
Collective behavior and parasite transmission

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5.1 Introduction

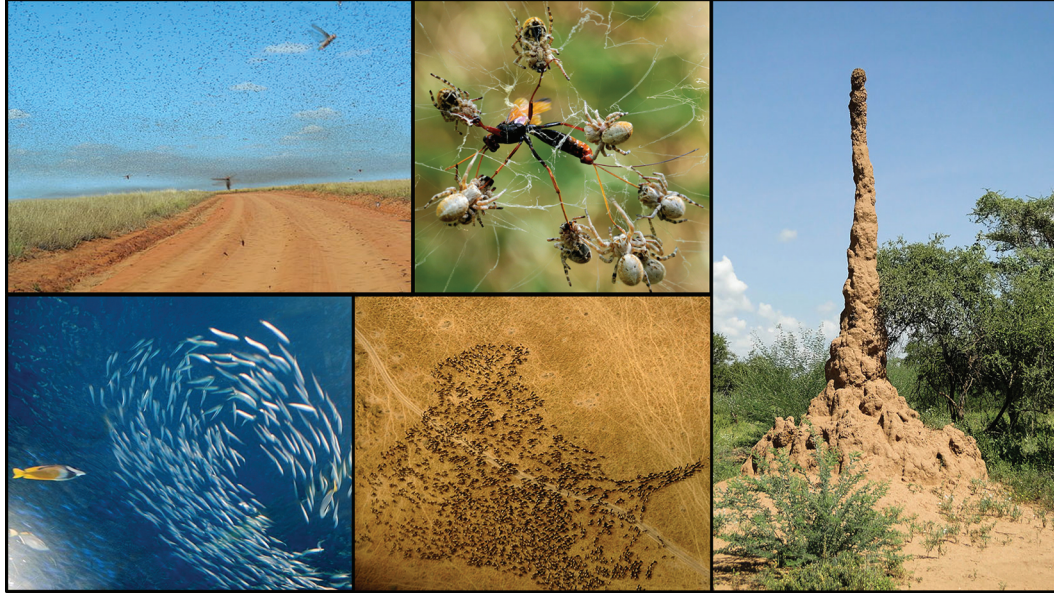
The fields of animal behavior and infectious diseases are both typified by multiscale research perspectives, combining research on individuals, social groups, populations, and communities. For example, the collective movements of fish schools and bird flocks are emergent, self-organizing properties of the behaviors of individual group members. Individual group members behave following sets of rules which vary depending on their own traits and the actions of individuals around them. Likewise, the dynamics of an infectious disease outbreak are emergent properties of individual-level host–parasite interactions. Individual hosts become infected based on their own behavioral and immunological traits, but transmission potential depends jointly on the actions of interacting individuals. One cannot truly understand the dynamics at one scale (e.g., individual) without incorporating information from the other (e.g., group, population).

How, then, do these multi-tier systems of **collective behavior** (see Box 5.1 for glossary) and disease interact? The relationship between individual behavior and infection risk is well-studied (1), (2), as is the effect of parasites on individual behavior traits (3). Less understood, however, are the ways in which the collective behavior of social groups influences the transmission dynamics of parasites. It is important to understand links between collective behavior and parasitism because sociality is such a pervasive and important phenomenon

characterizing animal life. Tight-knit social groups incur unique benefits (**social immunity**, resource acquisition) and costs (parasite exposure), all of which have the potential to impact parasite transmission. Here, I use examples from diverse animal societies to review (i) how individual and group behavior underlies the relationship between collective behavior and parasite transmission; (ii) mechanisms by which groups can modulate the benefits of collective behaviors and minimize the risk of parasitism; and close by (iii) highlighting some contemporary technological and conceptual advances pushing the frontiers of research in collective behavior and disease.

5.2 Individual differences and collective outcomes in behavior and disease

Individuals differ from each other in countless ways: body size, body condition, hunger, behavioral phenotypes, experience, parasite load, etc. How, then, do groups of animals produce concerted group-level outcomes? For an anthropocentric yet familiar example: how does a group composed of friends with different tastes, hunger states, and local experiences effectively choose a restaurant? Although this conundrum often results in long-winded discussions rarely concluding in a decision preferred by all members (4), the vast majority of animal societies arrive at collective decisions based on sets of individual-level rules. For example, studies on fish shoals and bird flocks suggest that individuals are attracted to others at long distances,

Box 5.1 Glossary

Box 5.1, Figure 1 Examples of collective behavior in animal groups with varying social systems. Photo sources: Wikimedia Commons. Clockwise from top left: locust swarm by Iwoelbern, social spiders by Wynand Uys, termite mound by Bernard Gagnon, wildebeest migration by T.R. Shankar Raman, shoaling fish by lifelish.

What is collective behavior? Through direct or indirect interactions between individuals, groups of animals produce coordinated actions at the group level. Collective behaviors are unachievable by individuals alone, and thus many collective behaviors represent emergent properties of social groups. As pictured earlier, collective behavior can emerge in locomotion, decision-making, group foraging and defense, construction of built environments, and more.

Allogrooming: Unidirectional and/or reciprocal grooming between individuals, including the removal of ectoparasites and debris.

Collective personality: Temporally consistent differences between groups of individuals in the execution of collective behavior.

Infection–information trade-off: Social interactions are the basis of beneficial information spread and harmful parasite transmission. A trade-off emerges if these two processes are regulated via the same social interactions.

Keystone individual: Akin to the keystone species concept of community ecology, keystone individuals are those that exert an inordinate influence over dynamics at higher levels of biological organization (social groups, communities, etc.).

Social context: Synonymous with “social environment,” conditions of the social group in which an individual resides (e.g., group size, sex ratio, group phenotypic composition), which often influence how individuals behave.

Social immunity: Antiparasitic defenses mounted by groups to protect individuals against disease and therefore protect the group from the loss of individuals or the transmission of parasites. Some researchers use the term social immunity exclusively in the context of collective behaviors in eusocial insects and highly complex primate societies, whereas others refer to social immunity more broadly as any immune response or antiparasitic defense that benefits others.

Social fulcrum hypothesis: In cases where trade-offs exist between the execution of a collective behavior (e.g., foraging, exploration) and the transmission of parasites, herein I propose the hypothesis that groups can resolve this trade-off by shifting the relative composition of different phenotypes within the group (see section 5.4 for more details).

Social heterosis: Benefits shared by group-mates via representation of diverse genotypes or phenotypes relative to monotypic groups.

repulsed by individuals at close distances, and align with group-mates depending on orientation and speed (5), (6). Most importantly, perhaps, are the rules regarding the source of social information: focal individuals respond to either every individual within a certain *distance* (7), a certain *number* of individuals (8), or only their single *nearest neighbor* (5). However, as we understand more about behavioral variation among individuals, contemporary studies aim to generate frameworks for how individual heterogeneity influences the mechanisms by which collective behaviors are organized (9)–(11).

Interestingly the ways in which individual behaviors contribute to the execution of collective behaviors can vary in response to infection. In shoaling fishes, individuals taking leading positions have a disproportionate influence over navigational decision-making (12). It has been hypothesized that individuals assume leading positions when most in need of finding a particular resource or locality (“lead according to need,” (13)), as nutritionally deprived fish often assume leading positions, acquire more food, and then retreat to posterior positions (14), (15). However, evidence also suggests that more experienced (16) or risk-tolerant fish (17) repeatedly take leading positions. Interestingly, Killifish infected with the trematode *Cras-siphiala bulboglossa* and sticklebacks infected with the microsporidian *Glugea anomala* are both more

likely to take leading positions in their shoals (18), (19) (Figure 5.1). The foraging benefits of a leading position may help ameliorate the deleterious effects of parasite infection, or perhaps leaders are simply more likely to encounter parasites. Experimental infections in laboratory shoals can help differentiate these competing hypotheses.

