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Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts

Received: 8 October 1999 / Accepted: 13 September 2000 / Published online: 7 December 2000
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Abstract Spatial variation in parasitism is commonly observed in intermediate host populations. However, the factors that determine the causes of this variation remain unclear. Increasing evidence has suggested that spatial heterogeneity in parasitism among intermediate hosts may result from variation in recruitment processes initiated by definitive hosts. I studied the perching and habitat use patterns of wading birds, the definitive hosts in this system, and its consequences for the recruitment of parasites in snail intermediate hosts. Populations of the mangrove snail, *Cerithidea scalariformis*, collected from mangrove swamps on the east coast of central Florida are parasitized by a diverse community of trematode parasites. These parasites are transmitted from wading birds, which frequently perch on dead mangrove trees. I tested the hypothesis that mangrove perches act as transmission foci for trematode infections of *C. scalariformis* and that the spatial variation of parasitism frequently observed in this system is likely to emanate from the distribution of wading birds. On this fine spatial scale, definitive host behaviors, responding to a habitat variable, influenced the distribution, abundance and species composition of parasite recruitment to snails. This causal chain of events is supported by regressions between perch density, bird abundance, bird dropping density and ultimately parasite prevalence in snails. Variation between prevalence of parasites in free-ranging snails versus caged snails shows that while avian definitive hosts initiate spatial patterns of parasitism in snails through their perching behaviors, these patterns may be modified by the movement of snail hosts. Snail movement could disperse their associated parasite populations within the marsh, which may potentially homog-

enize or further increase parasite patchiness initiated by definitive hosts.

Keywords *Cerithidea scalariformis* · Definitive host · Intermediate host · Spatial heterogeneity · Trematodes

Introduction

A fundamental goal in ecology is to determine the causes of variation in recruitment to a habitat. Like most free-living organisms, such as marine invertebrates and reef fish, the recruitment of parasites to host populations is variable in space and time (Martin 1955; Robson and Williams 1970; Loker et al. 1981; Sousa 1983, 1990; Kuris 1990; Williams and Esch 1991; Kuris and Lafferty 1994; Lafferty et al. 1994; Stevens 1996). This spatial and temporal variation may result from a variety of factors such as host movement, density, life history, susceptibility to infection; and parasite dispersal and behavior (Wakelin 1978; Anderson and Gordon 1982; Blower and Roughgarden 1989; Williams and Esch 1991; Sousa 1993; Grosholz 1994; Kuris and Lafferty 1994). The relative contribution of these factors on parasite distribution is likely to vary with spatial scale (see Wiens 1989).

Compared to the high mobility of definitive hosts (those that harbor the adult parasites) such as birds and fishes, intermediate hosts (those harboring the larval parasite stage) are relatively sessile. The heterogeneous distribution of parasites observed among intermediate hosts such as clams, gastropods, etc., has been suggested to emanate from the high mobility and behavioral patterns of definitive hosts, which are the source of parasites to intermediate hosts (Robson and Williams 1970; Kuris 1990; Sousa and Grosholz 1991; Williams and Esch 1991; Sousa 1993; Kuris and Lafferty 1994). For example, birds that migrate between marshes, along coastlines, or across continents, can link parasite communities of intermediate hosts that inhabit spatially separated sites (Kuris 1990; Sousa 1993). Definitive hosts that use habitats differentially will deposit their associated parasites

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unevenly (Kuris 1990; Sousa 1990; Sousa and Grosholz 1991). Consequently, parasite abundance in intermediate host populations is likely to be highest in frequently visited areas. On local scales (e.g. within marshes), feeding and perching behaviors of birds can also generate small-scale heterogeneity in the supply of parasite recruits. For example, the aggregation of definitive hosts around nesting or roosting sites can concentrate parasites at these sites, creating localized areas of high transmission.

