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INVITED REVIEW

How does host social behavior drive parasite non-selective evolution from the within-host to the landscape-scale?

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Abstract

Social interactions with conspecifics are key to the fitness of most animals and, through the transmission opportunities they provide, are also key to the fitness of their parasites. As a result, research to date has largely focused on the role of host social behavior in imposing selection on parasites, particularly their virulence and transmission phenotypes. However, host social behavior also influences the distribution of parasites among hosts, with implications for their evolution through non-random mating, gene flow, and genetic drift, and thus ability to respond to that selection. Here, we review the paucity of empirical studies on parasites, and draw from empirical studies of free-living organisms and population genetic theory to propose several mechanisms by which host social behavior potentially drives parasite evolution through these less-well studied mechanisms. We focus on the guppy host and *Gyrodactylus* (Monogenea) ectoparasitic flatworm system and follow a spatially hierarchical outline to highlight that social behavior varies between individuals, and between host populations across the landscape, generating a mosaic of ecological and evolutionary outcomes for their infecting parasites. We argue that the guppy-*Gyrodactylus* system presents a unique opportunity to address this fundamental knowledge gap in our understanding of the connection between host social behavior and parasite evolution. Individual differences in host social behavior generates fine-scale changes in the spatial distribution of parasite genotypes, shape the size, and diversity of their infecting parasite populations and may generate non-random mating on, and non-random transmission between hosts. While at population and metapopulation level, variation in host social behavior interacts with landscape structure to affect parasite gene flow, effective population size, and genetic drift to alter the coevolutionary potential of local adaptation.

Significance statement

Social interactions between animals shape the evolution of the pathogens that infect them. Most research exploring this phenomenon has focused on the selection such interactions impose, but social hosts also shape parasite evolution by determining the ability of their parasites to respond to that selection. Here, we explore how host social behavior drives parasite evolution by shaping non-random mating, gene flow, and genetic drift, from the scale of the individual to the landscape. The relative strength of these evolutionary mechanisms can have striking implications for the evolution of parasite traits such as virulence and alter the evolutionary trajectories of populations across the landscape. We emphasize the importance of studies combining parasite population genetics, host social behavior, and landscape processes to illuminate complex host-parasite coevolutionary dynamics.

Keywords Host social behavior · Host-parasite coevolution · Landscape population genetics · Spatial scale · Parasite non-selective evolution · Parasite transmission dynamics

Introduction

Host social behavior strongly influences parasite transmission between hosts and thus the ecological and evolutionary trajectories of parasite populations among individual hosts, between host populations, and across the landscape (Paull et al. 2012; Albery et al. 2021). We define social behavior as

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This article is a contribution to the Topical Collection Sociality and Disease

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Extended author information available on the last page of the article behavioral interactions between conspecific animals. These interactions may be negative (e.g., aggression, avoidance) or positive (e.g., allogrooming, affiliation) in nature and can occur within or outside the context of discrete social groups. We include mating interactions in this definition. A previous work exploring the evolutionary implications of host social behavior for metazoan parasites has focused almost exclusively on the form and strength of selection on parasite phenotypes, such as virulence (Boots and Sasaki 1999; van Baalen 2002; Walsman et al. 2021) and transmissibility (Stroeymeyt et al. 2018; White et al. 2018). Host social behavior also has the potential to affect other evolutionary processes, including gene flow, non-random mating, and genetic drift, but these have received substantially less research attention. This is especially true for directly transmitted parasites that reproduce in or on the host. However, the relative dominance and interactions among evolutionary mechanisms can have striking implications for parasite response to selection (Fig. 1). Understanding the parasite's population structure and genetic mating system (hereafter "mating system"; the manner in which gametes unite to form a zygote with particular regard to relatedness; Table 1) is therefore key to predicting virulence evolution (Frank 1996). Similarly, the spatial population structure of parasites and their hosts, the dispersal rates of each, and population-level differences in demographic processes—all affected by host social behavior—will shift host-parasite coevolutionary outcomes across the landscape (Lively 1999; Thompson 1999; King et al. 2009). We therefore highlight the often-overlooked importance of host social behavior for parasite non-random mating (i.e., mating system), gene flow (i.e., population substructure), and genetic drift (i.e., changes in population effective size, bottlenecks, and genetic diversity), and emphasize the importance of incorporating multiple spatial scales (Fig. 2).

Population genetics presents an important set of molecular tools to indirectly infer the ecological and evolutionary implications of host social behavior for parasite ecology and evolution (Criscione et al. 2005; Gorton et al. 2012). Disruptions to panmixia can occur at multiple scales and the patterns of genetic structuring depend on the ecological mechanism that generates these disruptions, many of which may work in concert to generate the observed genetic patterns. While there are many other potential candidates, we focus on host social behavior as one such ecological mechanism because much recent research has focused on its role in imposing selection on parasites. A key difference between free-living and parasitic organisms is that parasite populations are further subdivided through non-random transmission between the "infrapopulations" of individual hosts and thus additionally affected by host biology and behavior (Table 1, Fig. 2a). Genetic variation must be assessed across these hierarchical levels: disruptions to panmixia at the infrapopulation scale that go unrecognized can confound patterns detected at the larger spatial scales (Criscione et al. 2005; Prugnolle and De Meeus 2010; Gorton et al. 2012). Importantly, the rate of genetic exchange between infrapopulations depends on migration rates between them

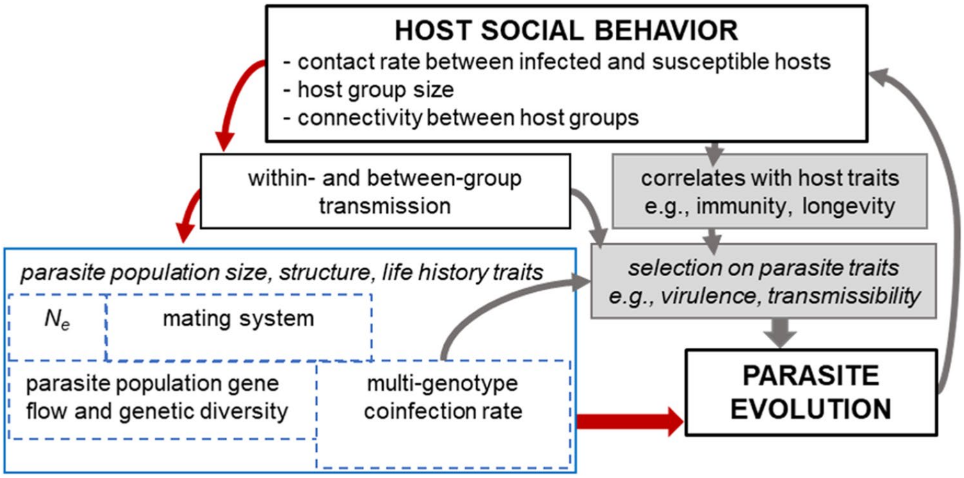

Fig. 1 Host social behavior and parasite evolution result in complex bidirectional interactions. Host social behavior may shape parasite evolution through multiple pathways, not all of which are included in this chart. Increased contact rate, group size, and connectivity between host individual and groups facilitate parasite transmission, effective population size, genetic diversity, mating system, and structure (dashed boxes), which can be directly or indirectly estimated through studies of parasite population genetics. The combination of the factors in the blue box affects the strength of selection and the ability of the parasite population to respond to selection, which will feedback to affect host social behavior and thus are essential to our understanding of these bidirectional interactions in wild populations. Red arrows indicate processes discussed in this review, while gray arrows have been covered extensively elsewhere. In this review, we focus on the effects of host social behavior on parasite population structure, mating system, and gene flow

