Parasitism and the tradeoffs of social grouping: The role of parasite transmission mode

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Keywords: collective behavior, disease ecology, ecology of fear, epidemiology, landscape of disgust, optimal group size, parasitism, sociability, transmission dynamics

Abstract

Animals use social grouping for numerous fitness-enhancing processes, such as foraging, social learning, defense, and energy expenditure. One broadly referenced negative consequence of social grouping is the increased risk of exposure to parasites, which are defined broadly here as organisms with obligate, persistent, and harmful consumer associations with a host. However, there is growing evidence that group living can also act as a defensive mechanism against parasites. Here, we present a conceptual framework that explores host sociability in the context of parasite life history, arguing that the positive or negative impact of a social lifestyle on infection risk is strongly linked to the parasite's transmission mode. We discuss the link between host sociability and infection risk with respect to common, non-mutually exclusive differences in transmission: direct vs. indirect, density- vs. frequency-dependent, and simple vs. complex life cycles. We then use our framework to discuss the mechanisms for active parasite avoidance, passive effects of infection-induced phenotypes, and their impacts on host social networks. Further, we highlight additional important factors that can modulate these dynamics (e.g., parasite virulence, infection intensity, co-infection by multiple parasites, and environmental factors). The goal of this broad, comparative approach is to provide researchers from multiple disciplines with a unified framework to better understand the relationship between social grouping and host-parasite interactions across diverse systems.

1. INTRODUCTION

Parasites make up approximately half of all species on the planet and a substantial proportion of its biomass (Dobson et al. 2008, Kuris et al. 2008), and thereby play a fundamental role in ecological processes, from the individual to the ecosystem (Mouritsen and Poulin 2002, Wood et al. 2007, Hechinger 2015). Despite growing evidence that links parasitism with many important animal processes, such as physiology, morphology, behavior, and cognition (e.g., Hamilton and Zuk 1982, Wisenden et al. 2009, Øverli et al. 2014, Binning et al. 2018), the role of parasites in generating intra- and interspecific variation in their hosts is understudied (Poulin and Thomas 1999, Thomas et al. 2011). Furthermore, while parasites can have diverse impacts on their hosts, studies rarely account for or even acknowledge the possibility of parasites' presence (Chretien et al. 2023), which may in some instances lead to unrecognized biases and incorrect conclusions (Timi and Poulin 2020). The reciprocal nature of parasitism and animal behavior is particularly underappreciated, as host infection risk and behavior are inextricably linked (Hawley and Ezenwa 2022).

Many animals engage in a social lifestyle, which we broadly define here as the tendency to live in groups for prolonged periods of time at some point in the animal's life history (Ward and Webster 2016). Group living exposes animals to a greater diversity of contagious parasites on a more frequent basis, through parasites that are transmissible via direct contact between individuals ('directly transmitted parasites'). This risk could influence individuals' tendency to socialize, their preferred characteristics in social partners, and in turn the dynamics within and among groups (e.g., group size, composition, assortment; Rifkin et al. 2012, Patterson and Ruckstuhl 2013). Parasites can also be transmitted through the environment or interactions with other species ('indirectly transmitted parasites') (May and Anderson 1979). For these parasites,

63 social grouping could aid hosts in reducing infection (Mooring and Hart 1992, Stockmaier et al.
64 2023), by reducing the per capita host attack rate by parasites (Duncan and Vigne 1979),
65 increasing detection of free-living parasites (Stumbo et al. 2012), and promoting cost-sharing of
66 anti-parasite defensive strategies (Brutsch et al. 2017). Fifty years after the link between host
67 sociability and parasitism was first proposed (Alexander 1974), the role of parasite transmission
68 mode in the tradeoffs of group living remains an area of active and ongoing research (Keiser
69 2022, Stockmaier et al. 2023), as disentangling the complex feedback loop between parasites and
70 social grouping remains difficult (Ezenwa et al. 2016b).
71 Here, we look at the role of parasitism in host group living through the lens of parasite
72 transmission mode and present a conceptual framework to help researchers from diverse
73 disciplines to understand how parasites can alter the tradeoffs of group living. We define parasite
74 transmission mode through dichotomies commonly used by disease ecologists, eco-
75 immunologists, and parasitologists (Figure 1). We discuss the mechanisms for active parasite
76 avoidance, passive effects of infection-induced phenotypes, and their combined impacts on host
77 social networks. We also highlight the importance of considering additional factors that
78 modulate these dynamics, including parasite virulence, infection intensity, co-infection, and the
79 environment. We aim to connect research at the intersection of behavioral ecology, physiology,
80 immunology, parasitology, and disease ecology, and thereby reach a more mechanistic
81 understanding of the effects of parasite transmission mode on social grouping of animal hosts.
82 Given the framework's multidisciplinary focus, we define a parasite broadly as any organism
83 with an obligate and persistent consumer association with an individual of another species,
84 which, upon associating with a host, causes it harm (e.g., viruses, bacteria, fungi, protozoa, and
85 metazoan; Anderson and May 1978, Combes 2001, Parmentier and Michel 2013).

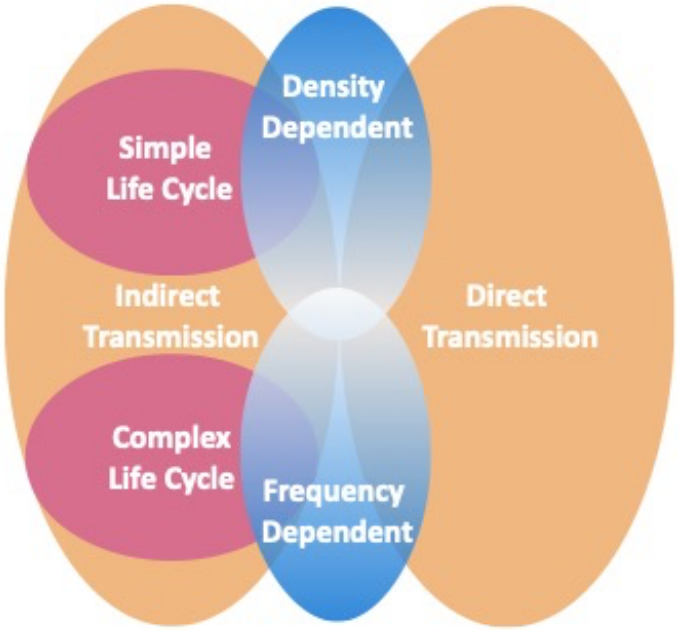

Figure 1. Venn diagram of parasite transmission modes that may impact the tradeoffs of host sociability. Transmission mode refers to the method that a parasite uses to infect a susceptible host. Overlap represents that certain routes of transmission may be found in multiple transmission mode categories.