Likewise, definitive host abundance may influence temporal patterns of parasitism in intermediate hosts (Kuris and Lafferty 1994). Definitive host abundance may vary daily, monthly or seasonally, creating temporal pulses in parasite recruitment to intermediate hosts. For example, the seasonal migration patterns of birds can generate high parasite prevalence (percentage of hosts infected; see Margolis et al. 1982) in intermediate host populations during particular times of the year along their migration routes.

Definitive hosts may also reduce genetic variation among parasite populations. Birds, which feed on infected hosts, pick up local populations of parasites. As birds move between sites, they disperse these parasites over large spatial scales. This host movement promotes gene flow among parasite populations even for genetically and geographically isolated intermediate hosts. Such dispersal also allows parasites to colonize new habitats (hosts), and replenish existing or extinct local parasite populations.

Correlative studies have found a positive relationship between definitive host abundance and parasite prevalence in intermediate hosts (Hoff 1941; Robson and Williams 1970). A few studies have examined factors that influence the transmission and distribution of parasites into intermediate host populations by manipulating the spatial distribution of intermediate hosts in the field and evaluated the consequences for parasite distribution. For example, Blower and Roughgarden (1989) found that host susceptibility to parasitism increased with host density and degree of host spatial aggregation. Further, host genotype and spatial distribution has also been shown to influence the intensity of parasitism in intermediate hosts (Grosholz 1994). However, while the role of host genetics and density on parasite distribution has received some attention, the role of definitive host behavior still remains unclear.

In this study, I tested the hypothesis that definitive hosts initiate spatial heterogeneity in infections in first intermediate hosts through their distribution and behavioral patterns. In the study system, the primary definitive hosts are wading birds, which frequently perch on dead mangrove trees. As a result of this behavior, bird feces (which contain parasite eggs) are aggregated around the base of dead mangroves. Previous work in this system has shown that parasitism among first intermediate hosts is spatially variable and that such variation may be contributed by the behavioral patterns of wading birds (Ruiz et al, unpublished data; personal observation). I hypothesized that dead mangroves serve as transmission foci for parasite infections to first intermediate hosts (snails) and that snails are more likely to become infected with parasites near perches than in non-perch areas. Further, I predicted that parasite recruitment would increase with the density of mangrove perches. This observational study represents the first step to understanding the linkage between definitive host behavior, spatial variation in mangrove density and spatial variation in parasitism in snail intermediate hosts.

Materials and methods

Natural history

My study system involves multiple species of digenetic trematodes, which infect several hosts during their life cycle. The first intermediate host is the snail, *Cerithidea scalariformis*, found in mangrove and salt marsh habitats of southern Florida. *Cerithidea scalariformis* exhibits rapid and direct development, and lives for 1–2 years (Houbriek 1984). Populations of *C. scalariformis* are parasitized by a diverse assemblage of larval trematodes (Holliman 1961; McNeff 1978). Snails become infected from either ingestion of trematode eggs or from attachment and penetration of free-swimming miracidia which emerge from eggs. While in the snail, trematodes undergo asexual reproduction (in the gonad, digestive gland, or mantle) and castrate the host. Free-swimming cercariae are produced, often in large numbers, by the asexual reproduction within the snails. Depending on the trematode species, cercariae penetrate and encyst in a second intermediate host (e.g. crustacean, fish) or they encyst on vegetation or other ingestible substrates such as a crustacean cuticle. Definitive hosts become infected by ingesting infected second intermediate hosts or cysts. The worms develop to sexual maturity within the definitive host, and the life cycle begins anew when eggs are passed in feces or urine. The life history of the trematode species that infect *C. scalariformis* is presented in Table 1.

