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Consistency of trematode infection prevalence in host populations across large spatial and temporal scales

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Abstract. Parasites can impart heavy fitness costs on their hosts. Thus, understanding the spatial and temporal consistency in parasite pressure can elucidate the likeliness of parasites' role as agents of directional selection, as well as revealing variable environmental factors associated with infection risk. We examined spatiotemporal variation in digenetic trematode infection in 18 populations of an intertidal host snail (*Littorina littorea*) over a 300 km range at an 11-yr interval, more than double the generation time of the snail. Despite a complete turnover in the snail host population, the average change in infection prevalence among populations was <1% over the 11-yr span, and all but three populations remained within 5 percentage points. This consistency of prevalence in each population over time suggests remarkable spatiotemporal constancy in parasite delivery vectors in this system, notably gulls that serve as definitive hosts for the parasites. Thus, despite gulls' high mobility, their habitat usage patterns are ostensibly relatively fixed in space. Importantly, this spatiotemporal consistency also implies that sites where parasites are recruitment limited remain so over time, and likewise, that parasite hotspots stay hot.

Key words: *biogeography; Cryptocotyle lingua; environmental heterogeneity; Larus spp.; metazoan parasites; recruitment limitation; transgenerational hotspots; trophically transmitted trematodes.*

INTRODUCTION

Environmental heterogeneity has long been of key interest to ecologists, in part because it can provide insights into underlying mechanisms and extrinsic factors that affect population size and structure (Tilman and Kareiva 1997). For example, in some instances, gradients in influential environmental variables may directly shape population abundance and even community assembly (Menge 1976). For parasites, there is additional impetus to examine such heterogeneity because it informs the variability in selection pressures on hosts, the identification of environmental risk factors associated with infection, and the construction of epidemiological models (Smith et al. 2002, Ostfeld et al. 2005, Reisen 2010).

Most heterogeneity in the abundance and prevalence of metazoan parasites is studied across space, and usually found to be highly variable (e.g., Kuris et al. 1980, Granovitch et al. 2000, Smith 2001, Torchin et al. 2001, 2005, Fredensborg et al. 2006, Hechinger et al. 2007, Thieltges et al. 2013). Studies addressing their temporal

heterogeneity are less common (Esch et al. 1997, Granovitch and Johannesson 2000, Johnson et al. 2009), and the majority of these have examined seasonal variation (e.g., Latham and Poulin 2003). Although a few studies have tracked parasite prevalence and composition at a handful of sites over longer time frames (Cort et al. 1960, Sousa 1993, Keas and Blankespoor 1997), many of these have often pooled data across sites, thus conflating spatial and temporal variation and making it hard to discern whether sites respond similarly or idiosyncratically across time (e.g. Schall and Marghoob 1995, Granovitch et al. 2000). Studies also pool across time, or disregard temporal dimensions. For example, meta-analyses of parasite metrics, such as abundance, prevalence, and species richness, often analyze spatial data collected in different years (e.g., Poulin and Mouritsen 2003, Poulin and Dick 2007). Such analyses implicitly assume that temporal patterns are constant enough that the analyses isolate factors that drive spatial variability. However, without knowledge of the temporal consistency in parasite patterns, we do not know the degree to which such analyses mix variation in space and time.

To differentiate spatial and temporal variability, one needs both a large spatial scale and a long time scale.

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However, because of the considerable effort involved, spatiotemporal studies of parasites (with the exception of human diseases, which are often under active treatment) are often conducted over small scales, incorporate only a few sites, or sample a low number of host individuals (e.g., Schall and Marghoob 1995, Granovitch et al. 2000, Faisal et al. 2011). The limited number of thorough spatiotemporal investigations of metazoan parasites have shown considerable heterogeneity in parasite prevalence, especially across space (e.g., Giovanelli et al. 2001, Lively and Jokela 2002, Gomes et al. 2012).

In this study, we quantify the spatiotemporal variability in trematode parasite prevalence in a snail host across a large spatial scale and across a temporal scale greater than the generation time of the host. Looking across this decade-long time interval allows us to quantify temporal patterns divorced of autocorrelation that could otherwise affect studies on shorter temporal scales, especially since the snail host is relatively long-lived and typically retains infections for life. Furthermore, present infection levels in snails should have no direct temporal dependence on past infection levels in snails because the trematodes have an obligate multi-host life cycle (described below), and thus do not transmit infection directly from snail to snail.

