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Microhabitat differences surrounding a pond affects the distribution of trematode parasites among a pulmonate snail community

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Summary

Anthropogenic disturbance associated with clear-cutting and changing the environmental landscape can lead to distinct microhabitat structure surrounding aquatic habitats. The transmission dynamics of trematode parasites in their snail first intermediate hosts were examined to determine if these alterations affect trematode parasite distribution. This was accomplished by examining 2,771 pulmonate snails belonging to two species (*Physa gyrina* and *Lymnaea columella*) over a three month period in a pond surrounded by distinct microhabitats as a result of anthropogenic changes to the environmental landscape. Trematode parasite distribution in the snail first intermediate hosts was largely tied to the microhabitat preference of their vertebrate definitive hosts. Autogenic species were found further away from the center of the open microhabitat and allogenic parasites were closer to the centralized point, most likely as a result of habitat preference by their frog and waterfowl definitive hosts, respectively. Additionally, there was increased parasitism in the molluscan hosts at the edges of the wooded environments due to habitat overlap of autogenic and allogenic species hosts, indicating that microhabitat structure can have profound effects on parasite distribution.

Keywords: trematode; snail; microhabitat; autogenic; allogenic

Introduction

Habitat disturbance (e.g., landscape changes, pollution, climate change) can have a major impact on the distribution of animals in both terrestrial and aquatic habitats (Khan, 1991; Lafferty, 1997; Alin *et al*., 1999; Rodríguez-Prieto & Fernández-Juricic, 2005; Marcogliese & Pietrock, 2011). Microhabitat changes caused by either natural or anthropogenic damage can alter the community composition and distribution of plants and animals within it. These alterations can have a major impact not only on the fauna,

but their parasites as well (Medeiros & Maltchik, 1999; Lafferty & Kuris, 2005; Morley, 2006; Urban, 2006; Morley, 2010). Disturbance can condense animal populations, consequently increasing parasite transmission (Kristofferson, 1991; Lafferty & Kuris, 2005; Urban, 2006). This situation can be extremely important for host species with low vagility (e.g., molluscs) via enhancement of the efficiency of parasite transmission by increasing proximity and encounter rate of parasites with their hosts.

Changes to the environmental landscape (Alin *et al*., 1999; Gill *et al*., 2001; Beale & Monaghan, 2004; Lafferty & Kuris, 2005; Rodriguez-Preito & Fernandez-Juricic, 2005), pollution (MacKenzie *et al*., 1995; Morley, 2006; Sures, 2008; Morley, 2010; Marcogliese & Pietrock, 2011), and other alterations to the aquatic environment (Lafferty, 1997; Gerard, 2001; Lafferty & Kuris, 2005; Koprivnikar *et al*., 2007; Gerard *et al*., 2008) can influence digenetic trematodes due to their complex life cycles. Multiple hosts involved in these life cycles result in a greater potential for at least one of them to be affected by changes in microhabitat. Most trematode life cycles require three hosts (at least one mollusc as an intermediate host, as well as one vertebrate as a definitive host where asexual and sexual reproduction of the parasite occurs, respectively), which may be influenced by these changes (Lafferty & Kuris, 2005; Urban, 2006). Although a wide array of host species are utilized by digenetic trematodes for life cycle completion, each parasite falls into one of two categories. Autogenic parasites have life cycles in which all hosts are present within a single aquatic system, unable to move between bodies of water, while allogenic parasites have life cycles in which at least one host is capable of moving between aquatic habitats (Esch *et al*., 1988). As a result, parasites in these two life-cycle categories often have distinct distributions not only between bodies of water, but within them as well (Esch *et al*., 1988; Criscione & Blouin, 2004; Fellis & Esch, 2005;).

Molluscan first intermediate hosts are extremely important in shaping the distribution and transmission dynamics of trematode parasites (Esch & Fernandez, 1994; Sapp & Esch, 1994; Detwiler & Minchella, 2009). Changing microhabitat may not only affect the distribution of aquatic snails, but may also indirectly affect the encounter rate of the gastropods with the definitive hosts (Huspeni & Lafferty, 2004; Lafferty & Kuris, 2005; Urban, 2006; Hechinger et al., 2007; Marcogliese & Pietrock, 2011). Consequently, the frequency of snails encountering eggs or miracidia of trematode parasites that infect them may be altered.

