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a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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Schistosomiasis, an extremely widespread parasitic disease, is caused by flatworm parasites that transmit between freshwater snails and humans. Humans become infected after coming into contact with juvenile worms (cercariae) that are released by infected freshwater snails. Infected snails that consume more and/or better food release more cercariae, and thus pose a greater risk for humans. However, competition for resources among snails can limit an individual's parasite production. Here, I examined how asymmetry in body size affects snail competition. Using the *Biomphalaria glabrata* (snail) – *Schistosoma mansoni* (trematode) system, I manipulated the size of a focal individual (small or large) and its competitive environment (no competitor, small competitor, or large competitor; thereby creating size-symmetric and size-asymmetric pairings) and measured growth, reproduction, and parasite production in two separate experiments over 80 and 42 days, respectively. I hypothesized that large infected hosts would exert greater competitive effects than small individuals. I also hypothesized that large individuals would be less sensitive to competition than small individuals.

Both experiments revealed competitive effects on focal snails. In the second experiment, which was conducted at a lower food level, larger competitors exerted greater effects than smaller ones, consistent with my hypothesis. Unfortunately, few snails became infected in either experiment, so I was unable to assess the effects of size asymmetry on infection dynamics. However, given the positive effect of resource acquisition on cercarial production, I suspect that competition involving relatively small infected hosts could disproportionately disrupt parasite transmission.

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Introduction

Schistosomiasis is one of the most widespread parasitic diseases afflicting the world today. In Africa alone, estimates suggest that 163 million people were infected in 2012 (Lai, et al. 2015). Schistosomiasis is present in 74 countries around the world, making it the most frequent water-borne disease of rural areas in developing countries (Gryseels, et al. 2006). Schistosome infections mainly afflict children and adolescents (Doumenge, Mott, and Cheung 1987). Its symptoms vary according to the intensity of infection, and range from anemia and impairment in cognition and growth to severe organ damage and urogenital scarring (Lai, et al. 2015). In its advanced forms, schistosomiasis infection is associated with bladder cancer (Botelho, Figueiredo, and Alves 2015). Schistosomiasis is considered a major threat not because of its death rate; in 2013, it was only associated with about 5.5k deaths. Instead, its symptoms put a heavy burden on its victims, significantly decreasing their life expectancy. This life expectancy decrease, or disability-adjusted life years (DALYs) and years lost to disability (YLDs), is extremely high in schistosomiasis victims. In 2013, schistosomiasis DALY output was estimated to be about 3.06 million and its YLD output 2.86 million, ranking schistosomiasis third in DALY and second in YLD counts for neglected tropical diseases (Herricks, et al. 2017). Of the *Schistosoma* parasites, *S. mansoni*, *S. haematobium*, and *S. japonicum* cause the vast majority of human infections (Doumenge, Mott, and Cheung 1987).

Schistosomiasis may be a major threat and widespread, but it cannot be spread directly from human to human host. Schistosomes have a complex life cycle that always requires infecting a snail intermediate host. Since no other vertebrate hosts can support *S. mansoni* persistence under natural conditions (Gryseels, et al. 2006), the schistosome life cycle starts out in the human host, where mature males and females mate and produce eggs. These eggs are either trapped in the human host, inflaming nearby tissue and causing pathology, or are released into the environment through defecation or urination. If the eggs reach fresh water, they hatch into miracidia and infect nearby freshwater snails of specific genera (e.g., the genus *Biomphalaria* for *S. mansoni*). For 4-7 weeks inside the snail, the miracidia develop into sporocysts, feed off the snail, and then begin to asexually produce cercariae. Snails release these cercariae into the surrounding water, where they can penetrate human skin and mature, successfully restarting their reproductive cycle (Colley, et al. 2014). Thus, *S. mansoni* cercariae released by snails are the culprit of human infection, and their production by snail populations is a major determinant of the ecological risk for human exposure.