Study system

On the coast of northeastern North America, the highly abundant, long-established non-native intertidal snail, *Littorina littorea*, serves as first intermediate host to five parasitic trematode species, all with obligate, multi-host life cycles (Pohley 1976, Stunkard 1983, Blakeslee and Byers 2008). *Littorina littorea* can live 5–10 yr (Hughes and Answer 1982) and once a snail becomes infected it typically remains infected for life (Rothschild 1942, Robson and Williams 1970). Infective stages of the trematodes are periodically shed from the snails as short-lived, free-swimming cercariae, which locate, penetrate, and encyst as metacercariae in the tissues of a second intermediate host. *Littorina littorea* hosts are primarily infected by one trematode species, *Cryptocotyle lingua* (Blakeslee and Byers 2008, Byers et al. 2008), which uses nearshore fishes as second-intermediate hosts (Stunkard 1930). Second intermediate hosts transmit infection when they are eaten by the definitive (final) host, typically a shorebird (e.g., gulls, cormorants, eiders) where the adult worms live for several weeks and produce eggs (Stunkard 1930, Lauckner 1985). The life cycle is completed when snails contract infections by ingesting parasite eggs, which are spread in the feces of infected birds. Gulls are ecologically the most important definitive host for *L. littorea* trematodes, and gull abundance is a good indicator of parasite prevalence at a site (Byers et al. 2008). The strong positive relationship between parasite prevalence in snails and the abundance of gulls across sites indicates that recruitment limitation of trematodes in this system is common (Byers et al. 2008).

Heterogeneity in abundance within and among parasite species is often generated by host and vector traits (e.g., Hechinger et al. 2007, Byers et al. 2015). Low mobility and restricted diets of hosts are factors that may generate stability and predictability in their parasite communities by contributing to regular and stable recruitment rates by different parasite species (Gonzalez and Poulin 2005). In this system with multiple obligate hosts, temporal consistency of spatial patterns in trematodes would seemingly require constancy in multiple host taxa, but especially in the final gull host, which is the most immediate upstream host to the focal trematode larval stages in the snails and whose abundance is tightly coupled with trematode prevalence in snails (Byers et al. 2008). Thus, similarities in trematode prevalence in snail hosts across years would suggest that gull populations, despite their omnivory and high mobility, are relatively consistent in their diets and site visitation and usage patterns. Gulls are known, for example, to show strong annual site fidelity in their choice of breeding grounds (Ludwig 1963, McNicholl 1975). Consistency in parasite prevalence could also be aided by the longevity of snail hosts (coupled with the near permanence of their infections), which integrates many infection episodes, and thus may buffer interannual vagaries in gull abundance and their associated parasite inputs (Esch et al. 2001).

METHODS

During summer 2013, we sampled *Littorina littorea* snails at 18 sites throughout New England that had been previously sampled in summer 2002 by Byers et al. (2008). The sites sampled in 2013 were well spaced throughout the entire ~300 km domain and were sites where we were certain we could sample the precise location as we had 11 yr prior. Sites were originally selected to span a wide variety of geographic settings (i.e., island, mainland, estuarine) and habitat attributes (e.g., sediment type, wave energy) from Maine to Connecticut. Our protocols for sampling infection prevalence in *L. littorea* snails were the same for both time points, as were two of the key personnel (i.e., Byers and Blakeslee).

At each site, we haphazardly collected ~200 *L. littorea* snails over a linear distance of approximately 40 m, stratifying half the collection from the high intertidal zone and half from the low intertidal zone. The high-tide contour was based on the onset of the fucoid layer in the intertidal zone [approximately +1.5 m above mean lower low water (MLLW)], and the low tide sampling area was at approximately +0.5 m above MLLW. Although tidal height was not an important explanatory factor of parasite prevalence across sites in the 2002 study (Byers et al. 2008), we replicated the sampling procedure in 2013 to be consistent with the 2002 protocol, collecting equally from both tidal heights and pooling the collections from both low and high tidal heights to yield a site-wide prevalence. Because trematodes typically infect the gonad of their snail hosts, only mature snails (≥ 8 mm) were collected.

Snail density was not quantified because prior work has shown no effect of this variable on trematode prevalence in this system (Byers et al. 2008), which is likely due to the trematodes' obligate multi-host lifecycle, where there is no direct horizontal transmission from snail to snail.