Just as individual-level differences in behavior show broad explanatory power for various topics in behavioral ecology, individual variation in disease susceptibility and transmission potential have been at the forefront of infectious disease research for decades (e.g., (20)). The influx of studies focusing on consistent individual differences in behavior (i.e., animal personalities, behavioral syndromes (21), (22)) over the past two decades has laid the framework for uniting animal behavior and research on host heterogeneity in wildlife diseases with multi-scale perspectives. Differences among individuals on axes of behavioral variation like activity, aggressiveness, and sociability that underlie ecological outcomes like exploration of new environments (23) and predator–prey dynamics (24) similarly influence host–parasite dynamics (1), (25). Although most personality studies on wild-caught animals are correlative, studies have demonstrated that more exploratory (26) or active (27) individuals are more likely to encounter and acquire parasites. Of course, correlations between behavior and immune

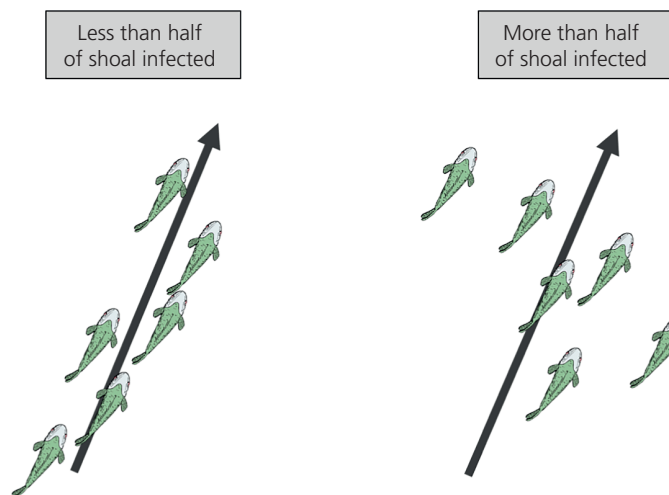


Figure 5.1 Example depicting one relationship between parasitism and collective behavior. Killifish in shoals where the majority of individuals are infected show a phalanx-like shoal formation relative to the direction of travel (\uparrow) compared to the processional shoal of majority uninfected groups. Adapted from Ward *et al.* (2002) (19).

traits likely play a role in behavior-parasitism relationships (2), (28), like the positive relationship between boldness and immunity in crickets (29).

The most extreme examples of individual variation are those where one or a few individuals exert an inordinately large influence over group outcomes, termed **keystone individuals** (30). For example, group exploration in guppies is not driven by social conformity of the entire group, but rather by the behavior of the least active member of the shoal (31). Keystone individuals may be beneficial to the groups in which they reside, like a small subset of “elite” workers in *Temnothorax* spp. that contribute to the majority of work in colony tasks (32). However, keystone individuals may also be detrimental to their groups, like disease superspreaders, where a large number of infections are caused by a small subset of infectious individuals (20). Martin *et al.* (33) hypothesized that correlated suites of behavioral and physiological traits associated with parasite exposure, susceptibility, and transmission have the potential to generate “extremely competent” individuals that have disproportionate impacts on disease spread, for example by generating an excess of infections. The degree to which underlying traits predict the influence of keystone individuals on both collective behavior and disease dynamics is an overlooked but important phenomenon that requires deeper study.

Some notable case studies have identified traits which may underlie keystone individuals’ joint influence over collective behaviors and disease. Sapolsky and Share (34) describe in detail a case where a number of highly aggressive male baboons, *Papio anubis*, ate contaminated meat from a garbage dump and died of bovine tuberculosis infections. The death of highly aggressive males left behind groups with altered sex ratios and a greater representation of non-aggressive survivors that persisted for over a decade. Here, aggressiveness *per se* (not dominance rank or age) predicted which individuals fed at the high-risk resource patch and subsequently engaged in more dominance interactions between infected and susceptible baboons (34). In the social spider *Stegodyphus dumicola*, the presence of highly risk-tolerant or “bold” individuals in a colony is associated with groups attacking prey more rapidly (35). When these potentially influential individuals are exposed to a cocktail of

harmful cuticular bacteria, collective prey capture is dampened even in the absence of spider mortality (36). Thus, collective behavior is dampened not because of the loss of participating individuals, but potentially because keystone individuals behaved differently after bacterial exposure and lost their influence over group-mates (e.g., (37)). Using simulations parameterized with data from laboratory colonies of *S. dumicola*, Pinter-Wollman *et al.* (38) suggest that keystone individuals might alter group-mates’ behavior via their interaction patterns which lead to trade-offs between disease risk and cooperative prey attack.

5.3 Collective behavior and group infection dynamics

Just as behavioral traits like sexual promiscuity, sociality, or territory size can be important predictors of parasite risk for individuals, the collective traits of social groups can similarly predict the likelihood of disease outbreaks therein. Group-level traits like density are often predictors of parasite transmission (39), and “crowding” behavior in beetle larvae (*Plagiodera versicolora*) is positively associated with group-level mortality from parasitoids (40). However, the effects of individual traits on individual infection risk will not always scale linearly to group behavior and group transmission dynamics. For example, *Poecilia reticulata* guppies experience female-biased parasite intensity, but no differences in disease dynamics are found between single-sex and mixed-sex groups (41). This is because the expression of individual behaviors, and their associated relationships with infection risk, change depending on **social context** (42). For example, glucocorticoids have immunosuppressive effects on low-ranking but not high-ranking baboons (43), and zebra finches respond to immune challenge by reduced activity level, but only in isolation; birds in a social setting do not exhibit this change in behavior (44). Therefore, studying group-level traits (group size, group composition, collective behaviors) and how individual traits contribute to them is important in predicting group-level disease dynamics.

In some cases, collective behaviors and infectious disease dynamics may be driven by the same underlying organizational forces. Modular

social network structures, where social interactions are more likely to occur within subgroups rather than between subgroups, are hypothesized to promote the evolution of cooperation (45), (46), and the severity of disease outbreaks decline at higher levels of network modularity (47). Similarly, the spatial and temporal separation of interactions between nurses (specializing on brood care) and foragers (specializing on food collection) in eusocial insect colonies may serve as a means to organize division of labor (48) and to restrict parasite transmission (49).

Particularly interesting cases are those where a collective behavior meant to decrease infection risk can also serve as a route for parasite transmission. **Allogrooming**, where individuals clean debris and ectoparasites off group-mates, results from emergent, self-organizing social behaviors that reduce parasite burden in many animal groups (50). *Formica* ants increase allogrooming when exposed to entomopathogenic fungal spores (51) and allogrooming decreases tick load in baboons (52). This collective behavior serves, in addition to social bonding in some mammals, to reduce parasite burden yet also facilitates additional routes for parasite transmission (53). However, in some animal societies where allogrooming and dominance are positively correlated (e.g., meerkats (54)) certain allogrooming strategies (e.g., indiscriminate allogrooming versus preferential allogrooming based on social connectedness) are ineffective in parasite removal and may rather serve to reinforce social bonding (50), (55). In contrast, in other societies, like baboons, allogrooming is both effective at parasite removal and positively correlated with dominance (52).

Allogrooming represents a promising phenomenon with which to test hypotheses linking the execution of collective behaviors with potential antiparasitic defenses across species with different systems of social organization. For example, in which social systems do the consequences of collective behaviors like allogrooming on group cohesion and parasitism align versus misalign? Are these contrasts driven solely by social organization, or under higher parasite intensity will these outcomes become aligned? Allogrooming is a major component of behavioral disease defenses in eusocial insects, referred to collectively as **social immunity**,

and how colonies execute various components of social immunity to optimize collective behavior and disease defenses is another interesting avenue of research (Box 5.2).