Schistosomes are considered macroparasites of humans because human pathology increases with infection intensity (the number of adult worms that have successfully established in a human; Gryseels et al. 2006). Historically, research and management has operated under the assumption that infected snails generally produce cercariae at a rate that is unaffected by the environment, so that the total number of infected snails would be a good predictor of human risk.(Woolhouse 1991; Woolhouse 1992; Sokolow, et al. 2015; Halstead, et al. 2018). However cercarial shedding is directly impacted by both intrinsic and extrinsic factors, such as snail body size, light, genotype, resource availability, and temperature (Karvonen, et al. 2006; Seppälä, et al. 2008; Anderson, et al. 1982; Kuntz 1947; Asch 1972; Lewis, et al. 1986; Richards 1975). Many of these effects are linked: large snails produce more cercariae (Karvonen, et al. 2006), possibly because they contain more resources for the parasite to exploit or because they feed faster than small snails (Civitello et al. 2018). Therefore, environmental conditions that influence the production of cercariae by snail populations can alter human risk of exposure and the severity of disease.

Given the powerful influence of body size and resource availability on cercarial production, resource competition among snails could alter human risk in unexpected ways. For example, resource competition can break the (assumed) correlation between snail population density and cercarial density (a key measure of human risk of exposure; Civitello et al. 2018). Body size can be an important determinant of competitive ability as well as competition sensitivity. If food resources are limiting, then infections in small snails that coexist with many large snails could be extremely unproductive. However, infections in large snails might be largely insensitive to competition from smaller snails, especially because large individuals feed disproportionately faster than small ones in almost every species (Kooijman 2010). Although this type of competition is commonly documented in plants (Weiner 1990), vertebrate animal examples also exist (Young 2004; Thompson and Fox 1993; Bassar, et al. 2016). Size-asymmetric competition could be extremely important for *B. glabrata* snails due to their large size range (1-40 mm in natural populations, corresponding to almost 1000-fold variation in biomass) (Slootweg 1987). Moreover, the distribution of body sizes in snail populations can vary seasonally or across space (Loreau and Baluku 1987).

I hypothesize that snail size and competition will interact to impact growth, reproduction, and cercariae shedding rate for several reasons. First, large snails consume food faster than small snails (Civitello et al. 2018). Therefore, they could more effectively compete and provide more resources for parasites. I predict an infected host size and competitor size interaction will occur, resulting in large competitors disproportionately affecting small hosts. Based on this interaction, I hypothesize that in a competitive environment, small snails will exert weaker competitive effects than large snails. I also hypothesize that compared to large snails, small snails will be more sensitive to competition by small or large snails. Therefore, I predict that the growth, reproduction, and parasite production of small focal snails will be most dramatically reduced by large competitors. Ultimately, understanding the strength and asymmetry of snail competition could help improve predictions and control measures for human schistosomes.

Methodology and Experimental Design

Albino Snail Growth, Maintenance, and Exposure

I obtained albino NMRI strain B. glabrata snails from a pre-existing colony maintained in High Hardness COMBO artificial lake water (Baer and Goulden 1998) with a 12:12 light:dark cycle at 26°C and fed a diet of organic chicken feed (Meatbird crumbles, Nutrena, Minneapolis, MN). I individually exposed 60 small (2.5-3.5 mm) and 60 large (7.5-8.5 mm) snails to 8 miracidia in 3 mL COMBO in 24-well plates. I also placed 60 snails of each size class individually in 24-well plates without exposure to parasites. For my second experiment, I followed an identical procedure, except that I only exposed sixty small snails to 10 schistosome miracidia each.

Snail Size Competition

I paired focal snails of each size with three different competitive scenarios: no competitor, a small (2.5-3.5 mm), or large (7.5-8.5 mm) competitor. I then maintained all individuals in lidded plastic containers with 160 mL COMBO in a constant-light incubator at 26°C.