The present study examined microhabitat differences around a pond on the distribution of two species of freshwater pulmonate gastropods (Physa gyrina and Lymnaea columella) and their larval trematode parasites to determine if changes in the habitat structure around an aquatic system affect the parasite distribution within it. Microhabitat differences relating to the surrounding vegetation, particularly open versus wooded habitat, were suspected to impact the trematode infection patterns in the snail community. In particular, the habitat preference of the definitive hosts can have an impact on trematode infection in the snail population (Smith, 2001; Huspeni et al., 2004; Hechinger & Lafferty, 2005; Urban, 2006). Differences in the microhabitat preferences of autogenic host species, e.g., Rana spp. frogs tend to inhabit densely wooded microhabitats (Woodford & Meyer, 2003; Gagne & Fahrig, 2007; Hamer & Parris, 2011), and allogenic host species, e.g., aquatic waterfowl prefer to forage in areas with little to no wooded vegetation (Darnell & Smith, 2004; Sanchez-Zapata et al., 2005; Ma et al., 2010), were predicted to impact the distribution of trematode infections in the molluscan hosts.

Materials and methods

Study Site
Coon Lake is a 1.5-ha pond located in the Piedmont region of North Carolina, USA (35°59'50" N, 80°24'31" W). This oligotrophic lake has a maximum depth of 5 – 7 m with extensive littoral zones in the western half of the pond on the northern and southern banks. Although located within a public park, Coon Lake is isolated from human access and is mostly surrounded by dense wooded vegetation. The western edge of the pond is cleared of all vegetation, with the exception of grass that was planted to prevent soil erosion and is trimmed weekly, due to the construction of a cart path associated with the golf course. Although stocked with largemouth bass and bluegill sunfish, the pond is rarely visited by the public. Abundant numbers of Rana spp. frogs and visiting waterfowl frequent the pond.

Sampling and measurements
The western half of the pond was divided into 40 transects (5-m long), each of which was put into one of three categories, i.e., open (N=18), wooded (N=18), or edge habitat (N=4) (Fig. 1). The pond was partitioned so that there was an equal number of open and wooded transects for sampling. Open habitat was devoid of trees and vegetation and was located exclusively on the western edge of the pond, wooded habitat was covered in dense vegetation and trees, and edge habitat was characterized by transects that were within 5 m of the edge of the tree line.

All snails were sampled from May to July 2013 by hand or dip netting within 2 m of the shoreline. Snail density was estimated by counting all snails present within a 0.05-m^2 rectangle prior to the collection of snails in each transect. The snails were then isolated in the laboratory in 55-mm finger bowls with aged tap water for 48 hours, and checked for emerging cercariae. Each snail was then measured to the nearest 0.05 mm.

A subset of 150 snails, 50 from each habitat classification that were randomly selected from multiple transects within each category, was necropsied each month for an estimation of how many snails harbored pre-patent infections (i.e., possessing asexually reproducing sporocysts or rediae, but not yet shedding cercariae) and to provide a better estimation of the infection dynamics of the trematode parasites. All shed cercariae were isolated, identified, and then sub-categorized into autogenic and allogenic species
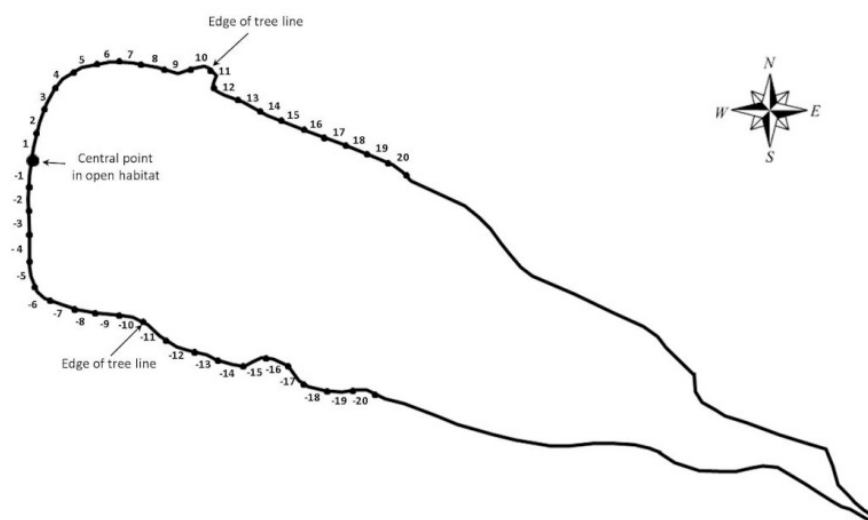