Extended phenotypes of animal collective behavior, like the built environment of social groups, can also influence infectious disease dynamics (56). Nest architecture has been a focus of evolutionary parasitology in eusocial insects, as the physical structures around individuals directly constrain the frequency, duration, and location of social interactions (57)–(59). Some features of nest architectures, like subdivision into separate chambers (57) or small nest entrances (60), have been hypothesized to reduce parasite transmission, but some experimental studies have found no effect of colony architecture on disease prevalence (e.g., (61)). The built environment represents an interesting phenomenon for the study of collective behavior and parasite transmission because the disease consequences of the collective behaviors involved in constructing that environment are temporally offset. That is, a social group builds a nest whose features will influence future social interaction patterns therein, and those patterns may differentially impact parasite transmission within groups (62).

5.4 Performing collective behaviors while minimizing parasite transmission

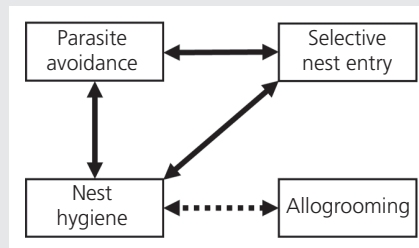
Although collective behavior and parasite transmission are often studied separately, these group-level outcomes may be interrelated in some cases. The collective outcomes of social groups are driven, in part, by the composition of individual phenotypes within the group. Groups of social spiders containing more risk-prone or bold individuals attack prey more quickly (74), and guppy shoals containing both bold and shy individuals experience increased collective foraging success compared to monotypic groups (75). However, the optimal mixture of phenotypes for one task may be detrimental in other contexts (Figure 5.2C). For example, the **infection–information trade-off** describes the trade-off between the sharing of beneficial information and the transmission of parasites via social interactions (76). Evans *et al.* (77) suggest that modular social network structures and long-term social bonds can promote the sharing of information

Box 5.2 Social immunity as a collective behavioral syndrome

Despite living in dense groups of highly related individuals, eusocial insects are remarkably proficient at reducing the risk of disease outbreaks within the colony (63). Eusocial insects mitigate outbreak risk via collective behaviors referred to as **social immunity** (64); a set of colony-level protections against parasites performed by workers either individually (e.g., corpse removal; antimicrobial secretions), in dyadic interactions (e.g., allogrooming), or collectively (e.g., social fever; altered social network structure) (65), (66). A few studies have quantified aspects of social immunity over time and identified consistent among-colony differences in the expression of social immunity under identical environmental conditions (i.e., social immunity as “collective personalities” (121)). For example, honey bees exhibit among-colony differences in hygienic behaviors which are repeatable across years (67), and defensive resistance against *Varroa* mites is a repeatable and heritable trait at the colony level (68). Social immunity traits also correlate with other collective behaviors, like a negative relationship between corpse-removal behavior and nest relocation in *Temnothorax* ants (69) and a positive relationship between corpse-removal and forging activity in honey bees (70). Therefore, factors of social immunity may similarly be related to one another in collective behavioral syndromes (correlations between collective personality traits), as has been found in other collective traits in ant societies (71).

For example, in the hypothetical population depicted in Figure 1, colonies that exhibit more stringent parasite avoidance or selective nest entry also express increased hygienic corpse-removal behaviors, but show decreased

time investment in allogrooming. Thus, depending on local parasite pressure, colonies may adjust the relative expression of different social immunity traits as alternative strategies to achieve a necessary level of colony protection. There has not yet been a study which explicitly addressed collective immune syndromes and their survival/fitness consequences in the face of parasitism, though some studies have shown that social immunity is negatively correlated with individual immunity (72). This suggests that colonies may regulate the expression of social immunity based on the physiological immunocompetence of workers therein. Cassidy *et al.* (73) found that *T. curvispinosus* ant colonies containing workers with weaker individual immune defenses showed increased social immunity (faster corpse removal). Future studies should test whether the relative investment in social versus individual immunity, or relationships between social immune traits, change across time and space based on local parasite pressures.



Box 5.2, Figure 1 Conceptual map depicting a hypothetical collective behavioral syndrome involving four social immunity traits, where arrows represent positive correlations and dashed lines represent negative correlations between traits.

while mitigating parasite transmission. Notably, they predict that behavioral plasticity modifying social interactions in the presence of parasites is “a key mechanism by which this balance between the costs and benefits of being highly socially connected is mediated.” (77) Therefore, trade-offs in collective outcomes may be resolved via the adaptive allocation of individual phenotypes within groups. For example, the trade-off between exploiting known resource patches and exploring new patches is mediated in honey bees via the mixture of different “finder” and “refiner” learning phenotypes (78).

Here, I propose the “social fulcrum hypothesis,” where shifting phenotypic composition is a mechanism by which groups can adaptively modulate the competing outcomes of collective behavior and disease risk (Figure 5.2D). Imagine a case where (i) groups containing more aggressive individuals outperform groups with fewer aggressive individuals in collective foraging, (ii) parasites are transmitted via aggressive interactions, and (iii) the benefits garnered from foraging are outweighed by the costs associated with parasitism. In the presence of parasites, the optimal group composition

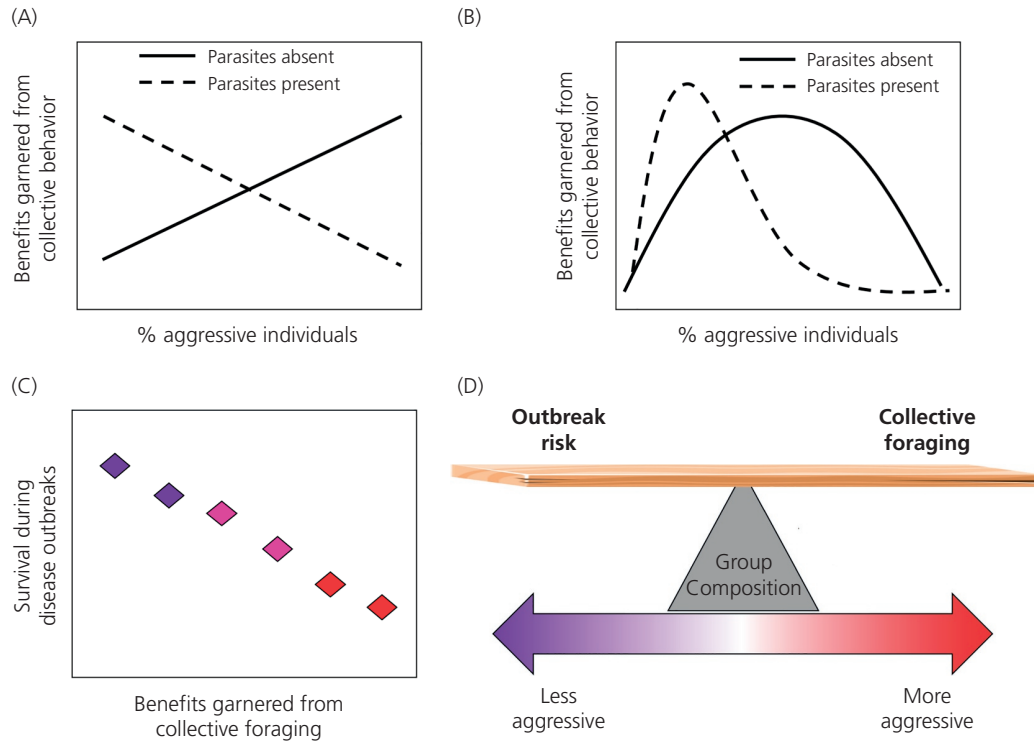


Figure 5.2 (A, B) Hypothetical relationships between group composition (the percentage of aggressive individuals in a group) and the benefits garnered from the execution of a given collective behavior like cooperative hunting. The optimal group composition may change depending on the presence of transmissible parasites, and these relationships may be (A) linear or (B) nonlinear. (C) Proposed trade-off between the benefits garnered from collective foraging and survival during disease outbreaks. Redder colors represent groups with more aggressive individuals while violet colors represent groups with fewer aggressive individuals. (D) The social fulcrum hypothesis of group composition posits that group phenotypic composition will shift towards the optimum to balance opposing demands of collective behavior and disease risk.