Table 1 Glossary of terms used throughout the paper

Automictic parthenogenesis	The production of diploid daughters from unfertilized eggs. The first stages of meiosis occur and diploidy is restored by the fusions of two nuclei originating from the same oocyte. Automictic parthenogenesis increases homozygosity in each generation but the rate of increase depends on the cytological mechanism restoring the diploidy
Between-clone mating	Mating between two individuals originally derived from parthenogenetic reproduction. The resultant offspring will have a reduction in heterozygosity akin to the rates generated by selfing
Clonemate	Genetically identical individuals generated through asexual reproduction
Clonal co-transmission	The clumped dispersal of clones from one host—the "donor"—to the next—the "recipient"
Component population	All the parasites infecting the host population
Effective population size (*Ne*)	The ideal population size is *N* in which all parents have an equal expectation of being the parents of offspring within the population. The size of *Ne* determines the rate of change in the population due to genetic drift. When the infrapopulation is stable over successive generations, genetic drift within the infrapopulation may weaken the force of selection. Note that the parasite effective population can be considered the infra-, component, or metapopulation, depending on the migration, or transmission rate between hosts
F_{IS}	The proportional change in heterozygosity relative to Hardy–Weinberg equilibrium is due to the non-random union of gametes in a subpopulation. Positive F_{IS} can be caused by mating between closely related individuals, or when two genetically differentiated populations are analyzed as one (see Wahlund effect)
F_{ST}	Proportional change in heterozygosity relative to Hardy–Weinberg equilibrium due to subdivision within the population. Larger values of F_{ST} indicate greater population subdivision
Genetic drift	Random changes in allele frequency in a finite population
Habitat configuration	Amount and spatial arrangement of biotic and abiotic components of the habitat
Inbreeding	Mating among individuals is more closely related than expected at random within the population. Inbreeding may be the result of self-fertilization or biparental inbreeding (mating between two closely related individuals, such as full siblings)
Infrapopulation	All the parasites infecting a single host at a particular point in time
Linkage disequilibrium	The non-random association of alleles on different loci (also called gametic disequilibrium). Detecting linkage disequilibrium among loci can be an indication of inbreeding or small effective population sizes. However, it may also be caused by sampling closely related individuals, such as siblings
Mating system	Here we use "mating system" to refer to the genetic mating system of parasites, not the behavioral mating system of hosts. Specifically, we use mating system to refer to the manner in which gametes unite to form a zygote. This may be random or non-random. We specifically focus on mating system regarding relatedness
Sibling co-transmission	The clumped dispersal of siblings to subsequent hosts
Social behavior	Behavioral interactions that occur among conspecific animals and vary in duration. These interactions can be "negative" (e.g., aggression, avoidance) or "positive" (e.g., allogrooming, affiliation) in nature and can occur within or outside the context of discrete social groups. We include mating interactions in this definition
Transmission bottleneck	A genetic reduction in diversity is when a small number of individuals or a number of genetically similar individuals are transmitted from one host to another. Large or wide transmission bottlenecks are less restrictive than small or narrow ones. Bottlenecks may occur between host individuals when the infrapopulation is the unit of evolution, or between component populations when infrapopulation turnover is high
Wahlund effect	The reduction in the proportion of observed heterozygotes relative to the expected Hardy–Weinberg proportions in a sample caused by population substructure

(Criscione and Blouin 2006; Prugnolle and De Meeus 2010) which, for many systems, will be dictated by the transmission opportunities afforded by social interactions between hosts. Host social behavior can therefore be expected to fundamentally shape both selections on parasites, and their gene flow and mating systems, and thus ability to respond to that selection (Fig. 1). Early work on the importance of spatial genetic structure on parasite population genetics stems from a series of multi-scale publications in a seabird tick system by McCoy and colleagues. This work, which is foundational to the parasite population genetics work we review here, compared fine-scale spatial genetic structure and tick diversity within and among nests of the seabird hosts (McCoy et al. 2003a) and regional scale host-driven differences in dispersal among tick races (McCoy et al. 2003b). (For a more detailed review of publications in this system, see Gorton et al. (2012).)

To date, there is a paucity of research explicitly testing the effects of host social behavior on parasite population genetics. Lumme and Zietara (2018) sequenced the infrapopulations of *Gyrodactylus arcuatus* infecting adult and juvenile three-spined stickleback in a single host population at three time points to examine how host mating and shoaling behavior affect parasite population structure. Initially, *G. arcuatus* infections on juvenile fish consisted of low-intensity infections composed primarily of clonally derived

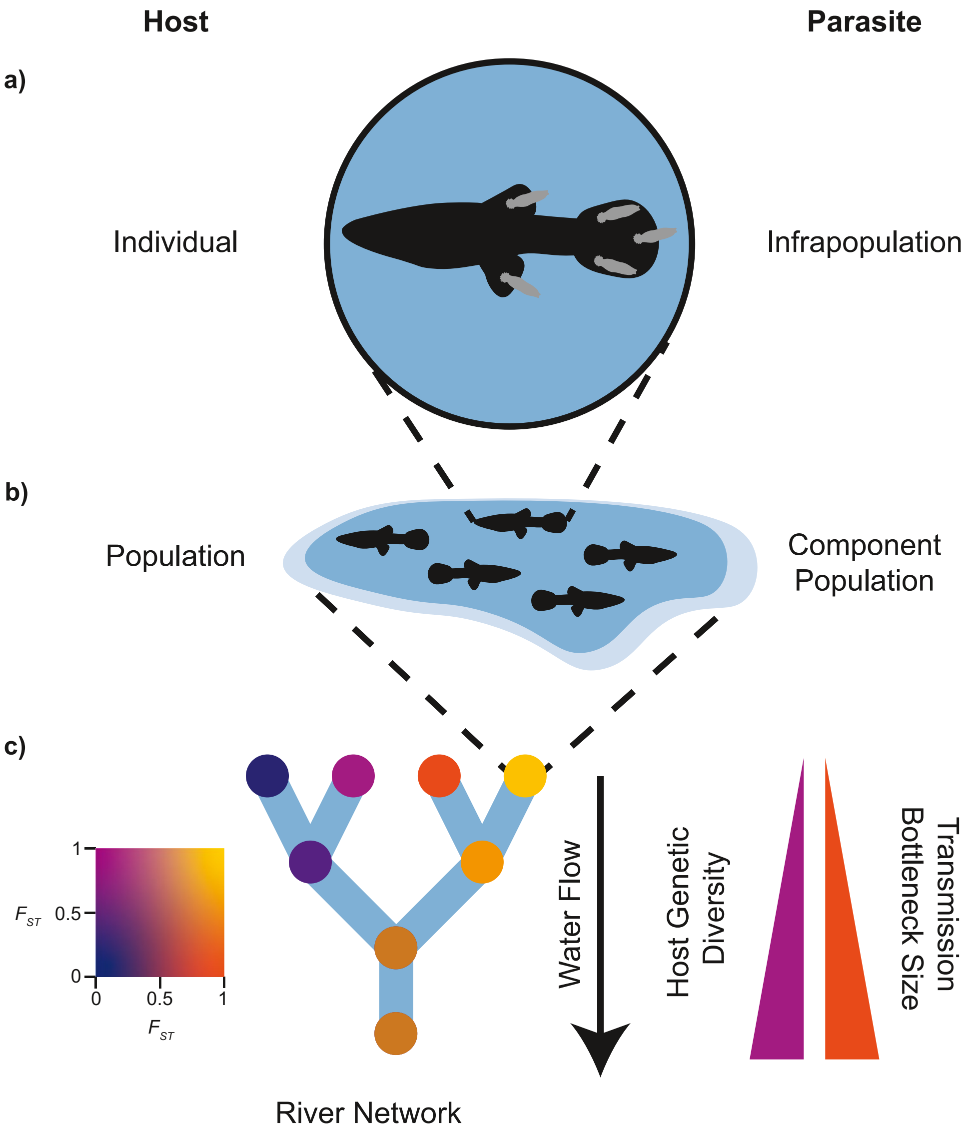

Fig. 2 At the finest scale, **a** parasites are subdivided among individual hosts, generating infrapopulations made up of the parasites infecting a particular host at a particular point in time. Parasite infrapopulations composed of successive recurrent generations of individuals will function as a deme and genetic drift will act within the infrapopulation. Transmission bottlenecks between individuals will influence the genetic diversity of parasites interacting within the infrapopulation. At the population scale, **b** the parasite component population is composed of all the parasites infecting all hosts. When infrapopulation turnover is high, genetic drift will occur within the component population. At the metapopulation scale, **c** the placement of a population within the complex habitat configuration and landscape processes directly affects the diversity of parasite genotypes to which a host is exposed. Dendritic branching interacts with host dispersal behavior to influence gene flow and subsequent genetic differentiation within the network. Genetic differentiation between populations is illustrated by circle color in which greater color differences between populations indicate greater genetic differentiation and higher F_{ST} values (adapted from Thomaz et al. 2016)—the inset color graph represents local population genetic identity in multivariate space. Asymmetric dispersal in response to unidirectional stream drift results greater genetic diversity downstream and in narrower parasite transmission bottlenecks farther upstream, increasing the strength of genetic drift upstream (see Fig. 3)