Table 1 The life history of trematodes that infect *Cerithidea scalariformis* in St. Lucie and Indian River Co., Florida

Trematode species	Miracidia	Stages in snail host	Foci of infection in snail	Definitive host
<i>Parorchis acanthus</i>	Penetrate	Redia	Gonad	Birds
<i>Euhaplorchis</i> sp.	Ingest	Redia	Gonad	Birds
<i>Phocitremonoides</i> sp.	Ingest	Redia	Gonad	Birds and mammals
<i>Renicola buchhanani</i>	Ingest	Sporocyst	Mantle	Birds
<i>Renicola</i> sp. A	Ingest	Sporocyst	Gonad	Birds
<i>Probolocoryphe lanceolata</i>	Ingest	Sporocyst	Gonad	Birds and mammals
<i>Mesostephanus appendiculatoides</i>	Penetrate	Sporocyst	Mantle	Birds and mammals

The principal definitive hosts in this host-parasite system include several species of wading birds, which are very abundant in salt marsh, estuarine and mangrove habitats occupied by the snails (Swain and Shenker 1993; personal observation). Many species of wading birds have been frequently observed to perch on dead mangroves, including the great egret (*Casmerodius albus*), snowy egret (*Egretta thula thula*), white ibis (*Eudocimus albus*), great blue heron (*Ardea herodias*), tricolored heron (*Egretta tricolor ruficollis*), wood stork (*Mycteria americana*), and roseate spoonbill (*Ajaia ajaja*) (personal observation). Egrets, white ibis, and herons are known to harbor a rich parasite community that includes many trematode species (Hutton and Sogandares-Bernal 1960; Hutton 1964; Bush and Forrester 1976), and some of these species use *C. scalariformis* as the first intermediate host (see Holliman 1961; McNeff 1978). A variety of small mammals such as cotton rats (*Sigmodon hispidus*), cotton mice (*Peromyscus gossypinus*), marsh rice rats (*Oryzomys palustris*), and raccoons (*Procyon lotor*) can also harbor several species of the trematodes that infect *C. scalariformis* (Hutton and Sogandares-Bernal 1960; Heard 1976; Kinsella 1988), but were in low abundance at this study site (unpublished data).

Study site

This research was conducted in a mangrove marsh south of Round Island State Park, Indian River Co., Florida (N 27° 33' 45" W 80° 20'). The marsh lies adjacent to the Indian River Estuary and has been physically modified by impoundment for mosquito control (Rey and Kain 1989). The marsh flora consists primarily of mangroves (black mangrove, *Avicennia germinans*; red mangrove, *Rhizophora mangle*) and other salt-tolerant plants (*Salicornia* sp. and *Batis maritima*). Approximately, 50% of the marsh is unvegetated (personal observation). In 1989, Florida suffered an unusually prolonged freeze that killed most of the black mangroves. Consequently, the landscape of the marsh is composed of hundreds of dead and young (<5 years) mangrove trees distributed over the 21 ha wetland.

Study design

I tested the hypothesis that spatial patterns of habitat use by wading birds can influence the distribution of parasites to first intermediate hosts by caging snails in one of three groups that differed in mangrove perch density. Each study plot contained 0, 1, or 2 mangrove perches, with 9 replicates of each group. Perches were identified as large dead mangroves with at least one horizontal branch on which a wading bird could perch. The minimum height of all perches was at least 6 m. Perches were randomly selected by numbering dead mangrove trees in the field according to the number of natural perches in a standardized plot, then selecting them using a random numbers table. Plots with one perch are referred to as solitary perches, and plots with two adjacent perches (within 0.5 m) are referred to as multiple perches. No-perch plots were also randomly selected using the same method as the perches. These were open mudflat areas with a few small, salt-tolerant plants, but no dead mangroves. All plots were the same size (31.4 m²) and were separated from each other by at least 10 m.

Snail enclosures were constructed of 4 mm Vexar mesh with a surface area of 0.30 m². Enclosing snails prevented them from dispersing in the field and allowed a standardized comparison of the effect of perch density on trematode infection. The top edges of the enclosure walls were folded towards the inner walls of the enclosure, so that the mesh would not completely shade the interior. All enclosures had a mixture of soft mud and sand, and experienced periodic floods during afternoon thunderstorms. Plants and woody debris were removed from within the enclosures to make the caged environment similar to each other. For each solitary perch, one enclosure was placed randomly at the base of the mangrove. For each multiple perch, one enclosure was placed between the two mangroves. For each no-perch plot, one enclosure was

