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# 15 The influence of habitat structure on the transmission of parasites

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To a parasite, a host represents a patch of habitat that provides metabolic resources or a protected environment in which to remain dormant. Since these resources are finite, and the host itself ephemeral, transmission to a new host must occur if the parasite is to persist. Coincidence of the infective stages of a parasite and susceptible hosts is prerequisite for transmission. Therefore, the structure of the habitat external to the host (see discussion below), can affect the rate of transmission in at least two ways. It can directly or indirectly determine the distribution and abundance of infective stages of parasites, whether free-living or transported by intermediate hosts or vectors. Similarly, habitat structure influences the distribution and abundance of susceptible hosts, often enhancing the heterogeneity of host spatial distributions. The great diversity of host-finding mechanisms exhibited by parasites is quite likely the product of strong selection for the ability to locate patchily distributed hosts.

This chapter examines the influence of habitat structure on the transmission of parasites between hosts. The diverse ways in which parasites are transmitted between hosts will be discussed, and a summary presented of some of the better-studied examples of host-parasite associations in which rates of transmission are influenced by habitat structure. This being the focus of the chapter, no consideration will be given to parasites that are directly transmitted between members of the same host species by social or sexual means, or parasites transmitted from parent to unborn offspring. The discussion will also be restricted to protozoan and metazoan parasites of animals. We believe this assemblage of parasites, although ignoring some potentially important prokaryotic and fungal parasites, provides a representative sample of the diverse transmission patterns exhibited by parasites of animals. Parasites of plants are not discussed since these taxa, and the effect of habitat structure on aspects of their movement and interaction with plant hosts, are treated in Chapters 8 and 13.

The idea that habitat structure influences rates of parasite transmission is

not new. Early appreciation of the association between parasites and habitat types developed from efforts to control the spread of human diseases. Audy (1958) reviews, with an ecological and evolutionary perspective, the history of research on the relationship between disease and habitat structure; this relationship has been a primary focus of parasitological research and disease control in Russia for at least 50 years (Pavlovsky, 1966). What Pavlovsky (1966) referred to as landscape epidemiology is essentially the study of the geographic coincidence of infected hosts, uninfected hosts, and vectors of the disease. When these coincide in sufficient numbers in space or time, a 'nidus' (nest or hotspot) for the disease exists:

The natural disease nidus exists under certain conditions of climate, vegetation, soil, and favorable microclimate in those localities in which vectors, donors, and recipients of the disease cluster. In other words, the natural nidus of a disease is characteristic for a definite geographic landscape . . . (Pavlovsky, 1966, p. 9)

A recent example of the application of these concepts to disease control in the United States is the investigation of the relationship between habitat variables, host and vector population characteristics, and the incidence of Colorado tick fever (Carey *et al.*, 1980; Bowen *et al.*, 1981; McLean *et al.*, 1981).

### 15.1 HABITAT STRUCTURE: THE PARASITE'S PERSPECTIVE

Before discussing structural features of parasite habitats that influence transmission, we must first clarify what constitutes a parasite's habitat. The complex life cycles of many parasites makes a simple definition difficult. For parasitic stages in the life cycle, the host itself comprises the parasite's habitat. As a habitat, an individual host possesses varying degrees of structure, e.g. internal organ systems and tissues for an endoparasite. A number of authors have reviewed the subject of hosts as heterogeneous parasite habitats (e.g. Crompton, 1973; Holmes, 1973; Kennedy, 1976; Kuris *et al.*, 1980). This level of habitat structure will not be considered further here.

The present review examines the influence of habitat structure on the transmission of parasites between hosts, rather than on the movements of parasites on or within them. Examples and discussion are therefore limited to (1) the movement of free-living stages in parasite life cycles, or (2) the transport of parasitic stages by intermediate hosts or vectors, through the environment external to the target host. It is this external environment, that in which the target host itself lives, which constitutes the habitat of free-living parasitic stages and of the species that serve as vehicles for transmission, i.e. vectors and intermediate hosts. The typical disparity in size between free-living stages or vectors and their target hosts means that their

perceptions of and responses to the habitat's three-dimensional structure will often be very different.

Both abiotic and biotic components of this habitat may represent structure to parasites and vectors that are in transit between hosts. Physical features of the habitat, including inanimate objects, can affect transmission by altering the active or passive movement of a dispersed stage, in addition to their influence on the spatial distribution of the host. As described below, living organisms other than the host, both plants and animals, can similarly influence host-finding by parasites.

What constitutes relevant habitat structure depends on the particular parasite and stage under consideration. For example, independent or vectored transmission via water or air is common to many parasite taxa. These fluid media possess physical structure in the form of velocity gradients and viscous forces (Vogel, 1981) that is not so different conceptually or functionally from the solid surfaces in aquatic or terrestrial environments to which the term 'habitat structure' has traditionally been applied (see also Chapter 5). This is especially true for small aquatic parasites that must overcome strong viscous forces associated with low Reynolds number conditions.