should shift from aggressive-dominated to potentially mixed behavioral composition. Regardless of whether the effect of group composition on collective behavior is linear (Figure 5.2A) or non-linear (Figure 5.2B), shifts in phenotypic composition may materialize via two non-mutually exclusive mechanisms: (i) there may be *local adaptation* in host-parasite coevolution as in geographic mosaic theory (79) where the collective behavior of social groups differs among populations depending on parasite pressure (Figure 5.3A); or (ii) groups may shift group phenotypic composition as a result of prevailing parasite cues (e.g., across a “landscape of disgust”; (80)) (Figure 5.3B). Shifts in group composition could occur via numerical changes in the relative representation of different phenotypes,

as in shifting caste ratios in response to competition in ants (81) and wasps (82) or individual phenotypic plasticity may shift group composition towards the optimum, as in task switching in harvester ants (83) or individualized changes of specialized roles in social groups (84). Alternatively, numerical changes in group composition may occur due to phenotype-biased mortality. The motivation for groups to modulate group composition will also depend on whether collective behaviors are associated with the transmission of *beneficial* microorganisms (85) or anti-parasitic substances (63). Currently, I am unaware of any direct evidence in support of the social fulcrum hypothesis. Rather, several systems provide indirect evidence from separate experiments that group

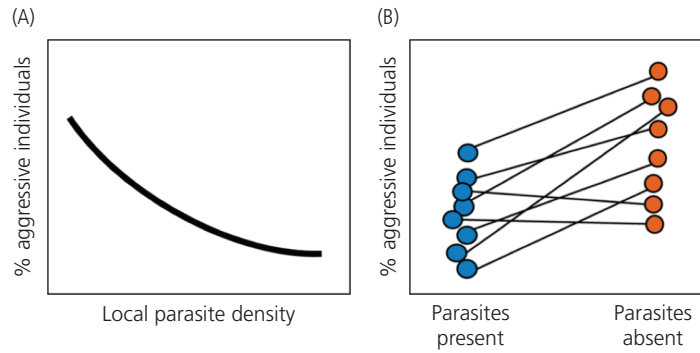


Figure 5.3 Two ways by which the social fulcrum hypothesis of group composition could manifest. (A) Local adaptation in host–parasite coevolution where the percentage of aggressive individuals in social groups differs among populations, and therefore the execution of collective behaviors also varies, depending on local parasite pressure (B) Active shifts in group composition, and thereby changes in collective behavior, as a result of parasite presence. Variation in group composition in the absence of parasites may be due to prey availability, whereas variation in group composition in the presence of parasites may be due to differences in parasite pressure. Shifts in group composition may be numerical via differential mortality from parasite infection, or individual phenotypic plasticity may adaptively shift group composition.

composition underlies both collective behavior and disease dynamics (Table 5.1). For example, the same group compositions that benefit social spider group foraging (74), (86) also increase the transmission of cuticular bacteria (87). And female-biased groups of *Drosophila melanogaster* exhibit more cohesive aggregation when choosing food patches (124), but experience more severe outbreaks of a fungal pathogen (42). Future studies can utilize these systems to test for direct trade-offs between collective behaviors and disease risk, and whether phenotypic composition varies among groups to resolve these conflicting demands.

5.5 Frontiers in collective behavior and disease

Researchers interested in the interface between collective behavior and parasite transmission are fortunate to have multiple fields from which theory and methodology can be drawn. Here I highlight some of the current conceptual advances (e.g., parasite–collective behavior feedbacks) and methodological advances (e.g., multi-level network modeling, animal tracking) in research uniting collective behavior and parasitism, along with some currently unanswered questions to inspire future research.

5.5.1 Parasite–collective behavior feedbacks

Ezenwa *et al.* (89) provide a framework for studying feedbacks between host behavior and parasite infection where there is a reciprocal exchange between host behavior and parasitism. Host behavior influences parasite infection risk, parasite infection influences host behavior, and these dynamics do not occur in isolation of each other. The framework of behavior–parasitism feedbacks can similarly be applied to feedbacks between parasite transmission and the execution of collective behaviors. For example, aggregation in locusts can increase the transmission of the microsporidian parasite *Paranosema locustae*, though infection suppresses the hindgut bacteria that produce aggregation pheromones in their locust hosts, thereby preventing swarming behavior (Box 5.3; (88)). Future research should identify systems where there is evidence for reciprocal effects of collective behavior on parasite transmission and parasite presence on collective behavior, and use longitudinal observations to identify whether these effects are indeed linked via a feedback loop. Then, time series analyses can be used to test for temporal associations between collective behavior and parasite prevalence over time or parameterize simulations to generate predictions regarding these potentially reciprocal interactions.

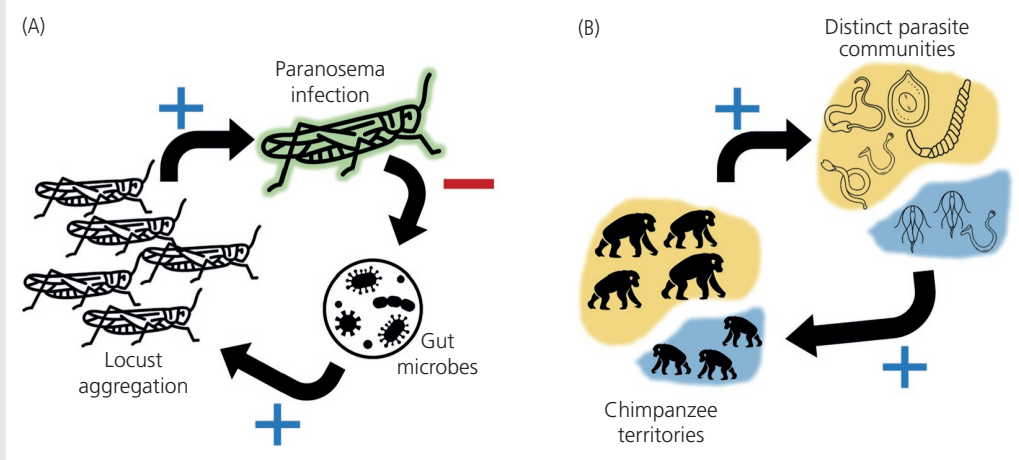
Table 5.1 Examples of study systems in which group composition effects have been described as predictors of both collective behavior and disease. Each of these systems represent promising cases in which the social fulcrum hypothesis may be tested directly. Group composition in these examples is broken up into mixtures of behavioral phenotypes, group genotypic composition, and demographics like caste ratio, sex ratio, and age class distribution.