Fig. 1. Map of Coon Lake divided into 40 transects (5-m long) with the central point in the open habitat and the edge of the tree line labeled

Table 1. Sample sizes, density, and prevalence of trematode infection in three categories of microhabitat surrounding the pond in *Physa gyrina* and *Lymnaea columella* in Coon Lake from May to July 2013

	Open Habitat			Edge Habitat			Wooded Habitat			Totals		
	N	Density	Prevalence	N	Density	Prevalence	N	Density	Prevalence	N	Density	Prevalence
Physa gyrina	925	21.8 ± 1.1	10.5 % ± 1.0 %	326	17.1 ± 2.1	13.5 % ± 1.4 %	840	16.1 ± 1.4	8.0 % ± 1.2 %	**2091**	**18.7 ± 1.4**	**9.9 % ± 0.7 %**
Lymnaea columella	485	8.6 ± 0.7	1.2 % ± 0.4 %	81	7.9 ± 0.6	4.9 % ± 0.5 %	114	6.3 ± 0.9	0.8 % ± 0.1 %	**680**	**8.1 ± 0.7**	**1.6 % ± 0.3 %**
Totals	**1410**	**15.7 ± 0.8**	**7.1 % ± 1.0 %**	**407**	**15.8 ± 1.7**	**11.8 % ± 1.4 %**	**954**	**14.8 ± 1.1**	**7.3 % ± 1.2 %**	**2771**	**15.4 ± 1**	**7.9 % ± 0.7 %**

(Schell, 1985; Faltynkova *et al.*, 2007, Faltynkova *et al.*, 2008). The population was described in terms of prevalence (i.e., a binary measurement referring to the presence or absence of a trematode infection) according to the terminology of Bush *et al.* (1997) and is expressed as a percentage by dividing the number of infected snails by the total number of snails sampled.

Statistical Analyses
Generalized additive models (GAMs) were used to determine if the differences in microhabitat surrounding the pond affected the population structure and distribution of parasites within the body of water. A centralized point in the open habitat was marked (Fig. 1), and distance from this location was used to determine the influence of the microhabitat surrounding the pond on the spatial patterns of the trematode parasites. This centralized point was equidistant from the wooded habitat on either side of the pond. The GAMs used prevalence of autogenic and allogenic parasites and distance from the centralized point for the construction of the models. Additionally, 1-way ANOVA was used to compare snail densities and lengths between sites and Chi square analysis was used to compare prevalence of parasites between the 3 habitat categories and snail species. All models and statistical analyses were performed using R (R Development Core Team, Vienna, Austria). Data are presented as means ± standard error.

Results

A total of 2,771 pulmonate snails was collected belonging to *P. gyrina* (N = 2,091) and *L. columella* (N = 680). Total snail density did not differ significantly between habitat types (ANOVA, $P = 0.3566$), but did deviate between snail species (ANOVA, $P < 0.0001$; Table 1). Additionally, snail density did not differ between months of collection for either snail species (ANOVA, $P > 0.05$), nor was there a difference in snail length between habitat categories (ANOVA, $P > 0.05$).