In the lab, we measured snail size as the shell length from the apex to the anterior tip of the aperture using vernier calipers. Because size and age are well correlated in *L. littorea* (Robson and Williams 1970), increasing size represents increased exposure time to trematodes in the environment (Byers et al. 2008). Thus, snail size is important to track because it is positively correlated with infection status, and as such, changes in size at a population level could account for some proportion of any observed change in population infection prevalence. We dissected snails to examine the gonad and digestive tissues under a stereo-microscope (40 \times) to determine the occurrence of trematode parasites. We identified trematode species under a compound microscope using published keys (James 1968, Werding 1969, Stunkard 1983).

To provide a broad description of prevalence patterns across time, we first calculated the prevalence of trematode infection at each site and averaged these across sites for each of the two sampling years. To evaluate the

overall trend in site-specific trematode prevalence over this 11-yr period (2002–2013) we used a paired *t*-test to compare the change in prevalence of trematode infection at each site. To visualize the data and the consistency of prevalence within sites over time, we plotted the prevalence of trematode infection in *L. littorea* at each site in 2013 against its 2002 value along with the 1:1 identity line ($y = x$), which denotes the predicted prevalences for 2013 if they were identical to those measured in 2002. We also regressed the change in infection prevalence at a site against the change in the average snail size at a site to quantify how much of the change in prevalence between years could be explained by changes in the size structure of the host population.

Next, to more formally evaluate the temporal and spatial consistency of prevalence from 2002 to 2013, we ran a generalized linear model to analyze snail infection status with a binary distribution and a logit link function (SAS 9.4) that examined the influences of site and year as main effects and snail size as a covariate, each treated as a fixed factor. The fully orthogonal model and all its reduced subsets were compared using Akaike's Information Criterion (AIC) to select the best performing model (i.e., lowest AIC). We also calculated each model's Akaike

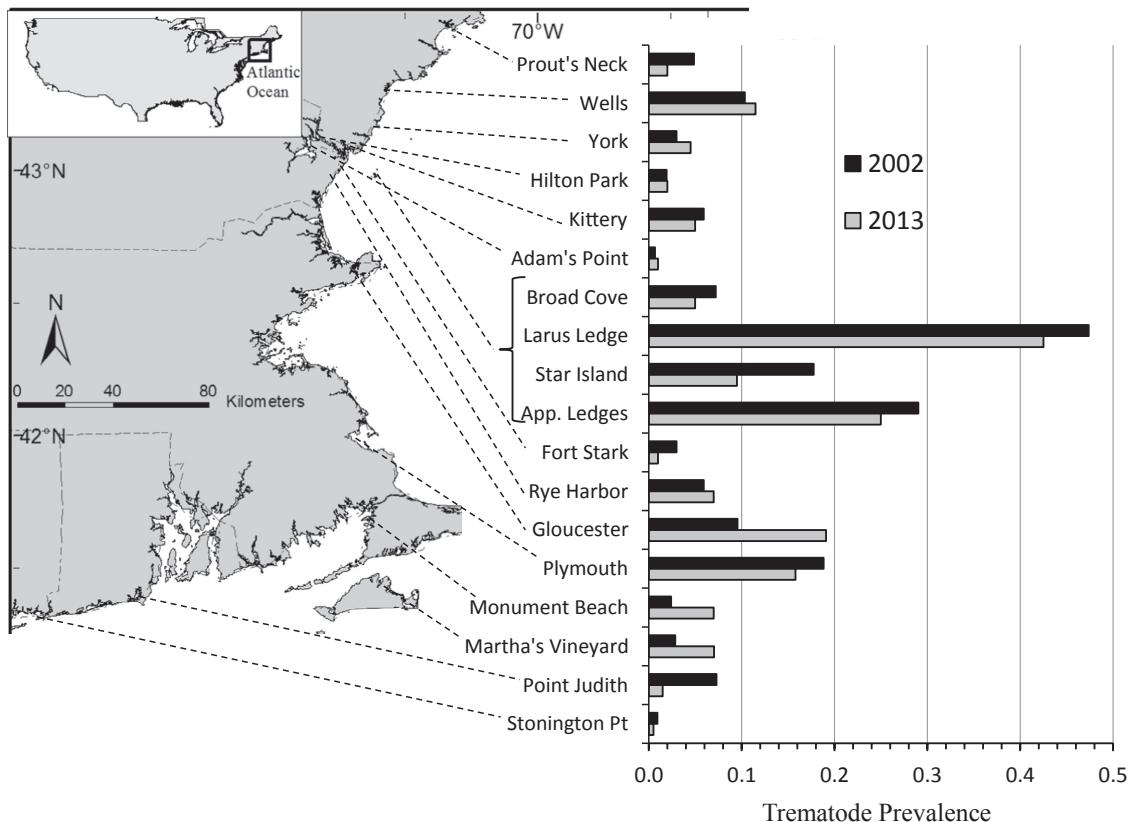


FIG. 1. Trematode prevalence in the 18 intertidal populations of *Littorina littorea* sampled in New England, USA in 2002 and 2013. The four bracketed sites are located on the Isles of Shoals archipelago.