parasites, but diversity rapidly increased to levels similar to infrapopulations on adults, despite juveniles having overall smaller infrapopulation sizes. These results suggest that host social behavior permits continuous parasite transmission, resulting in diverse mitochondrial haplotypes at the infrapopulation level and low levels of relatedness over the course of the infection (Lumme and Zietara 2018). Host social behavior also appears to have an important role in structuring the populations of mites infecting bats: Bruyndonckx et al. (2009) found patterns of isolation by distance and strong population subdivision between, but not within, wing mite (*Spinturnix bechsteini*) populations infecting colonies of Bechstein's bat (*Myotis bechstienii*), indicative that host social roosting behavior limits long-distance mite dispersal. Additionally, a cross-species comparison indicated that *S. myotis*, which infects a more social bat host, *Myotis myotis*, exhibited higher intensity of infection, greater genetic diversity, and lower genetic differentiation among colonies, when compared to *Spinturnix bechsteini* infecting the less social *Myotis bechstienii* (van Schaik et al. 2014). Further work in the genus *Spinturnix* demonstrated that both host social organization and mating system shapes mite aggregation, prevalence, and intensity (van Schaik and Kerth 2017). The authors note that these patterns are likely to have consequences for the population genetic structure of the parasite but did not include population genetic analysis within the study. Wohlfeil et al. (2020) found that tick relatedness increased with increased spatial proximity and asynchronous shared refuge spaces within social networks of their hosts, Australian sleepy lizards (*Tiliqua rugosa*). However, Portanier et al. (2019) found no evidence that social behavior in Mediterranean mouflon (*Ovis gmelini musimon*) generates fine-scale spatial genetic structure in *Haemonchus contortus*, a nematode with direct transmission, likely because the free-living stage of the parasite, coupled with a broad host range, facilitates parasite genetic mixing beyond that suggested by the host social behaviors.

Future work should build on these foundational studies of host social behavior driving parasite population structure: deeper analysis across hierarchical scales can address the implications of this structure for parasite mating within the host, and subsequent transmission between hosts. For the remainder of the review, we use empirical data and population genetic theory to suggest likely important, but as yet unstudied, patterns at this exciting early stage of investigations into how host social behavior shapes parasite non-selective evolution. We highlight that future research incorporating field sampling in natural experiments, experimental manipulations, and population genetic hypothesis testing is sorely needed to elucidate how ecological mechanisms, including host social behavior, may structure parasite populations. We structure our review by spatial scale, first examining the impact of individual-level host social behavior, and then population- and metapopulation-level variation in host social behavior, on the structure of parasite populations at the corresponding scales of within-host (infrapopulation), between-host (component population), and metapopulation. Wherever possible, we focus on host-specific metazoan ectoparasites with direct transmission and simple, one-host life cycles because their population size and structure are intuitively most likely to be influenced by host social behaviors. Furthermore, host social behavior is likely to be particularly important in structuring the populations of directly transmitted parasites: social interactions involving infected hosts facilitate their direct transmission, but pathology caused by the infection, particularly if parasites reach high loads on individual hosts, may induce susceptible hosts to actively avoid infected hosts.

With this review, we aim to highlight the utility of the well-characterized Trinidadian guppy (*Poecilia reticulata*) and its directly transmitted monogenean ectoparasites, *Gyrodactylus* spp., as a model system both to address the existing knowledge gap and also provide a useful illustration of the patterns and processes, we predict are likely important. Guppies are a classic ecoevolutionary model (Reznick et al. 1997; Magurran 2005) because the geographic mosaic of Trinidadian river ecosystems generates a "natural laboratory" for studying guppy evolution in response to variation in predation pressure: waterfalls form upstream migration barriers to large piscivorous fish, resulting in upper and lower course guppy populations experiencing dramatically different predation regimes. Since the 1960s, researchers have worked to demonstrate that this difference in predation regime has resulted in repeated evolution of divergent guppy life history, behavior, and morphology (reviewed in Magurran 2005). The interactions between the guppy and its directly transmitted ectoparasites, *Gyrodactylus turnbulli* and *G. bullatarudi*s, have also received some research attention (Cable and van Oosterhout 2007; Martin and Johnsen 2007; Fraser and Neff 2009; Fraser et al. 2010; Gotanda et al. 2013; Stephenson et al. 2015a, b; Xavier et a. 2015; Mohammed et al. 2020), and molecular genetic tools provide new and rare opportunities to investigate parasite response to host social behavior (Konczal et al. 2020, 2021). Gyrodactylid reproduction in the wild is complex, which presents opportunity for future study (Shelkle et al. 2012). Gyrodactylids produce two daughters asexually, after which individuals grow a penis and can reproduce either sexually or asexually (Cable and Harris 2002). The first daughter is produced through asexual proliferation which would result in an offspring with an identical multilocus genotype to the mother (Cable and Harris 2002). The mating between two genetically identical clonally derived individuals results in patterns of reduced heterozygosity analogous to selfing (Svendsen et al. 2015; Criscione and Blouin 2006). Self-fertilization reduces heterozygosity by 50% compared to the parent generation, while the expected heterozygosity decreases due to parthenogenesis depend on the phase of meiosis in which the fusion of the meiotic products takes place and the form of automictic parthenogenesis (Svendsen et al. 2015). The second asexually produced daughter is generated through automictic parthenogenesis, although the automictic mechanism is unknown (Cable and Harris 2002). Automixis by gamete duplication and terminal fusion will increase homozygosity, while central fusion will maintain heterozygosity in the offspring relative to the adult (Engelstädter 2008; Tanaka and Daimon 2019). Thus, they exhibit acyclical partial clonality, where sexual reproduction, clonality, and parthenogenesis co-occur in time (Rouger et al. 2016). Infection by a single individual can result in epidemic infections that induce significant host morbidity and mortality (Harris and Lyles 1992; Bakke et al. 2007). Crucially for our review, guppy behavior, including social interactions, has been extensively characterized both in the wild and in the laboratory (reviewed in Houde 1997; Magurran 2005), and *Gyrodactylus* spp. transmission has been linked directly to host social behavior. We therefore draw from theoretical models, population genetic analyses from free-living wild systems, and the highly characterized Trinidadian guppy model system to generate predictions of how host social behavior could shape parasite population genetic structure, and thus parasite evolution through both selective and non-selective processes.

How do individual host social interactions determine parasite population genetic structure and mating system?

We draw from our focal system, Trinidadian guppies and their Monogenean ectoparasites, *Gyrodactylus* spp., and the wealth of knowledge about the host's behavior, to illustrate that host social behaviors affect the frequency and type of contact between hosts, and the identity of the interacting hosts. The extent to which host social decisions mean they encounter the same subset of conspecifics will determine the extent to which transmission is clustered and therefore the identity of parasite individuals that interact. This section is divided into two subsections: in the first, we focus on guppies to illustrate how host social behaviors may affect the distribution of parasites among hosts. In the second, we draw from theory and empirical work on free-living and parasitic animals to generate general, testable predictions about the implications of these host behaviors for parasite population genetic structure and mating system.

