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The Decoy Effect in the Snail-Schistosome System

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Abstract

The Decoy Effect in the Snail-Schistosome System

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The presence of non-host species can divert parasites away from susceptible host individuals, reducing parasite transmission, a process termed the “decoy effect”. Previously, we found that the body size of host snails susceptible to human schistosomes influenced their exposure rate and susceptibility to infection. Therefore, we investigated whether the body size of non-host decoy snails could affect their exposure rates, thereby influencing transmission in snail communities. We examined two hypotheses: (1) that non-host snails would significantly act as decoys to disrupt schistosome transmission to host snails and (2) that the strength of the decoy effect would increase with increasing body size of the non-host species. We conducted transmission trials with *Biomphalaria glabrata* as a host species and *Helisoma anceps* as a non-host species to quantify these decoy effects. Populations with greater body sizes of non-host snail species had lower prevalence of infection in host snails. We then created a size-dependent transmission model for non-host snails that incorporated body size of non-host snails, susceptibility of host snails, and exposure of host snails. Fitting this model to our data indicated that (1) schistosomes cannot effectively distinguish host and non-host snails, resulting in decoy effects, and (2) larger decoys exerted stronger decoying, consistent with our predictions. This study demonstrates the potential for body size-dependent decoying in the snail-schistosome system and raises the possibility that the body size structure of host communities could influence parasite transmission more broadly.

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INTRODUCTION

Parasite transmission can be influenced by a variety of factors from both the host and the parasite, including genetic, behavioral, and ecological processes. For example, certain parasite genotypes might only be able to infect certain subsets of host genotypes (Rahmati-Holasoo 2024). In other systems, seasonal factors like temperature drive parasite population dynamics and prevalence (Lass 2006). Physiologically, host size and/or age can influence exposure rate and susceptibility to infection given exposure (Théron 1997). Ecologically, the presence of non-host species can divert parasites away from susceptible host individuals, reducing transmission by serving as "decoys" (Johnson *et. al* 2009). Understanding how these factors, which influence individual-level traits of hosts or parasites, scale up to influence parasite transmission on the population or community level is a key challenge for disease ecologists to identify new approaches to inhibit the spread of problematic parasites.

The dilution effect describes a phenomenon in which disease transmission decreases as species diversity increases (Keesing *et al.,* 2006). Host quality, abundance, and susceptibility are all factors that impact the strength of the dilution effect (Keesing *et. al* 2006). Although many systems exhibit this negative correlation between species diversity and parasite prevalence, some systems counteract this phenomenon in a process known as amplification (Civitello 2015). One particular mechanism that can cause dilution is the decoy effect. Dilution and decoy effects are thought to be particularly important in the epidemiology of human schistosomiasis (Johnson *et al.* 2009).

Schistosomiasis is a Neglected Tropical Disease that affects 200 million people worldwide and causes 280,000 deaths annually (Nelwan 2019). The disease is caused in humans primarily by three species: *Schisostoma manosni, S. haematobium,* and *S. japnicum* (LoVerde

2019). These parasites obligately cycle between freshwater snails and human hosts using free-living stages that swim through water and burrow through host skin (Niemann and Lewis 1990). The "decoy effect" has been observed frequently in studies of schistosomes transmitting through snail communities. This phenomenon suggests that while schistosomes are effective at locating snails in aquatic environments, they cannot perfectly differentiate between host and non-host snail species (Johnson *et al.* 2009). This idea has been applied as a form of biocontrol against human schistosomiasis: fully resistant snail species have been deliberated added to sites occupied by susceptible snail species to interrupt transmission. However, biocontrol success has varied substantially, depending on the region and environment; certain places successfully eliminated the disease while others exacerbated the effects of schistosomiasis (Giovanelli 2002). Therefore, understanding which factors influence the strength of decoy effects could help identify new ecological interventions for human schistosomiasis.

Recently, we found that the body size of individual snails in susceptible species strongly affected their infection risk by predictably changing their exposure rate and susceptibility to infection (Shaw *et. al* 2023). Specifically, schistosomes actively seek out host snails in water bodies in a size-dependent manner – they are better able to locate larger snails (Niemann and Lewis 1990). Thus, we hypothesized that larger individuals of decoy species could more potently disrupt transmission to susceptible snails if they also exhibit this size-dependent increase in exposure rate.