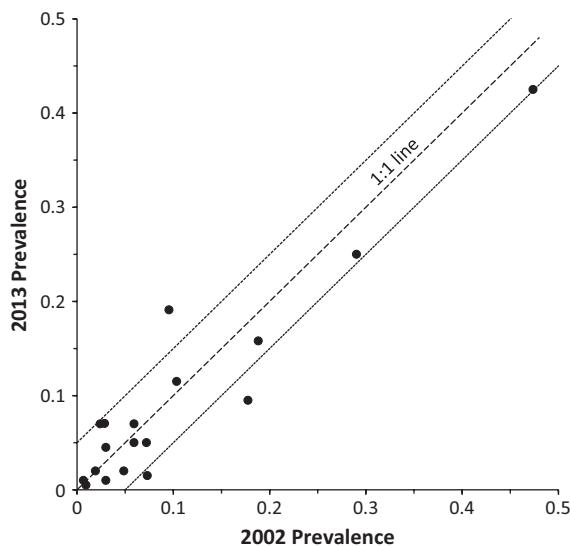


FIG. 2. The relationship of trematode prevalence in *Littorina littorea* populations in 2013 and 2002 at each of the 18 intertidal sites. Dashed line is the identity (1:1) line if prevalences were identical at each site in both years. Dotted lines bracket values five percentage points above and below the identity line. Thus, prevalence values within the dotted lines changed fewer than five percentage points across the 11-yr sampling interval.

weight (w_i), which is the model likelihood normalized by the sum of all model likelihoods, where values close to 1 indicate greater confidence in the selection of the best model. This provided a measure of the strength of the best fitting model against all others. For the generalized linear model analysis, we excluded the Point Judith, Rhode Island site because exploratory analyses showed this site to be an outlier, exhibiting a different direction of the effect of snail size on infection across years.

RESULTS

At the regional level across all sites, overall trematode prevalence and variability were very similar between sampling periods [2002: $9.9\% \pm 11.9$ (mean \pm SD); 2013: $9.3\% \pm 10.7$]. In both years, prevalence of trematodes varied substantially by site, ranging from 0.7% to 47% in 2002 and 0.5% to 42.5% in 2013 (Fig. 1). Also, in both years, the median site-level prevalence was 6%, reflecting that the distribution of trematode infection rates was heavily biased toward low prevalence (i.e., overdispersed). In addition, species specific prevalence of trematodes across all sites showed only marginal differences between the years, especially for *L. littorea*'s two most common trematodes. Specifically, *Cryptocotyle lingua* accounted for 87.4% of all infections and had an infection prevalence of 9.73% in 2002 vs. 7.89% in 2013, and *Cercaria parvicaudata* accounted for 10.4% of all infections and had an infection prevalence of 0.94% in 2002 vs. 1.14% in 2013 (Appendix S1).

Trematode prevalence changed little at the site level between 2002 and 2013. The average difference in

site-level prevalence across years was -0.66% (± 4.2 , SD) and was not significantly different from zero ($t = -0.67$, $df = 17$, $P = 0.51$). Overall, observed values for prevalence in 2013 corresponded well to the identity line (Fig. 2). In 2013, prevalence of infection at all but three of the 18 sites was within 5 percentage points of its 2002 value (Fig. 2, Appendix S2). The largest change was a 9.5 percentage point increase at Gloucester, Massachusetts. Sites where snail size increased from 2002 to 2013 tended to also increase in parasite prevalence, whereas sites with decreased mean size from 2002 to 2013 tended to decline in prevalence (Fig. 3). A sizable, marginally significant portion of the variation in the change in prevalence was explained by the change in average snail size at a site ($F_{1,16} = 3.93$, $R^2 = 0.20$, $P = 0.065$; Fig. 3). One site, Pt. Judith, RI (bottom rightmost point in Fig. 3) had substantial weight in this analysis. Highlighting its previously identified role as an outlier, exclusion of this one point more than doubled the fit of the relationship ($F_{1,15} = 11.02$, $R^2 = 0.42$, $P = 0.005$). The generalized linear model analysis corroborated the temporal consistency of infection levels at sites, showing that site and size and their interaction significantly affected snail infection status, while year and site \times year had no significant effects (Table 1). This reduced model was heavily favored over all others with $w_i = 0.67$.