2. PARASITE TRANSMISSION MODE

Transmission is a function of interacting processes among the parasite, its host, and their shared environment (Francl 2001, Antonovics et al. 2017). Transmission mode refers to the method by which a parasite moves between susceptible hosts in a population (Antonovics 2017) and must be considered for a comprehensive understanding of the ecological impacts of parasites across biological levels (e.g., population, community, ecosystem) (Cortez and Weitz 2013). Below, we describe common transmission dichotomies that influence the ecological and evolutionary processes that shape social grouping (Figure 1). These dichotomies include direct versus indirect transmission, density- versus frequency-dependent transmission, and simple versus complex

lifecycle (presented and described here as a sub-category of indirect transmission). Note that while we present dichotomies as distinct categories for clarity, arguably, host-parasite systems may fall on a continuum between each category depending on, for example, the host and parasite's life history (Roche et al. 2011, Antonovics et al. 2017, Hopkins et al. 2020). Further, while the hierarchical ordering of these dichotomies varies depending on the host-parasite system (Antonovics et al. 2017), this classification provides a framework to hypothesize about the ecological implications of parasite infection risk on a host's social preferences.

2.1. Direct versus indirect transmission

In direct transmission (DT), infection occurs through physical contact or close proximity between infectious and susceptible individuals (Anderson and May 1979). As group living promotes close proximity among individuals, it increases the transmission risk for any DT parasites present within a social group. Tactile transmission of DT parasites in groups includes, for example, ectoparasite transfer (skin-skin; Hillgarth 1996), ingestion of infectious agents (skin-oral; Hernandez and Sukhdeo 1995), and transmission through sexual activity (genital-genital; Mansuy et al. 2016). If the parasite is droplet- or air-borne (Ghosh et al. 2015), transmission can occur through proximity without tactile contact between hosts, when droplets contact the host's eyes, nose, or mouth (McCallum et al. 2001). Given the connection between social interactions and infection risk by DT parasites, DT parasites present a substantial potential cost of social grouping, and often reduce individual social tendencies in the short term (Hawley et al. 2021, Stockmaier et al. 2023).

Parasites with an indirect transmission mode (IT) are transmitted either through free-living infectious stages present in the environment or interactions with infected hosts from other

taxa (Begon et al. 2002, Antonovics et al. 2017). IT parasites undergo a developmental phase outside their final host before infecting a new susceptible host (Lafferty and Kuris 2002). This developmental phase can take place outside of the host in a particular environmental medium (simple life cycle) or in intermediate host species (complex life cycle) (Chernin 2000). As transmission of IT parasites is a multi-step process, gregarious species may use social grouping as a mechanism to dilute their individual infection risk (Mooring and Hart 1992).

2.2. Density- versus frequency-dependent transmission

Density-dependent (DD) transmission rate increases with host population density as susceptible hosts are more likely to encounter an infectious host, but these types of parasites require a minimum host population size: below this population threshold, the parasite cannot be sustained (Anderson and May 1981, McCallum et al. 2001). For example, for crucian carp (*Carassius carassius*) hosts, both the abundance and species richness of monogenean ectoparasites vary directly with the host's population size (Bagge et al. 2004). Hence, DD parasites likely present the greatest cost of social grouping as both larger groups and a higher group density will result in higher transmission rates and more easily sustain parasites, with reductions to group size being a potential strategy that leads to parasite extinction (Lloyd-Smith et al. 2005a).

Frequency-dependent transmission (FD) occurs when the rate of contact between susceptible and infectious individuals is independent of population density (Best et al. 2011, Antonovics 2017). For example, FD transmission becomes a better representation at a population level if the overall population is subdivided into smaller groups of varying sizes (Antonovics 2017), as in human villages (Sauvage et al. 2007) and territorial pack animals (White et al. 2017). Sexually transmitted diseases also fall under this type of transmission whereby the mating

system dictates the number of partners that a susceptible individual encounters (Thrall et al. 1993), and the rate of infections can even be determined by a single promiscuous infected host (Best et al. 2011). Given the nature of FD transmission, the role of FD parasites on social grouping varies depending on the social trait examined and the life history of each specific parasite and host. Further, while DD and FD transmission have traditionally been considered distinct categories, principles associated with both have been identified within host-parasite systems, varying depending on the patterns of social behavior through time (e.g., seasonal variation and across contexts) (Smith et al. 2009). Thus, rather than a true dichotomy, host-parasite systems lie on the spectrum from pure DD to pure FD (Hopkins et al. 2020).

2.3. Simple versus complex life cycle

In parasites with a simple life cycle (SLC), parasites pass from one host to another through infectious propagules deposited in the environment. After a developmental phase (Roche et al. 2011, Sih et al. 2018), which can vary from days to months (Brooker et al. 2006), these propagules can be transmitted to a new, susceptible host via a specific medium, such as water or feces, and/or via shared habitat (Caraco and Wang 2008, Sih et al. 2018). While SLC parasites often lack mechanisms for active movement, there are some mobile SLC parasites, which overcome physical processes in their environment to seek new hosts. For example, SLC-transmitted isopod parasites have a swimming stage as juveniles, which aids them in finding a suitable fish host (Bunkley-Williams and Williams 1998). For sedentary SLC parasites, the encounter rate with susceptible hosts is generally directly proportional to the propagules' density and distribution in the environment (Boldin and Kisdi 2012). If transmission of sedentary SLC parasites to new hosts relies on spatial overlap, the timing must occur in parallel with the

parasite's infectious period following its developmental phase (Wohlfiel et al. 2013). For parasites with a long developmental period, the timing could decouple the connection between social grouping and SLC infection risk (Sih et al. 2018), such that these parasites have a lower or negligible impact on host social grouping. However, social individuals may be at higher risk of encountering infectious SLC parasites that have a short developmental phase (Rifkin et al. 2012).