Here we used short-term transmission experiments to test the hypotheses that (1) non-host snails significantly act as decoys to disrupt schistosome transmission to host snails, and (2) the strength of effect increases with increasing body size of the non-host species. Studying these phenomena across non-host snail species is useful in understanding parasite dynamics across the

individual and population level. Because of the complexity of the snail-schistosome and its interactions with the environment, uncovering this phenomenon is important in decreasing infection prevalence and decreasing the spread of schistosomiasis.

METHODS:

Snail Maintenance:

We maintained *Biomphalaria glabrata* (NMRI strain) in favorable conditions conducive to snail growth and proliferation (Baer and Goulden 1998). These conditions include a 12:12 light-dark cycle at 26ºC in HHCOMBO artificial lake water (Baer and Goulden 1998). Changeover of lake water occurred once a week. We fed host snails with abundant food twice a week. Food consisted of a combination of fish flakes (Omega One) and chicken feed (Nutrena Meatbird Crumbles) that was suspended in 1% agar.

Transmission Trials:

We used *Biomphalaria glabrata* as the host snail species due to its role in the schistosome life cycle (Colley 2014). We used one non-host snail species that is resistant to schistosomes: *Helisoma anceps* because of their presence in endemic transmission sites (Joubert 1990). During the transmission trial, all snails were exposed to parasites for 24 hours due to the lifespan of miracidia (Esch 2001).

We used a block design to conduct transmission trials, resulting in two blocks of *Helisoma* used for analysis. For each block, we filled 15 L tanks with HHCOMBO, or artificial lake water (Baer and Goulden 1998). For each non-host snail species, we had six tanks per experimental block. Each block contained two replicates for a total of twelve tanks per block for varying size structures. In these tanks, there were 9 host snails and 9 non-host snails, resulting in a total of eighteen snails per tank. This creates a 1:1 ratio of host snails to non-host snail species. Host snails ranged in size from 2.3 to 6.0 mm in diameter, a size that exhibits high susceptibility to infection while also allowing for growth throughout the experiment (Shaw *et al.* 2023). Each

tank contained a specific size structure of non-host snails; however, non-host snails varied in size across treatments. Each replicate per block had a range of non-host snail species of different sizes, with minimal variation within tanks. The replicates with *Helisoma* contained non-host snails with average body sizes of 3.1 ± 0.2%, 4.8 ± 0.6%, 6.6 ± 0.6%, 8.2 ± 0.6%, 10.7 ± 1.7%, and 13.3 ± 2.4% mm individuals.

As a control group, we had three tanks per experimental block that consisted of 18 *Biomphalaria* snails ranging from 3.1 to 4.7 mm ± 0.52% in size. These control groups allowed for comparisons within and across blocks. This uniformly small size of snails allowed for high susceptibility to infection and low exposure rates (Shaw *et. al* 2023).

In separate well plates, we placed medium sized snails, ranging from 7.0 mm to 8.5 mm ± 0.5%, in small amounts of HHCOMBO. These snails were exposed to either 2 parasites per snail, 8 parasites per snail, or 14 parasites per snail. This condition was used to control for inter-block infectivity of parasites. We assumed that the snails were exposed to all of the parasites because of the small volume of HHCOMBO in the individual well plates (Niemann and Lewis 1990).

Infection Diagnosis:

During weeks 4 and 5, snails were shed to check for successful infections (Niemann and Lewis 1990). During shedding, snails were placed in well plates for two hours with HHCOMBO. The well plates were observed underneath a microscope to determine if infected snails have shed schistosome cercariae. A snail was considered “positive” and therefore infected when at least one cercariae was present in the well plate. During week 4, if cercariae were present, then the positive snails were separated from the maintenance tanks. If cercariae were not present, then the

negative snails remained in the maintenance tanks until the end of week 5. During week 5, shedding was repeated to determine successful infection.

Generalized Linear Models:

We used the glmmTMB package in R and created a generalized linear model (GLM) to compare prevalence of infection across different experimental blocks (fixed factor) with the *Helisoma* non-host snail species treatment, with the body size of the *Helisoma* non-host as the other fixed factor (Brooks *et al*., 2017). We used a binomial distribution due to the binary nature of infection status as either positive or negative. We viewed the effect of *Helisoma* body size as the focus of our hypotheses whereas we incorporate the block effect simply to acknowledge and account for temporal variation in the infectivity of parasites. We created one model that included our uniform small host snail controls.