DISCUSSION

Even after the passage of two generations of snail hosts, trematode prevalence remained remarkably similar within each of the 18 populations across a 300 km domain. Although spatial differences and effects of host size are readily apparent, neither of the two variables involving time had significant effects on parasite infection

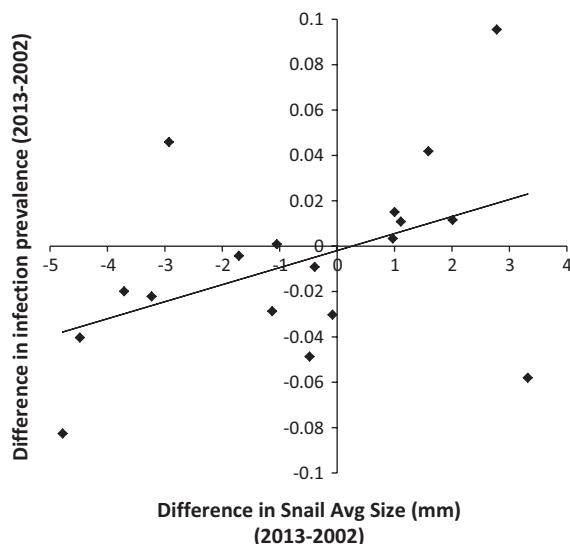


FIG. 3. The influence of the change in snail size from 2002 to 2013 at each site on the change in trematode infection prevalence over the same time period ($F_{1,16} = 3.93$, $R^2 = 0.20$, $P = 0.065$).

TABLE 1. Results of the best performing (i.e., lowest AIC) generalized linear model examining the effects of site, year, size and their interactions on the probability of snail infection. With AIC = 3474.9 and $w_i = 0.67$, this reduced model performed substantially better than the second best model that also included the non-significant factor size \times year (AIC = 3476.9, $w_i = 0.25$), or the third best (fully factorial) model (AIC = 3480.3, $w_i = 0.046$). All other models had $w_i \leq 0.02$.

Effect	Numerator df	Denominator df	F	P
Site	16	6470	2.11	0.0059
Year	1	6470	0.24	0.62
Size	1	6470	25.32	<0.0001
Site \times year	16	6470	0.86	0.61
Site \times size	16	6470	2.28	0.0025

probability (Table 1). That is, parasite hotspots stayed hot, and low infection sites stayed low. The values of parasite prevalence for each snail population at the second time point of the sampling interval are not biased by previous infection levels because ostensibly no individuals of the host populations sampled in 2002 were still alive in 2013. Thus, the consistency in prevalence across this time scale suggests a strong site-specific consistency in trematode recruitment. Definitive hosts, especially shorebirds like gulls (*Larus* spp.), are the primary trematode recruitment vector in this system and their integrated abundance is a principal driver of trematode infection prevalence (Byers et al. 2008). Thus, infection levels of gulls (contracted predominantly through their consumption of infected fish) and their habitat usage patterns, including their breeding grounds and loafing areas, must be remarkably consistent over time (Ludwig 1963, McNicholl 1975). For example, the highly infected snail populations at Larus Ledge and Appledore Ledges on the Isles of Shoals are known to be adjacent to consistently dense gull breeding grounds (Ellis et al. 2006). In contrast, several sites (e.g., Adams Point, Hilton Park, Stonington Point) had very low infection prevalence across years, and were also consistently low in gull abundance (Byers et al. 2008, *personal observation during 2013 sampling*).

The temporal consistency in prevalence is especially remarkable given that three host species are needed for the trematodes to complete their life cycle. Second intermediate hosts of the predominant parasite in this system are nearshore fish (e.g., cunner [*Tautoglabrus adspersus*], rock gunnel [*Pholis gunnellus*]). Theoretically, shifts in fish distributions could cause definitive gull hosts that prey on the fish to alter foraging patterns and home ranges. However, these fish host species are not long-ranging, and thus perhaps it is not surprising that their populations would undergo little consequential large-scale redistribution. The temporal consistency in trematode parasite prevalence in *L. littorea* may also be buttressed by the longevity of the snail hosts, which integrates exposure to upstream bird hosts, and thus may

buffer interannual variation in parasite recruitment (Esch et al. 2001).