In contrast, complex life cycle (CLC) parasites require one or more intermediate hosts for growth and development prior to reaching the final host, where the parasite reproduces (Parker et al. 2015). At each developmental stage, parasites may specialize in infecting just one host species (i.e., host specialist) or be able to infect multiple species (i.e., host generalist). Various factors can alter this host specificity, such as the temporal and spatial overlap of hosts and parasites, sensory mechanisms for the parasite to detect a suitable host, and strategies for the parasite to evade host anti-parasite defenses (Adamson and Caira 1994, Poulin et al. 2011, Doherty et al. 2022). Transmission of CLC parasites between host species can occur via multiple routes, including passive transport, active movement, vector-borne, and trophic interactions (Haas 2003, Grear et al. 2013, Hobart et al. 2022). With passive transport, the infectious propagules are transmitted through the environment via physical processes, such as wind and water currents (Akullian et al. 2012, Behringer et al. 2018). In these parasites, transmission requires some action by the host to facilitate encounters, such as suspension or filter feeding (Ben-Horin et al. 2015, Hobart et al. 2022). Many CLC parasites have a mobile phase that can actively seek out a subsequent host, allowing them to overcome environmental obstacles to transmission (e.g., air or water turbulence) and rely less on host-parasite spatiotemporal overlap (Fingerut et al. 2003a, Buck and Lutterschmidt 2016). Vectors (often haematophagous arthropods like mosquitos and ticks) carry disease-causing infectious agents from infected to

susceptible individuals (Rappole and Hubalek 2003, Wilson et al. 2017). In trophically-transmitted parasites, infectious propagules are transmitted through predation events where the next host consumes the previous intermediate host (Grear et al. 2013, Buck and Ripple 2017). For each CLC transmission route, an individual's infection risk may be diluted through group living, as the infectious propagules in a particular area are divided among more available susceptible hosts and thus reduces the per capita risk (Mooring and Hart 1992, Cote and Poulin 1995).

3. SOCIAL CONSEQUENCES OF PARASITES

As parasitism is ubiquitous, most social animals inevitably harbor parasites, and often many different species of parasite (McCabe et al. 2015). To properly understand the role of parasite transmission mode on host social behavior, the mechanisms for active parasite avoidance, passive effects of infection-induced phenotypes, and its role in social networks need to be considered (Table 1; Hawley et al. 2021).

Mechanism	Host	Parasite	Transmission Mode	Impact on social grouping	References
Active avoidance	House mouse *Mus musculus*	*Eimeria vermiformis* (protozoa)	SLC (stationary, 1-2 day development period)	Uninfected individuals only avoid infected group-mates once infection is transmissible despite earlier cues of infection.	Kavaliers & Colwell 1995; Kavaliers et al. 1997
Active avoidance	Mandrill *Mandrillus sphinx*	Varied gut protozoans (protozoa)	SLC (stationary, rapid development period)	Uninfected individuals avoid grooming infected groupmates.	Poirotte et al. 2017
Active avoidance	Dampwood termite *Zootermopsis angusticollis*	*Metarhizium anisopliae* (fungus)	DD	Infected individuals alert others in the colony of parasite exposure using mechanical cues.	Rosengaus et al. 1999
Active avoidance	Caribbean spiny lobster *Panulirus argus*	*Panulirus argus* virus 1 (virus)	DD	Individuals avoid den-sharing with infected conspecifics.	Behringer et al. 2006; Behringer and Butler 2010
Active avoidance	Fathead minnows *Pimephales promelas*	*Ornithodiplostomum ptychocheilus* (metazoa)	CLC (mobile)	Individuals increase shoal cohesion by up to 15 times in response to free-living parasites (i.e. cercariae).	Stumbo et al. 2012
Passive effects	Western fence lizard *Scleroporus occidentalis*	*Ixodes pacificus* (metazoa)	SLC (mobile, develop over several months)	Infection reduces male success in intrasexual contests.	Lanser et al. 2021
Passive effects	Rainbow trout *Oncorhynchus mykiss*	*Diplostomum spathaceum* (metazoa)	CLC (mobile)	Reduced vision following infection of the eye lens reduces the social group's ability to maintain cohesion.	Seppälä et al. 2008
Passive effects	Milkweed leaf beetles *Labidomera clivicollis*	*Chrysomelobia labidomerae* (metazoa)	FD	Infected males interact with other males, and steal females from established mating pairs, more than uninfected males.	Abbott & Dill 2001
Passive effects	Three-spined stickleback *Gasterosteus aculeatus*	*Schistocephalus solidus* (metazoa)	CLC (trophically transmitted)	Mixed-infection groups take greater risks and reduce cohesion.	Demandt et al. 2018, 2020; Jolles et al. 2020b
Social network	Guppy *Poecilia reticulata*	*Gyrodactylus* spp. (metazoa)	DD	Introduction of infected newcomers increases the frequency of fission-fusion events.	Croft et al. 2011; Stephenson et al. 2018
Social network	Giraffe *Giraffa camelopardalis*	*Trichostrongylus* spp., *Trichuris* spp. (metazoa)	FD, SLC (stationary, 5-10 day development period)	Sub-grouping within populations relies on weak ties among cliques for transmission.	VanderWaal and Ezenwa 2016
Social network	Sleepy lizard *Tiliqua rugosa*	Tick *Amblyomma limbatum* (metazoan)	SLC (mobile, 8 day development period)	Highly connected lizards with consistent refuge sharing had higher tick loads than less connected individuals.	Leu et al. 2010
Social network	Black garden ant *Lasius niger*	*Metarhizium brunneum* (fungus)	DD	Parasite exposure caused increased social network modularity, clustering and assortativity.	Stroeymeyt et al. 2018

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Table 1. Examples of the impact of parasite transmission mode on social grouping, based on a subset of the studies compiled in this review. Additional information is provided for indirectly transmitted parasites, as the nature of the parasite's life cycle can influence its social impact. For simple life cycle parasites, the parasite's mobility (stationary, mobile) and length of environmental development period are noted, while routes of transmission are included for complex life cycle (e.g., mobile, trophically transmitted) parasites.

3.1. Active parasite avoidance

Once cues of parasites or infection are detected, individuals may use active avoidance mechanisms to minimize their risk of parasite exposure and infection (Lopes et al. 2022), including choosing to associate with or avoid certain individuals, substances, and/or (micro-) habitats where parasites or infected group-mates are found (Curtis 2014). Similar to the non-consumptive physiological and behavioral effects that predators impose on their prey (i.e., landscape of fear) (Clinchy et al. 2013), parasites can impact susceptible hosts over diverse spatial and temporal scales (Buck et al. 2018) (i.e., landscape of disgust; Weinstein et al. 2018), with wide-ranging consequences for the dynamics and structure of animal groups (Doherty and Ruehle 2020).