Host species	Group composition	Collective behavior outcome	Disease outcome	Notes
Social spider, <i>Stegodyphus dumicola</i>	Bold and shy behavioral types	More bold spiders in colony increase attack speed and repeatability of collective foraging (74), (86)	More bold spiders increase bacterial transmission rates (87)	Bacteria used in transmission experiments were naturally occurring and likely non-pathogenic
Cavity-nesting ants, <i>Temnothorax</i> spp.	Aggressive and non-aggressive behavioral types	More aggressive individuals in colony associated with more rapid nest relocation behavior (112)	Colonies with greater nest relocation tendency have greater immune defenses (69)	An example of a non-contrasting outcome, though positive selection for "all-aggressive" colonies is unlikely due to social heterosis (113), (114)
Honey bee, <i>Apis mellifera</i>	Aggressive and non-aggressive behavioral types	Colonies containing more aggressive bees exhibit more rapid nest defense (115)	Aggressive and mixed-phenotype colonies exhibit enhanced nest hygiene compared to non-aggressive colonies (115)	This was a single study that manipulated worker composition and measured collective behaviors related to colony defense and nest hygiene
Guppy, <i>Poecilia reticulata</i>	Bold and shy behavioral types	Shoals containing bold individuals discover novel food sources more quickly (116)	Shy fish acquire more ectoparasites within shoals (117)	A potential case where phenotype-biased illness/mortality underlies shifts in group composition
Threespine sticklebacks, <i>Gasterosteus aculeatus</i>	Sociability and boldness scores	Trait compositions explain the emergent structure and coordination of self-organized shoaling, also driving foraging success (118)	Collective movement in pairs of infected fish is less cohesive and coordinated than non-infected pairs; mixed pairs largely led by the non-infected fish (119)	One piece of evidence missing in this example is whether shoals containing different mixtures of behavioral types are more or less likely to encounter parasites and experience different rates of transmission/infection
Honey bee, <i>Apis mellifera</i>	Genotypic composition	Genetically diverse colonies show enhanced collective foraging and weight gain compared to uniform colonies (120)	Colonies containing workers from breeding lines predisposed to hygienic behavior perform more hygienic behaviors (121)	Genetic variation may benefit colonies under some circumstances, but if parental genotypes not selected for hygienic behavior, then genetic composition may have maladaptive effects on the distribution of anti-parasite behavior

continued

Table 5.1 *Continued*

Host species	Group composition	Collective behavior outcome	Disease outcome	Notes
Bumble bee, <i>Bombus impatiens</i>	Body size variation	Colony body size variation does not affect colony thermoregulation, where bees fan their wings to cool the nest after heating.	Colonies with similarly sized bees outperform those with a wider range of body sizes in corpse-removal behavior.	This was a single study that manipulated worker body size composition and measured collective behaviors related to colony thermoregulation and nest hygiene (122)
Cavity-nesting ants, <i>Temnothorax curvispinosus</i>	Queen presence	Queenless colonies discover food more slowly and exhibit less brood-care behavior.	Queenless colonies experience more rapid disease-associated mortality.	Single study; queenless colonies that exhibited more brood care (i.e., behaved more like queenright colonies) experienced less severe outbreaks (123)
Guppy, <i>Poecilia reticulata</i>	Sex ratio	Male-biased sex ratios reduce group cohesion (males disperse; (124))	Despite female-biased parasite intensity, no difference in disease dynamics between single-sex and mixed-sex groups (41)	Groups may benefit from female-biased sex ratios, but this depends on whether the benefits of group cohesion are sex-biased
Fruit fly, <i>Drosophila melanogaster</i>	Sex ratio	Female-biased groups exhibit more cohesive aggregation when choosing food patches (125)	Female-biased social groups experience more severe outbreaks of a fungal pathogen (42)	Promising system to test the social fulcrum hypothesis, as one metric of group composition (sex ratio) affects collective behavior and disease risk, with a potential trade-off in group outcomes

Box 5.3 Parasite-collective behavior feedbacks

Box 5.3, Figure 1 Potential positive (A) and negative (B) feedbacks between collective behavior and parasitism. Icons obtained from the Noun Project. Grasshopper by Yu Luck; chimpanzee by Abby; parasites by Olena Panasovska.

Ezenwa *et al.* (89) provide a framework for studying feedback between host behavior and parasite infection. This framework can similarly be applied to feedbacks between parasite transmission and the execution of collective behaviors. Figure 1A gives an example of a negative feedback between parasite transmission and collective behavior. The microsporidian parasite *Paranosema locustae* can be transmitted horizontally in aggregations of their locust host (90). Microsporidian infection suppresses the hindgut bacteria responsible for producing aggregation pheromones, thereby reducing

swarming tendencies generated through aggregation and reducing horizontal transmission. Figure 1B shows an example of a positive feedback between parasite transmission and collective behavior. Chimpanzees maintain territories via aggressive interactions at territory borders. Within territories, chimpanzees accumulate locally abundant parasites (91) and parasite load increases with levels of aggression/dominance via immunosuppression from testosterone and cortisol (92). This establishes a potential positive feedback between group-level aggression and parasite transmission.

5.5.2 Multi-level network modeling

The analysis of social networks has been an invaluable tool in the study of social behavior and infectious disease epidemiology (93). One criticism of traditional social network analysis is that a connection (edge) between two individuals (nodes) is often meant to represent a single action, like grooming, information transfer, bodily contact, or mere proximity. However, this singular view of social behavior ignores the multifaceted nature of social interactions. The advent of multi-level network

modeling integrates multiple network topologies atop one another either simultaneously or over time to address interrelatedness between different contexts of social interactions (94). For example, one could use multi-level network models to ask how different types of social interaction (e.g., allogrooming versus cooperative hunting) underlie the transmission of different pathogens, and how those transmission dynamics may interact (95). This powerful analytical tool could be applied to any system, from social insects (96) to bird flocks (97) and mass migrations (98).

5.5.3 High-resolution tracking

Advances in real-time tracking technology have facilitated leaps in progress in studying collective behaviors. As questions about living systems become grander, so do the tools required to address them and the resulting scale and dimensionality of datasets (99). For example, automated tracking via miniature QR codes attached to *L. niger* ants demonstrated that colony social networks change after parasite introduction (49). By tracking juvenile white storks using high-resolution GPS and accelerometers, Flack *et al.* (100) discovered that clear leaders and followers emerge in flocking dynamics, where leaders discover thermal uplifts and are followed by followers. In this example, leaders spend more time in thermals, requiring less flapping during flight, and migrate further annually. The migration of juvenile white storks has been the source of introduced avian diseases in the past, like West Nile Virus in Israel in 1998 (101) and Newcastle Disease Virus in Germany in 1992–1993 (102). Given that some sub-genotypes of Newcastle Disease Virus exhibit significant panzootic potential (103), this study system has the potential to link individual traits and collective flocking behavior with migration outcomes to predict and prevent disease outbreaks (104), (105).

5.5.4 Collective behavior of clones

Given how important inbred genotype lines in model systems (*Drosophila* flies and *C. elegans* nematodes) have been to understanding the intrinsic and extrinsic factors of behavior, clonal animals are a growing tool for the study of social behavior. Bierbach *et al.* (106) used tightly controlled ontogenetic experiments with the clonal Amazon molly to identify the degree to which behavioral individuality emerges despite no differences in genotype, no social input, and near-identical rearing conditions. They discovered substantial individual variation among genetically identical siblings isolated directly after birth into standardized environments, and the degree of variation did not change depending on varying levels of social exposure. Laskowski *et al.* (107) highlight the untapped potential of clonal vertebrates in experimental animal behavior, and how systems like the Amazon Molly may be

predisposed for incorporating parasite transmission dynamics due to a history of studies on the major histocompatibility complex and its regulation on genotypic immune variation (108), (109). In some cases, research on vertebrate models is not feasible, and fruit flies represent an amazing system for studying collective behavior (e.g., aggregation) and disease dynamics in single and mixed-genotype populations (110). Using inbred laboratory lines of *Drosophila melanogaster*, one can generate replicate social groups of specific genotype combinations over a relatively short time span (111), allowing for large-scale testing of hypotheses combining collective behavior and disease outcomes.

5.6 Conclusions

The transition from solitary life to social living was one of the major biological transitions in evolution and as such, social animals are amazingly successful with huge impacts on ecological communities. Quantifying the dynamics which influence parasite transmission in social groups is complicated because the collective behaviors of animal societies incur unique benefits and costs associated with parasitism. The goals of this chapter were threefold: (i) describe notable phenomena and trends in research focusing on animal collective behavior and its disease outcomes, (ii) propose a mechanism (the social fulcrum hypothesis) by which selection may operate on group traits and their joint outcomes on collective behavior and parasitism, and (iii) describe burgeoning research frontiers in which the dynamics of collective behavior and parasitism can be tested. With advances in tracking technologies and the computational power that facilitates analyses of tracking data, identifying the costs and benefits of complex collective behaviors for social groups becomes more feasible. Experiments designed to test hypotheses explicitly regarding potential trade-offs in collective outcomes, and how they are resolved, are likely to expand our foundational understanding of how disease dynamics play out in animal societies.