Host demographic changes can be one of the largest influences on temporal variation in parasite prevalence (e.g., Mullowney et al. 2011). In our study, changes in the average snail size in each population explain a large part of a population's deviation from its previous infection prevalence (Table 1, Fig. 3). As in many snail-trematode systems, because larger snails are older snails, and older snails have more time to accrue infection, a positive relationship of host size and infection probability exists in this system (Byers et al. 2008). Thus, snail demography is a useful proxy for average parasite exposure time. Sites with an increase in average snail size (and thus presumably age) were 0.67 mm (± 1.83 , SD) larger in 2013 and were commensurately 1.7 percentage points (± 4.6 , SD) higher in prevalence; conversely, sites with a decrease in average snail size in 2013 were 1.65 mm (± 2.47) smaller and were 2.2 percentage points (± 3.2) lower in prevalence. These levels of change in parasite prevalence are consistent with the changes in snail size not only in direction, but also to a certain extent, in magnitude. That is, a change in size on the order of 1–3 mm, represents several months of growing time, an amount of parasite exposure time that can affect prevalence by up to a few percent if gulls are abundant (Byers et al. 2015).

Understanding temporal consistency in parasite prevalence could help to illuminate possible differences in site-specific variation in both selective pressures from parasitism and ecological processes affected by parasitism. From an evolutionary perspective, temporally consistent but spatially heterogeneous parasite pressure may cause natural selection to act on snail hosts differentially across sites. For example, high trematode loads have large fitness consequences (castration) on a snail host, however immune investment can be costly, so tailoring immune defense to match the local level of infection risk is important for maximizing fitness (Sheldon and Verhulst 1996, Zuk and Stoehr 2002, Keogh et al. 2016). For a broadcast spawning species like *L. littorea* where recruitment is mostly decoupled from the local adult population, its ability to adapt its parasite defenses to match local conditions may be reduced. In fact, the consistency of low infection risk at a majority of sites across which *L. littorea* may be connected by dispersal may overwhelm any strong localized selection favoring immunity at the handful of consistently high infection-risk sites. However, two congeneric direct-developing *Littorina* species in this system that share many of the same trematodes have shown evidence of parasite resistance that matches local parasite risk (Keogh et al. 2016). From an ecological perspective, there may be effects of temporally consistent parasite loads on intertidal communities since altered grazing by trematode-infected *L. littorea* causes differential change to the emergent algal community composition, which is a basal resource for many intertidal species (Wood et al. 2007).

Thus, it is instructive to know the degree to which a singular, static measurement of prevalence characterizes

long-term parasite pressure. As we have shown here, to evaluate the representativeness of a single prevalence measurement, one needs data on temporal variation in parasite prevalence across multiple years, especially across multiple sites, data that are rarely gathered in metazoan parasite studies. In a notable exception, Lively and Jokela (2002) examined trematode infection in populations of a New Zealand annual snail in 20 lakes after an interval of 10–15 yr and found spatial consistency in prevalence similar to the levels reported here.

In contrast to the system studied here, infection prevalence may be less consistent in dynamic systems where host and parasite populations vary in their degree of openness. For example, the prevalence of human trematodes (i.e., schistosomes) is highly variable across both space and time in their first intermediate snail hosts (e.g., Wilkins 1987, Webster and Davies 2001). In part, this is attributable to variation in the degree to which the trematodes are locally adapted to their snail host populations (e.g., Manning et al. 1995, Webster et al. 2004, Ibikounle et al. 2012). Compared to our system with highly mobile definitive bird hosts and broadcast spawning snail hosts, human schistosome-snail systems often vary along a temporal and spatial continuum of openness (e.g., ponds to streams to large lakes), with local adaptive advantages accruing differentially to the schistosomes where the system is more closed. Temporal changes in system openness and connectance (e.g., with changes in water flow or human movement patterns) would presumably also affect gene flow and the subsequent strength of parasite local adaptation, increasing fluctuations in prevalence.

In sum, we show that although parasite prevalence is highly variable spatially across host populations, within a population the prevalence is remarkably consistent across multiple host generations. Our findings suggest that upstream definitive bird hosts, especially their diets and habitat usage patterns, may be relatively fixed in space and across time. This site-level temporal consistency, coupled with the strong influence of birds on trematode recruitment, implies that sites that are parasite recruitment limited will consistently remain so. It will be informative if future studies can examine the generality of this finding across multiple host-parasite systems. Ultimately, understanding the spatial and temporal consistency in parasite infection risk can further elucidate the potential of parasites as agents of directional selection in host populations and as proxies for the integrated presence of their free-living hosts.

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