3.1.1. Sensory basis for parasite and infection detection

Detection of infections that can be transmitted among group-mates through tactile contact or spatial overlap (i.e., DT, DD, FD, and some SLC parasites) involve using multiple senses, including visual, olfactory, auditory, and mechanical cues (Behringer et al. 2018). Visual cues of infections can either be physical changes in a host's appearance (Rahn et al. 2015) or

231 recognizable behaviors associated with “sickness” (Hart and Hart 2021). Rahn et al. (2015) show
232 that uninfected three-spined sticklebacks (*Gasterosteus aculeatus*) avoid conspecifics with a
233 *Gyrodactylus aculeatus* DD ectoparasite infection, due to their visibly poorer body condition.
234 Conversely, sickness behaviors, such as reduced overall activity, exploration, and grooming, are
235 visible symptoms induced by infection (Lopes et al. 2021), which may cause uninfected group
236 members to avoid close contact with an infectious individual until they recover (Hart and Hart
237 2021). In the canary *Serinus canaria domestica*, visual cues of infection by the DD parasite
238 *Mycoplasma galliseptum* stimulated multiple immune responses in uninfected group mates that
239 enhance readiness to fight a potential infection (Love et al. 2021). Parasite infection can also
240 alter an individual’s odor, which may be used to actively discriminate between infected and
241 uninfected individuals (Stephenson et al. 2018), even in the absence of cues typically attributed
242 to “sickness” (Kavaliers et al. 2004). These changes in chemical profile can stem from
243 fluctuations in an individual’s commensal microbial community, release of metabolic by-
244 products associated with the immune response, or suppression of androgenic hormones (Penn
245 and Potts 1998). The ability to distinguish infected from uninfected group-mates based
246 exclusively on olfactory cues has been demonstrated in mice (Kavaliers and Colwell 1995),
247 bullfrogs (Kiesecker et al. 1999), guppies (Stephenson et al. 2018), mongooses (Mitchell et al.
248 2017), and mandrill monkeys (Poirotte et al. 2017). Infection status may even be transmitted
249 through auditory cues, such as vocal signals (Lopes et al. 2022). For example, when yellow-
250 bellied marmots are infected with *Eimeria* (SLC parasite with a 1-2 day environmental
251 development phase), individuals exhibit noisier and less structured vocal signals than uninfected
252 conspecifics (Nouri and Blumstein 2019). These sensory cues of infection may not be isolated to

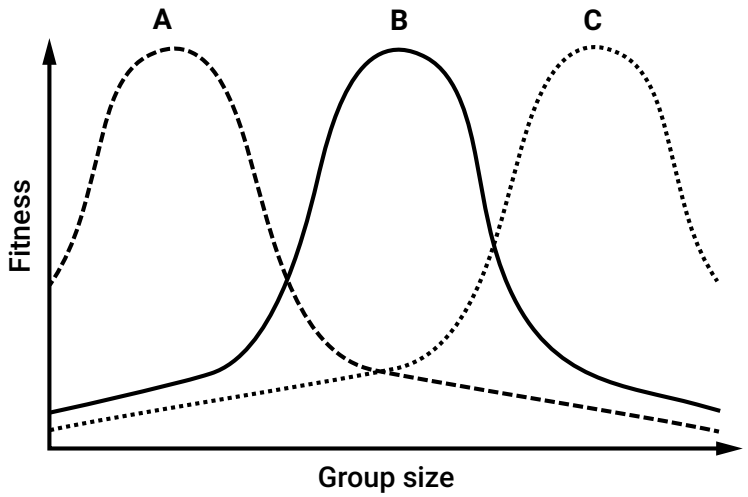
a single modality, as sensory redundancy can ensure communication of infection risk to group-mates (Reichert et al. 2023).

3.1.2. Avoidance of infected group-mates by uninfected individuals

Once an infectious group-mate is detected, uninfected individuals may actively avoid socializing with them (Figure 3; Barber et al. 2000, Kavaliers and Choleris 2018). This aversion is more likely towards the infected individual than the parasite. Dugatkin et al. (1994) showed that uninfected three-spined sticklebacks avoid conspecifics infected with the mobile SLC ectoparasite *Argulus canadensis* but show no aversion to the parasite itself. Such aversive behavioral responses can arise even before hosts become visibly symptomatic. For example, the social Caribbean spiny lobster (*Panulirus argus*) can discriminate between uninfected individuals and those infected with the DD *Panulirus argus* virus 1 (PaV1), avoiding den-sharing with infected conspecifics even when they lack any visible signs of infection (Behringer et al. 2006, Behringer and Butler 2010), potentially due to olfactory signals of infection (Penn and Potts 1998). Susceptible individuals can also modulate the strength of their avoidance behavior depending on an associate's infection stage (Stephenson et al. 2018). In the mouse (*Mus musculus domesticus*), avoidance of individuals infected by the stationary SLC parasite *Eimeria vermiformis* (2-7 day environmental development period; Fayer 1980) is lower prior to the infection being transmissible, even if infected individuals exhibit detectable cues of the infection (Kavaliers et al. 1997). Effective infection avoidance behaviors can be associated with improved fitness outcomes, such as greater fecundity (Newey and Thirgood 2004).

Changes in social preference in response to parasites can also alter the tendency for groups to split (fission) and merge (fusion). For DT parasites, individuals that would typically

maintain fidelity to a single group may choose to leave groups when infection risk becomes high (Freeland 1976) or initiate a fission event following the introduction of an infected newcomer (Croft et al. 2011). This wariness of newcomers may be advantageous. Newly immigrated members of European badger (*Meles meles*) groups are more likely to be infected by the parasite *Mycobacterium bovis* (which can be transmitted both through tactile contact and spatial overlap) than existing group members (Woodroffe et al. 2009). Reducing group size may also be an effective strategy to reduce the transmission rate of a DT parasite (Figure 2). Ritchie et al. (2021) showed that the transmission rate of the DT-transmitted fungus *Batrachochytrium dendrobatidis* is significantly faster in larger groups of the California slender salamander (*Batrachoseps attenuatus*) than smaller ones, even when infection prevalence was initially low in the group. While, intuitively at least, parasites that are transmitted through social interactions or spatial overlap (e.g., DT, some SLC parasites) may increase the frequency of fission events, we know little about how environmentally transmitted parasites (e.g., IT, CLC) alter fission-fusion dynamics and if these changes are driven by active avoidance or passive processes due to the phenotypes expressed following infection.



