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How do infections impact social relationships?

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Infectious disease dynamics are both a cause and a consequence of variation in sociality. Social interaction rates can shape parasite transmission, and conversely, parasite infection can alter social interaction rates. At the core of this feedback is a trade-off: although many social interactions yield fitness benefits, parasites impose fitness costs on infected hosts and risks to uninfected partners. Both the benefits of social interaction and the costs of infection are context-dependent, dynamic and often asymmetric within dyads. We therefore hypothesize that variation in this cost–benefit trade-off explains how and why behavioural responses to parasitism differ between individuals across stages of relationship development and across different types of social relationships (parent–offspring, pair-bond, affiliative, dominance relationships). We use these hypothetical cost–benefit trade-offs to generate testable predictions about how parasites will impact the behaviour of infected and uninfected hosts across different social relationships. We also explore the potential for acute infections to have long-term social consequences by influencing the development of social relationships.

1. Introduction

Host contact networks shape the transmission patterns of disease-causing organisms (i.e. parasites). In most epidemiological models, every host individual has an equal probability of contacting others (e.g. [1]; figure 1A). Yet interaction rates are often non-random, forming structured social networks that can influence epidemic outcomes (figure 1B). For example, disease spread can be accelerated by highly connected 'superspreaders' [2] and slowed by network modularity [3]. Social network structure has important implications for both short-term epidemic dynamics and the long-term coevolution of hosts and parasites [4–7], and network-based models can guide disease control strategies in humans [8] and wildlife [9,10].

Parasites are also powerful agents that can influence contact rates through the behaviour of both infected and uninfected hosts [11,12], which can feed back on transmission dynamics [13–15]. While some host behavioural changes involve parasite manipulation of hosts [11,16], other responses are by-products or adaptive responses to infection. Infected individuals often reduce their movement or social interactions following infection [12,17–19]. Uninfected hosts can either avoid infected conspecifics [20–23] or provide care [24,25]. These parasite-driven changes in contact rates can scale up to affect broader social networks and epidemiological dynamics [26–29] (figure 1C).

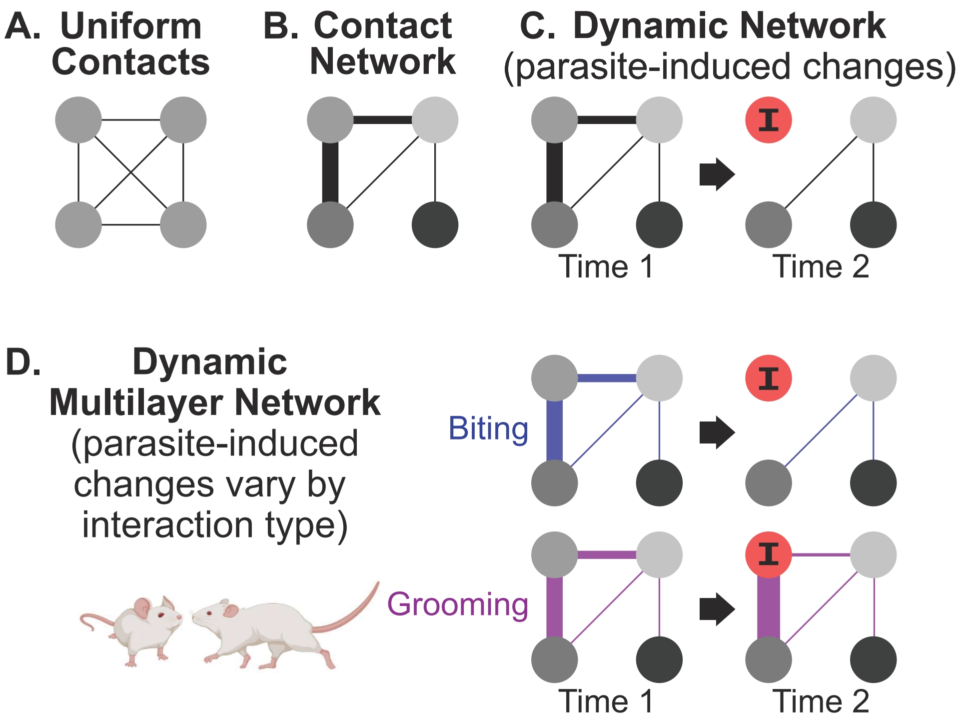

Figure 1. Increasingly complex representations of social structure in social networks can reflect how relationships change with infection. An infected individual (shown in red and marked with **I**) is embedded in a social environment that can be modelled using (A) uniform contacts, (B) variation in pairwise contact rates aggregated over time (i.e. a social network), (C) dynamic changes in those contact rates over time, including changes caused by infection and (D) parasite-induced behavioural changes that vary across interaction types and/or social relationships.