Structure is expressed at a series of hierarchical scales in natural habitats (Allen and Starr, 1982). The transmission of a parasite may be influenced by more than one scale of habitat structure. For example, hymenopteran parasitoids may initially be attracted to certain vegetation types or plant species that harbour appropriate hosts, then search among various plant microenvironments, e.g. leaf faces, flower heads, etc., for individual hosts to attack (Vinson, 1976). Similarly, on the large scale a parasite might attain higher densities in forest than field habitats. At a smaller scale, within a forest, the parasite may be concentrated in particular microenvironments, such as the forest edge. Within forest edge vegetation, the parasite may preferentially aggregate on particular species of woody plants. Thus, the structure of a habitat cannot be unambiguously defined without specifying the spatial scale of interest. In other words, a habitat does not have a single structure; rather, there exists a hierarchy of structures, one at each scale of observation. Each structure may facilitate or interfere with parasite dispersal, in some cases providing cues or stimuli to which parasites, their vectors, or intermediate hosts may behaviourally respond.

## 15.2 MODES OF PARASITE TRANSMISSION

The influence of habitat structure on host-finding by parasites is most evident if viewed in the context of parasite life cycles, in particular, the modes of transmission involved. Table 15.1 provides a general summary of the modes of transmission in the life cycles of the parasitic taxa circumscribed above. These modes are divided into two broad categories with corresponding headings: (1) transmission stages that are free-living in the

environment, and (2) transmission stages that inhabit an intermediate host or vector, and are transported via the movements of this host. Transmission stages are further classified by the activity of the stage immediately upon release from the first host, its infectivity upon release, and the mechanism by which it infects the next host (columns 1–3, respectively, in Table 15.1). The fourth column lists taxa in which the majority of the species exhibit the indicated mode of transmission; these lists are not meant to be exhaustive. Below, the classification criteria are discussed briefly as they apply to each of the two major categories of transmission.

### 15.2.1 Transmission in the external environment

Active stages (see column 1 in Table 15.1) are independently mobile; they move through the environment, seeking either a new host or a microhabitat in which the likelihood of encountering such a host is high. Examples of active stages include trematode miracidiae and cercariae, cestode coracidiae, and some nematode larvae. Passive stages are immobile and cannot move around in the environment without the aid of physical forces such as air or water currents. The eggs and cysts in the life cycles of many parasitic taxa are examples of passive stages. After transmission stages enter the environment, they may either be immediately infective, such as trematode cercariae, or require a period of development before they are infective to the next host, as is true of many nematode larvae (see column 2 in Table 15.1).

Common mechanisms of infection (column 3 in Table 15.1) exhibited by parasites whose juvenile stages disperse freely in the external environment are: (1) penetration of the stage into the body of the host, or attachment to the exterior of the host, and (2) ingestion of the stage by the host. The importance of this distinction is that ingestion of the stage by the host may be less a function of parasite behaviour and more a function of host behaviour, than in the situation where the parasite can choose the site of attachment or penetration.

A quite different mode of external transmission is exhibited by blood-feeding ectoparasites and insect parasites and parasitoids. In both categories of parasite, the adult is a host-finding stage responsible for some or all of the dispersal between hosts. In life cycles of blood-feeding ectoparasites, adults are parasitic; juveniles can be either free-living (e.g., Diptera) or parasitic (e.g., Acarina). In contrast, the adults of most insect parasites and parasitoids are free-living, but seek hosts in/on which to deposit eggs or larvae. To highlight the distinctive life cycles of these two groups they are listed separately in Table 15.1, which also indicates that the adult is the host-finding stage that interacts with the external environment. Acarina are also listed under the active-juvenile heading since a number of species in this group have life cycles in which nymphs and larvae (as well as adults) actively seek hosts by movement through the external environment. In some parasitic taxa, juvenile stages are the only parasitic phase and do all the host-

*Table 15.1* Classification of the modes of transmission exhibited by protozoan and animal parasites of animals. For each exemplary taxon, the phylum is given, followed by lower taxonomic levels at which important differences in transmission modes can be seen. A lower taxon is listed under a single transmission mode if most, or all, of the members of that taxon exhibit that mode. If more than one transmission mode is common within a given lower taxon, this taxon is listed under each of these common modes. See text for an explanation of the classification criteria. An asterisk indicates a taxon in which adults are free-living and play no role in transmission; in these taxa, juveniles are the exclusive, host-seeking, parasitic stage in the life cycle

<i>Activity of transmission stage</i>	<i>Infective at release</i>	<i>Mechanism of infection</i>	<i>Taxa</i>
<b>I. Transmission stage in external environment (cont'd)</b>			
Active	Yes	Penetrate/ Attach	Cnidaria* Ctenophora* Platyhelminthes : Trematoda : Digenea : Turbellaria : Cestoda : Pseudophyllidea : Trypanorhyncha  Nemertina Nematoda : Metastrongyloidea Mollusca : Gastropoda : Entochoinchidae : Bivalvia : Unionidae* Insecta : Strepsiptera
Active	Yes	Ingested	Platyhelminthes : Trematoda : Digenea Nematoda : Camallanina : Gnathostomatoidea : Thelazioidea
Active	No	Penetrate/ Attach	Mesozoa Nematoda : Strongylida : Ascarida : Rhabditoidea

Table 15.1 – cont'd

<i>Activity of transmission stage</i>	<i>Infective at release</i>	<i>Mechanism of infection</i>	<i>Taxa</i>
<b>I. Transmission stage in external environment (contd)</b>			
Active adult stage	No	Penetrate/ Attach	Chelicerata : Acarina Crustacea : Cirripedia : Copepoda : Cyclopoida : Notodelphyoida : Caligoida : Montrilloida* : Amphipoda : Isopoda : Flabellifera : Epicaridea : Gnathiidea
		Blood feeding adult	Annelida : Hirudinea Insecta : Hemiptera : Diptera : Siphonaptera Chelicerata : Acarina Chordata : Pisces : Cyclostomata : Trichomycteridae : Mammalia : Microchiroptera
Active adult stage		Penetration of larvae	Insecta : Hymenoptera : Diptera : Oestridae : Tachinidae : Calliphoridae : Sarcophagidae