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294 **Figure 2.** A potential theoretical relationship between host group size and fitness under varied
295 parasite risk, assuming all other factors kept constant (e.g., foraging efficiency, competition for
296 resources, predator defense, and parasite avoidance). Curve A represents social contexts in which
297 reducing social contacts through lower group sizes would be the most effective strategy to reduce
298 transmission, such as directly transmitted parasites. Curve C illustrates environments in which
299 larger group sizes dilute the risk of parasite infection, including indirectly transmitted parasites
300 with a simple (mobile or have a long environmental development phase) or complex (mobile,
301 vector, or trophically transmitted route of infection) life cycle. Curve B represents environments
302 in which risk of any parasite infection is low. Note that curve shape is for illustrative purposes
303 only.

304

305 3.1.3. Avoidance initiated by infected group-mates

306 Infected individuals may also actively spend less time with uninfected group mates or disperse to
307 a new area, particularly when species live in societies with high levels of kin structure (e.g.,
308 social groups with high genetic relatedness; Iritani and Iwasa 2014). For example, nestling cliff
309 swallows (*Hirundo pyrrhonota*) disperse to non-natal breeding colonies following heavy DD-

ectoparasite infection (Brown and Brown 1992). Alternatively, some social species have evolved 'warning' signals of infection. In single or mixed familial dampwood termite (*Zootermopsis angusticollis*) colonies, individuals infected by the DT fungus *Metarhizium anisopliae* use a mechanical alarm signal to warn nest-mates to stay away (Rosengaus et al. 1999). While social isolation protects uninfected group-mates, it can be associated with higher mortality risk in infected individuals. For example, when the European earwig *Forficula auricularia* were experimentally isolated following infection by the DD fungus *Metarhizium brunneum*, they experienced higher mortality than those that were socialized (Kohlmeier et al. 2016). Whether infected individuals initiate avoidance will likely depend on a combination of factors related to the parasite's transmissibility, the severity of infection costs, and inclusive fitness benefits associated with leaving the group (Iritani and Iwasa 2014).

3.1.4. Use of social grouping to reduce infection and its severity

To reduce infection from some DT parasites, individuals in a cooperative social group can mount a stronger anti-parasite defense when working together, using behavioral and physiological mechanisms (i.e., social immunity; Cremer et al. 2007, Cotter and Kilner 2010, Cremer et al. 2018). For example, ants indiscriminately partake in allogrooming regardless of infection status to achieve frequent, low-level exposure to fungal parasites, increasing both individual and colony-level survival following outbreaks (Konrad et al. 2012). When risk of mobile parasite stages typical of CLC parasites is high, individuals may choose to stay with a group that they would otherwise leave, as even brief periods of isolation while moving between groups could expose them to large numbers of free-living parasites (Figure 3). Stumbo et al. (2012) illustrated this effect in fathead minnows *Pimephales promelas*, in which individual risk of infection by

free-living *Ornithodiplostomum ptychocheilus* larval trematode parasites (i.e., cercaria) was three times higher for solitary versus shoaling individuals. In their meta-analysis, Patterson and Ruckstuhl (2013) show that infection intensity by mobile parasites decreases as group size increases in diverse host and parasite taxa, likely due to the encounter-dilution effect (Mooring and Hart 1992). While this dilution effect of group behavior has historically been applied to predation risk (Foster and Treherne 1981), the same principles apply to attacks by mobile (typically CLC) parasites, such as aquatic free-living trematode parasites (i.e., cercariae) that latch onto then penetrate the epidermis of second intermediate fish hosts (e.g., Stumbo et al. 2012, Buck and Lutterschmidt 2016). Individual risk of parasite attack is diluted if the parasite cannot attack a greater number of individuals in a larger group (Hart 1994, Patterson and Ruckstuhl 2013), suggesting that social grouping or plasticity in group size could evolve in response to mobile parasite prevalence (Figure 2). Individuals may also use social grouping to reduce infection risk through social learning, which can promote more effective parasite avoidance behaviors (Kavaliers et al. 2019). In mice, a single observation of another mouse being attacked by a mobile, blood-feeding fly promoted the learning of defensive behaviors and mounting of comparable endocrine, corticosterone stress responses following future encounters (Kavaliers et al. 2001, 2003). In theory, an individual's parasite exposure history and variation in the prevalence of parasites with different transmission modes could lead to the evolution of behavioral plasticity in social preferences through time but remains an unexplored area that requires investigation.

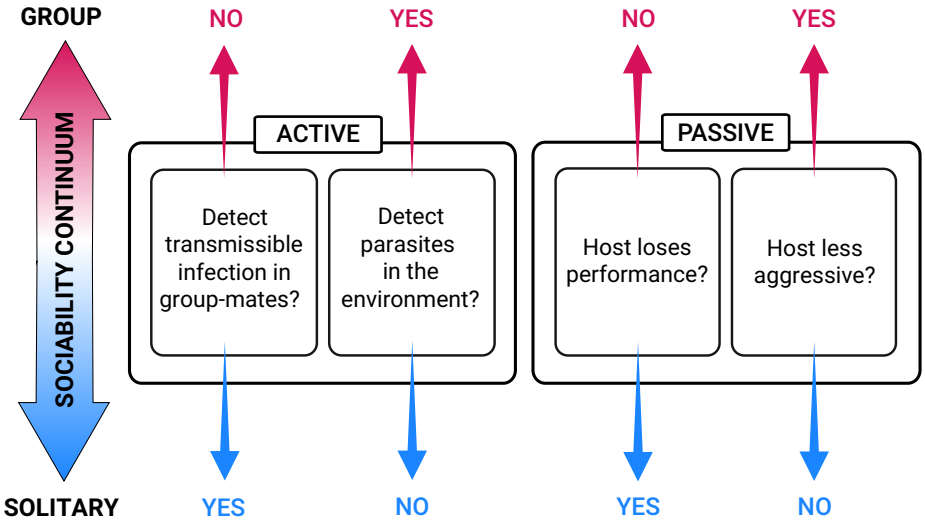

Figure 3. Predictions for how parasites with varying transmission modes could influence host behavior along the sociability continuum from a solitary to a group lifestyle because of active parasite avoidance ('active') and passive effects of infection-induced phenotypes ('passive'). Arrows marked 'yes' indicate the directionality that the mechanism pushes the individual along the sociability continuum.