Transmission Model

GLMs offer one statistical view of this experiment, but they cannot accommodate our directional hypotheses and do not represent the specific mechanism by which we predict the decoy effect to operate. Therefore, we fit a mechanistic transmission model to our dataset. Specifically, we adapted our previously published size-dependent transmission model (Shaw *et. al* 2023) to a scenario involving a fixed size cohort of susceptible host snails coexisting with a cohort of a putative decoy species that could vary in size. The model contains three coupled ordinary differential equations that track changes in the densities of susceptible (S) and infected, (I) snails as well as parasites in the water (Z) during a short-term transmission scenario that

excludes processes at longer timescales, such as births and deaths. No short-term processes affect the density of decoy snails (D); therefore their density remains constant in the model:

$$\frac{dS}{dt} = -\varepsilon\sigma SZ \quad \text{(Eq. 1)}$$

$$\frac{dI}{dt} = \varepsilon\sigma SZ \quad \text{(Eq. 2)}$$

$$\frac{dZ}{dt} = -(\varepsilon S + \varepsilon_D D)Z \quad \text{(Eq. 3a)}$$

Susceptible snails (S) become exposed to schistosome parasites (Z) at the *per capita* exposure (ε). Given exposure, a schistosome parasite causes an infection with a probability determined by host susceptibility (σ). Importantly, schistosome exposures result in the irreversible loss of parasites from the environment (Eq. 3a). In other words, schistosomes either infect or die, and no individual schistosome can invade more than one snail host. Therefore, schistosomes are lost from the environment upon exposure to susceptible snails at rate (ε) and upon exposure to decoy snails at rate (ε_D) (Eq. 3a). In this model, decoys interfere with transmission only through their exposure to and removal of parasites from the environment. Note that if the decoy exposure rate (ε_D) equals zero, then parasites would perfectly discriminate between susceptible hosts and decoys and transmission would be completely independent of decoy density. Alternatively, if $\varepsilon_D = \varepsilon$, then parasites would exhibit no preference between host types. Lastly, if $\varepsilon_D > \varepsilon$, then decoys would represent an "ecological trap", i.e., a habitat that appears attractive to a dispersing organism, but results in low fitness (Dennehy 2007).

To evaluate the size dependence of decoying, we made one further change to the model, we allowed ε_D to be an exponential function of decoy body length, L:

$$\frac{dZ}{dt} = -(\varepsilon S + \varepsilon_{D0} e^{\varepsilon_{DL} L} D)Z \quad \text{(Eq. 3b)}$$

In this size-dependent model, the parameter ε_{D0} represents the estimated exposure rate for 0 mm decoy and the parameter ε_{DL} represents the relative increase in the exposure rate for every additional mm of body length.

We then found the analytical solution for prevalence of infected snails after a $t = 1$ day exposure, $P(1)$, for the two model variants, respectively:

$$P(1) = 1 - e^{\frac{-Z_0\varepsilon\sigma\left(1-e^{-(\varepsilon S_0+\varepsilon_D D)}\right)}{\varepsilon S_0+\varepsilon_D D}} \quad \text{(Eq. 4a)}$$

$$P(1) = 1 - e^{\frac{-Z_0\varepsilon\sigma\left(1-e^{-\left(\varepsilon S_0+\varepsilon_{D0}e^{(\varepsilon_{DL}L)}D\right)}\right)}{\varepsilon S_0+\varepsilon_{D0}e^{(\varepsilon_{DL}L)}D}} \quad \text{(Eq. 4b)}$$

Here, S_0 and Z_0 refer to the initial densities of susceptible hosts and parasites, respectively, i.e., at time $t = 0$. We note again that the decoy density, D, is fixed and is therefore always equal to the density at time $t = 0$.

We then used the MCMC() function in the adaptMCMC package (Scheidegger 2024) in the R statistical programming language to estimate the parameters of these models. Following established theory for transmission experiments (Shaw *et. al* 2023), the equations for expected prevalence provide the expectation for the probability of successful infection for a binomially-distributed variable representing the number of infected snails (successes) and uninfected snails (failures) of the susceptible host species per replicate in our experiments. S_0, Z_0, D, and L were all under our experimental control for each replicate, leaving us to estimate σ, ε, and ε_D (for the model represented by Eqs. 1, 2, 3a, and 4a) or σ, ε, ε_{D0}, and ε_{DL} (for the model represented by Eqs. 1, 2, 3b, and 4b). We assumed uninformative priors for all free parameters and fit models with replicate adaptive-MCMC chains using a 100,000 iteration adaptation/burn-in period followed by 500,000 iterations that we retained for statistical analysis.