I performed weekly changeovers to ensure water quality. During this procedure, I measured maximum shell diameter and counted eggs laid using a dissecting microscope. In my first experiment, I fed the snail pairs biweekly 15.25 mg dry weight of a 1:1 chicken feed:fish flake (Freshwater Flakes, OmegaSea, NJ, USA) mixture solidified in 1% agar. In previous research, this amount has been sufficient to exhibit competition's effects on one small snail in competition with 1-7 similarly-sized snails (Civitello, et al. 2018). In my second experiment, I fed the snail pairs 10.08 mg food per feeding to produce a more limiting competitive environment.

Visual Diagnosis of Parasite Shedding

Beginning on the fourth week post-infection, I measured the number of cercariae released by exposed snails during a two-hour “shedding” trial. Between 9 and 10am, when parasite shedding is at its peak, I removed infected snails from their environment and placed them in individual 30mL beakers filled with about 15mL of COMBO. For two hours, I incubated these beakers at 26°C with constant light. I then returned the infected snails to their respective environments. I stained cercariae with Lugol’s iodine and counted them with a dissecting scope at 10-40x magnification. If cercarial counts were greater than 200, I took two independent pictures per beaker at 10x magnification and counted a subsample of cercariae digitally with ImageJ software, multiplying by a previously determined scaling factor (3.47) to estimate total counts.

Statistical Analysis

I performed all analyses with R. Because time series observations of snail diameter and reproduction are almost always nonlinear (Gerard and Theron 1997; Civitello, et al. 2018), I used Generalized Additive Mixed Models (GAMMs) to fit a smoothed spline to the temporal trend, control for repeated measurements on each individual, and test for effects of the treatments (infection, size of the focal host, and competitor size). I used a Gaussian error distribution for snail diameter measurements and a quasipoisson distribution for the cumulative counts of snail eggs. I omitted snails from the analysis if they were exposed but never released cercariae, because I could not confirm their infection status.

Results

Snail Size is Restricted by Competition

Competition reduced growth by the focal snail in the first experiment (Figure 1A). Small focal snails were smaller than large focal snails ($t = -4.97$, $P < 0.0001$) and all snails grew significantly during the experiment ($t = 9.39$, $P < 0.0001$). Snails paired with either a small competitor ($t = -1.08$, $P < 0.016$) or a large competitor ($t = -1.26$, $P < 0.037$) were smaller than snails without competitors. However, there was no difference between focal snails competing with small or large individuals ($P > 0.05$), and there were no significant interactions between size of the focal snail and competitor size for focal snail growth.

Snail Reproduction is Restricted by Competition

Similar to effects on snail size, competition also reduced snail reproduction (Figure 2A). Matching their significant growth, reproduction for all snails increased significantly through time ($t = 2.41$, $P = 0.016$). Snails paired with a small ($t = -3.66$, $P = 0.0003$) or a large ($t = -3.01$, $P = 0.0028$) competitor demonstrated reduced per capita egg laying than those paired with no competitor, but no significant interactions between small and large competitors were detected.

Snail Size can be Restricted by Size Asymmetric Competition

My second experiment, using a lower feeding rate and only small focal snails over a period of 42 days, produced similar results (Figure 1B). Compared to a small snail in isolation, competition with small and large individuals resulted in a significant impairment of focal snail size over time ($t = -6.94029, -13.57879$, respectively; both $P < 0.0001$). Here I also observed an interaction with time ($P < 0.0001$): snails paired with large snails grew significantly slower than both other treatments, and snails paired with small competitors grew significantly slower than snails without competitors. So, under stringent competitive parameters, small snails are more sensitive to a large than a small competitor.

Parasite Production Interaction with Size Asymmetric Competition is Unknown

Unfortunately, few snails became patently infected, 7.5% (n = 120) and 0.0% (n = 45) infection rates in the two experiments, respectively. Therefore, I cannot determine the effects of competition on infection dynamics.