Guppy individual-level social behavior likely changes the frequency and type of transmission opportunities for their parasites

Larger host social groups and higher host density should intuitively lead to increased contact rates between hosts and therefore more parasite transmission and thus larger parasite populations (Côté and Poulinb 1995; Patterson and Ruckstuhl 2013). From the parasite's perspective, it is likely more complicated: host social interactions within a population are often non-random, resulting in higher contact between particular individuals than otherwise expected due to chance. Thus, group size alone likely does not capture how host social behavior drives parasite transmission. Indeed, our focal guppy hosts tend to live in social groups, "shoals", as an anti-predator defense (Farr 1975) and to improve foraging efficiency (Day et al. 2001), the composition of which is highly non-random. Individual guppies discriminate between potential shoalmates based on their size (Croft et al. 2003b), sex (Magurran et al. 1992), familiarity (Magurran et al. 1994; Sievers and Magurran 2011), reproductive receptivity (Guevara-Fiore et al. 2009; Brask et al. 2012), personality (Lucon-Xiccato and Dadda 2017; Kniel and Godin 2019), cooperativeness (Brask et al. 2019), diet (Morrell et al. 2007), relatedness (Griffiths and Magurran 1998; Piyapong et al. 2011), and population of origin, as well as rearing density (Song et al. 2011).

These individual-level decisions affect the conspecifics a guppy electively interacts with, and therefore the shape of their social networks (Croft et al. 2005a, b), and vary both between individuals and contexts. The structure of a social network is therefore dependent on its members and can be highly dynamic. For example, female guppies shoal more than males (Magurran et al. 1992), preferentially with familiar (Griffiths and Magurran 1998) and same-sex conspecifics (Shohet and Watt 2004), unlike males (Godin et al. 2003). Females therefore have more stable social interactions than males (Croft et al. 2005a; Krause et al. 2017). Further to this, these individual differences in shoaling are context-dependent: for example, the visual stimulus of a male decreases shoaling tendency in single-sex female shoals (Darden and Watts 2012). Indeed, sexual behavior further shapes the host social network. Female guppies in many populations prefer males with larger areas of orange coloration (Houde and Endler 1990), who exhibit mate choice copying (Dugatkin and Godin 1992), and with size-assortative mating (Auld et al. 2016), potentially clustering social networks around a few key males. However, both sexes exhibit a preference for novelty (Hughes et al. 1999; Eakley and Houde 2004; Zajitschek et al. 2006; Mariette et al. 2010; Macario et al. 2017), which decreases the modularity of contacts. Relatedness may or may not affect mate choice: Viken et al. (2006) found that mature virgin females may not actively discriminate between related and unrelated males, and inbreeding can be favored for optimizing offspring genotypes (Neff 2004). Overall, guppy networks are highly modular with short path lengths: individuals within a shoal directly contact only about 15% of the network (Croft et al. 2004). Importantly, individual network position remains stable over time (Krause et al. 2017). Collectively, these studies indicate how individual variation in guppy social behavior can generate fine-scale spatial variation in parasite transmission opportunities.

This remarkable body of work (our review of which is not exhaustive) yields a deep understanding of the factors affecting guppy social interactions and enriches our predictions about parasite transmission in this system. Our focal parasites, *Gyrodactylus* spp., are transmitted through close contact during social interactions (Johnson et al. 2011), so guppy social network structure likely influences the identity of hosts coming into transmission-relevant contact, and the rate of transmission between them. As guppies are live-bearing fish with internal fertilization (Houde 1997), these parasites are also sexually transmitted (Houde and Torio 1992; Able 1996). Importantly, males vary in the extent to which they court females or attempt coercive mating, both within and between individuals, and within and between populations (Houde 1997). If sneak mating decreases the amount of close contact relative to courting, this variation in mating tactics then drives individual- and population-level variation in transmission. Finally, females are more likely to contract *G. turnbulli* than males in single-sex shoals (Croft et al. 2005a; Richards et al. 2010; Krause et al. 2017), but males tend to move between shoals more frequently (Croft et al. 2003a), potentially facilitating parasite transmission between social networks or even populations.

However, inferences about transmission through social networks based on data from uninfected individuals are likely flawed (Stroeymeyt et al. 2018): the presence of infection can change the social behavior of both infected (Croft et al. 2011), and uninfected hosts in the network (Hart 1990; Loehle 1995). Non-discriminative shoaling allows epidemics of *Gyrodactylus* spp. even at low host densities (Johnson et al. 2011): unsurprisingly, then, guppy social decisions are affected by infection. Conspecifics actively avoid infected guppies (Croft et al. 2011) based on visual and olfactory cues (Houde and Torio 1992; Stephenson and Reynolds 2016) which change with transmission risk (Stephenson et al. 2018). In theory, such avoidance behaviors reduce transmission and increase aggregation on infected individuals. In contrast, infected guppies increase their social contacts (Stephenson 2019). Early life infection exposure can, again, be formative: juvenile guppies exposed to infected conspecifics associated more with them as adults (Stephenson and Reynolds 2016). Infection also shapes guppy mate choice: females tend to prefer uninfected and relatively resistant males (Kennedy et al. 1987; McMinn 1990; Houde and Torio 1992; Stephenson et al. 2020). However, because sneak mating undermines female mate preferences (Magurran 2005), and therefore a females' ability to avoid mating with infected males, it decreases clustering and increase opportunities for transmission. Female guppies also lose their choosiness when infected (López 1999), potentially increasing transmission between the sexes. Therefore, discrimination against infected conspecifics, combined with the social behavior of those infected individuals, shapes host social networks and thus parasite transmission.

We can draw from the broader literature to inform how guppy social networks may affect *Gyrodactylus* spp. transmission and thus population genetic structure (Fig. 3a). Across systems, an individual's position in the network can predict its probability of parasite infection (Godfrey 2013; White et al., 2017). For *Gyrodactylus* spp., modeling suggests that guppies with the highest network rank are more than twice as likely to become parasitized than guppies of low network rank (Krause et al. 2017). Further to this, modeling reveals that the more highly structured the network, the more transmission is constrained within local clusters, generating non-random distributions of parasite populations and genetic diversity (Newman 2003; Griffin and Nunn 2012; Mohr et al. 2018; Romano et al. 2018; Webber and Vander Wal 2020). Thus, the structure of the host social network likely dictates non-random mating and fine-scale gene flow among parasites (Fig. 3b).

Individual-level guppy behavior therefore dictates the structure of their social networks, and therefore likely the transmission and population genetic structure of their directly transmitted gyrodactylid parasites (Fig. 3b). Social behavior that increases transmission opportunities or results in unclustered transmission allows greater mixing of the parasite population, while behaviors that increase transmission clustering or drive down transmission opportunities impose decreased connectivity in the parasite population (Fig. 3b). Male sneaky mating, or loss of female choosiness when infected, for example, both increase transmission opportunities while potentially decreasing the clustering of female-male interactions, resulting in greater mixing of the parasite population. By contrast, preferences for uninfected, familiar fish would result in the opposite. Some host social behaviors could result in contrasting effects on the parasite population, possibly negating each other: as mentioned above, females shoal more but preferentially with other females, possibly both increasing and clustering parasite transmission opportunities within limited parts of the overall host social network. Sexual transmission allows for bridging between female and male social networks, while vertical transmission could occur if *Gyrodactylus* spp. are transferred during guppy live-birth, potentially tying parasite populations to guppy lineages. Host social behaviors also have the potential to facilitate transmission opportunities within modular networks, while limiting transmission among networks. Thus, network stability can generate fine-scale population substructure among parasites originating from different networks.