Using the first model, we assessed the ability of schistosome parasites to discriminate between susceptible hosts and decoys. We generated a test statistic, $\varepsilon_D/\varepsilon$, which represents the relative exposure rate for decoys. If this quantity equals zero, then schistosomes perfectly differentiate between the species. If it equals one, then schistosomes invade snails indiscriminately. Lastly, if it exceeds one, then decoys are disproportionately invaded, despite their death sentence for the parasite, representing an ecological trap.

Next, we compared the fit of the two models for our dataset using Bayes factors, which represent the relative support for candidate models following data analysis. Here, we assumed equal prior probability for the two models, therefore the resulting Bayes factor completely represent the models' relative performance for this dataset.

Last, we used the analysis of the second model to test the hypothesis that the decoy exposure rate increases with body size. In the model, the size-dependence of exposure rate for decoys is fully specified by the ε_{DL} parameter. Therefore, we generated a histogram of the posterior distribution for this parameter and evaluated whether the 5th percentile of this distribution was greater than zero. We then used the joint posterior distribution of ε_{DL}, ε_{D0} and ε to generate a posterior distribution for a compound function representing the relative exposure rate for decoys, $\varepsilon_{DR}(L)$ along a body length gradient compared to the susceptible host species:

$$\varepsilon_{DR}(L) = \frac{\varepsilon_{D0} e^{(\varepsilon_{DL} L)}}{\varepsilon}$$

We drew 1000 parameter estimates from the joint posterior distribution and generated a 90% credible interval for the resulting function along a size gradient of 0 – 20 mm.

RESULTS:

GLMs:

The overall prevalence for *Helisoma* is 0.62 ± 0.17 (mean ± SD). When modeling solely *Helisoma* abundance against prevalence, we did not find a significant effect on prevalence in *Biomphalaria* (P-value = 0.44). When testing whether *Helisoma* body size affected *Biomphalaria* prevalence, we found a negative, but not quite significant effect of body size of *Helisoma* on prevalence (P-value = 0.11; Figure 1). In this model, we included our *Helisoma* free controls, with a decoy body size set to zero mm (Figure 1).

Transmission Model:

We fit two closely related transmission models to the infection data. In the first model, *Helisoma* have a size-independent exposure rate, and in the second, *Helisoma* exposure rate could change with body size. Using the first model, we found that the exposure rate for *Helisoma* was roughly equal to the exposure rate for *Biomphalaria* (Figure 2). Then, using the second model, we found that the highest posterior density estimates indicated that *Helisoma* exposure rates increase with body size, with >95% of the posterior density greater than zero for this parameter (Figure 3). Applying these parameter estimates to the exposure rate function itself, we found that across the range of sizes tested, small *Helisoma* had exposure rates comparable to *Biomphalaria,* and larger *Helisoma* had exposure rates exceeding our estimates for *Biomphalaria* (Figure 4).

FIGURES:

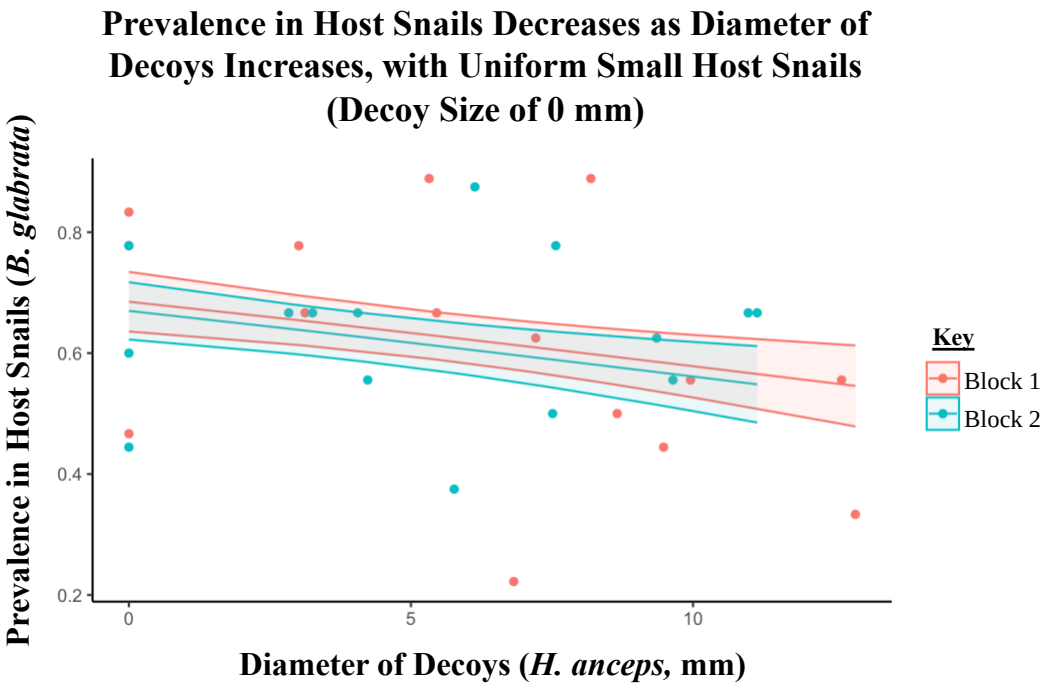

Figure 1. **Schistosome prevalence in *B. glabrata* host snails decreases as body size of *H. anceps* non-host decoy snails increase, with uniform small host snails**

Schistosome prevalence in *Biomphalaria glabrata* populations coexisting with *Helisoma anceps* populations of various body sizes. Points represent prevalence in each replicate. Lines represent best model fits from the GLM testing effect of decoy size. Peach represents Block 1 (exposure date of 8/31/23), and blue represents Block 2 (exposure date of 10/22/23). Body size was not statistically significant (P-value = 0.11); however, there was a negative relationship between the diameter of decoys and prevalence of infection in host snails. We represented the control treatment, which lacked *Helisoma,* with a decoy size of zero mm.

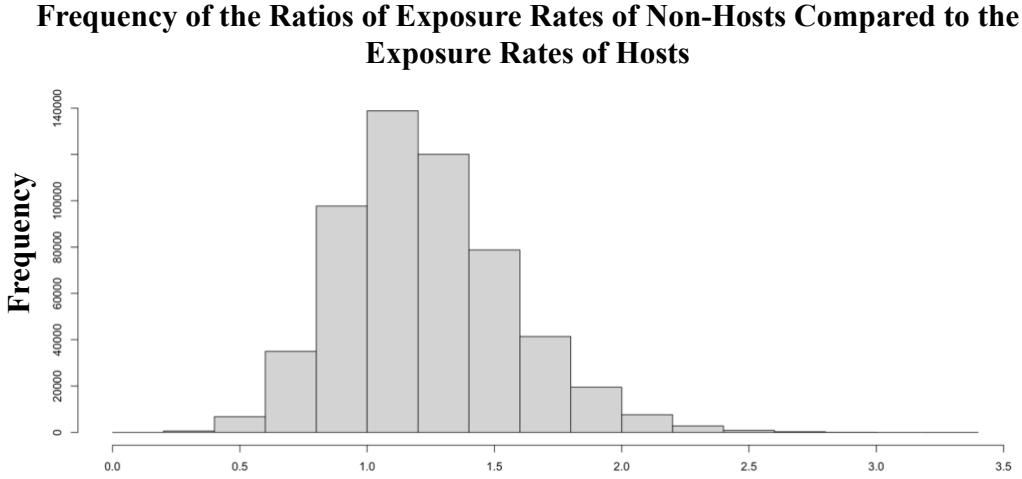

Figure 2. Modeling the frequency of exposure rates for *H. anceps* non-host snail species compared to the exposure rates for *B. glabrata* host species

After creating a size-independent transmission model, we used this model to assess the ability for schistosome parasites to discriminate between susceptible hosts and decoys. We did not consider size as a factor in this model and solely focused on the exposure rates for *Helisoma* and *Biomphalaria*. We plotted the ratio of the *Helisoma* exposure rate compared to the *Biomphalaria* exposure rate. We found that exposure rate for *Helisoma* was roughly equal to the exposure rate for *Biomphalaria*.