Table 15.1 – cont'd

Activity of dispersal stage	Infective at release	Mechanism of infection	Taxa
I. Transmission stage in external environment (cont'd)			
Passive	Yes	Ingested/ absorbed	Apicomplexa : Gregarina : Coccidia Ciliophora : Trichostomatida Sarcostomatophora : Sarcodina : Opalinata : Zoomastigophora : Hexamitidae  Myxozoa : Microsporoa : Acetosporoa : Platyhelminthes : Trematoda : Digenea : Cestodaria : Amphiliinidea : Cestoda : Protocephalidea : Cyclophyllidea  Acanthocephala Nematoda : Oxyurida : Ascaridida : Thelazioidea
Passive	No (become passive infective)	Ingested	Apicomplexa : Gregarina Apicomplexa : Coccidea : Eimeriidae Nematoda : Trichuroidea : Oxyuroidea : Ascaridoidea : Strongyloidea : Mermithoidea*  Nematomorpha* Pentastomatida

Table 15.1 – cont'd

Activity of dispersal stage	Infective at release	Mechanism of infection	Taxa
I. Transmission stage in external environment (cont'd)			
Passive	No	Penetrate/attach	Sarcomastigophora : Dinoflagellida : Sarcodina
	(become active infective)		Ciliophora : Holotrichida Platyhelminthes : Monogenea : Trematoda : Digenea : Cestoda : Protocephalidea : Cestodaria : Gyrocotylidea Nematoda : Strongyloidea : Rhabdiasoidea : Syngamoidea : Ancylostomatoidea : Trichostrongyloidea : Rhabditoidea : Mermithoidea* Chelicerata : Acarina* Insecta : Siphonaptera*
Passive	No	Ingested	Platyhelminthes : Aspidogastrea : Cestoda : Pseudophyllidea Nematoda : Strongyloidea : Spiruroidea : Trichostrongyloidea : Metastrongyloidea : Thelazioidea
	(become active infective)		
II. Transmission stage in host/vector			
Passive	Yes	Blood feeding	Apicomplexa : Coccidia : Lankesterellidae



seeking; adults are free-living and have no role in the transmission of juvenile parasitic stages between hosts.

### 15.2.2 Transmission via an intermediate host or vector

By definition, vectored parasites or those infecting intermediate hosts rely on their hosts for transport and do not move through the external environment under their own power; their activity has thus been classified as passive. Parasites that are transmitted via an intermediate host or vector must often undergo some development in, or on, that host, before they are infective to the next host. The primary influence of habitat structure on the transmission of such parasites is through its effect on the distribution and abundance of the vector or intermediate host.

It should be pointed out that blood-feeding ectoparasites, in addition to being parasites in their own right as discussed above, are potential vectors for microparasites, especially parasitic protozoa. The vector becomes infected by stages of the microparasite acquired in a blood meal, and transmits the parasite to another vertebrate host as it draws a second blood meal. Transmission of the vectored microparasite is, therefore, synonymous with transmission of, or host-finding by, the blood-feeding adult stage of the ectoparasite, and is identically influenced by habitat structure.

Helminth parasites encysted within intermediate hosts are transferred to definitive hosts (in which the adult stage develops) when the former hosts are consumed by the latter. In some systems, the behaviour of the intermediate host is altered by the parasite in such a way that the chance of its being eaten by the definitive host is increased. These behavioural modifications commonly take the form of altered responses to habitat structure, especially small-scale environmental heterogeneity. In Table 15.1, parasite taxa that have been shown to modify the behaviour of their intermediate hosts are listed separately from those in which such modifications have yet to be observed.

## 15.3 INFLUENCE OF HABITAT STRUCTURE ON TRANSMISSION: SOME EXAMPLES

In this section, host–parasite associations are described in which rates of parasite transmission are influenced by habitat structure. Not all modes of transmission listed in Table 15.1 are represented by the chosen case studies.

### 15.3.1 Free-living larval parasites

#### Trematode larvae

The cercarial and miracidial larvae of digenetic trematode life cycles are free-living, motile stages. Miracidial larvae generally hatch from eggs that have been deposited in the external environment with host faeces. For most

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digeans, these stages are aquatic and their success at host-finding can be greatly influenced by the structure of the water medium, as described above. Rates of miracidial transmission also depend on the spatial distribution of target hosts which themselves may be affected by heterogeneity in the aquatic and benthic environments.