Figures

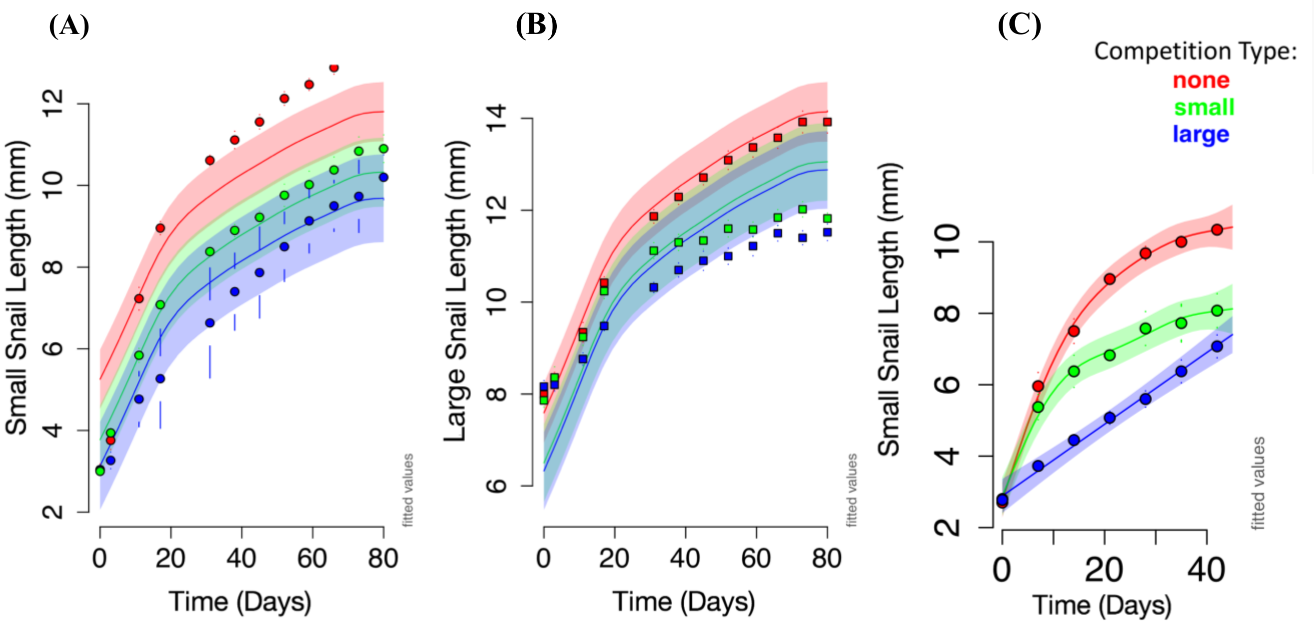

Figure 1. Size asymmetric competition restricts snail size over time. To determine if size asymmetric competition can regulate snail size, I conducted two experiments that compared a focal snail's size in three different competitive environments: no competitor, one small competitor, and one large competitor. In the first experiment, focal snails were placed in one of three different grades of competitive environments for 80 days. Focal snails started out either **(A)** small (2.5-3.5mm; n = 16) or **(B)** large (7. 5-8.5mm; n = 19), and each snail pair was fed 15.25mg food biweekly. Throughout the 80 days, focal small snails stayed smaller than their large counterparts (t = -4.97, $P < 0.0001$), and focal snails grew significantly (t = 9.39, $P < 0.0001$). Focal snails paired with a small (t = -1.08, $P < 0.016$) or large (t = -1.26, $P < 0.037$) competitor were smaller than snails with no competitor, but there was no difference between focal snails competing with small or large snails ($P > 0.05$). So, competition restricted snail size over time.