The frequency and type of transmission opportunities likely shape parasite population genetic structure and mating system

Non-random interactions between social hosts, such as have been extensively described in the guppy system, can have profound implications for the structure of their parasite populations both at the within- and between-host scales. In this subsection, we draw on theory and empirical work from free-living systems to suggest general patterns. Our central

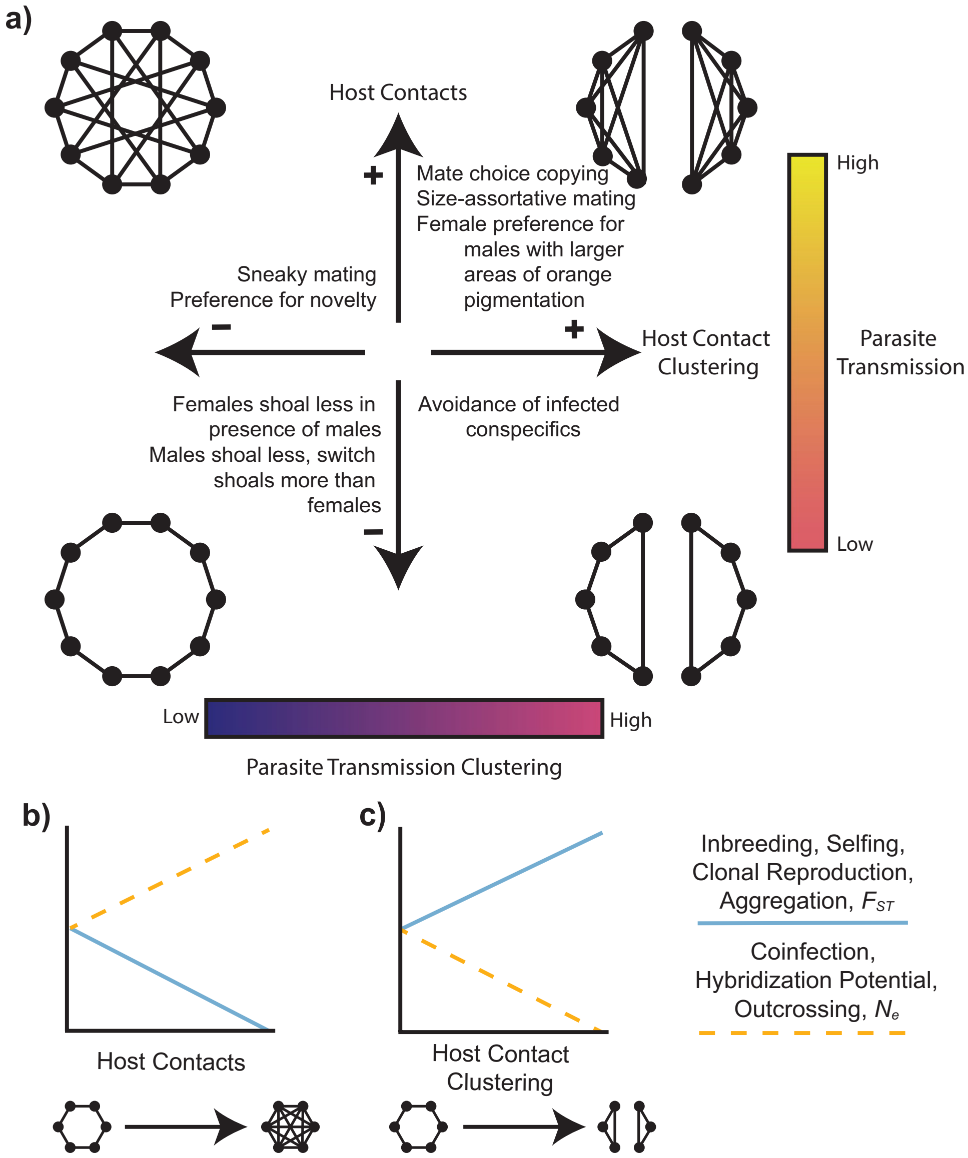

Fig. 3 Individual host social behaviors shape the rate of contact between hosts and the identity of interacting hosts (**a**). Social behaviors which facilitate high contacts (indicated by positive arrows) or decrease network modularity will increase opportunities for parasite transmission and decrease parasite aggregation. Thus, host social behaviors and network structure will shape the genetic identity and turnover of interacting parasite individuals. **b** Social behaviors that result in lower host contact rates or networks are highly modular, parasite transmission among individuals and within networks may increase deviations from panmixia due to non-random mating driven by reductions in transmission opportunity and population subdivision

thesis is that host social behavior likely shapes the distribution of parasite genotypes within a host, which would in turn dictate the parasite mating system. Together, population genetic structure and mating system have implications for parasite evolution at the within- and between-host scales, and indeed the scale at which evolution can act: limited and clustered transmission events increase the extent to which the infrapopulation is considered the evolutionary unit, but when transmission facilitates rapid changes in infrapopulation genetic composition, evolution will act at the component population (Fig. 2b) (Criscione and Blouin 2006).

Host social behaviors that increase transmission, and decrease the extent to which transmission is clustered, theoretically increase the size and diversity of parasite infra- and component populations. Such conditions should approximate panmixia and increase the importance of selection while reducing the effects of drift (Hedrick 2010). Less aggregated, more even distribution among hosts may reduce parasite intraspecific competition and variation in parasite reproductive success, potentially increasing effective population sizes (Dharmarajan 2015). Host social behaviors that generate larger group sizes and transmission opportunities also increase the probability of multigenotype coinfections and thus the genetic diversity of infrapopulations. In such host populations, larger and more diverse infrapopulations will result in relatively wider transmission bottlenecks, which perpetuates the relative importance of selection over drift across multiple hosts (Fig. 4). Our current understanding of the role of coinfection in parasite evolutionary outcomes is incomplete, but their important impact on virulence evolution