Trematode miracidia are well equipped with sense organs (Brooker, 1972; Smyth and Halton, 1983), and respond to a variety of environmental stimuli including light, water flow, temperature, and gravity (Ulmer, 1971; Wright, 1971; Cable, 1972; Chernin, 1974; Brown, 1978). Under natural conditions these responses may be quite complex, as illustrated by Shiff's (1974) study of the host-seeking behaviour of *Schistosoma mansoni* miracidia in a natural pond on the highveld plateau of Zimbabwe. In this system, transmission is influenced by a strong link between spatial and temporal variation in the physical environment, spatial distribution of susceptible hosts, and the host-seeking behaviour of miracidia. The structure and relative quality of the pond habitat as perceived by the host snails (*Bulinus (Physopsis) globosus*) changes seasonally. In winter, the host snails aggregate in large numbers at the warm surface of the pond, avoiding colder bottom areas. In summer, their spatial distribution reverses: snails spend much of their time feeding on the bottom, and in shaded, vegetated areas near the surface. The responses of the miracidia to these seasonal changes in the environmental structure of the pond habitat match those of the snails, resulting in the aggregation of the parasites in areas where the likelihood of encountering a host is high. In summer, the miracida are negatively phototactic and most infections of caged, uninfected, 'sentinel' snails occurred at the bottom of the pond, and in shaded areas near the surface. None of the snails in cages placed in open, unshaded surface sites became infected. Experiments conducted during cooler winter months revealed the opposite pattern of miracidial behaviour. Many infections occurred in surface snails, and few bottom snails became infected. Laboratory experiments confirmed that a reduction in water temperature could reverse the negative phototaxis exhibited by miracidia under warm conditions.

The biotic component of habitat structure can also affect the rate of miracidial transmission. Several studies conducted in laboratory aquaria, outdoor experimental ponds, and seminatural transmission sites have demonstrated that the presence of non-host species of aquatic animals reduces the rate at which target host snails become infected (Chernin, 1968; Chernin and Perlstein, 1969; Upatham, 1972; Upatham and Sturrock, 1973). The mechanism producing this deterrent effect has only been investigated in the case of 'decoy', non-host snail species: miracidia attempt to penetrate these snails, but are 'irreversibly damaged' in the process and die (Chernin and Perlstein, 1969). It is interesting that this biotic component of habitat structure would affect transmission given that miracidia are attracted to chemical stimuli emitted from snails (see reviews in Ulmer, 1971; Cable, 1972; Chernin, 1974; MacInnis, 1976; Brown, 1978; Smyth and Halton,

1983). However, this response of miracidia to host chemicals is only observed when the larvae are in very close proximity to a snail, and is apparently not specific or strong enough to prevent the larvae from mistakenly attempting to penetrate non-host organisms.

Habitat structure can also determine the success of miracidial transmission to intermediate hosts indirectly through its influence on the distribution and abundance of definitive vertebrate hosts. If resources exploited by the definitive host are patchily distributed in space, this host will spend more time in some parts of the habitat than others, and deposit more trematode eggs (and miracidia) in these areas. The chance that a first intermediate molluscan host will become infected should therefore be higher in areas preferred (for completely different reasons) by the definitive vertebrate host. Circumstantial evidence for this indirect effect comes from studies of the prevalence of trematode infections in populations of intermediate molluscan hosts. Rates of infection are often highest near sites where birds roost or spend a disproportionate amount of time foraging (Robson and Williams, 1970; Pohley, 1976; Hughes and Answer, 1982; Sousa and Grosholz, unpublished).

Like the miracidial stage, trematode cercariae are equipped with numerous sensory structures (Whitfield, 1979) that can detect environmental stimuli such as light and shadow, temperature, gravity, water currents, and host-emitted chemicals. Larval responses to gradients in these environmental features often facilitate contact with the next host (Whitfield *et al.*, 1977; Smyth and Halton, 1983).

One kind of habitat structure commonly encountered by aquatic cercariae is spatial and temporal variation in water flow. Studies of *Schistosoma mansoni* cercariae have shown that they may be injured by the extreme turbulence encountered in fast-flowing streams, reducing their infectivity to definitive mammalian hosts (Upatham, 1973; Jewsbury, 1985). Maximal infection occurs at a water velocity of 30–40 cm s<sup>-1</sup> with fewer infections becoming established at higher or lower velocities (Radke *et al.*, 1961; Webbe, 1966; Ulmer, 1971; Upatham, 1974; Jordan and Webbe, 1982). The reduction in infection rate at low water velocities is probably a consequence of the reduced rate of contact between parasite and host, while at high velocities turbulence probably interferes with cercarial penetration (Jewsbury, 1985).

### **Nematode larvae**

Some groups of nematodes are transmitted between hosts by active larval stages. Nematode larvae generally do not move (under their own power) very far in the external environment; at most, they may crawl a few centimetres from the location at which they are defaecated by their vertebrate host (Croll, 1972; Kennedy, 1976). Some species, however, rely on non-host organisms for their dispersal.

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The life cycle of the bovine lungworm, *Dictyocaulus viviparus*, provides a dramatic example of this kind of phoretic dispersal by a non-host species (Robinson, 1962). The infective, third-stage larvae are found along grass blades, and are accidentally ingested by grazing cows, the only host in this parasite's life cycle. This unusual nematode is transmitted between bovine hosts as follows. Larvae are released into the grass when an infected cow defaecates. If the cow pat contains sporangiophores of the fungus *Philobolus* spp. and the pat is exposed to light, the usually inactive larvae will ascend the sporangiophore and rest on the upper surface of the sporangium. The daily discharge of the sporangia is quite powerful and can send fungal spores up to three metres away from the pat, and the nematode larvae along with it. Since cows tend to avoid grazing in areas adjacent to pats, the discharged larvae may be ingested at a higher rate by cattle than are those remaining on the pat, however, this has yet to be demonstrated. Thus, the microhabitat of the cow pat, in particular, whether it was deposited in a sunny or shady part of the pasture, may affect the spread of nematode larvae and therefore their chances of infecting a new host.