In the second experiment **(C)**, all focal snails were small (n = 13), and each snail pair was fed 10.08mg food biweekly for 42 days. Again, focal small snails paired with a small or large competitor (t-values = -6.94029, -13.57879; both $P < 0.0001$) were smaller than snails with no competitor, but focal snails paired with large snails grew significantly slower than both other treatments, and snails paired with small competitors grew significantly slower than snails without competitors. Thus, under stringent competitive parameters, small snail growth was restricted more when paired with a large than a small competitor.

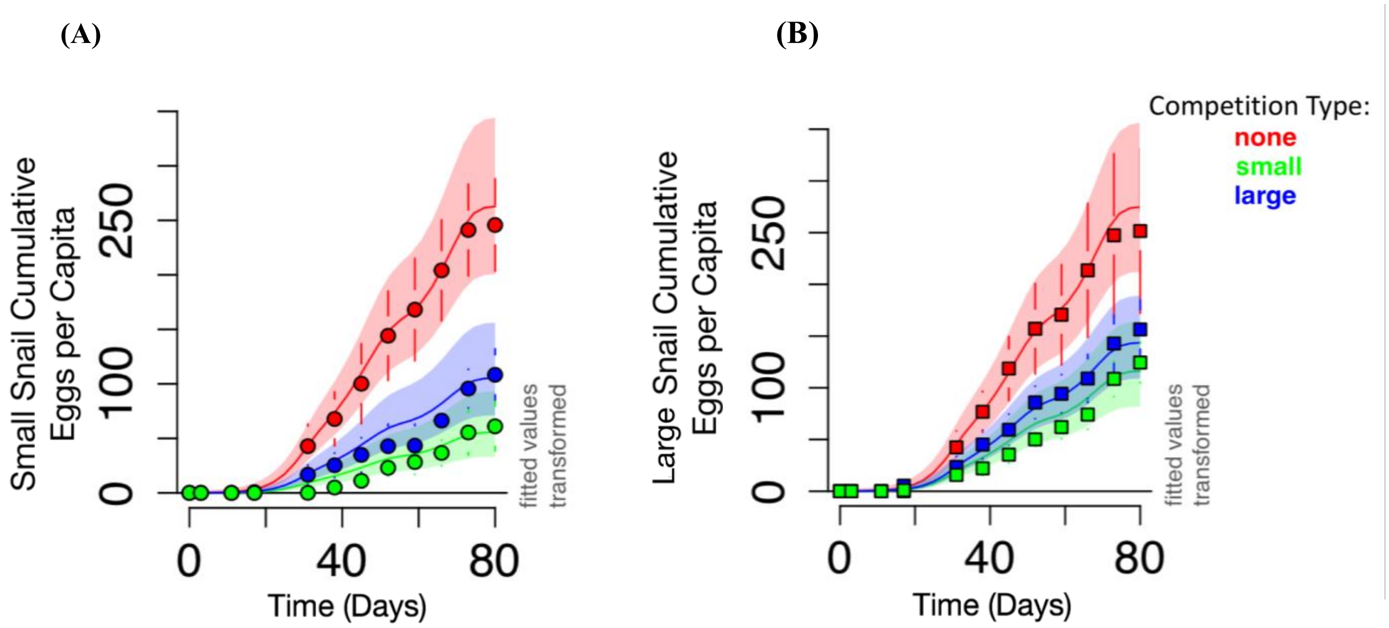

Figure 2. Competition restricts reproduction over time. To determine if size asymmetric competition can inhibit snail reproduction, I compared focal snails' eggs per capita over time, **(A)** small (2.5-3.5mm; n = 16) and **(B)** large (7.5-8.5mm; n = 19) focal snails were placed in three different competitive environments (no competitor, small competitor, and large competitor). Cumulative eggs per capita through time were compared between the competitive environments. All snails increased reproduction through time (t = 2.41, P = 0.016). Snails paired with a small (t = -3.66, P = 0.0003) or a large (t = -3.01, P = 0.0028) competitor demonstrated reduced per capita egg laying than those paired with no competitor, but no significant interactions between small and large competitors were detected. So, competition restricts snail reproduction rate over time.