A total of 10 species of trematode parasites, among them, three autogenic species and seven allogenic species, was collected from the snails in Coon Lake, with a total prevalence of 7.9 % ± 0.7 % (Table 2). *Physa gyrina* were more frequently infected by trematodes than *L. columella* (Table 1), with allogenic parasites (6.7 % ± 0.8 % and 1.3 % ± 0.3 %, respectively) infecting these snails more frequently than autogenic species (3.3 % ± 1.2 % and 0.3 % ± 0.1 %, respectively) (Chi square test, $P < 0.05$). Dissections demonstrated the existence of pre-patent infections and allowed the determination of the real prevalence of trematode infection in the snail hosts. The prevalence of pre-patent infection gives information on the moment at which gastropods were infected by miracidium, based on a typical pre-patency period of four weeks. Dissections revealed that parasite prevalence was under-
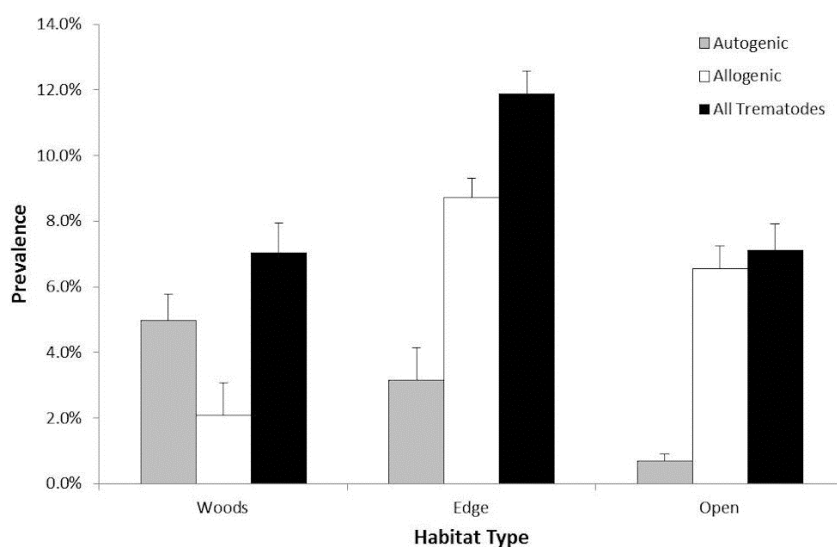

Fig. 2. Prevalence (± standard error) of autogenic, allogenic parasite, and all trematode parasite species infecting snails in the 3 habitat categories in Coon Lake

Table 2. Trematode prevalence in *P. gyrina* and *L. columella* with information on their life cycle (vertebrate definitive host, autogenic vs. allogenic) in Coon Lake between May and July 2013

Parasite Species	Gastropod Intermediate Host	Prevalence (Estimated)	Prevalence (Real)	Definitive Host	Life Cycle Type
Glypthelmins quieta	*P. gyrina* *L. columella*	2.4 % ± 0.1 %	2.7 % ± 0.2 %	*Rana* spp.	Autogenic
Haematoloechus complexus	*P. gyrina*	0.5 % ± 0.3 %	0.6 % ± 0.3 %	*Rana* spp.	Autogenic
Megalodiscus temperatus	*P. gyrina*	0.4 % ± 0.3 %	0.4 % ± 0.3 %	*Rana* spp.	Autogenic
Australapatemon burtii	*L. columella*	0.7 % ± 0.3 %	0.8 % ± 30.0 %	Waterfowl	Allogenic
Australapatemon canadiensis	*L. columella*	0.2 % ± 0.1 %	0.2 % ± 0.1 %	Waterfowl	Allogenic
Echinoparyphium recurvatum	*L. columella*	0.3 % ± 0.1 %	0.3 % ± 0.3 %	Waterfowl	Allogenic
Notocotylus attenuatus	*P. gyrina*	5.0 % ± 1.0 %	5.3 % ± 1.1 %	Waterfowl	Allogenic
Plagiorchis sp.	*P. gyrina*	1.8 % ± 0.2 %	2.6 % ± 0.3 %	Waterfowl	Allogenic
Tylodelphis sp.	*P. gyrina*	0.3 % ± 0.1 %	0.3 % ± 0.1 %	Waterfowl	Allogenic
Total Prevalence		**7.9 % ± 0.7 %**	**9.1 % ± 0.6 %**		

