient? For some particular problems, such as nutrient cycling, one can probably combine some of Lafferty and Kuris's (2002) categories into a smaller subset, perhaps through application of size-energetic scaling relationships. After all, relative body size differences among consumers and resources appear to determine which of the eight to ten life history strategies is most profitable for consumers (see figures 10.2 and 10.3; Lafferty and Kuris 2002). Given that logic, the argument posed by the apparent dichotomy in this essay ultimately swings full circle. Perhaps, then, the ultimate answer lies somewhere between the two positions. Or perhaps the strategies used by predators and parasites (Lafferty and Kuris 2002) would emerge as stable strategies produced by the same evolutionarily explicit consumer-resource model. In this case, the two positions juxtaposed here become one and the same. We hope that a reader pursues this challenge.

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