Discussion

Most studies that integrate competition and infection focus on competitive effects driven by changes in population density (Brown 1982; Coles 1973; Barbosa, Barbosa, and Arruda 1993; Michelson and Dubois 1979; Richards 1975). However, individuals within populations are not all identical, and body size variation can influence competitive ability and sensitivity through resource acquisition. For example, I hypothesized that small snails will compete less effectively and be more sensitive to competition, and thus acquire fewer energy resources, than large snails, likely due to their slower feeding rate. More specifically, I predicted that in a competitive environment, infected small snails paired with an equal-sized competitor would shed fewer cercariae than large snails under the same conditions. I also predicted that compared to large snails, small snails will have a more drastic decrease in parasite shedding rates as competitor size increased, due to differences in feeding rates.

To examine this relationship, I paired two size classes (small and large) of focal snails with three competitive scenarios (no competitor, small competitor, and large competitor) and measured focal snail size, reproduction, and parasite production. Under higher resource conditions, any competitor reduced the growth of a focal snail. However, under low resource conditions I observed asymmetric effects: small snail growth was restricted more with increasing competitor size (i.e. small to large).

Snail sensitivity to competition was likely due to resource acquisition. Since my experiment focused on exploitative competition, with food as the limiting resource, any decrease in this resource results in negative consequences for snails. In the experiment, both snails by themselves and snails with competition were given the same amount of food, so snails with competition must split the food between themselves and their competitor. This results in a decrease in resources for snails with competition and thus negative consequences. Thus, when snails are paired with any size of competition, snails acquire fewer resources, producing less energy for the snail to allocate to growth and reproduction. This results in lower growth and reproduction rates.

My second experiment demonstrated that large snails exert stronger competitive effects than small snails. The lower food supply in this experiment likely produced this observable effect. Thus, the importance of resource competition in nature could depend on the productivity of the environment.

Although sufficiently low resources are needed to observe size asymmetric competitive effects, size asymmetry likely still has significant impacts on snail populations in the field. Snail populations exhibit population size structures that fluctuate with season (Loreau and Baluku 1987). The fluctuation and maintenance of these size structures may be influenced by size asymmetric competition effects, which likely play different roles according to the time of year. For example, at one time of the year, *B. pfeifferi* snail populations are mainly populated by large snails (Loreau and Baluku 1987). During this time, because the main competitors are large snails, small snails are likely severely impacted by the size competition and exhibit a decreased growth rate. This likely impairs them from reaching a reproductive size, and, due to decreased resource acquisition, they may even exhibit a higher mortality rate. These size asymmetric competitive effects may drive the snail population size distribution to lean towards large snails. In contrast, at another time of year, snail populations are mainly composed of small snails (Loreau and Baluku 1987). When most of the competition is small, small snails' growth rates will likely only be moderately inhibited. These small snails will likely grow more quickly and reach reproductive size, and their mortality rates will likely be much lower than before. This lower small snail mortality rate supports an overall population increase, which is reflected in high population density at this time of year (Loreau and Baluku 1987). Snail population density and size distribution may be driven by size asymmetric competition.

Similarly, patterns of resource availability could feed back to alter or reinforce snail population structure. The vegetation dry weight, and thus snail food availability, of the Riachuelo river basin fluctuates with season (Rumi and Hamann 1992). Although this is a *G. occidentalis* habitat, it is likely that *B. glabrata* and other snail habitats also exhibit similar features, which should be quantified in future ecological studies. In this river basin, the vegetation dry weight is the lowest during the summer (December – February) and highest during the spring (July – November). So, size asymmetric effects would likely be most pronounced during the summer months because of the low resource availability. Snail populations during the summer months may be more highly populated with large snails because the small snails are faced with pronounced size asymmetric competitive effects, decreasing their size, resource acquisition, and likely increasing their mortality (a scenario termed "juvenile bottlenecking" in population ecology). However, during the spring when resources are more available, size asymmetric effects are likely lessened, if at all observable. More resources allow small snails to grow and survive, which changes the population size distribution to include more small snails. However, this trend may be inverted should resource availability become sufficiently low at any point. If there are not enough resources, larger snails may be more affected by competition than small snails because it may be difficult to acquire enough resources to support themselves. So, size asymmetric effects may reverse, resulting in a higher large snail mortality rate, allowing the small snails to benefit from the size asymmetric effects instead.