Parasite risk can also alter the tradeoffs associated with different positions in a social group, resulting in altered position shuffling. Individuals at the front of a mobile group generally benefit from having first access to any food encountered (Krause et al. 1998, Domenici et al. 2017), but may also be associated with higher predation risk (Morrell and Romey 2008). Thus, these positions may also come with a higher risk for parasites with a mobile phase. Newsom et al. (1973) showed that leaders in herds of East African Zebu cattle (*Bos indicus*) had a higher infection intensity of the mobile SLC brown ear tick (*Rhipicephalus appendiculatus*) than followers. As leader positions provide individuals with first access to food, these positions, in

theory, may also come with a higher risk of acquiring trophically-transmitted CLC parasites, but this idea has yet to be studied. Conversely, central positions in groups may provide safety from mobile parasites in a similar way as has been documented in groups attacked by predators with certain hunting strategies (Krause and Ruxton 2002, Ward and Webster 2016), with individuals at the group's periphery more susceptible to infection by mobile parasites than individuals in the center (Stumbo et al. 2012).

Group cohesion varies in response to parasite exposure and risk, but the directionality of the change (i.e., increasing or decreasing) depends on the parasite's transmission mode and mobility. When mobile parasite stages are attacking (e.g. CLC), the cohesion of social groups increases in a similar way to when predators attack (Stumbo et al. 2012). When encountering DT or SLC parasites with limited mobility and short developmental periods, individuals can reduce their infection risk through reduced group cohesion. Conversely, as risk of these types of parasites decreases, group cohesion may increase. Friant et al. (2016) found that social cohesion of red-capped mangabeys (*Cercocebus torquatus*) increased in response to antiparasitic treatment that killed off DT and SLC protozoan and helminthic parasites, presumably due to reduced infection risk from social grouping following treatment. Taken together, the limited available evidence suggests that mobile CLC parasites may impact group dynamics similarly to predators, while parasites that can be transmitted among group members reduce group cohesion and coordination as group members try to limit their infection risk. Yet, these ideas have been tested in a limited number of host-parasite systems and warrant broader investigation.

3.2. Passive effects of infection-induced phenotypes

Passive effects of infection-induced phenotypes on social grouping result indirectly due to the phenotype expressed following infection, rather than in direct response to the infection itself.

392 Even minor differences in host physiology or movement behavior can have substantial social
393 repercussions (Jolles et al. 2020a). The tradeoffs of group membership will be linked to the
394 pressures of the animal's unique environment, such as its need to avoid predators and parasites,
395 acquire resources, and minimize energy expenditure during movement (Krause and Ruxton
396 2002, Ward and Webster 2016).
397 Parasite infections can also alter host behavioral phenotypes and responses to sensory
398 cues, either due to impairments imposed by the infection or manipulations by the parasite to
399 enhance transmission. In several DT host-parasite systems (e.g., Bouwman and Hawley 2010,
400 Lanser et al. 2021), reduced host aggression has been observed (Figure 3), with a range of
401 consequences for social interactions, including reduced host competitive abilities (Lanser et al.
402 2021) and enhancing group-mate collective foraging (Bouwman and Hawley 2010). Some
403 parasite infections, particularly endoparasites typical of IT infections, can alter sensory abilities
404 (e.g., visual acuity) that individuals need to maintain social cohesion (Seppälä et al. 2008). In
405 addition to impairment, individual behavior may also change as the parasite hijacks its host's
406 phenotype to enhance its own fitness (Godfrey and Poulin 2022), with impacts on host social
407 grouping. For example, males of the milkweed leaf beetles *Labidomera clivicollis* that are
408 infected by the FD-transmitted subelytral mite *Chrysomelobia labidomerae* interact more with
409 other males and are more likely to steal a female from an established mate pair than uninfected
410 males, which likely enhances transmission to both males and females (Abbott and Dill 2001). In
411 trophically-transmitted CLC parasites, infection may alter host behaviors that increase
412 detectability by predators (e.g., increasing activity or conspicuous behaviors) and reduce their
413 host's anti-predator responses (Godfrey and Poulin 2022). Conversely, as particularly DT
414 parasites require close proximity between social group-mates for transmission, the parasite may

415 increase their host's social tendencies to promote transmission (Godfrey and Poulin 2022). These
416 changes in the host social tendencies result from a change in their behavioral phenotype due to
417 parasite infection, rather than being an active choice by the host, and thus have passive effects on
418 the social phenotype at both the individual and group level.

419 Parasites can alter host behavior and physiology in a range of ways that alter their host's
420 interactions with their group-mates. Hosts may experience energetic consequences following
421 infection, such as: 1) increased maintenance metabolic rate as parasites extract resources from
422 their host; 2) reduced maximum metabolic rate and aerobic capacity as host tissues involved in
423 metabolically-costly processes are damaged; and 3) altered locomotor performance due to host
424 responses to the parasite and host manipulation by the parasite (Binning et al. 2017). Any
425 increase in maintenance metabolic rate can shift the tradeoff from prioritizing defense to
426 acquiring food despite risk. The CLC tapeworm *Schistocephalus solidus* consumes much of their
427 three-spined stickleback intermediate host's overall food intake (Giles 1983), which causes more
428 risk-taking behavior as the host prioritizes foraging over defense. Both endo- and ectoparasites
429 (often DT or SLC) may alter their host's ability to stay with a social group through impaired
430 locomotor performance (Allan et al. 2020) and increased energetic costs of movement (Binning
431 et al. 2013; Figure 3). These changes can lead individuals to occupy positions towards the back
432 of groups or break up and join others with a slower preferred locomotor pace (Killen et al. 2017).
433 Jolles et al. (2020b) showed that when only one individual in a three-spined stickleback pair is
434 infected with the tapeworm *S. solidus*, the infected individual primarily assumes the follower
435 role while the uninfected individual leads. Although infected individuals may either occupy
436 follower positions at the back of the group or be unable to keep pace with the rest of the group,