placed next to a wooden stake centered in that plot. A total of 725 snails were collected on 1 May 1997 within the size range 10.0–14.9 mm. Fifty snails were dissected to estimate parasite prevalence at the commencement of the study. Snails examined for trematodes at this size range and during this time of year are usually uninfected (unpublished data), and because these marine snails cannot be reared in the laboratory, only field collected snails could be used. The rest of the snails were randomly distributed to each cage on 7 May 1997 with 25 snails per cage. This density (25 snails/30 m²) is within the typical range of natural densities encountered in the field (unpublished data). All snails were painted with acrylic paint on the apex of their shells to distinguish them from free-ranging snails. To maintain density, missing painted snails were replaced by local snails of similar size. These replacement snails were not used in any of the analyses. On 29 September 1997, snails were removed from each enclosure and dissected for parasites. Specifically, the mantle, digestive gland and gonad were examined for larval trematodes, and if present, were identified according to Holliman (1961). In addition, all free-ranging snails of similar size range found within 0.50 m of each enclosure were also collected on 29 September 1997 and examined for parasites to determine if these snails experienced similar infection patterns as sentinel snails. For most plots, at least 25 free-ranging snails were collected, while at a few plots, less than 25 snails were collected. The sample sizes of this group were variable mainly due to their patchy distribution, which often reflected changes in environmental conditions (see Discussion). For all snails, size, sex, and infection status were recorded.

Wading bird and bird dropping surveys

Because wading birds are mobile and the scale of the plot may be too small to adequately describe the wading bird community, I counted all wading birds within the entire study site over an area of 5,000 m² in addition to counting birds within each plot. I documented the abundance and distribution of wading birds by surveying the entire study area and each plot twice a week from 7 May to 28 September 1997. For each census, wading birds were identified and counted during the same time of day (1200–1300 hours), a time when wading birds were most frequently observed perching. Immediately following the bird counts, the number of bird feces within each perch group was counted. Each dropping was then marked with a wooden dowel to prevent it from being recounted.

Data analysis

Associations between wading bird abundance within plots, bird dropping abundance, perch density and prevalence of parasitism were tested using regression analyses. A logistic regression model analyzed by a chi-square test was used to compare parasite prevalence of caged snails among perch densities. Using the same analytical method, I also compared parasite prevalence of each trematode species among perch densities. Analysis of variance was used to test for differences in wading bird abundance and bird dropping abundance among perch densities. A student's *t*-test was used to test for differences in parasite prevalence (arcsine transformed) between caged and free-ranging snails for each perch group. Analyses with parasite prevalence were conducted on caged snails, unless otherwise noted.

Results

Bird community

The wading bird community comprised primarily white ibis, herons, egrets and several other species of marsh birds (Table 2). White ibis was the most common wading

Table 2 List of wading birds that were observed perching and feeding within the entire study area. The last column represents the percentage of the total number of counts represented by each species of wading bird

Common name	Scientific name	Number perching	Number feeding	%
White Ibis	<i>Eudocimus albus</i>	98	65	70.9
Tricolored Heron	<i>Egretta tricolor</i>	8	7	6.5
Snowy Egret	<i>Egretta thula thula</i>	7	8	6.5
Great Egret	<i>Casmerodius albus</i>	8	5	5.7
Little Blue Heron	<i>Egretta caerulea</i>	1	4	2.2
Roseate Spoonbill	<i>Ajaia ajaja</i>	2	2	1.7
Wood Stork	<i>Mycteria americana</i>	3	0	1.3
Yellow-crowned Night Heron	<i>Nyctanassa violacea</i>	2	1	1.3
Black-crowned Night Heron	<i>Nycticorax nycticorax</i>	1	0	0.4
Great Blue Heron	<i>Ardea herodias</i>	0	1	0.4
Reddish Egret	<i>Egretta rufescens</i>	0	1	0.4
Other marsh birds				
Osprey	<i>Pandion haliaetus</i>	5	0	2.2
Black Vulture	<i>Coragyps atratus</i>	1	0	0.4
Total		136	94	