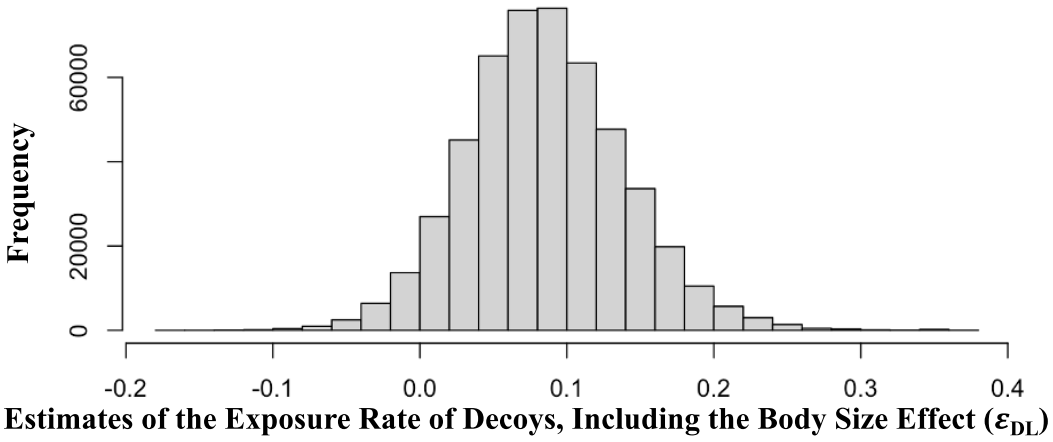

Figure 3. Histogram of posterior density estimates for body size dependence of exposure rate for *H. anceps* non-host snails

Posterior density estimates for the body size dependence of exposure rate for *Helisoma*. The highest posterior density estimate for this parameter is approximately 0.1, indicating a 10% increase in exposure rate with every increase of 1 mm in length. Less than 5% of the posterior distribution of this parameter was ≤ 0, providing significant evidence that the ability for *Helisoma* to act as a decoy increases as the body size of *Helisoma* increases, resulting in decreased prevalence in *Biomphalaria* with increasing body size.

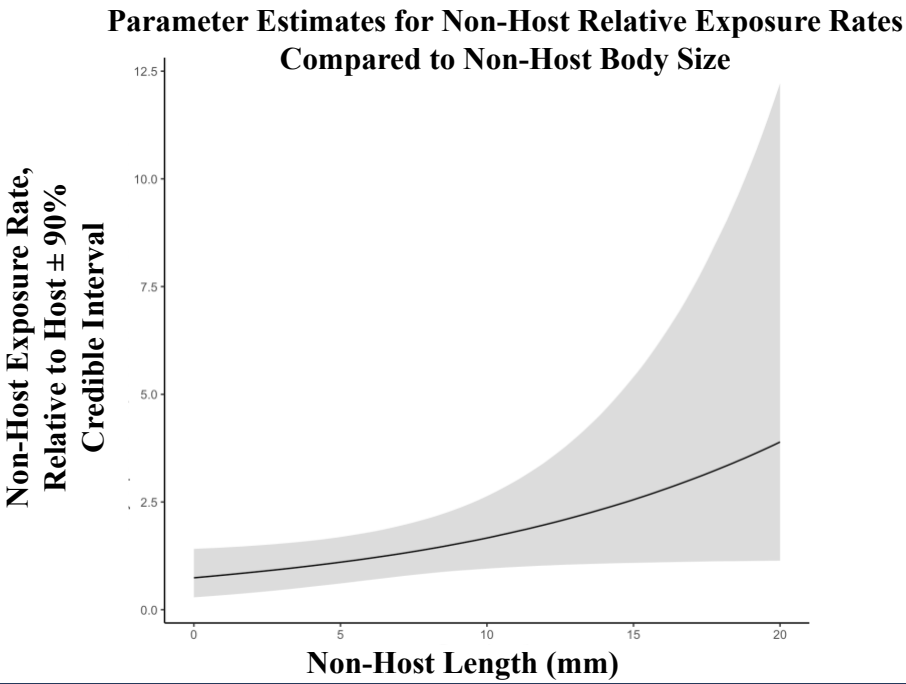

Figure 4. **Parameter Estimates for Non-Host Relative Exposure Rates Compared to Non-Host Body Size**

Using the joint posterior density for all parameters related to *Biomphalaria* or *Helisoma* exposure, we determined the exposure rate for decoy individuals relative to *Biomphalaria* as a function of decoy size. By definition, decoy exposure rate equals the exposure rate estimated for *Biomphalaria* hosts when this quantity is 1. The solid black line represents the highest posterior density prediction, and the shaded region represents the 90% credible interval. This indicates that 90% of the time this pattern will have the shape specified in the shaded region. Across the range of sizes tested, small *Helisoma* had exposure rates comparable to *Biomphalaria*, and larger *Helisoma* (greater than approximately 5 mm in length) had exposure rates exceeding our estimates of *Biomphalaria.* Again, the lower end of the credible interval remained positive and increased across the body size range, indicating significant increases in exposure rate with body size.