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References

1. Barber I and Dingemanse NJ. Parasitism and the evolutionary ecology of animal personality. *Phil Trans Roy Soc B*. 2010;365(1560):4077–88.
2. Hawley DM, Etienne RS, Ezenwa VO, and Jolles AE. Does animal behavior underlie covariation between hosts' exposure to infectious agents and susceptibility to infection? Implications for disease dynamics. *Integr Comp Biol*. 2011;icr062.
3. Poulin R. Parasite manipulation of host personality and behavioural syndromes. *J Exp Bio*. 2013;216(1):18–26.
4. Conradt L. Group decisions: How (not) to choose a restaurant with friends. *Curr Bio*. 2008;18(24):R1139–R40.
5. Herbert-Read JE, Perna A, Mann RP, Schaerf TM, Sumpter DJ, and Ward AJW. Inferring the rules of interaction of shoaling fish. *PNAS*. 2011;108(46):18726–31.
6. Lukeman R Li Y-X, and Edelstein-Keshet L. Inferring individual rules from collective behavior. *PNAS*. 2010;107(28):12576–80.
7. Couzin ID, Krause J, James R, Ruxton GD, and Franks NR. Collective memory and spatial sorting in animal groups. *J Theoretical Bio*. 2002;218(1):1–12.
8. Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, et al. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *PNAS*. 2008;105(4):1232–37.
9. Jolles JW, King AJ, and Killen SS. The role of individual heterogeneity in collective animal behaviour. *Trends Ecol Evol*. 2020;35(3):278–91.
10. Farine DR, Montiglio P-O, and Spiegel O. From individuals to groups and back: The evolutionary implications of group phenotypic composition. *Trends Ecol Evol*. 2015;30(10):609–21.
11. LeBoeuf AC and Grozinger CM. Me and we: The interplay between individual and group behavioral variation in social collectives. *Curr Opin Insect Sci*. 2014;5:16–24.
12. Bumann D and Krause J. Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). *Behaviour*. 1993;125(3-4):189–98.
13. Conradt L, Krause J, Couzin ID, and Roper TJ. "Leading according to need" in self-organizing groups. *Am Nat*. 2009;173(3):304–12.
14. McLean S, Persson A, Norin T, and Killen SS. Metabolic costs of feeding predictively alter the spatial distribution of individuals in fish schools. *Curr Bio*. 2018;28(7):1144–49.e4.
15. Hansen MJ, Schaerf TM, Krause J, and Ward AJW. Crimson spotted rainbowfish (*Melanotaenia duboulayi*) change their spatial position according to nutritional requirement. *PLoS One*. 2016;11(2):e0148334.
16. Reebs SG. Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim Behav*. 2000;59(2):403–9.
17. Reebs SG and Leblond C. Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour*. 2006;143(10):1263.
18. Ward AJW, Duff AJ, Krause J, and Barber IJ. Shoaling behaviour of sticklebacks infected with the microsporidian parasite, *Glugea anomala*. *Env Bio Fishes*. 2005;72(2):155–60.
19. Ward AJW, Hoare DJ, Couzin ID, Broom M, and Krause J. The effects of parasitism and body length on positioning within wild fish shoals. *J Anim Ecol*. 2002;10–14.
20. Lloyd-Smith JO, Schreiber SJ, Kopp PE, and Getz W. Superspreading and the effect of individual variation on disease emergence. *Nature*. 2005;438(7066):355–9.
21. Sih A and Bell AM. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*. 2008;38:227–81.
22. Bell AM, Hankison SJ, and Laskowski KL. The repeatability of behaviour: A meta-analysis. *Anim Behav*. 2009;77(4):771–83.
23. Cote J, Clobert J, Brodin T, Fogarty S, and Sih A. Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Phil Trans Roy Soc B*. 2010;365(1560):4065–76.
24. Toscano BJ, Gownaris NJ, Heerhartz SM, and Monaco CJ. Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. *Oecologia*. 2016;182:55–69.
25. Kortet R, Hedrick AV, and Vainikka A. Parasitism, predation and the evolution of animal personalities. *Eco Lett*. 2010;13(12):1449–58.
26. Gyuris E, Hankó JF, Feró O, and Barta Z. Personality and ectoparasitic mites (*Hemipteroseius adleri*) in firebugs (*Pyrrhocoris apterus*). *Behav Proc*. 2016;122:67–74.
27. Paquette C, Garant D, Savage J, Réale D, and Bergeron PJ. Individual and environmental determinants of *Cuterebra* bot fly parasitism in the eastern chipmunk (*Tamias striatus*). *Oecologia*. 2020;193(2):359–70.

28. Demas GE and Carlton ED. Ecoimmunology for psychoneuroimmunologists: Considering context in neuroendocrine-immune-behavior interactions. *Brain Behav Immunity*. 2015;44:9–16.
29. Niemelä PT, Dingemans NJ, Alioravainen N, Vainikka A, and Kortet RJ. Personality pace-of-life hypothesis: Testing genetic associations among personality and life history. *Behav Ecol*. 2013;24(4):935–41.
30. Modlmeier AP, Keiser CN, Watters JV, Sih A, and Pruitt JN. The keystone individual concept: An ecological and evolutionary overview. *Anim Behav*. 2014;89:53–62.
31. Brown C and Irving E. Individual personality traits influence group exploration in a feral guppy population. *Behav Ecol*. 2014;25(1):95–101.
32. Pinter-Wollman N, Hubler J, Holley J-A, Franks NR, and Dornhaus A. How is activity distributed among and within tasks in *Temnothorax* ants? *Behav Ecol and Sociobiol*. 2012;66(10):1407–20.
33. Martin LB, Addison B, Bean AG, Buchanan KL, Crino OL, Eastwood JR, et al. Extreme competence: Keystone hosts of infections. *Trends Ecol Evol*. 2019;34(4):303–14.
34. Sapolsky RM and Share LJ. A pacific culture among wild baboons: Its emergence and transmission. *PLoS Biol*. 2004;2(4):e106.
35. Hunt ER, Mi B, Geremew R, Fernandez C, Wong BM, Pruitt JN, et al. Resting networks and personality predict attack speed in social spiders. *Behav Ecol Sociobiol*. 2019;73(7):1–12.
36. Keiser CN, Wright CM, and Pruitt JN. Increased bacterial load can reduce or negate the effects of keystone individuals on group collective behaviour. *Anim Behav*. 2016;114:211–18.
37. Beros S, Jongepier E, Hagemeyer F, and Foitzik SJ. The parasite's long arm: A tapeworm parasite induces behavioural changes in uninfected group members of its social host. *Proc R Soc B: Biol Sci*. 2015;282(1819):20151473.
38. Pinter-Wollman N, Keiser CN, Wollman R, and Pruitt JN. The effect of keystone individuals on collective outcomes can be mediated through interactions or behavioral persistence. *The Am Nat*. 2016;188(2):240–52.
39. Brown CR and Brown MB. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology*. 1986;67(5):1206–18.
40. McCauley DE. Intrademic group selection imposed by a parasitoid-host interaction. *Am Nat*. 1994;144(1):1–13.
41. Tadiri C, Scott M, and Fussmann GJ. Impact of host sex and group composition on parasite dynamics in experimental populations. *Parasitol*. 2016;143(4):523–31.
42. Keiser CN, Rudolf VHW, Sartain E, Every ER, and Saltz JB. Social context alters host behavior and infection risk. *Behav Ecol*. 2018;29(4):869–75.
43. Archie EA, Altmann J, and Alberts SC. Social status predicts wound healing in wild baboons. *PNAS*. 2012;109(23):9017–22.
44. Lopes PC, Adelman J, Wingfield JC, and Bentley GE. Social context modulates sickness behavior. *Behav Ecol Socio*. 2012;66(10):1421–8.
45. Marcoux M and Lusseau DJ. Network modularity promotes cooperation. *J Theoretical Bio*. 2013;324:103–8.
46. Gianetto DA and Heydari BJ Sr. Network modularity is essential for evolution of cooperation under uncertainty. *Sci Rep*. 2015;5:9340.
47. Sah P, Leu ST, Cross PC, Hudson PJ, and Bansal S. Unraveling the disease consequences and mechanisms of modular structure in animal social networks. *PNAS*. 2017;201613616.
48. Mersch DP, Crespi A, and Keller LJ. Tracking individuals shows spatial fidelity is a key regulator of ant social organization. *Science*. 2013;340(6136):1090–93.
49. Stroeymeyt N, Grasse AV, Crespi A, Mersch DP, Cremer S, and Keller L. Social network plasticity decreases disease transmission in a eusocial insect. *Science*. 2018;362(6417):941–5.
50. Wilson SN, Sindi SS, Brooks HZ, Hohn ME, Price CR, Radunskaya AE, et al. How emergent social patterns in allogrooming combat parasitic infections. *Front Ecol Evol*. 2020;8:54.
51. Reber A, Purcell J, Buechel SD, Buri P, and Chapuisat M. The expression and impact of antifungal grooming in ants. *J Evol Biol*. 2011;24:954–64.
52. Akinyi MY, Tung J, Jeneby M, Patel NB, Altmann J, and Alberts SC. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Anim Behav*. 2013;85(3):559–68.
53. Nowak MA and May RM. Superinfection and the evolution of parasite virulence. *Proc R Soc B: Biol Sci*. 1994;255(1342):81–9.
54. Kutsukake N and Clutton-Brock TH. Social functions of allogrooming in cooperatively breeding meerkats. *Anim Behav*. 2006;72(5):1059–68.
55. Madden JR and Clutton-Brock TH. Manipulating grooming by decreasing ectoparasite load causes unpredicted changes in antagonism. *Proc R Soc B: Biol Sci*. 2009;276(1660):1263–8.
56. Pinter-Wollman N, Jelić A, and Wells NMJ. The impact of the built environment on health behaviours and disease transmission in social systems. *Proc R Soc B: Biol Sci*. 2018;373(1753):20170245.
57. Pie MR, Rosengaus RB, and Traniello JF. Nest architecture, activity pattern, worker density and the