Table 3 List of wading birds that were observed perching and feeding within plots

Common name	Scientific name	Number perching	Number feeding	%
White Ibis	<i>Eudocimus albus</i>	18	0	56.3
Roseate Spoonbill	<i>Ajaia ajaja</i>	1	4	15.6
Tricolored Heron	<i>Egretta tricolor</i>	3	0	9.4
Great Egret	<i>Casmerodius albus</i>	2	1	9.4
Wood Stork	<i>Mycteria americana</i>	2	0	6.3
Little Blue Heron	<i>Egretta caerulea</i>	0	1	3.1
Total		26	6	

Table 4 *R*-square values from regression analyses between wading bird abundance, bird dropping abundance, parasite prevalence of sentinel snails, and perch density. The *R*-square values in bold face represent the causal chain of events: perch density to bird abundance to bird droppings to parasite prevalence

	Bird abundance	Bird droppings	Parasite prevalence
Perch density	0.190*	0.199*	0.249*
Bird abundance		0.349**	0.240*
Bird droppings			0.386***

* $P > 0.05$, ** $P > 0.005$, *** $P = 0.0001$

bird species observed during the censuses, accounting for 71% of counts over the entire study area (Table 2) and 56% of the plot counts (Table 3). Wading birds exhibited a strong preference for perching on dead mangroves or on logs lying on the mudflat. No wading birds were observed perching on live mangrove or other live vegetation.

Mean wading bird abundance increased with perch density (no-perch: 0.11 ± 0.10 SE, solitary perch: 0.79 ± 0.26 SE, and multiple perch: 2.56 ± 1.15 SE) and was significantly associated with perch density (Table 4). The effect of the perch density on bird abundance approached significance in an ANOVA ($F = 3.06$, $P = 0.06$).

Distribution of bird droppings

In general, bird droppings were aggregated around dead mangrove perches and significantly increased with perch density (Table 4). Further, there was a significant difference in the abundance of bird droppings among perch densities (ANOVA, $F = 4.32$, $P < 0.05$) with a mean abundance of 8.33 ± 1.86 SE for the no-perch, 8.33 ± 1.89 SE for the solitary perch and 16.0 ± 2.29 SE for the multiple perch. The number of bird feces in the multiple perch was significantly different from dropping counts in the no-perch and solitary perches, but drop counts in the no-perch and solitary perches were not significantly different from each other (Tukey's studentized range test, $P = 0.05$). Further, bird abundance within plots was significantly associated with the abundance of bird droppings (Table 4).

Prevalence of parasitism

At the commencement of the study, the prevalence of parasitism was 4%, and only *Probolocoryphe lanceolata* was present. By the end of the study, a total of seven trematode species were found among the caged snails. With all parasite species combined, prevalence of parasitism in caged snails significantly increased with perch density (Table 4, Fig. 1), and was significantly different among perch

Table 5 Trematode species prevalence (\pm SE) for each perch density. Last column represents results of the logistic regression model analyzed by a chi-square test to compare the prevalence of each parasite species among perch densities

Trematode species	Perch density			
	Control	Perch	Multiple	χ^2
<i>Parorchis acanthus</i>	1.8 (0.01)	6.7 (0.02)	10.7 (0.02)	10.05*
<i>Euhaplorchis</i> sp.	2.4 (0.01)	4.2 (0.02)	6.5 (0.02)	3.42n.s.
<i>Phocitremonoides ovale</i>	1.2 (0.01)	2.4 (0.01)	3.2 (0.01)	1.57n.s.
<i>Renicola buchhanani</i>	0.0	1.2 (0.01)	1.9 (0.01)	0.24n.s.
<i>Renicola</i> sp. A	0.6 (0.01)	0.6 (0.01)	0.4 (0.00)	0.05n.s.
<i>Probolocoryphe lanceolata</i>	0.6 (0.01)	1.8 (0.01)	2.3 (0.10)	1.54n.s.
<i>Mesostephanus appendiculatoides</i>	9.6 (0.02)	9.1 (0.02)	5.6 (0.02)	3.06n.s.
Total prevalence	16.2 (0.03)	26.1 (0.03)	30.6 (0.03)	10.17*