DISCUSSION:

In this study, we investigated the impact of non-host body size on the decoy effect and parasite transmission in heterospecific communities. We predicted that larger body size of the non-host species would decrease parasite transmission and overall prevalence and conducted transmission trials to further solidify this connection between exposure and body size of non-host snails.

We observed a lower schistosome prevalence in *Biomphalaria* snails when they were exposed to parasites in the presence of larger-bodied non-host snails (Figure 1). This data supports the decoy effect in which *Helisoma* decreases prevalence and schistosomiasis transmission as it increases in size. In other words, *Helisoma* acts as a potential "parasite sink" in which free-living parasites cannot perfectly discriminate between *Biomphalaria* and *Helisoma.* This lack of distinction indicates that *Helisoma* acts as parasite sink that stops the complex life cycle of schistosomes from proceeding (Johnson *et. al* 2009).

After creating a GLM that examined body size in relation to the uniform small snails, we identified that prevalence decreases as the body size of *Helisoma* increases. We compared *Helisoma* prevalence against uniform small *Biomphalaria* without decoys (indicated in our model as a decoy body size of 0 mm) (Figure 1). This comparison allows us to identify if there is a positive or negative correlation with size and the decoy effect. Although this model did not detect a significant effect of body size, the estimated effect was in the direction we hypothesized. Given the near significance and directional consistency of the observed data with our hypotheses, we conducted an analysis with a mechanistic transmission model, which could give us more statistical power to assess the specific way we hypothesized that decoy body size would influence transmission in these communities.

Our size-independent transmission model found that exposure rates for *Biomphalaria* and *Helisoma* were generally comparable, indicating poor ability of schistosomes to discriminate between host and non-host snails (Figure 2). Our size-dependent model, which fit better overall, showed that exposure rate increased with increasing body sizes of *Helisoma* snails, supporting our hypothesis that bigger decoys would be more effective in disrupting transmission (Figure 3).

In this experiment, *Helisoma* serves as better diluters when increasing in body size, indicating body size can serve as a moderating factor regarding the decoy effect. When *Helisoma* are approximately 4-5 mm in size, they have the same exposure rate as *Biomphalaria* (Figure 4). When *Helisoma* are bigger than 5 mm, they are better diluters, as indicated by decreased prevalence in transmission tanks with larger non-host snails (Figure 4).

In this experiment, we focused on smaller *Biomphalaria* because they have a lower exposure rate and high susceptibility to infection (Shaw 2023), thereby increasing the potential to observed decoy effects. While our observations demonstrate the phenomenon of size-dependent decoying, conducting further transmission trials with a variety of sizes of *Biomphalaria* and non-host snail species could further our understanding of the ecological relevance of these decoy effects. In addition, this study was conducted with a strain of *S. mansoni* that has been maintained in the laboratory for decades. Therefore, future studies can be conducted to compare the decoy effect with both the lab and wildtype strains. Because the lab strain has had easy, deliberate exposures to snails for many generations, there may not be as much of a selective pressure for parasites to discriminate between the host and non-hosts.

Schistosomiasis interventions can be costly and ineffective, so finding specific ways to control transmission in regions endemic to the disease can be helpful in decreasing prevalence of the disease in human populations. While the decoy effect and body size are known phenomena

that impact *B. glabrata* growth and reproduction (Johnson *et. al* 2009, Niemann and Lewis 1990), it is unknown whether the combination of these two variables can impact schistosomiasis transmission. This study found an interaction among these two concepts in the snail-schistosome system.

Helisoma have been previously used as a biocontrol agent for schistosomiasis in certain regions endemic to the disease, as indicated by a decreased infection rate and cercarial production in environments with its presence (Joubert 1990, Johnson *et. al* 2009). However, these experiments have not factored body size as a potential for further exacerbating the decoy effect and decreasing schistosomiasis transmission. The study created certain water environments with intention; therefore, further studies in the field can help in solidifying this effect in the natural world. The decoy effect can not only mitigate the spread of schistosomiasis but also other diseases (Johnson *et. al* 2009). Ecologists should consider how the relative body sizes of organisms influence parasite transmission in complex communities, especially because biodiversity loss disproportionately affects larger species (Dirzo *et. al* 2014). Considering how these systemic changes in size structures of communities can affect parasites could give ecologists new insights to predict or manage parasite outbreaks as biodiversity continues to change in the Anthropocene.