estimated by 20.3 % in May, 9.4 % in June, and 5.8 % in July due to pre-patent infections of trematodes. However, no significant differences in the underestimation of trematode parasites were observed between life cycle strategy or habitat classification in any given month ($P >$ 0.05), despite the overall prevalence being underestimated by 1.2 % due to pre-patent infections (Table 2). The frequency of all trematode parasites, both autogenic and allogenic, were similar in both the open (7.1 % ± 0.7 %) and wooded (7.3 % ± 0.7 %) transects, but a significantly higher prevalence was observed in the edge habitat (11.9 % ± 0.5 %; Chi square test, $P < 0.0001$) (Fig. 2). Both categories of parasites had distinct distribution patterns across transects and habitat types. Autogenic species had the highest prevalence of infection in snails inhabiting transects in the densely wooded vegetation (5.0 % ± 0.8 %). The prevalence in the wooded transects was significantly greater than both the edge (3.1 % ± 1.0 %) and open habitats (0.7 % ± 0.2 %; Chi squared test, $P < 0.0001$) (Fig. 2). Additionally, the generalized additive model showed that the further away from the central point in the open habitat, the higher the prevalence of infection of trematode parasites with autogenic life cycles (Generalized Additive Model, $P < 0.0001$, $R^2 = 0.91$) (Fig. 3). Allogenic parasites showed the opposite trend and were significantly more likely to occur in the open (6.5 % ± 0.7 %) and edge (8.7 % ± 0.6 %) habitats than in the wooded habitat (2.1 % ± 1.0 %; Chi-squared test, $P < 0.0001$) (Fig. 2).
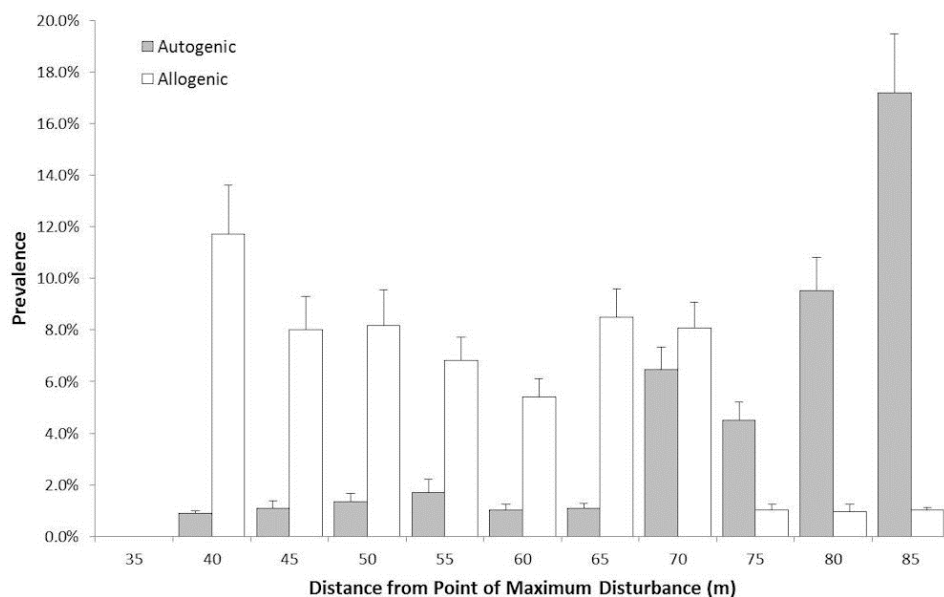

Fig. 3. Prevalence (± standard error) of autogenic and allogenic parasites in relation to the distance from the central point in the open habitat in Coon Lake

Furthermore, the generalized additive model indicated that the closer the collected snails were to the middle of the open habitat, the higher the prevalence of infection by allogenic parasites (Generalized Additive Model, $P = 0.0016$, $R^2 = 0.68$) (Fig 3).