The restricted movement and resultant patchy distribution of nematode larvae make it possible for potential hosts to reduce their chances of infection by avoiding portions of the habitat where the density of larval nematodes is high. This is one hypothesized explanation for the observation that yellow baboons (*Papio cynocephalus*) in Amboseli Park, Kenya, alternate their use of groves of yellow-barked acacia trees for sleeping sites (Hausfater and Meade, 1982). A sleeping grove is a discrete cluster of 2–12 trees, separated from other sleeping-groves by a few hundred metres of open savanna. The soil beneath sleeping-trees becomes contaminated with the baboons' faeces which contain numerous ova and larvae of their intestinal nematode parasites. The eggs develop into preinfective larvae, and then infective larvae within one to six days after their defaecation. Baboons acquire nematode parasites by contact with, or ingestion of, late stage, soil-dwelling larvae. This is likely to occur each morning when the baboons descend from their sleep sites and spend minutes to hours resting, foraging, and socializing on the ground beneath the trees in which they slept the night before.

The main study group monitored by Hausfater and Meade (1982) had nearly exclusive use of at least 15 different sleeping-groves during the study period. This group used a particular grove for one to two nights in succession, before shifting to another grove in their home range. Peak hatching of nematode eggs occurs between 48 and 96 hours after faeces have been passed, so the timing of the baboons' shift to a new grove is consistent with the hypothesis that they do so in order to reduce the risk of nematode infection. Under the climatic regime of Amboseli, infective nematode larvae are abundant in the soil beneath a sleeping grove for about 8.5 days following its use by baboons (Hausfater and Meade, 1982). The average time for a baboon group to return to a grove after having switched to another

is at least nine days. In other words, baboons return to a grove only when the density of infective larvae has declined, and the chance of infection is low. Thus, the fact that dense populations of larval nematodes are restricted to certain discrete patches in the habitat (i.e., soil beneath sleep trees), allows the host behaviourally to avoid contact with the parasite and thus reduce transmission. In an analogous situation, rotational use of pastures by livestock, or pasture spelling, has proved to be an effective means of controlling the transmission and abundance of one-host ticks (Harwood and James, 1979).

### 15.3.2 Insect parasitoids

Free-living, flying adults are commonly the dispersive phase in the life cycle of insect parasitoids. Spatially variable environmental conditions may limit access of the adult insect to the host. An extensive literature regarding parasitoids of crop pests, reviewed by Vinson (1976), suggests that on relatively large scales, physical attributes of the environment such as temperature, humidity, windspeed, and light may limit successful host finding to certain regions of the habitat where conditions are favourable. On a smaller scale, within these suitable areas, parasitoids may use the host's food plants as a predictor of host presence, and may selectively attack the host on certain food plants but not others (Fox *et al.*, 1967; Rabb and Bradley, 1968). In addition, parasitoids may use the structure of the plant itself and may search for the host only in particular areas of a given plant (Varley, 1941; Smith, 1943).

Pounds and Crump (1987) studied patterns of attack by a sarcophagid fly, *Notochaeta bufonivora*, on the harlequin frog, *Atelopus varius*, along a montane, gallery forest stream in Costa Rica. Frogs were found to be aggregated in areas receiving waterfall spray, and individuals in these areas were more likely to be parasitized than those in areas lacking spray. An experimental manipulation of frog density demonstrated that this increased risk of parasitism was associated with moister patches of habitat *per se*, rather than being a response of the parasitoid to locally dense aggregations of hosts (e.g. Hassell, 1978). Why the parasitoid exhibits this pattern of attack is not known. Several investigators have suggested that insect parasitoids locate their hosts by a two-step process in which the parasitoid first locates an appropriate patch of habitat in which to search, then selects hosts to attack (Vinson, 1976).

Tidal fluctuations may limit the rate of attack by the parasitoid wasp *Anagras delicatus* on eggs of the plant hopper *Prokelisia marginata* (Stiling and Strong, 1982). Planthopper eggs are laid in the leaves of the salt marsh cord grass, *Spartina alterniflora*. Wasps cannot enter water, and therefore can only attack eggs that are not submerged. The higher, distal tips of cordgrass plants and leaves are exposed to the air longer than are more basal parts. Planthopper eggs laid in these distal plant parts may therefore be at

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greater risk of attack by wasps. Consistent with this hypothesized constraint of habitat structure on transmission, Stiling and Strong (1982), working in Gulf coast salt marshes of Florida, found that the rate of egg parasitism increases towards both the leaf apex and the more apical leaves. A similar study in California (Roderick, 1987), did not find this within-plant pattern of egg parasitism; however, on a larger spatial scale, rates of parasitism increased with tidal elevation. One plausible, but as yet untested, explanation for this pattern is that eggs within plants growing at higher tidal heights are exposed in air, and therefore to wasp attack, for longer periods of time.

### 15.3.3 Blood-feeding ectoparasites

#### Acarina

Ticks provide some of the best examples of how habitat structure, at several spatial scales, can influence host-finding by parasites. The host-seeking, or questing, behaviours of ticks are very stereotyped (Camin, 1963). Questing ticks (larval, nymphal, or adult) crawl to the tips of vegetation, and after a period of 'testing', position themselves with the capitulum directed upwards, and anterior legs outstretched. There they remain quiescent until a sudden decrease in light intensity or movement of the vegetation, as might be caused by a passing host, elicits the 'questing' response, i.e., the extended anterior legs are waved in the air beyond the branch tip in anticipation of contacting the host.