REFERENCES:

Baer, K. N., & Goulden, C. E. (1998). Evaluation of a high-hardness COMBO medium and frozen algae for Daphnia magna. Ecotoxicology and Environmental Safety, 39(3), 201–206. https://doi.org/10.1006/eesa.1997.1627

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Civitello, D. J., Angelo, T., Nguyen, K. H., Hartman, R. B., Starkloff, N. C., Mahalila, M. P., Charles, J., Manrique, A., Delius, B. K., Bradley, L. M., Nisbet, R. M., Kinung'hi, S., & Rohr, J. R. (2022). Transmission potential of human schistosomes can be driven by resource competition among snail intermediate hosts. Proceedings of the National Academy of Sciences, 119(6), e2116512119. https://doi.org/10.1073/pnas.2116512119

Dennehy, J. J., Friedenberg, N. A., Yang, Y. W., & Turner, P. E. (2007). Virus population extinction via ecological traps. *Ecology letters*, *10*(3), 230–240. https://doi.org/10.1111/j.1461-0248.2006.01013.x

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. Science, 345(6195), 401–406. https://doi.org/10.1126/science.1251817

Esch, G. W., Curtis, L. A., & Barger, M. A. (2001). A perspective on the ecology of trematode communities in snails. Parasitology, 123 Suppl, S57-75. https://doi.org/10.1017/s0031182001007697

Giovanelli A, Vieira MV, Coelho da Silva CL. Interaction between the intermediate host of Schistosomiasis in Brazil Biomphalaria glabrata (Planorbidae) and a possible competitor Melanoides tuberculata (Thiaridae): I. Laboratory experiments. Mem Inst Oswaldo Cruz. 2002 Apr;97(3):363-9. doi: 10.1590/s0074-02762002000300016. PMID: 12048567.

Johnson, P. T. J., Lund, P. J., Hartson, R. B., & Yoshino, T. P. (2009). Community diversity reduces Schistosoma mansoni transmission, host pathology and human infection risk. Proceedings of the Royal Society B: Biological Sciences, 276(1662), 1657–1663. https://doi.org/10.1098/rspb.2008.1718

Joubert, P. H., & De Kock, K. N. (1990). Interaction in the laboratory between Helisoma duryi, a possible competitor snail, and Biomphalaria pfeifferi, snail intermediate host of Schistosoma mansoni. Annals of Tropical Medicine & Parasitology, 84(4), 355–359. https://doi.org/10.1080/00034983.1990.11812480

Keesing, F., Holt, R. D., & Ostfeld, R. S. (2006). Effects of species diversity on disease risk. Ecology Letters, 9(4), 485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x

Lass, S., & Ebert, D. (2006). Apparent seasonality of parasite dynamics: Analysis of cyclic prevalence patterns. Proceedings of the Royal Society B: Biological Sciences, 273(1583), 199–206. https://doi.org/10.1098/rspb.2005.3310

Nelwan, M. L. (2019). Schistosomiasis: Life Cycle, Diagnosis, and Control. Current Therapeutic Research, Clinical and Experimental, 91, 5–9. https://doi.org/10.1016/j.curtheres.2019.06.001

Niemann, G. M., & Lewis, F. A. (1990). Schistosoma mansoni: Influence of Biomphalaria glabrata size on susceptibility to infection and resultant cercarial production. Experimental Parasitology, 70(3), 286–292. https://doi.org/10.1016/0014-4894(90)90110-X

Rahmati-Holasoo, H., Niyyati, M., Fatemi, M., Mahdavi Abhari, F., Shokrpoor, S., Nassiri, A., & Marandi, A. (2024). Molecular identification, phylogenetic analysis and histopathological study of pathogenic free-living amoebae isolated from discus fish (Symphysodon aequifasciatus) in Iran: 2020–2022. BMC Veterinary Research, 20(1), 54. https://doi.org/10.1186/s12917-024-03902-6

Scheidegger, A. (2024). adaptMCMC: Implementation of a Generic Adaptive Monte Carlo Markov Chain Sampler (1.5) [Computer software]. https://cran.r-project.org/web/packages/adaptMCMC/index.html

Shaw, K. E., Cloud, R. E., Syed, R., & Civitello, D. J. (2024). Parasite transmission in size-structured populations. Ecology, 105(2), e4221. https://doi.org/10.1002/ecy.4221

Théron, A., Pages, J.-R., & Rognon, A. (1997). Schistosoma mansoni:Distribution Patterns of Miracidia amongBiomphalaria glabrataSnail as Related to Host Susceptibility and Sporocyst Regulatory Processes. Experimental Parasitology, 85(1), 1–9. https://doi.org/10.1006/expr.1996.4106