437 the consequences of parasite infection for collective movement of social groups remains
438 understudied.
439 Individual-level changes often scale up to shifting collective phenotypes at the whole-
440 group level. This effect has been illustrated for multiple behavioral traits in three-spined
441 stickleback groups that contain at least one individual infected with the CLC tapeworm *S.*
442 *solidus*, even if the group contains uninfected group-members. Groups of three-spined
443 sticklebacks that contain *S. solidus*-infected individuals engage in more risky behaviors overall
444 and reduce social information transmission about risk (Demandt et al. 2018, Demandt et al.
445 2020). Similarly, Jolles et al. (2020b) found that mixed infection groups are slower, less
446 cohesive, and less aligned than uninfected groups.
447
448 *3.3. Role of parasite transmission mode in social networks*
449 Host social networks (i.e., structure of social interactions and/or social associations in a
450 population or group) and parasite transmission are closely interlinked (Mistrick et al. 2022). Not
451 only does social network structure play a fundamental role in the epidemiological dynamics of
452 many parasites, but parasite spread and prevalence can also influence social network structure
453 (Ezenwa et al. 2016a). This bidirectional relationship has important implications not only for
454 ongoing parasite transmission, but also for other ecological and evolutionary processes, such as
455 information transmission and behavioral contagions within groups (Evans et al. 2020).
456 The direct role of social networks in shaping parasite spread is clearest for parasites that
457 are transmissible among social group-mates (e.g., DT, some SLC parasites), as specific types of
458 social association or interactions offer the primary route of transmission (White et al. 2017).
459 Variation in the network connectivity of individuals (degree heterogeneity) can generate more

explosive infectious disease outbreaks, with onward infection dominated by particular highly-connected individuals (Lloyd-Smith et al. 2005b). Simultaneously, sub-divisions in the social network that result in a more modular structure can limit parasite spread, by trapping infections within subsets of the overall group or population (Sah et al. 2017). Correspondingly, the social network position of individuals is correlated with their infection status (VanderWaal and Ezenwa 2016). While well-connected individuals may be at greater infection risk due to a higher frequency of social encounters, it is also possible that less socially integrated individuals can be more susceptible to parasites when they encounter them, if these social network positions are associated with poor condition and reduced immune performance (Balasubramaniam et al. 2016, Ezenwa et al. 2016b). For DT parasites, the sickness behaviors of infected individuals can reduce social network connectivity in some host-parasite systems (Lopes et al. 2016) but could also increase connectivity to facilitate parasite persistence in others, such as the increased number of contacts of dogs with the furious form of rabies (Brookes et al. 2019).

While social networks may not play a direct role in transmission of IT parasites, they will often shape which individuals use similar habitats or share food and water sources, meaning that social network connections may still be correlated with routes of infection. Because of this difference between DT and IT parasites, network approaches can therefore help tease apart the relative importance of each transmission mode for parasite species with varied transmission. For example, network approaches have shown the greater relative importance of IT ticks (Leu et al. 2010) than DT *Salmonella* (Bull et al. 2012) in sleepy lizard hosts (*Tiliqua rugosa*). While time-delay networks are often correlated with SLC parasite transmission (due to the varied length of the environmental development phase in SLC parasites) (Sih et al. 2018), this asynchronicity is typically not found in networks associated with CLC parasite transmission (Grear et al. 2013).

However, past studies have only examined CLC parasites with a trophically-transmitted route of infection (Grear et al. 2013). No studies, to the best of our knowledge, have examined how social networks impact transmission of mobile stages typical of CLC parasites (e.g., vectors, trematode cercariae), which would be an area of potential interest for future empirical research.

The types of passive and active social responses to parasites described in previous sections can have implications for social network dynamics. For example, infection avoidance behaviors against DT parasites can lead to predictable changes to social network structure, such as uninfected individuals having a higher and more variable number of social interactions than infected individuals (Shaw and Schwartz 2008) and being assorted or clustered together within the network (Gross et al. 2006). These changes can shape longer-term parasite dynamics by promoting disease re-emergence or persistence (Gross et al. 2006). Empirical studies have investigated these parasite-driven network dynamics in non-human animals. An experimental manipulation of the DT ectoparasite *Gyrodactyalus* sp. load in guppies *Poeclia reticulata* showed that avoidance of an infected individual resulted in treatment groups having less clustered social networks than control groups (Croft et al. 2011). In contrast, in the ant *Lasius niger,* parasite exposure caused behavioral changes that increased modularity, clustering and assortativity in colony social networks, and reduced network efficiency, in a manner that reduced parasite transmission in the colony (Stroeymeyt et al. 2018). The latter study is particularly important, as it suggests that changes in individual behavior in response to infection can lead to adaptive group or population-level changes in social network structure that match theoretical models in network science.

The consequences of active avoidance behaviors on social network structure may change for the DT-IT and SLC-CLC transmission mode dichotomies. Importantly, variation in the

landscape of disgust according to transmission mode (see "Active parasite avoidance" section) may cause different changes to social network structure. For IT parasites, any active infection avoidance behavior will be tied more to the ecological (e.g., habitat, food resource) than social environment (see previous sections). For some CLC parasites, avoidance behaviors are either ineffective or the impact of the parasite on the host is so minimal that no pressures would exist to promote avoidance, in which case no landscape of disgust would be predicted to evolve (e.g., trophically transmitted CLC parasites; Øverli and Johansen 2019). However, assuming there are cues for parasite presence in the environment (e.g., cues of fecal matter for SLC parasites or chemical alarm cues for mobile cercariae parasites; Poulin et al. 1999, Hutchings et al. 2000), avoidance of extended risky or contaminated areas could influence network structure, such as by causing social network structures to be more clearly sub-divided if they restrict opportunities for different parts of the population to mix. If infection risk with CLC parasites varies with time across daily, tidal or seasonal cycles (e.g., Fingerut et al. 2003b), then the result could be predictable changes to social network structure if social contact rates are altered by changes to spatial behavior. Despite this, social network studies have focused predominantly on DT parasites, while IT parasites (particularly mobile parasite stages common in CLC parasites) require much greater theoretical and empirical attention.

OTHER PARASITE CHARACTERISTICS

While transmission mode plays a pivotal role in driving the relationship between infection and host sociability, other factors may shift this dynamic and should be considered, including characteristics specific to the parasite (e.g., virulence and infection intensity) and ecological interactions (e.g., co-infection by multiple parasites and host-parasite interactions with their

environment). Below, we highlight some examples of potential ways that these factors can shape the links between parasite transmission mode and social grouping in hosts.