Experimental studies of questing behaviour in several tick species have found that the height at which ticks prefer to quest corresponds to that of the target host species (Camin and Drenner, 1978; Loye and Lane, 1988). Characteristics of the vegetation are also important. Using glass rods to simulate branches, Camin and Drenner (1978) found that questing larvae of the rabbit tick (*Haemaphysalis leporispalustris*) preferred to climb rods of greater surface curvature. Milne (1944) found in a field study that the density of *Ixodes ricinus* increased with the thickness of vegetation, regardless of the plant species. These studies demonstrate that relatively small-scale differences of habitat structure, i.e., the height, stem diameter, and branching patterns of vegetation, can influence the abundance of host-seeking ticks (Chapter 6). Thus far, there is little evidence that ticks prefer particular species of plants on which to quest. Lane *et al.* (1985) found no difference in the propensity of *Dermacentor occidentalis* to quest on different species of chaparral shrubs. A variety of environmental variables (both air and soil) that vary in space and time affect the rate of questing by ticks, including levels of light, humidity and temperature (e.g., Camin, 1963; Camin and Drenner, 1978; Lane *et al.*, 1985; Hair and Bowman, 1986; Loye and Lane, 1988).

The abundance of questing ticks is also influenced by larger scales of habitat, or vegetational, structure. Questing ticks are often most abundant

at vegetational ecotones. For example, adult and nymphal *Amblyomma americanum* reach their highest densities in secondary growth vegetation at the interface of meadow and forest (Semtner *et al.*, 1971; Hair and Bowman, 1986). Other sites supporting high numbers of *A. americanum* are small openings and old fire or game trails in woodlands. Similarly, Lane *et al.* (1985) found much higher densities of questing adult *Dermacentor occidentalis* at the ecotone between grassland and chaparral; the density of ticks decreased sharply within 3–5 m on either side of it.

The exact reason for the aggregation of questing ticks at vegetational ecotones has yet to be rigorously demonstrated (Lane *et al.*, 1985), but one of the most plausible explanations is that these are areas of increased host activity, and, therefore, tick transmission. For example, black-tailed deer, a major host of adult *D. occidentalis* in Lane *et al.*'s (1985) study area, most commonly graze along the edge of chaparral brushland. The abundance of small mammals, hosts for larval and nymphal stages, is also highest in the ecotone (R. Lane, personal communication).

## **Insecta**

Habitat structure also influences the ability of blood-feeding insects to contact their hosts. Such insects are rarely distributed uniformly across a habitat. Hosts can reduce their contact with these parasites by moving to those portions of the habitat where the density of blood-feeding insects is low. For example, during warm summer days, reindeer are attacked by dense swarms of blood-sucking and parasitic insects, especially mosquitoes and warble flies (White *et al.*, 1975; Halvorsen, 1986; J. Anderson, personal communication). At moderate levels of harassment, reindeer aggregate locally on remaining snow patches or elevated, windy sites where insect densities are lower. Under extreme harassment, herds move towards areas of the tundra with the least insect activity. Reindeer near Prudhoe Bay, Alaska, move towards the coast, where the prevailing north wind is strong (White *et al.*, 1975). As they approach the coast, moving north into the wind, they congregate on sand dunes exposed to the wind or on the gravel bars of river deltas where mosquitoes are uncommon for lack of vegetational cover. Herds may even move some distance out into rivers, or the Arctic Ocean, and stand in shallow water where insects are absent.

### **15.3.4 Vectored microparasites**

The structure of the habitat can affect the transmission of vectored parasites through its influence on the spatial distribution and activity of both the invertebrate vector and the vertebrate hosts. Studies in the Hawaiian islands have demonstrated the effects of habitat structure at several spatial scales on transmission of malaria in native bird populations (van Riper *et al.*, 1986). The introduced parasite, *Plasmodium relictum capistranoae* is transmitted by

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the culicine mosquito *Culex quinquefasciatus* and has a wide host range including most native birds and many seasonal migrants.

The prevalence of avian malaria on the island of Hawaii is highest at intermediate elevations where the altitudinal overlap of the vector and susceptible native birds is greatest (van Riper *et al.*, 1986). The native birds are most abundant at higher elevations, becoming progressively rarer at lower altitudes. The mosquito vector has the opposite distributional pattern: it decreases in abundance with increasing altitude.

Habitat structure at smaller spatial scales may also affect the transmission of the parasite between the vector and the avian host. At mid-elevations, contact between vector and host is further enhanced by the presence of habitat patches called kipukas (Goff and van Riper, 1980). Kipukas are islands of older vegetation surrounded by recent lava flows on which younger vegetation predominates. These areas of older vegetation are sites of increased activity of both birds and mosquitoes, and therefore malarial transmission (van Riper *et al.*, 1986). The prevalence of malaria is also higher in mesic than xeric habitats, probably because vector breeding sites are more abundant in the former areas. Gillies (1972) describes analogous effects of habitat structure on the distribution and movements of the mosquito vectors of human malaria in tropical Africa.