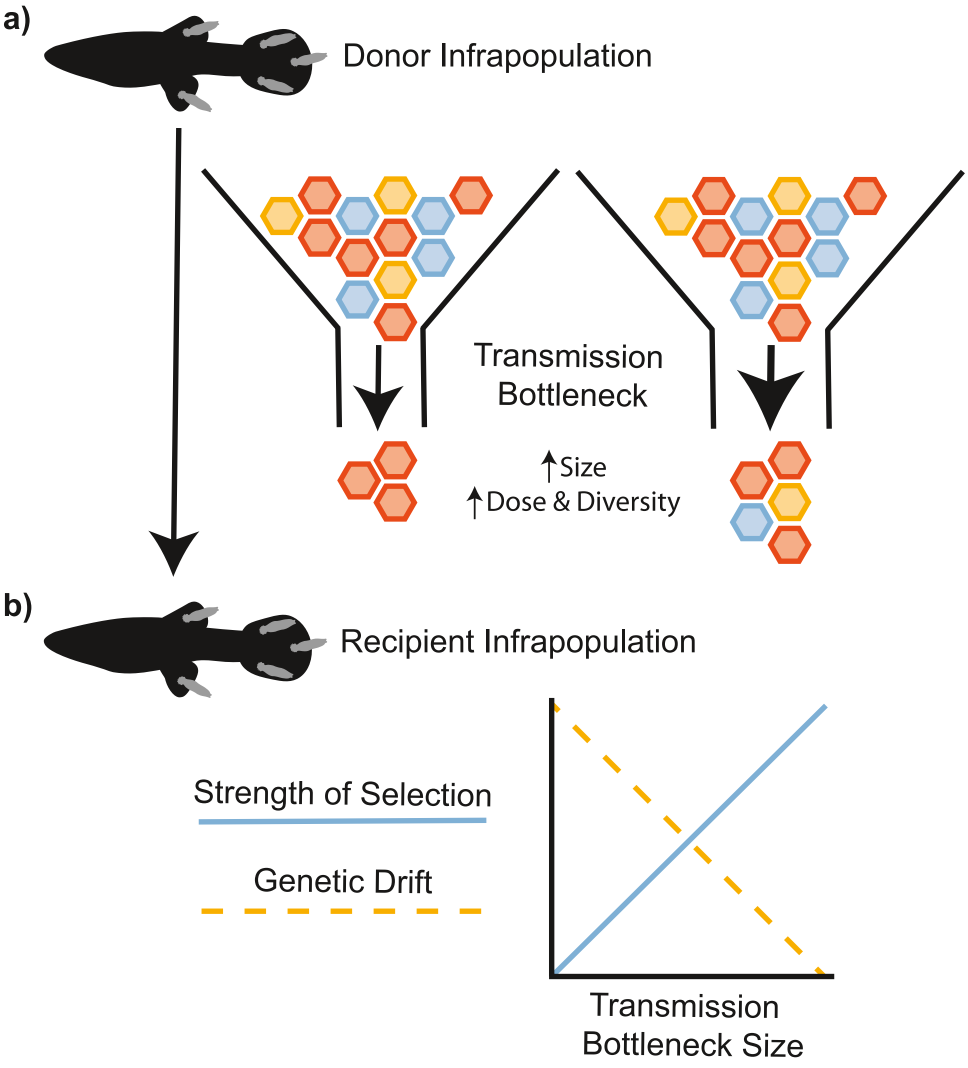

Fig. 4 Transmission bottlenecks are a key, underappreciated process affecting a parasite's ability to respond to selection. The size, genetic identity, and genetic diversity of parasite individuals transmitting from host **a** to host **b** determine the outcome of interactions on the subsequent host (i.e., sibling co-transmission facilitates sibling mating). Small, genetically depauperate founding populations, a result of narrow transmission bottlenecks, weaken the force of selection and increase the importance of genetic drift relative to selection. Transmission bottlenecks may occur at the scale of infrapopulations or between populations. The graph depicts linear relationships to illustrate the predicted direction of association, but the actual shape of these relationships could take several forms such as asymptotic

(Alizon et al. 2013; Gleichsner et al. 2018) suggests this is likely an important avenue for future research.

By increasing the genetic diversity of infrapopulations, reducing relatedness of coinfecting parasite individuals, and reducing parasite aggregation among hosts, host social behavior drives parasite evolution through non-selective processes. These conditions may promote outcrossing, detectable as F_{ST} values approaching zero (Table 1) (Detwiler et al. 2017), and allowing for novel combinations of alleles which can be especially advantageous for the parasite during coevolutionary arms races (Lighten et al. 2017; Park and Bolker 2019). Host social behaviors that facilitate parasite outcrossing will also reduce the effects of genetic drift at the infrapopulation level by preventing the loss of alleles due to random sampling and repeated recolonization and extinctions events (Price 1977; Nadler 1995).

By contrast, host social behavior that limits or clusters transmission opportunities may contribute to the aggregation of closely related parasites, forcing parasites to inbreed, self, or exclusively clonally reproduce, with potentially substantial negative fitness consequences (Fig. 3) (Detwiler et al. 2017). Inbreeding can decrease offspring survival and fecundity (Charlesworth and Willis 2009), and high population-level rates of inbreeding and selfing increase the relative importance of genetic drift, reducing both the effective population size and within-population genetic variance relative to outcrossed populations (Pollak 1987; Charlesworth 2003; Jullien et al. 2019). By increasing homozygosity across all alleles, thus limiting the generation of potentially advantageous novel genotype combinations (Jullien et al. 2019), selfing can reduce genetic diversity to the extent that populations cannot adapt to changing host or environmental conditions (Charlesworth and Charlesworth 1995). Over the longer term, however, the benefits of inbreeding may outweigh its costs, particularly for parasites when repeated historical purging of deleterious alleles allows parasites, as it does with other non-parasitic organisms, to escape inbreeding depression (Lande et al. 1994; Porcher and Lande 2016;

Caballero and Criscione 2019). In fact, it is possible that some level of inbreeding may be an essential parasite mating system characteristic that facilitates rapid evolutionary change in response to host immune systems or environmental stochasticity. Inbreeding also maintains locally adapted gene complexes which outcrossing disrupts (Peer and Taborsky 2005). Elucidating the transmission dynamics that either facilitate or reduce inbreeding rates in wild populations is therefore fundamental to our understanding of host-parasite coevolutionary dynamics.

Despite its importance, there remain few studies that address the effects of parasite transmission, and none that directly address the impact of host social behavior, on parasite mating system. Theory suggests that spatial structuring of parasite transmission among hosts, as we predict would be generated by host social behaviors, significantly increases parasite inbreeding by increasing the probability of multiple parasites from one infrapopulation being contracted by a host in the next generation, and thus the probability that infrapopulations will contain multiple closely related parasites (Dharmarajan 2015). Empirical estimates of parasite inbreeding to test these ideas are limited. Significantly positive F_{IS} values and deficits of heterozygotes, both indicators of inbreeding, have been detected among cestodes (Lymbery et al. 1997), nematodes (Picard et al. 2004; Churcher et al. 2008), ticks (Dharmarajan et al. 2011), and trematodes (Vilas et al. 2012). Inbreeding depression has been demonstrated among some tapeworms (Christen et al. 2002; Christen and Milinski 2003; Benesh et al. 2014), while other species of tapeworm exhibit none, despite high rates of both selfing and sibling mating (Detwiler and Criscione 2017; Caballero and Criscione 2019). By contrast, trematodes infecting salmon (Criscione and Blouin 2006), European conger eel (Vilas and Paniagua 2004), and tapeworms infecting salmonid and coregonid fishes (Šnábel et al. 1996), all parasites with complex life cycles and aquatic transmission, appear to outcross whenever possible and self only when hosts are infected with a single individual. The mating system, as well as the ecological and life history characteristics that influence mating systems, remains largely unknown for most parasites. Generally, parasite mating systems represent a substantial knowledge gap: a deeper understanding of this fundamental aspect of parasite biology is urgently needed. The task will not be a small one: parasites include organisms from a huge phylogenetic range (Flatworms, which alone include 130,000 described species, Nematodes and insects to name a few), which infect a massive diversity of hosts in terrestrial and aquatic habitats. Substantially more empirical examinations of the parasite mating system, and how it is affected by transmission and host social behavior, are sorely needed. It is important to note as well, that technical artifacts such as null alleles and sampling biases can also generate high F_{IS} values and heterozygote deficits in non-model organisms (see de Meeus (2017) for a discussion in detecting the presence of null alleles and Prugnolle and De Meeus (2010) for the importance of sampling biases). Thus, both sampling scheme and marker development should be carefully designed in future studies.

Parasite primary mating system has important genetic implications at the between-host scale. In populations in which host social behavior results in low contact rates between hosts, when contact does occur, the accumulation of closely related and clonal individuals on a host between transmission events increases the probability that siblings and clones will transmit together to subsequent hosts. The founder effects resulting from such transmission bottlenecks have been documented in a number of systems: sibling co-transmission has been implicated as an important characteristic of infrapopulation composition for many nematodes (Cole and Viney 2018), and the co-transmission of closely related strains of *Plasmodium falciparum* in the definitive mosquito host is increasingly recognized as an important factor in shaping malaria infection outcomes (Wong et al. 2018; Nkhoma et al. 2020). Infection of the next host by clumps of multiple genetically identical or genetically closely related individuals further increases the probability of non-random, inbred mating within infrapopulations across multiple generations of hosts. These processes can significantly increase the frequency of selectively advantageous rare parasite genotypes (Cornell et al. 2003), or conversely increase the importance of genetic drift and reduce the strength of selection. Co-transmission of clonemates in natural systems also has important ramifications for models that incorporate kin selection (e.g., as a mechanism for the evolution of host manipulation) (Poulin and Maure 2015) or kin shading (kin shading as a mechanism for virulence evolution) (Cressler et al. 2016). Clumped transmission to subsequent hosts will likely increase F_{IS} within the infrapopulation and, assuming variation between parasite lineages in their reproductive success, should increase the degree of genetic differentiation, measurable as high F_{ST}, among infrapopulations (Prugnolle et al. 2005).