This size asymmetric competition could also be used to more effectively utilize interspecies competition as schistosomiasis intervention strategies. Currently, *B. glabrata* are known to compete with other snails in the field. One of these species, *Melanoides tuberculata*, has been previously shown to be an effective competitor (Pointier, Théron, and Borel 1993). However, the size of interspecific competitors used has yet to be considered. For example, in *M. tuberculata,* different morphs can reach different sizes in laboratory conditions (Pointier, et al. 1992). To more effectively employ *M. tuberculata* as a competitor, perhaps a morph that grows larger should be selectively used to use size-asymmetric competition to our advantage in reducing schistosomiasis. Intervention strategies may focus on crowding, too, because crowded, infected snails grow slower, reproduce less, and produce fewer cercariae (Cooper, et al. 1992; Chernin, Michelson, and Augustine 1956). Thus, crowding snails with larger snails, especially of resistant competitor species, may increase the effectiveness of this intervention method.

Due to my low infection rates, I was unable to detect any relationship between competition and cercarial output. However, I still predict asymmetric competitive effects on cercarial production because it is related to host size and resource acquisition (Chu and Dawood 1970; Civitello, et al. 2018).

We were unable to provide such empirical evidence due to the low infection rates throughout both experiments. At present, no definite cause has been pinpointed, but it is likely due to a fault in my infection procedure. Although I increased the miracidia dosage per snail from 8 to 12 in my second experiment I still experienced extensive infection failure, so miracidia concentration is not likely the cause. It is also interesting to note that traditional infection procedures use glassware, while mine used plastic. How exactly the miracidia and plastic may be reacting is unclear, but it is possible that this step was critical to the infection process. While all of these theories are possible, the root cause of my infection failure is still unclear.

Along with abnormal infection rates, my data also produced unexpected reproduction results; however, unlike the infection rates, these results are likely due to the ambiguity inherent in my experimental set-up. According to my results, it would seem that reproduction by small focal snails were largely unaffected by the degree of their competition while, in my second experiment, their growth was significantly reduced. While this is possible, another, simpler reason is more likely. Due to my experimental set-up, the eggs laid by either the focal or competitor snail are indistinguishable. So, to determine the eggs laid per snail, the total number of eggs from each environment was counted and halved. This procedure contributed considerable ambiguity to my results, especially when an unequal number of eggs were laid per snail, which would be expected for pairs differing in size. So, it is more likely that the eggs laid by the large competitor were contributing to the per capita eggs of the focal small snails, masking the focal small snails' reproductive sensitivity. This effect can also be seen in the results of my second experiment, in which I observed reproduction in containers of some focal snails that were too small to be reproductively active. To ascertain whether this sensitivity is masked within my data due to procedural ambiguity, additional research that explores size asymmetric competition among snails with distinguishable eggs is essential. This could likely be done with heterospecific competitors that produce distinguishable eggs from *B. glabrata*.

Conclusion

My results indicate that size asymmetric competition is observable for *B. glabrata*. Small snail growth is decreased as the size of their competition increased, while large snail growth and reproduction only decreased with competition. This interaction is crucial to our understanding of the *Biomphalaria glabrata* (snail) – *Schistosoma mansoni* (trematode) system and snail host dynamics in general, as the relationship parasite production is linked to host size, which impacts host resource acquisition. Due to time and experimental constraints, I was unable to directly determine the effect of size asymmetric competition on infected hosts.

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