### 15.3.5 Larval parasites infecting intermediate hosts

Larval parasites sometimes alter the behaviour of the intermediate hosts they infect (Holmes and Bethel, 1972). If consumption of an infected intermediate host by a definitive host is the mechanism by which the latter becomes infected, then the parasite may alter its own rate of transmission by altering intermediate host behaviour. If the intermediate host's risk of predation varies spatially in a manner correlated with certain environmental variables, parasite-induced changes in this host's response to these variables can alter the rate at which it is preyed upon. Infection of the host may have a generalized, debilitating effect, slowing down or impairing its response to environmental stimuli. Alternatively, it may qualitatively alter the response of the host to various features of the environment, including gradients in moisture, gravity, pressure, or light.

The best examples of this interaction between habitat structure and parasite-induced changes in intermediate host behaviour come from studies of larval acanthocephalans and digenetic trematodes. Bethel and Holmes (1973, 1977) showed that responses of the intermediate amphipod hosts *Gammarus lacustris* and *Hyaella azteca* to light and disturbance by predators were altered by infections of larval acanthocephalans. Uninfected amphipods of both species avoid lighted areas of the water column, and are distributed primarily in the benthic and heavily vegetated zones of lakes, where light intensities are low. When disturbed at the surface, they dive towards the bottom. In contrast, *G. lacustris* infected with *Polymorphus*

*paradoxus* move towards light, and cling to floating vegetation or skim along the surface when disturbed. The definitive hosts of *P. paradoxus* are mallards, beavers, and muskrats which feed extensively along the surface of the water and amongst floating vegetation. In feeding experiments using mallards and muskrats, both hosts consumed more amphipods infected by *P. paradoxus* than uninfected ones.

*Hyalella azteca* infected with *Corynosoma constrictum* were also found to be positively phototactic. However, instead of clinging to vegetation or skimming along the surface when disturbed, over half the infected individuals dived towards the pond bottom. This variable response is consistent with the fact that both the mallard, a surface feeding, dabbling duck, and the lesser scaup, a diving duck, are definitive hosts of *C. constrictum*. In feeding experiments with mallards, significantly more infected hyalellids were captured than uninfected ones (Bethel and Holmes, 1977). Comparable feeding trials were not conducted with scaups.

*Gammarus lacustris* infected with *Polymorphus marilis* are also positively phototactic, but consistently dive to the bottom, like uninfected gammarids, when disturbed. In feeding trials with mallards and muskrats, neither infected nor uninfected gammarids were caught. Consistent with this pattern of behavioural modification, the definitive host of *P. marilis* is the diving, lesser scaup.

These studies demonstrate that the structure of the lake and associated vegetation, together with parasite-induced changes in intermediate host behaviour, influence the rate of transmission of particular species of larval acanthocephalans from intermediate amphipod to definitive avian hosts.

In another study involving larval acanthocephalans, Moore (1983) demonstrated that terrestrial isopods *Armadillidium vulgare* infected with *Plagiorhynchus cylindraceus* show positive phototaxis and preference for areas of lower humidity, in contrast to uninfected isopods which show negative phototaxis and preference for areas of higher humidity. In field predation experiments, Moore demonstrated that infected isopods were captured as food for nestlings more often than uninfected ones by adult starlings (*Sternus vulgaris*). Since the altered response of the isopod host determines the rate of transmission of the parasite between hosts, transmission rates will be a function of the response of infected isopods to the distribution of light and humidity within the habitat. Infected isopods spend more time in open areas away from refugia.

A final example of this type of modified host behaviour occurs in formicine ants infected by metacercariae of the digenetic trematode *Dicrocoelium dendriticum* (Carney, 1969). When the air temperature drops in late afternoon and early evening, infected ants climb to the tops of grass blades and attach to the blade with their mandibles until temperatures rise again in the morning. By contrast, uninfected nestmates return to the nestsite in response to lower temperatures. This altered behaviour is therefore temperature and possibly light dependent (Carney, 1969). It has been suggested, but

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not yet demonstrated, that this parasite-induced response of the intermediate host to frequent the tops of grass blades, a microhabitat in which they are particularly vulnerable to accidental consumption by the definitive herbivore host, increases their rate of transmission.

### 15.4 CONCLUSIONS

Finding hosts is a problem faced by all parasites. Formulating generalizations regarding the influence of environmental structure on parasite transmission is treacherous in view of the vast number of parasite species (Price, 1980), and the diversity of life cycles, transmission mechanisms, and habitat types. From the examples discussed in this review, we have identified several important elements of the interactions between habitat structure and parasite transmission. Hopefully, these elements, as described below, can provide a framework for future research.

The effects of environmental structure operate at a variety of different spatial scales, and its influence on host finding is likely to differ with scale. At the largest scale, only certain habitats provide the conditions necessary for the completion of a particular parasite's life cycle, including a physical environment conducive to successful transmission and an adequate density of hosts and vectors. In some cases, dispersal processes may restrict the distribution of a parasite species among otherwise suitable habitats. The dispersal of a parasite into a particular habitat may be by passive or active movement of free-living stages, or the parasite may be transported as a parasitic stage by a mobile host and subsequently released in habitats frequented by that host. It would seem that heterogeneity in parasite distributions at larger spatial scales, where not attributable to physiological constraints, is often due to differential habitat use, and therefore transport of the parasite, by the host. For example, the accumulation of ticks at vegetational ecotones is probably a consequence of the differential use of such areas by mammalian hosts, and the resulting deposition of nymphal and adult stages of the parasite. Similarly, the distribution of parasites among Amboseli acacia groves is a function of baboon troop movement and selection of sleep sites. It is unlikely, however, that the spatial distributions of hosts and parasites will be as tightly associated when the parasites possess widely dispersing, free-living stages. Antolin and Strong (1987) found that the parasitoid wasp, *Anagrus delicatus*, regularly disperses 1 km or more in a north Florida saltmarsh. On some sampling dates, substantial numbers of the wasps were trapped at sites where the host was rare or absent (D. Strong, personal communication). Clearly, the distribution of this highly mobile parasitoid among local saltmarshes is not limited by the movements of its planthopper host.