For example, decreases in human contact rates caused by influenza symptoms were associated with a near 75% reduction in transmission potential [30].

Shifts in contact rates in response to parasites emerge from decisions made within individual dyadic relationships. Within these pairs, uninfected and infected hosts face a trade-off between the benefits of social interactions and costs imposed by parasites, but these costs and benefits may differ between infected and uninfected partners. For uninfected hosts, social interactions can increase infection risk [31], and reducing social interactions can limit this risk [22,32,33]. In contrast, infected hosts already suffer the fitness costs of infection, arising from parasite damage and energetic costs of immunity [34]. Reducing social interactions may conserve energy for recovery [17], but infected hosts may also benefit from social interactions (e.g. caretaking) that facilitate host defences [35]. For both uninfected and infected hosts, however, foregoing social interactions also means losing any survival or reproduction-related benefits of the relationship [12,36–39].

The ratio of social benefits to infection costs is context-dependent, dynamic and asymmetric within a dyad, shaping how uninfected and infected hosts should navigate trade-offs. Many factors can influence how individuals balance social benefits and parasite costs, including perceived infection risk or severity [40,41], immunity [42], sex [43], the presence of potential mates [44,45] and predation risk [38]. Differences in which social interactions individuals prioritize or forego create variation in behavioural responses to infection [37,38,46] that scale up to context-dependent shifts in contact networks (figure 1D).

The costs and benefits of social interactions underlying trade-offs can also change as a pair of individuals forms differentiated *social relationships*—a term we use for unobserved social preferences that one animal has for affiliating with or avoiding another. Social relationships vary in strength, predictability and effect on fitness [47]. Behavioural ecologists often attempt to infer these latent social relationships from estimates of interaction or contact rates [48–51]. While disease ecologists often focus on contact rates as drivers of parasite exposure, social interactions and their underlying social relationships shape the social benefits hosts experience [47], influencing trade-offs and thereby potentially shaping how social behaviour may change in response to parasites (figure 1D).

Social relationships are also dynamic, and how relationships change over time may be both a cause and consequence of variation in how hosts respond to infection within dyads. Through repeated, mutually beneficial interactions, individuals can form stable associations that reduce conflict and increase cooperation, thereby developing a 'stake' in the survival of their partner due to the benefits of that partner's continued existence, a factor called 'fitness interdependence' [52–54]. However, because social relationships are dynamic, the cost–benefit trade-offs between sociality and infection will likely change as social relationships form, strengthen, stabilize, weaken or dissolve. A strong social relationship may represent a significant social benefit justifying infection risk for uninfected partners or energy expenses by infected hosts, while a weak or dissolving relationship may favour avoidance or isolation. Therefore, we suggest that the current state of the relationship is a primary driver of immediate behavioural decisions in the face of disease.

Crucially, present social interactions and disruptions thereof can impact the long-term future trajectory of social relationships. Growing evidence, for example, suggests that animals preferentially associate and interact with partners who have provided greater benefits, which can change over time [55–58]. Several experiments also suggest that long-term social relationships can be impacted by relatively short-term social perturbations. For example, male prairie voles (*Microtus ochrogaster*) separated from their pair-bonded female for four weeks lost their partner preference [59], and monk parakeets (*Myiopsitta monachus*) removed from their group for eight days lost and could not immediately regain their previous social rank [60], while female vampire bats (*Desmodus rotundus*) that were co-housed for one week were more likely to establish allogrooming relationships that persisted for months and could develop into life-saving food-sharing relationships [49,61]. These findings raise an interesting question about the potential for short-term social impacts of parasites to affect the long-term trajectory of social relationships.