Parasite virulence

Parasites exhibit intra- and inter-specific variation in virulence (i.e., infection-induced reduction in host fitness) (Read 1994, Cressler et al. 2016), varying from subclinical (i.e. not severe enough to present measurable effects) to lethal effects (Bull and Lauring 2014). The transmission-virulence trade-off theory predicts that parasites evolve a virulence level that maximizes their transmission (Alizon et al. 2009). Thus, virulence should be higher in IT parasites since these parasites are not dependent on host movement and social interactions for their own transmission. Empirical and theoretical evidence supports the idea that some IT parasites are more virulent than their DT counterparts (e.g., Walther and Ewald 2004, Cressler et al. 2016). However, host-parasite systems exhibit plasticity in virulence with individual-to-individual transmission rates, host population density, and contact rates among social groups (Frank & Schmid-Hempel, 2008; Cressler et al., 2016). High virulence may lead to higher rates of host mortality, which, in parasites that require host survival for transmission, could drive selection for lower levels of virulence to preserve host (and hence parasite) survival (Godinho et al. 2023). Heterogenous contact rates among potential hosts (e.g., through sub-grouping) in the population can also drive reduced virulence, since transmission opportunities to new groups are rare and host mortality is costly for the parasite's fitness (Walther & Ewald, 2004; Cressler et al., 2016).

Infection intensity

While infection is often treated as binary (uninfected vs infected), in reality, individuals vary in the number of parasites found on (and/or in) a single host (i.e., infection intensity; Rózsa et al. 2000). Heterogeneity in infection intensity can occur due to diverse factors, including differences in individual resistance to parasites, acquired immunity following previous infections, and host behavior modulating parasite encounter rate (Poulin 2007, Lopes et al. 2022). Not surprisingly, higher parasite intensities are typically associated with more dramatic host effects (Moretti et al. 2017, Ryberg et al. 2020). For example, social investigations (i.e., olfactory exploration of group-mates' bodies) decline in mice as infection intensity with the trophically-transmitted SLC nematode *Trichinella spiralis* increases. Social standing in other interactions can also be impacted. In the treefrog *Hypsiboas prasinus*, male calling performance declines directly with rising SLC-helminth parasite intensity, which would decrease males' ability to attract high quality female mating partners. Given the evidence available on the link between infection intensity and various social phenotypes, group social dynamics may be driven by variation in infection intensity but this remains an understudied area.

Co-infection by diverse parasites

Animals are often co-infected by several parasite species (Pedersen and Fenton 2007, Viney and Graham 2013). These parasites may have conflicting strategies to maximize their fitness, with consequences for the host's social phenotype. For instance, conflict between parasite species can arise when a host is infected by both DT and IT parasites (Haine et al. 2005, Cezilly et al. 2014, Hafer 2016). DT parasites benefit from increased host sociality to maximize encounters with susceptible individuals, while transmission routes for IT parasites (e.g., trophic transmission, active migration) are often limited by social mechanisms that can dilute individual's risk of

574 infection (Rahn et al. 2015, Buck and Lutterschmidt 2016). The degree to which these co-
575 infections interact to shift the host's social phenotype remains largely unexplored.
576
577 *Environmental factors*
578 The factors discussed above do not occur in a vacuum: animals and their parasites experience
579 environmental conditions that can alter transmission rates and the spatial-temporal distribution of
580 both parasites and hosts, including both natural (e.g. droughts, seasonality, heat waves) and
581 anthropogenic (e.g. pollution, habitat fragmentation) factors (Lafferty and Kuris 2005, Cable et
582 al. 2017). Variation in climate likely disproportionately impacts parasites with an
583 environmentally transmitted stage, common in IT parasites. For instance, parasite development
584 slows during dry and cold seasons (Turner and Getz 2010, Kutz et al. 2014) and the emergence
585 patterns of free-living, aquatic parasites are dictated by temperature, light and water depth
586 (Fingerut et al. 2003b). For hosts, activity and exploration generally increase at warmer
587 temperatures, which could lead to higher host encounter rates with IT parasites and greater social
588 interactions that facilitate DT parasite transmission (Barber et al. 2016, Gopko et al. 2020).
589 Seasonal and anthropogenic changes in water flow can also impact parasite transmission, with
590 Reynolds et al. (2019) showing that interrupted water flow leads to higher transmission of the
591 DD ectoparasite *Gyrodactylus turnbulli* and reduced shoal cohesion in guppy hosts (*P.*
592 *reticulata*). Habitat fragmentation may lead to reduced host contact rates and thus reduce
593 transmission, especially for DT parasites (Hess, 1996). Alternatively, habitat loss and
594 urbanization could enhance parasite richness when host density increases in a fragmented
595 ecosystem (McCallum and Dobson 2002). For instance, Froeschke and Matthee (2014) found
596 that an increased density of the four-striped grass mouse (*Rhabdomys pumilio*) in fragmented

areas led to higher parasite abundance and richness compared with rodents from natural areas. This unpredictable cocktail of environmental factors enhances the complexity of parasite transmission and its interaction with host sociability.

CONCLUSIONS

The diversity and abundance of parasites in animal communities contributes to intra- and interspecific variability in the distribution of social phenotypes. Although it has been 50 years since Alexander (1974) first proposed a link between social grouping and parasitism, we are only beginning to crack the surface of the complex interactions between gregarious hosts and their parasites. Further, we know little about how parasite exposure history could influence social phenotypes, even when the host successfully fights off the parasite's invasion. Recent work suggests that parasite exposure can alter the host's behavior, even in the absence of any detectable parasite infection following exposure (Parker et al. 2023, Vindas et al. 2023). These results highlight that the parasites found in study animals could be just the tip of the iceberg in terms of that animal's parasite exposure through its ontogeny and the species' evolutionary history. Further, we still have much to learn about the bidirectional relationship between social dynamics and infection risk, including factors like group positioning, composition, and social network structure and dynamics, and represent exciting opportunities for new research in this area.

ACKNOWLEDGEMENTS

LEN is supported by funding from the University of Southampton, and SAB is funded by an NSERC Discovery Grant and the Canada Research Chair Program. JDB is funded by an FRQNT doctoral scholarship. MJS is funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska Curie grant agreement No. 101023948 and Royal Society University Research Fellowship URF\R1\221800. SSK is supported by Natural Environment Research Council Standard Grant NE/T008334/1.

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