The focus of this chapter, however, is not on the ecological or evolutionary processes by which parasites come to occupy particular habitats. Rather, we are interested in the influence of environmental structure at

smaller scales: within habitats where a parasite population can persist. On these smaller spatial scales, the mobility of parasites and hosts, relative to each other and to the three-dimensional space of the habitat, is a key determinant of transmission success and the distribution of parasites among microhabitats. Some parasites or their vectors search for hosts or for microhabitats where hosts are likely to be encountered, whereas others 'sit and wait' for hosts to contact or consume them. Similarly, some host species are mobile, others sessile. The movements of active parasites and hosts will be affected to varying degrees by the structure of the habitat spaces they traverse, depending on such things as the organism's agility and its size relative to the structural components.

To predict the effects of a particular scale of habitat structure on the success of searching parasites or vectors, one must assess: (1) the parasite's abilities to use structure at that scale to predict the host's location and abundance, and (2) how easily the parasite can move in search of a host at that spatial scale. If habitat structure is a good predictor of the whereabouts of the host, and if the mobility of the parasite within the habitat is such that it can rapidly and completely search the area, then habitat structure is likely to facilitate host finding. On the other hand, if habitat structure is a poor predictor of host presence, and/or interferes with parasite mobility, then host finding may be unaffected or impaired by habitat structure, at the scale considered. For example, questing ticks use the structure of the vegetation to guide their movements to specific sites where the probability of host encounter is high. In contrast, the same vegetational structure may interfere with the flight of parasitoids searching for host larvae or eggs, and thereby limit their access to suitable hosts.

The transmission success of free-living, but passive, stages in parasite life cycles depends to a large degree on the movement patterns of the host, more so than in the case of actively searching parasites. Therefore, the scale of host mobility relative to habitat structure will strongly influence the frequency of contact between passive stages and their target hosts. Some active parasites, e.g. larval ticks, adopt a 'sit and wait' strategy after successfully locating an appropriate microsite. Once in a stationary questing posture, transmission becomes a function of the pattern of host movements, as for completely passive parasite stages.

For parasites that are transmitted via an intermediate host, the mobility of both intermediate and definitive hosts with respect to habitat structure may have considerable influence on transmission rates. In these cases, habitat structure may facilitate transmission by guiding the active search of the predatory definitive host or by providing camouflage for definitive hosts that use a 'sit and wait' hunting strategy. Alternatively, habitat structure may reduce transmission if it affords the intermediate host a spatial refuge from its predator. Parasite-induced changes in the responses of intermediate hosts to environmental characteristics can further modify the above relationships, as described earlier.

Finally, habitat structure influences the spatial pattern of potentially stressful environmental conditions, and the abundance and activity of non-host predators and pathogens of free-living transmission stages, vectors, or intermediate hosts. For example, transmission of an aquatic parasite could be limited by a swift current which damages its active transmission stages. Transmission of a terrestrial parasite might be higher in mesic than xeric microhabitats because the former allow extended survival of a passive stage. Forms of habitat structure could also decrease the survival of transmission stages by attracting non-host predators. Alternatively, habitat structure could decrease the intensity of such predation by providing refugia for the transmission stages.

In summary, in order to predict the effects of habitat structure on host finding, one must be explicit about the scale of habitat structure in question. Second, the ability of the transmission stage or host to perceive habitat structure and to use it as a predictor of host or parasite distribution, respectively, must be considered. Finally, it is necessary to know the mobility of the transmission stage and the host with respect to that particular scale of habitat structure.

The case studies presented above provide examples of the ways in which habitat structure can affect parasite transmission between hosts. However, few natural host–parasite systems have been studied in sufficient detail to provide more than anecdotal information on these effects or the mechanisms involved. In fact, for some of the host–parasite associations discussed above, information has had to be pieced together from several sources.

Much will be learned by examining host-finding under field conditions using systems in which habitat structure can be manipulated and movements of parasites, vectors, and hosts monitored. Studies that manipulate habitat structure on more than one biologically meaningful spatial scale will be especially valuable. For example, an investigation of the searching behaviour and success of parasitoids could include manipulation of both plant architecture and inter-plant spacing. A slightly different approach might be taken with parasites that have inactive transmission stages. By experimentally varying characteristics of the habitat, perhaps on different scales, one could study how habitat structure affects host movement and the resulting consequences for transmission. Finally, systems in which parasites change the behaviour of their hosts or vectors provide special research opportunities. Since movement of the intermediate host or vector is equivalent to movement of the parasite in these systems, ‘host finding’ would be easily observable and experimental investigations of the effect of habitat structure on ‘parasite’ movement would be feasible.

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