- dynamics of disease transmission in social insects. *J Theoretical Biol.* 2004;226(1):45–51.
58. Fefferman NH, Traniello JF, Rosengaus RB, and Calleri DV. Disease prevention and resistance in social insects: Modeling the survival consequences of immunity, hygienic behavior, and colony organization. *Behav Ecol Sociobiol.* 2007;61(4):565–77.
 59. Pinter-Wollman N, Fiore SM, and Theraulaz GJ. The impact of architecture on collective behaviour. *Nature Eco Evo.* 2017;1(5):1–2.
 60. Drum NH and Rothenbuhler WC. Differences in non-stinging aggressive responses of worker honeybees to diseased and healthy bees in May and July. *J Apicultural Res.* 1985;24(3):184–7.
 61. Loreto RG and Hughes DP. Disease in the society: Infectious cadavers result in collapse of ant sub-colonies. *PLoS One.* 2016;11(8):e0160820.
 62. Pinter-Wollman N, Penn A, Theraulaz G, and Fiore SM. Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour. *Phil Trans Roy Soc B* 2018; 373:20170232.
 63. Hughes WO, Eilenberg J, and Boomsma JJ. Trade-offs in group living: Transmission and disease resistance in leaf-cutting ants. *Proc R Soc B: Biol Sci.* 2002;269(1502):1811–19.
 64. Cremer S, Armitage SAO, and Schmid-Hempel P. Social immunity. *Curr Biol.* 2007;17:R693–R702.
 65. Cremer SJ. Social immunity in insects. *Curr Biol.* 2019;29(11):R458–R63.
 66. Pull CD and McMahon DP. Superorganism immunity: A major transition in immune system evolution. *Front Ecol Evol.* 2020;8:186.
 67. Facchini E, Bijma P, Pagnacco G, Rizzi R, and Bras-camp EW. Hygienic behaviour in honeybees: A comparison of two recording methods and estimation of genetic parameters. *Apidologie.* 2019;50(2):163–72.
 68. Villa JD, Danka RG, and Harris JW. Repeatability of measurements of removal of mite-infested brood to assess varroa sensitive hygiene. *J Apicultural Res.* 2017;56(5):631–4.
 69. Scharf I, Modlmeier AP, Fries S, Tirard C, and Foitzik S. Characterizing the collective personality of ant societies: Aggressive colonies do not abandon their home. *PLoS One.* 2012;7(3):e33314.
 70. Wray MK, Mattila HR, and Seeley TD. Collective personalities in honeybee colonies are linked to colony fitness. *Anim Behav.* 2011;81(3):559–68.
 71. Bengtson S and Dornhaus AJ. Be meek or be bold? A colony-level behavioural syndrome in ants. *Proc R Soc B: Biol Sci.* 2014;281(1791):20140518.
 72. Cotter SC, Littlefair JE, Grantham PJ, and Kilner RM. A direct physiological trade-off between personal and social immunity. *J Anim Ecol.* 2013;82(4):846–53.
 73. Keiser CN and Pruitt JN. Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proc R Soc B: Biol Sci.* 2014;281(1796):20141424.
 74. Dyer JR, Croft DP, Morrell LJ, and Krause J. Shoal composition determines foraging success in the guppy. *Behav Ecol.* 2009;20(1):165–71.
 75. Romano V, Sueur C, and MacIntosh AJ. The trade-off between information and pathogen transmission in animal societies. *Oikos.* 2021;00:1–11.
 76. Evans JC, Silk MJ, Boogert NJ, and Hodgson DJ. Infected or informed? Social structure and the simultaneous transmission of information and infectious disease. *Oikos.* 2020. 129:1271–88.
 77. Lemanski NJ, Cook CN, Ozturk C, Smith BH, and Pinter-Wollman N. The effect of individual learning on collective foraging in honey bees in differently structured landscapes. *Anim Behav.* 2021;179: 113–23.
 78. Nuismer SL. Parasite local adaptation in a geographic mosaic. *Evolution.* 2006;60(1):24–30.
 79. Weinstein SB, Buck JC, and Young HS. A landscape of disgust. *Science.* 2018;359(6381):1213–14.
 80. Passera L, Roncin E, Kaufmann B, and Keller LNJ. Increased soldier production in ant colonies exposed to intraspecific competition. *Nature.* 1996;379(6566): 630–1.
 81. Harvey JA, Corley LS, and Strand MR. Competition induces adaptive shifts in caste ratios of a polyembryonic wasp. *Nature.* 2000;406(6792):183–6.
 82. Gordon DM. Dynamics of task switching in harvester ants. *Anim Behav.* 1989;38(2):194–204.
 83. Réale D and Dingemanse NJ. Personality and individual social specialisation in Székely T, Moore AJ, and Komdeur J (eds), *Social Behaviour: Genes, Ecology and Evolution.* Cambridge: Cambridge University Press, 2010, 417–41.
 84. Keiser CN, Wantman T, Rebolgar EA, and Harris RN. Tadpole body size and behaviour alter the social acquisition of a defensive bacterial symbiont. *Roy Soc Open Sci.* 2019;6(9):191080.
 85. Lichtenstein JL, Wright CM, and Pruitt JN. Repeatability of between-group differences in collective foraging is shaped by group composition in social spiders. *J Arachnology.* 2019;47(2):276–79.
 86. Keiser CN, Howell KA, Pinter-Wollman N, and Pruitt JN. Personality composition alters the transmission of cuticular bacteria in social groups. *Bio Lett.* 2016;12(7).
 87. Shi W, Guo Y, Xu C, Tan S, Miao J, Feng Y, et al. Unveiling the mechanism by which microsporidian parasites prevent locust swarm behavior. *PNAS.* 2014;111(4):1343–8.