In summary, individual host social behaviors can shape the number and identity of individual parasites that infect them. Future research using fine-scale population genetics data to quantify parasite infrapopulation structure and primary mating system will shed much-needed light on how non-selective evolutionary processes act in concert with selection to shape host-parasite coevolution.

How might population-level differences in host social behavior interact with habitat configuration to alter parasite evolutionary trajectories?

Spatial variation in the distribution of resources, conspecifics, communities, and the physical structure of the environment can result in significant differences in social behaviors between populations. In this section, we explore how population-level differences in host social behaviors alter the distribution of parasite genotypes among hosts, shifting the relative dominance of evolutionary processes. We also discuss how the location of the host and parasite populations in the landscape, coupled with host dispersal, contribute to the relative rates of host and parasite gene flow, and can also contribute to the maintenance and distribution of genetic diversity for both species. We draw from population-level variation in Trinidadian guppy social behaviors, and the structure of the dendritic rivers they inhabit, to examine how these features could influence parasite mating systems and gene flow across the landscape. In the first subsection, we focus on population-level variation in behavior and transmission opportunities and draw from theory and data from free-living organisms to present general, testable predictions about how this variation shapes parasite mating system. In the second subsection, we discuss how the effects of dendritic habitat configurations and unidirectional stream drift in rivers alter coevolutionary dynamics and local adaptation.

Population-level differences in host social behavior may drive population-level differences in parasite evolution

Social behaviors are shaped by interactions between conspecifics, the broader community, and the physical environment. Resources, mates, predators, and competitors are unevenly distributed across the landscape due to complex multispecies interactions and geographic features which facilitate physical movement for some species but act as dispersal barriers for others. Separation of populations across this complex landscape both imposes differential selection through a set of given environmental and ecological conditions and can result in non-uniform gene flow among spatially separated subpopulations. As a result of these landscape-scale processes, guppies from populations experiencing high levels of predation risk exhibit a dramatic, sometimes 12-fold increase in time spent shoaling, and have larger, more cohesive shoals, compared to guppies from populations experiencing low levels of predation risk (Magurran and Seghers 1990; Seghers and Magurran 1991). Variation in predation risk also significantly alters fine-scale social interactions and the degree of connectedness in fission–fusion social systems, such as guppies: high predation guppies have stronger, non-random affiliations, and more tightly connected networks, perhaps promoting parasite transmission (Kelley et al. 2011). Similarly, males from high predation populations exhibit more structured networks, indicative of greater subdivision of interactions within high predation populations, and fewer male-male interactions (Edenbrow et al. 2011). On the other end of the spectrum, low predation populations would generate less stable social networks which would act to decrease F_{ST} and F_{IS} through movement among shoals. While the guppies offer an extreme example of population-level differences in social behavior, other coevolved host-parasite systems such as the *Spinturnix*-bat system or lice and their avian hosts may present opportunities to develop a comparative framework to understand the effects of host social behavior on parasite genetic structuring. In reality, many host social behaviors will vary between populations on a continuum rather than a dichotomy, thus generating a multitude of possible outcomes for their infecting parasite populations. Quantifying the genetic consequences of population-level variation in social behaviors is essential to our understanding of host-parasite coevolutionary dynamics.

Divergence of animal social behavior between geographically separate populations likely results in spatial variation in the non-random transmission of parasites. Host populations that differ in the transmission opportunities their social behavior provides to their parasites will likely have significantly different distributions of parasite infection and prevalence, as has been found across high and low predation guppy populations (Stephenson et al. 2015a,b). In populations such as low predation guppy populations, in which host social behavior likely causes isolated infrapopulations and clumped transmission, we predict higher F_{ST} values among infrapopulations, indicative of parasite population subdivision, and positive F_{IS} values associated with increased inbreeding. Population-level variation in network structure and the resulting clustered transmission opportunities would alter infrapopulation composition by concentrating parasite infection within a subset of the total host population, increasing the size and diversity of the infrapopulations of just a few individuals. Such local variation in stable network modularity can generate differences in fine-scale population substructure, which has significant impacts on the local maintenance of genetic variation and decreases in the effective population size (Whitlock and Barton 1997).

In addition to shaping variation in transmission opportunity, we propose that population-level variation in host social behavior, and thus parasite transmission opportunities, will generate geographic variation in the distribution of parasites within host populations, parasite population structure, and ultimately, mating system (Criscione and Blouin 2006; Detwiler et al. 2017). Our ideas are informed from theory and empirical work mostly available for free-living systems: geographic variation in mating systems has yet to be directly addressed in metazoan parasites, despite the fact that many are capable of outcrossing, selfing, and parthenogenesis (e.g., gyrodactylids). However, potential support for geographical variation in parasite mating systems can be indirectly inferred from phylogeographical studies when populations vary in F_{IS} (for example, see, Beesley et al. 2021 and Lymbery et al. 1997).

Theory predicts geographic variation in mating system, such as "geographic parthenogenesis," should result from variation in metapopulation dynamics and the probability of encountering a potential mate (Glesener and Tilman 1978; Haag and Ebert 2004). Local extinction and recolonization events both reduce the probability of encountering another individual and increase the probability of inbreeding when another individual is encountered (Haag and Ebert 2004; Rossi and Menozzi 2012). Mating systems dominated by selfing sometimes avoid the potentially deleterious effects of geographically imposed small populations and high rates of inbreeding (Hartfield 2016). Geographic parthenogenesis can generate clear patterns in population genetic data: where inbreeding and parthenogenesis are common, populations exhibit low genetic diversity and smaller effective population sizes, experience greater genetic drift, and are more genetically isolated (Haag and Ebert 2004; Tilquin and Kokko 2016; Laine et al. 2019; Wu et al. 2020). By contrast, populations dominated by outcrossing have high local diversity, high heterozygosity, and increased generation of novel multilocus genotypes (Laine et al. 2019). There is strong evidence that free-living organisms with mating system flexibility exhibit geographic variation in the dominant mating systems, including plants, plant pathogens (including aphids and fungi), snails, insects, and planarian flatworms (D'Souza et al. 2004; Haag and Ebert 2004; Laine et al. 2019).

For gyrodactylids, like other parasites, geographic parthenogenesis will likely be tied to the opportunity for outcrossing and coinfection (Gorton et al. 2012; Laine et al. 2019). Variation in parasite primary mating system generates hot spots and cold spots of genetic variation, parasite effective population sizes, and the relative importance of genetic drift and selection (Laine et al. 2019). The generation of novel genetic diversity also increases the evolutionary potential of outcrossing populations as they adapt to both hosts and the abiotic environment (Greischar and Koskella 2007; Wolinska and King 2009). Parasites are often predicted to have an adaptive advantage relative to hosts due to their short generation time, larger population sizes, and higher migration rates (Price 1977; Gandon and Michalakis 2002). However, high rates of inbreeding and parthenogenesis, small effective population sizes, low genetic diversity, and high population subdivision in populations of geographic parthenogens represent a substantial caveat to this idea. Elucidating parasite mating systems across the landscape is an important and almost entirely uninvestigated prerequisite to understanding the geographic mosaic of coevolution (Thompson 2005).