Discussion

Differences in the microhabitat surrounding the pond influenced the infection patterns of trematodes in the molluscan first intermediate hosts, particularly between autogenic and allogenic species, but did not affect the distribution of the snail hosts. Although snail density did not differ significantly between microhabitat categories, it did vary between the snail species that were collected (Table 1). *Physa gyrina* was far more abundant than *L. columella* and also occurred at a much greater density. Additionally, the prevalence of trematode infection was significantly greater in the former species. The ecology and feeding biology of these snail species are similar (Dillon, 2000), indicating that density and abundance of the gastropod hosts may have led to differences in their infection. Furthermore, digenetic trematodes typically have high specificity for their gastropod first intermediate hosts, oftentimes with affinity to a single genus or species of snail (Haberl *et al.*, 2000; Haas, 2003; Sapp & Loker, 2009). The two snail species in this study belong to different families and only *Glypthelmins quieta* was found to infect both species. It is possible that parasites specific for infecting *L. columella* were less abundant in this system, however, this was not tested since no definitive hosts were necropsied. Despite significant differences in trematode prevalence between snails, there were similar trends and spatial patterns of trematode infection.

Allogenic species outnumbered autogenic parasites in terms of both diversity and prevalence of infection in this system. Definitive hosts of autogenic parasites, such as the *Rana* spp. in Coon Lake, are restricted to a single body of water, due to their reliance on an aquatic habitat, while definitive hosts of allogenic parasites can move between aquatic systems. As a result, a lake may be visited by not only multiple individuals of potential allogenic parasite hosts, but a wide variety of species as well, consequently increasing the diversity of allogenic parasites in an aquatic system. This allows for the potential to introduce more allogenic parasite species to a body of water.

The underestimates of parasite prevalence are not uncommon among these types of studies (Goater *et al.*, 1989). Most trematode species have pre-patent periods of 4 – 8 weeks, indicating that a majority of the parasites in Coon Lake were recruited in March and April due to the high degree of underestimation of infection in May and nearly a 4-fold reduction by July. These are common findings among trematodes in the Piedmont region of North Carolina (Fernandez & Esch, 1991; Sapp & Esch, 1994; Negovetich & Esch, 2007). Snails are in torpor and largely inactive between November and March before they emerge from the substrata. This emergence coincides with water-

fowl migrating to and inhabitating this region of North Carolina, resulting in high recruitment of allogenic parasites during this time period (Zimmermann, 2010; Zimmermann, 2014). Parasite recruitment begins to taper off as summer approaches and the migratory waterfowl travel north to their breeding grounds and the residual effects of the parasites begin to decline (Zimmermann, 2010; Zimmermann, 2014).

Autogenic species however, are present year round and could potentially induce infection in the snail intermediate hosts throughout the collection season. This can occur among trematode species that use fish as definitive hosts, since they are active and feeding throughout the year (McDaniel & Bailey, 1974). However, all of the autogenic parasites in Coon Lake cycle through *Rana* spp. Neither the largemouth bass nor the bluegill sunfish harbored adult trematode parasites with autogenic life cycles using snails as intermediate hosts (K. Luth, pers. comm.). Since *Rana* spp. were the only hosts for autogenic parasites, comparable patterns in the initial infection dynamics of parasites were observed between the autogenic and allogenic species. Similar to the snail hosts, frogs typically go through a period of hibernation and inactivity in the winter months (Holenweg & Reyer, 2000; Regosin *et al.*, 2003). This results in parallel timing of infection and pre-patent periods between the autogenic and allogenic species in the spring. The lack of differences between the different types of parasites, and the various habitat classifications, allows all the data between months to be combined.

The distribution of both the autogenic and allogenic parasites in Coon Lake appears to be the by-product of the differences in microhabitat surrounding the pond. The western bank was devoid of any vegetation aside from the grass that was planted to prevent soil erosion. These microhabitat differences affected the distribution of the definitive hosts, both visiting and permanent. Three *Rana* spp. have been frequently observed at Coon Lake, *Rana pipiens*, *R. catesbeiana*, and *R. palustris*. All of these species are ambush predators and inhabit the shallow regions of the pond and the bank surrounded by dense and emergent vegetation (Zelmer & Esch, 1999; Gagne & Fahrig, 2007; Hamer & Parris, 2011). These densely vegetated habitats offer the frogs protection from predators as well as an abundant supply of insects that also use the habitat for refuge. Similar to other studies, frogs were rarely observed in open habitats, presumably due to the risk of predation and a less abundant food supply (Paloski, 2006; Hamer & Parris, 2011).