* $P < 0.01$, n.s. not significant

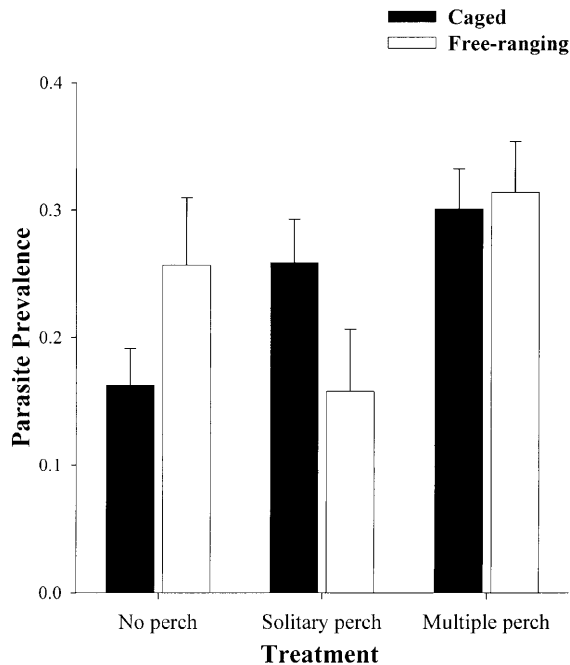


Fig. 1 Prevalence of parasitism (+ SE) of caged sentinel and free-ranging (non-caged) snails for each perch density

groups ($\chi^2=10.2$, $P < 0.01$). The percent of missing snails (presumably dead or escaped) for each group was 26%, 27%, and 4% for the no-perch, solitary perch and multiple perches, respectively. The associations of wading bird abundance and bird dropping counts with parasite prevalence were both positive and significant (Table 4). By species, most trematodes increased in prevalence with perch density. In this case, *Parorchis acanthus* was the only species significantly associated with perch density (Table 5).

The spatial variation in prevalence of parasitism among free-ranging snails was somewhat different from that of caged sentinel snails (Fig. 1). My results show that parasite prevalence of free-ranging snails was not significantly different from sentinel snails in the no-perch ($t=1.69$, $df=234$, $P > 0.05$), solitary perch, ($t=-1.64$, $df=221$, $P > 0.05$), and multiple perch plots ($t=0.31$, $df=351$, $P > 0.05$; Fig. 1). In contrast to caged sentinel snails, there was no significant difference in parasite prevalence among perch densities for free-ranging snails ($\chi^2=0.55$, $P > 0.05$).

Discussion

Spatial heterogeneity in parasitism is commonly observed in intermediate host populations and has been an important topic of discussion in ecological parasitology (Robson and Williams 1970; Loker et al. 1981; Sousa 1983, 1990; Kuris 1990; Williams and Esch 1991; Kuris and Lafferty 1994; Lafferty et al. 1994; Stevens 1996). My results suggest that heterogeneity in parasitism in intermediate hosts is strongly influenced by the distribution and abundance of definitive hosts as suggested from the literature (Robson and Williams 1970; Kuris 1990; Williams and Esch 1991; Sousa 1993; Kuris and Lafferty 1994). For example, Robson and Williams (1970) attributed the relatively high prevalence of trematode infections in *Littorina littorea* to the large numbers of gulls observed feeding, preening and roosting at such sites. Similarly, Hoff (1941) found high prevalence of trematode infections in *L. littorea* collected from and near roosting and nesting sites of gulls. He attributed these spatial patterns to the limited dispersal of trematode eggs, that, when deposited with fecal material, adhered to the algae and were subsequently ingested by snails (Hoff 1941).