Host social behavior and habitat configuration may both influence parasite gene flow and evolutionary trajectories across the landscape

The landscape itself, and the configuration of host and parasite habitat within that landscape, shapes the extent to which host social behaviors drive parasite evolutionary trajectories (Fig. 2c). Dispersal of both host and parasite across the landscape, and subsequent mating events, underpin gene flow within metapopulations. Dispersal of infected hosts increases infection persistence within the metapopulation as well as facilitates parasite gene flow (Tadiri et al. 2018). Recent models that explicitly account for both landscape structure and variation in group size of social hosts indicate that pathogen persistence increases with landscape complexity and competition-induced host dispersal (Scherer et al. 2020). Indeed, migration rates for both host and parasite vary across the landscape due to variation in host movements and landscape resistance, and these processes result in asymmetry in host and parasite gene flow in some but not all populations (Gandon and Michalakis 2002; Louhi et al. 2010; Blasco-Costa and Poulin 2013; Paz-Vinas et al. 2013). Host-parasite coevolutionary dynamics are dependent on the relative migration rates of host and parasite (Gandon et al. 1996b). When migration rate is high among hosts and low among parasites, as occurs if infected hosts are unable to disperse, hosts will be locally adapted and the parasites will not (Gandon et al. 1996a; Gandon and Michalakis 2002; Johnson et al. 2021). Parasite transmission bottlenecks that result from the dispersal of only a few infected individuals will increase the importance of drift and weaken the effects of selection (Fig. 4). Quantifying both host and parasite migration and population connectivity, as can be inferred through population genetic data, is thus key to understanding host-parasite coevolution.

Animal dispersal often depends on social interactions: dispersal occurs when the benefits of leaving the group, such as reduced competition and parasite transmission, outweigh the costs of losing group membership (Krause and Ruxton 2002). In many cases, dispersal is an adaptive response to avoid inbreeding and competition between kin and non-kin and to find a mate. Guppy dispersal is density-dependent, consistent with competition avoidance, though the pattern differs between age classes and throughout colonization events (De Bona et al. 2019). Kinship also plays an important role in guppy dispersal (Piyapong et al. 2011; De Bona et al. 2019). Once dispersal has occurred, the organization, social structure, and strength of individual ties in the new location together influence the successful gene flow of the disperser through social resistance (Armansin et al. 2020).

Dispersal is also influenced by habitat configuration and the location of a population within that configuration. The habitat configuration of rivers has two unique features that can work in concert to influence host and parasite dispersal: (1) unidirectional stream drift and (2) dendritic ecological networks (DEN) of rivers (Fig. 2c). Differences in species-specific responses to river network architecture and unidirectional drift can fundamentally alter each species' evolutionary potential (Crispo et al. 2006; Pilger et al. 2017). The unidirectional flow of water within streams biases downstream migration for organisms with short dispersal capabilities (Pilger et al. 2017; Blondel et al., 2019). Headwater populations are predicted to experience small population sizes, repeated local extinction, and recolonization events, leading to small effective population sizes and greater strength of genetic drift (Fig. 2c) (Thornton 2007).

Consistently, guppies in isolated headwater populations experience downstream dispersal bias, small effective population sizes, and low genetic diversity (Barson et al. 2009; Blondel et al. 2019). Downstream guppy populations in lowlands are both highly diverse and highly connected (Barson et al. 2009). Male downstream dispersal is further facilitated by *Gyrodactylus* infection (van Oosterhout et al. 2007), though there is likely substantial asymmetry in whether the host and parasite go on to contribute to the gene pool in their recipient populations. Work focused on lake and river three-spined sticklebacks (*Gasterosteus aculeatus*) implicates distinct parasite communities in limiting the invasion success of downstream migrants due to local adaptation in immune response of the fish (Erin et al. 2019). The asymmetrical downstream export of migrants has ramifications for both upstream population persistence and the downstream movement of genotypes and phenotypes (the stream drift paradox: Anholt 1995; Pachepsky et al. 2005). These processes are further magnified for parasites, whose progressive transmission bottlenecks also strengthen the effect of drift (Fig. 4).

The second feature of river habitat that interacts with host dispersal behaviors is the DENs formed by repeated, arborescent bifurcations that form landscape pathways of branches and nodes in a hierarchy of headwaters, tributaries, streams, and reaches (Fig. 2c) (Campbell Grant et al. 2007). Dendritic networks affect the demographic processes of species within them. Variation in connectivity within the network can promote local extinction events, especially for species with low dispersal abilities (Labonne et al. 2008). The DEN configuration drives differences in dispersal and demographic processes which generate two distinct genetic patterns: (1) population location affects the diversity of host and parasite genotypes and (2) network placement affects genetic differentiation among populations (Fig. 2) (Pilger et al. 2017; Whelan et al. 2019). In the simplest networks, genetic diversity will be lowest in headwater and tributaries and highest at river confluences and on mainstem branches (Thomaz et al. 2016). Network models predict increasing complexity in the arrangement of the network will generate increasing genetic diversity, and increased genetic differentiation within the entire river network (Chiu et al. 2020). These predictions are empirically supported: effective population size and thus the strength of genetic drift within populations is driven by network properties in fish assemblages (Pilger et al. 2017).

While the effects of DEN complexity have not been explicitly tested in guppies, guppy populations are highly structured among upland river drainages and contemporary migration rates vary between rivers facilitated by differences in physical riverine features (Barson et al. 2009). Guppy populations in the Caroni drainage exist in a complex metapopulation of source-sink dynamic (Barson et al. 2009). Lowland populations experience generally downstream-biased geneflow among rivers in the Caroni River drainage basin (though upstream between the Lopinot and Caura Rivers; Barson et al. 2009). Corresponding information on *G. turnbulli* and *G. bullatarudis* population structure is currently limited to two studies. Konczal et al. (2020) used resequencing data and polymorphic SNPs from 11 *G. bullatarudis* individuals from three rivers (Lopinot, Santa Cruz, and Laura River) to suggest parasite population subdivisions among the rivers. Konczal et al. (2021) also used resequencing data from 30 individuals of *G. turnbulli* from three rivers (Aripo, Caura, and Lopinot) and found a significant population subdivision associated only with the Caura River. Based on the available evidence, there are therefore discordant patterns of gene flow for guppies, *G. turnbulli* and *G. bullatarudis* within the Caroni drainage in northern Trinidad. However, small sample sizes and limited geographic sampling of parasites limits our understanding of how characteristics of riverine habitat (i.e., number of tributaries, confluence position, river length, and stream drift) interact with host social behavior to drive host and parasite population genetic structure and local adaptation across the landscape (Thomaz et al. 2016; Pilger et al. 2017).

Conclusions

Host social behaviors are essential to the transmission of many parasites. As such, they shape parasite ecology and evolution through complex interactions within the context of the landscape. At a time where social distancing is widely recognized for its importance in limiting transmission among individuals and between populations, the ecological and evolutionary consequences of these behaviors for infectious parasites that extend beyond selection need to be investigated (Stockmaier et al. 2021). Fine-scale spatial patterns in parasite infection are common across wildlife parasites of social organisms, even within very small areas (under 0.01 km^2) yet the mechanism which generates these patterns, and their ecological and evolutionary consequences are extremely understudied (Albery et al. 2020). Several recent reviews have called for integrating animal behavior, spatial analysis, and parasite transmission data to better understand parasite ecology and evolution in wild systems (He et al. 2019; Albery et al. 2020, 2021). These data are required to understand emerging infectious diseases in wildlife and human systems (Townsend et al. 2020). The realized outcomes of parasite evolution in complex socio-spatial systems will be highly influenced by variation in mating systems, gene flow, and population demographics. With this review, we aimed to highlight the need for incorporating parasite molecular ecology with host behavioral research to more fully understand the bidirectional eco-evolutionary interactions between sociality and parasites. Understanding deviations from panmixia in parasite populations across scales is fundamental to our understanding of parasite evolution because parasites routinely do not respond in predictable ways (Criscione et al. 2011; Criscione et al. 2010; Betts et al. 2016). Population genetics tools allow us to both identify these deviations and design and implement new research questions to better understand how and why parasite population genetics may deviate from our predictions. We argue that while the limited empirical data and theory we review here strongly suggest that host social behavior should generate certain patterns of parasite population connectivity and genetic diversity, testing these predictions is urgently needed. We acknowledge that the field is complex and remains largely unexplored. We highlight the opportunity provided by the guppy-*Gyrodactylus* system to test these ideas, but ideally, future research from multiple systems should integrate host social behavior, parasite genetic data, and multi-scale spatial analysis to understand and mitigate parasite evolution in social organisms.

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