Parasites employing allogenic life cycles in Coon Lake all used aquatic waterfowl as definitive hosts. Their behavior and habitat preference were opposite those of the frog species. The birds preferred the open habitat more than the densely wooded areas. Waterfowl were frequently observed inhabiting and grazing in the thick grass filled patches adjacent to the golf course and the wooded areas. These findings are similar to other studies in which vegetation surrounding the pond is negatively correlated with waterfowl inhabitance (Rumble & Flake, 1983; Baker, 2003; Ma *et al.*, 2010) and

that most waterfowl species prefer to forage in open areas free of vegetated cover (Darnell & Smith, 2004; Sanchez-Zapata *et al.*, 2005; Ma *et al.*, 2010). The area closest to the golf course had an extremely steep drop-off into the pond, with limited to no littoral zone. The open edges adjacent to the woods, however, offered a flat bank with an extensive littoral zone; these areas have high traffic from the waterfowl entering and exiting the pond, which probably contributed to the high prevalence of allogenic parasites in the edge regions of this system.

Other studies have shown that the environmental landscape surrounding a body of water can be an important indicator of trematode diversity (Koprivnikar *et al.*, 2006; Koprivnikar *et al.*, 2007; King *et al.*, 2010; Harston *et al.*, 2011; Schotthoeffer *et al.*, 2011), particularly among parasites infecting amphibian hosts. Additionally, non-agricultural ponds, i.e., those surrounded by at least some wooded vegetation, offer preferred habitats for aquatic waterfowl and the introduction of allogenic parasites (Bishop & Meyers, 2005; Koprivnikar *et al.*, 2006; Koprivnikar *et al.*, 2007). However, these studies are on a large-scale, with little attention given to the infection patterns of the parasites associated with the microhabitat directly surrounding a body of water. In the current study, not only did the microhabitat differences around the pond affect the distribution of the vertebrate definitive hosts, but this trickled down to affect the parasites and their distribution as well. As a result of the frog hosts inhabiting the microhabitat surrounded by dense wooded vegetation, these areas are where the autogenic parasites infected the snail intermediate hosts (Fig. 2). This resulted in the autogenic parasites being distributed further away from center of the open habitat (Fig. 3). In this particular case, snails distributed deeper in the woods were more likely to be infected by an autogenic parasite. The opposite trend was observed among the allogenic species that used waterfowl as definitive hosts. The avian hosts inhabited the regions of open and edge habitats due to the abundance of food and ease of access to enter and exit the pond. This resulted in the allogenic parasites being distributed closer to the centralized point in the open habitat and an increased likelihood of being present in the open and edge areas (Figs. 2 and 3).

The changing distribution of the hosts, and consequently their parasites, as a result of microhabitat differences can be important to the dynamics of the inhabitants of an aquatic ecosystem. Due to an overlap in the distribution of the parasites in the edge habitat, increased parasite transmission occured at these locations. Parasite prevalence in the edge habitat was significantly greater than that of the open or wooded habitats because of compound effects due to overlap in definitive host distribution. A 70 % increase in trematode infection between the edge habitat and both the wooded and open habitats was observed, however, there were fewer transects categorized as edge habitat compared to the open and wooded areas, which may have potentially influenced the results.

Microhabitat differences surrounding a body of water can have an enormous impact on the distribution and transmission patterns of parasites within it. Differences in the landscape, and potentially the distribution of the definitive hosts, can result in changes in their parasite distribution in intermediate hosts. This can create compounding effects and increased transmission in areas of extensive host overlap, significantly shaping the distribution and transmission dynamics of the parasites. This study supports the idea that microhabitat differences that are often associated with a changing environmental landscape can significantly affect both parasites and their hosts, potentially resulting in increased parasite transmission and may possibly serve as indirect markers of definitive host behavior and inhabitation in and around aquatic environments.

Acknowledgements

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