Specifically, this study demonstrated that perching behaviors may govern the spatial variation of parasitism within the host population at that site. The quantity of bird droppings accounted for 39% of the variance in parasite prevalence among perch densities. While bird abundance, dropping abundance and perch density may influence spatial patterns of parasitism; parasite prevalence could itself be correlated with other factors associated with bird abundance or perch density, although these are likely to be relatively minor contributions. For example, it is likely that all snails experienced similar water levels and heat stress, minimizing the effect of environmental variation on parasitism. Since trematodes are directly transmitted from birds to snails, the factors most likely to shape parasitism are those associated with bird abundance, distribution and behavior. Future studies that manipulate the recruitment of parasites to snails by altering natural perch density or definitive host abundance will be necessary to determine whether these factors are the primary causes of spatial variation in parasitism in intermediate hosts.

As shown, dead mangroves or other habitat structures that are used as perching sites by definitive hosts can

serve as transmission foci for parasites to infect snails. Changes in habitat features over large and small spatial scales can directly or indirectly influence transmission dynamics, and thus, the recruitment of parasites to their hosts (Sousa and Grosholz 1991). Further, since habitat features may influence parasite prevalence in host populations (see Sousa and Grosholz 1991 for a review), small alterations in a habitat can have significant implications for the transmission of medically important parasites (Lafferty and Kuris 1999). Habitat alterations can increase the prevalence of parasitic diseases by increasing the likelihood of transmission between hosts (Lafferty and Kuris 1999). For example, habitat alterations such as deforestation have often led to an increase in the number of habitats that are suitable as breeding sites for mosquitoes, and consequently, have increased the transmission of malaria in those regions (Desowitz 1981). Changes in a habitat can also lead to a decrease in parasitism. As an example, Cort et al. (1960) found a decline in trematode species diversity in the gastropod, *Stagnicola emarginata angulata*, over a 20 year period, and this decrease was associated with an increase in human disturbance and a decline in shorebird abundance. Alterations of habitats can also potentially reduce the impact and spread of medically important parasites by reducing conditions necessary for successful transmission (Desowitz 1981).

Due to the high dispersal ability of avian definitive hosts, parasite recruitment can occur over large spatial scales. The scale of parasite dispersal by their associated definitive hosts is comparable or sometimes greater than the dispersal of marine or estuarine free-living larvae by currents, tides and other oceanographic processes (e.g. Gaines et al. 1985; Boicourt 1982; Shanks 1983; Roughgarden et al. 1988; Kingsford 1990), where new individuals recruiting to a settlement habitat are likely to originate from other source populations (Victor 1983; Gaines and Roughgarden 1985; Mapstone and Fowler 1988; Jones 1990; Raimondi 1990). Thus, at some scale, the recruitment of parasites to their hosts is effectively open.

Within a habitat, the distribution of parasites in a host population may depend on the movement patterns of their intermediate hosts. In this study, the overall prevalence of parasites in the free-ranging snails did not parallel the spatial infection patterns of sentinel snails. The lack of a significant difference in prevalence among perch densities suggests that their movement or behavior may influence the dispersion of parasites from the foci of transmission. This may either homogenize or intensify spatial variation in the patterns of infection (Kuris 1990; Stevens 1996). Snails typically do not stay in exposed or open mudflat areas for extended periods (personal observation). Rather, they are rather mobile and are found in shady areas under vegetation, woody debris or in the crevices of tree trunks; presumably to escape from intense heat. Snails are also found on mangrove trunks during periods of high tides and rainfall to escape from flooding.

In another trematode-host system, Snyder and Esch (1993) showed that the most mobile snail species in their

system contacted and ingested the spatially patchy trematode eggs more frequently. Consequently, the mobile snail host had relatively higher parasite prevalence than did the less mobile snail species (Snyder and Esch 1993). Further, Stevens (1996) also noted that movement of the snail host, *Cerithidea californica*, may increase encounter rates with trematode eggs, which are patchily distributed. Such patterns have also been found in insect-pathogen systems where the dispersal of larval moths was associated with the spread of a virus (Dwyer and Elkinton 1995). Further studies in this system are needed to specifically test for the effect of movement by *C. scalariformis* on spatial patterns of parasitism to resolve whether snail behavior can influence contact rates with trematode eggs or miracidia, and if their movement patterns can modify initial infection patterns.