88. Ezenwa VO, Archie EA, Craft ME, Hawley DM, Martin LB, Moore J, *et al.* Host behaviour–parasite feedback: An essential link between animal behaviour and disease ecology. *Proc R Soc B: Biol Sci.* 2016; 283:20153078.
89. Wang-Peng S, Zheng X, Jia WT, Li AM, Camara I, Chen HX, *et al.* Horizontal transmission of *Paranosema locustae* (Microsporidia) in grasshopper populations via predatory natural enemies. *Pest Management Sci.* 2018;74(11):2589–93.
90. Nunn CL and Dokey AT-W. Ranging patterns and parasitism in primates. *Bio Lett.* 2006;2(3):351–4.
91. Muehlenbein MP and Watts DP. The costs of dominance: Testosterone, cortisol and intestinal parasites in wild male chimpanzees. *Biopsych Social Med.* 2010;4(1):1–12.
92. White LA, Forester JD, and Craft ME. Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biol Rev.* 2017;92(1):389–409.
93. Silk MJ, Finn KR, Porter MA, and Pinter-Wollman N. Can multilayer networks advance animal behavior research? *Trends Ecol Evol.* 2018;33(6):376–8.
94. Finn KR, Silk MJ, Porter MA, and Pinter-Wollman N. The use of multilayer network analysis in animal behaviour. *Anim Behav.* 2019;149:7–22.
95. Lemanski NJ, Cook CN, Smith BH, and Pinter-Wollman N. A multiscale review of behavioral variation in collective foraging behavior in honey bees. *Insects.* 2019;10(11):370.
96. Papageorgiou D, Christensen C, Gall GE, Klarevas-Irby JA, Nyaguthii B, Couzin ID, *et al.* The multilevel society of a small-brained bird. *Curr Biol.* 2019;29(21):R1120–R1.
97. Torney CJ, Hopcraft JGC, Morrison TA, Couzin ID, and Levin SA. From single steps to mass migration: The problem of scale in the movement ecology of the Serengeti wildebeest. *Phil Trans Roy Soc B.* 2018;373(1746):20170012.
98. Graving JM and Couzin ID. VAE-SNE: A deep generative model for simultaneous dimensionality reduction and clustering. *BioRxiv.* 2020. Available from: <<https://doi.org/10.1101/2020.07.17.207993>>.
99. Flack A, Nagy M, Fiedler W, Couzin ID, and Wikelski M. From local collective behavior to global migratory patterns in white storks. *Science.* 2018;360(6391):911–14.
100. Malkinson M, Banet C, Weisman Y, Pokamunski S, King R, Drouet M-T, *et al.* Introduction of West Nile virus in the Middle East by migrating white storks. *Emerg Infect Dis.* 2002;8(4):392–7.
101. Kaleta EF and Kummerfeld N. Isolation of herpesvirus and Newcastle disease virus from White Storks (*Ciconia ciconia*) maintained at four rehabilitation centres in northern Germany during 1983 to 2001 and failure to detect antibodies against avian influenza A viruses of subtypes H5 and H7 in these birds. *Avian Path.* 2012;41(4):383–9.
102. Miller PJ, Haddas R, Simanov L, Lublin A, Rehmani SF, Wajid A, *et al.* Identification of new sub-genotypes of virulent Newcastle disease virus with potential panzootic features. *Infect Genet Evol.* 2015;29:216–29.
103. Fritzsche McKay A, and Hoyer BJ. Are migratory animals superspreaders of infection? *Int Comp Biol.* 2016;56(2):260–7.
104. Altizer S, Bartel R, and Han BA. Animal migration and infectious disease risk. *Science.* 2011;331(6015):296–302.
105. Bierbach D, Laskowski KL, and Wolf M. Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nature Commun.* 2017;8(1):15361.
106. Laskowski KL, Doran C, Bierbach D, Krause J, and Wolf M. Naturally clonal vertebrates are an untapped resource in ecology and evolution research. *Nature Ecol Evol.* 2019;3(2):161–9.
107. Warren WC, García-Pérez R, Xu S, Lampert KP, Chalopin D, Stöck M, *et al.* Clonal polymorphism and high heterozygosity in the celibate genome of the Amazon molly. *Nature Ecol Evol.* 2018;2(4):669–79.
108. Schaschl H, Tobler M, Plath M, Penn DJ, and Schlupp I. Polymorphic MHC loci in an asexual fish, the amazon molly (*Poecilia formosa*; *Poeciliidae*). *Mol Ecol.* 2008;17(24):5220–30.
109. White LA, Siva-Jothy JA, Craft ME, and Vale PF. Genotype and sex-based host variation in behaviour and susceptibility drives population disease dynamics. *Proc R Soc B: Biol Sci.* 2020;287(1938):20201653.
110. Wice EW and Saltz JB. Selection on heritable social network positions is context-dependent in *Drosophila melanogaster*. *Nature Commun.* 2021;12(1):3357.
111. Modlmeier AP, Keiser CN, Shearer TA, and Pruitt JN. Species-specific influence of group composition on collective behaviors in ants. *Behav Ecol Sociobiol.* 2014;68(12):1929–37.
112. Modlmeier AP, Liebmann JE, and Foitzik S. Diverse societies are more productive: A lesson from ants. *Proc R Soc B: Biol Sci.* 2012;279(1736):2142–50.
113. Modlmeier AP and Foitzik S. Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behav Ecol.* 2011;22(5):1026–32.
114. Paleolog J. Behavioural characteristics of honey bee (*Apis mellifera*) colonies containing mix of workers of divergent behavioural traits. *Anim Sci Pap.* 2009;27(3):237–48.

115. Dyer JRG, Croft DP, Morrell LJ, and Krause J. Shoal composition determines foraging success in the guppy. *Behav Ecol.* 2008;20(1):165–71.
116. Richards EL. Foraging, personality and parasites: Investigations into the behavioural ecology of fishes. PhD dissertation, Cardiff University (United Kingdom). 2010.
117. Jolles JW, Boogert NJ, Sridhar VH, Couzin ID, and Manica A. Consistent individual differences drive collective behavior and group functioning of schooling fish. *Curr Biol.* 2017;27(18):2862–68. e7.
118. Jolles JW, Mazué GPF, Davidson J, Behrmann-Godel J, Couzin ID. Schistocephalus parasite infection alters sticklebacks' movement ability and thereby shapes social interactions. *Sci Rep.* 2020;10(1):12282.
119. Mattila HR and Seeley TD. Genetic diversity in honey bee colonies enhances productivity and fitness. *Science.* 2007;317(5836):362–46.
120. Arathi HS and Spivak M. Influence of colony genotypic composition on the performance of hygienic behaviour in the honeybee, *Apis mellifera* L. *Anim Behav.* 2001;62(1):57–66.
121. Jandt JM and Dornhaus A. Bumblebee response thresholds and body size: Does worker diversity increase colony performance? *Anim Behav.* 2014;87:97–106.
122. Keiser CN, Vojvodic S, Butler IO, Sartain E, Rudolf VHW, and Saltz JB. Queen presence mediates the relationship between collective behaviour and disease susceptibility in ant colonies. *J Anim Ecol.* 2018;87(2):379–87.
123. Croft DP, Albanese B, Arrowsmith BJ, Botham M, Webster M, and Krause J. Sex-biased movement in the guppy (*Poecilia reticulata*). *Oecologia.* 2003;137(1):62–8.
124. Lihoreau M, Clarke IM, Buhl J, Sumpter DJT, and Simpson SJ. Collective selection of food patches in *Drosophila*. *J Exp Biol*. 2016;219(5):668–75.