At the scale of a perch, the distribution and abundance of trematodes may be influenced by the limited dispersal abilities of free-swimming larval stages. The strong association between bird dropping abundance and parasite prevalence indicates that miracidia and trematode eggs do not disperse too far from where they were deposited and that the successful transmission of trematodes occurs on the scale of a few meters, near the source of miracidia. Trematode infections observed in sentinel snails in the no-perch plots may have resulted from droppings deposited during feeding or from bird fly-overs. Wading birds were observed feeding and defecating in these open areas during low tides (personal observation). In addition, the small size of miracidia, their limited swimming abilities, and short life span, would not allow them to disperse far from where they were deposited, especially under low flow conditions (Upatham 1973), as in ponds and marshes. Most miracidia are ephemeral, living just a few hours (Prah and James 1977). Temperature stress and UV radiation can significantly decrease their infectivity, activity and survival (Prah and James 1977). In this habitat, while some miracidia could potentially move between plots, most would not survive due to the high surface water temperatures (daily water temperature range 40–45°C) and prolonged periods when the mudflat was completely dry (personal observation). In contrast, where water flow is unidirectional and relatively strong, parasite prevalence may considerably increase downstream, as these populations become sinks for parasites in their snail hosts. A striking example here is the carefully documented study of the distribution of *Schistosoma mansoni* in *Biomphalaria glabrata* along a small canal in Guadeloupe, where the downstream snail populations experienced higher prevalence of *S. mansoni* than did upstream snail populations (Théron et al. 1978).

While the potential of parasitic infection is influenced by behavioral and ecological factors, the outcome of infection strongly depends on the susceptibility or resistance of the snail to the parasite (Wakelin 1978). Susceptibility to infection by trematodes has been found to have a partial genetic basis in natural populations of the snail, *Potamopyrgus antipodarum*, resulting in locally adapted parasite populations (Lively 1989). As direct developers,

there may be spatial variation in susceptibility to parasitism within the *C. scalariformis* population. If genetic variation in susceptibility is present, this may interact with spatial variation to produce non-random distributions of parasites among snails, and thus, may be an important factor in contributing to the patterns of parasite dispersion in this system.

While the distribution, abundance, and behavioral patterns of definitive hosts play an important role in shaping patterns of parasite recruitment, the distribution of trematodes among snails can also be influenced and modified by post-recruitment processes. Specifically, interspecific interactions among larval trematodes have been commonly observed in snail hosts (Lim and Heyneman 1972; Kuris 1990; Fernandez and Esch 1991; Sousa 1993; Kuris and Lafferty 1994). There is substantial evidence that these interactions result in the loss of subordinate species to competitively dominant species (Lim and Heyneman 1972; Lie 1973; Yoshino 1975; Combes 1982; Kuris 1990; Sousa 1993), and therefore, interactions among trematodes may influence the prevalence and distribution of trematode species within the host population. Recent effort by Lafferty et al. (1994) has focused on whether and how spatial heterogeneity of trematode recruitment can influence interactions between trematodes. By applying their model to this field study, my results show that mangrove perch density served to intensify trematode species interactions, which resulted in a substantial loss of subordinate species to competitively dominant species (unpublished data). Consequently, these losses influenced the distribution and abundance of larval trematodes in snail intermediate host populations. These findings underscore the need to examine the factors that may influence recruitment processes, as well as any interactions that may occur during and after recruitment.

Acknowledgements I would like to thank K. Rapacon and S. Reed for their generous assistance in the field. A. Alldredge, A. Kuris, G. Ruiz, K. Hill, S. Gaines, W. Coats and two anonymous referees provided valuable comments on the manuscript. I would like to thank the Indian River County Mosquito Control District for access to the study site. Special thanks to the Smithsonian Marine Station in Fort Pierce, Florida, for their assistance and use of their facilities while conducting this research. This paper represents contribution number 496 of the Smithsonian Marine Station at Fort Pierce.

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