Here, we address three questions: How do social relationships influence behavioural responses to parasites? Do parasites alter the formation and maintenance of relationships? And how might parasite-induced changes in social behaviour differ across relationship types? We hypothesize that variation in the parasite-cost-to-social-benefit trade-off explains how and why behavioural responses to parasitism differ across stages of relationship development and across different types of social relationships (e.g. parent–offspring, pair-bond, affiliative, dominance relationships). We then use these hypothesized cost–benefit trade-offs to generate testable predictions about how parasites impact the behaviour of infected and uninfected hosts across different social relationships. We also explore when acute infections might have long-term social consequences by affecting how social relationships develop.

(a) How do social relationships shape behavioural responses to parasites?

Parasites impose a trade-off between the benefits of social interaction and the costs of either parasite exposure [22,38,39,62] or excess energy expenditure during infection [17]. An optimal response, therefore, requires balancing the social benefits against the likelihood and costs of infection. Consequently, less beneficial social interactions and more costly parasites (e.g. those with higher transmissibility or severity) should favour greater avoidance by healthy hosts or greater social isolation by infected hosts (figure 2A,B). Conversely, hosts should maintain their investment in social relationships that are sufficiently beneficial, even when parasite costs are high. In some cases, individuals may increase their investment in relationships if there are unique benefits under infection, such as care or sanitary behaviours [63]. Similarly, growing evidence suggests that infected hosts may uniquely benefit from social interactions that improve access to resources or antipredator defence [64–66], potentially leading to asymmetries in infection costs and social benefits for sick versus healthy individuals (figure 2B).

The role of social relationships in this cost–benefit framework is well demonstrated by how responses to infection can differ by sex. Females often show a stronger aversion to infection cues than males [67]. In olive baboons (*Papio anubis*), for instance, females avoid mating with males that have visible yaws lesions, whereas males mate irrespective of infection cues [68]. While these results could represent female choice based on male immune quality [69], they can also be explained by sex-dependent cost–benefit trade-offs: for males, the additional mating opportunity may outweigh the costs of a possible infection, while for females, the same cost of possible infection may exceed the marginal reproductive benefits. Similarly, immune-challenged male zebra finches (*Taeniopygia guttata*) reduce activity in isolation but increase courtship when exposed to females [44], suggesting that the potential reproductive benefits outweigh the investment in immune defence. Sex-based differences in cost–benefit tradeoffs are also present in non-reproductive behaviours. For example, virus-infected male fruit flies (*Drosophila melanogaster*) socially distance while virus-infected females remain clumped [70]. Male social distancing likely reduces competition and energetically costly aggression, saving resources for immune defence [70]. In all these examples, the benefits of social interactions differ by sex, influencing how hosts balance social benefits and parasite costs. Next, we turn to the question of if and how parasites impact social relationships.

(b) Can parasites influence the development of long-term social relationships?

If social benefits increase in frequency and certainty over time as social relationships develop, then infections can be more disruptive to relationship formation than to relationship maintenance. Consider the simple case of two unrelated individuals developing a symmetrical, non-reproductive affiliative relationship, which is inferred from reciprocal allogrooming (or allopreening). Without an infection, allogrooming rates might increase over time during relationship formation (figure 2C) and stabilize once established (figure 2D). When the individuals first meet, there is no shared history to inform social interactions, the benefits of the social relationship are least certain, and fitness interdependence is absent. Therefore, at this stage, the cost of a potential infection should be most likely to exceed the social benefits (figure 2C,D). Yet the ability of an uninfected host to avoid a new infected partner requires detecting infection. When future social rewards are high or exclusion is costly, infected individuals may even conceal infection, as commonly observed in humans [71]. Additionally, uninfected hosts may be poor at detecting conspecifics' infections early in relationships if symptoms are progressive or if recognizing symptoms is easier with more familiar individuals [12].

In some cases, the impact of infection-induced behavioural changes on new relationships might delay or entirely prevent the establishment of a possible long-term relationship (figure 3A). This prediction is consistent with recent opportunistic observations of a *Staphylococcus* outbreak among female vampire bats captured from different wild populations and introduced in captivity [72]. Infected bats were lethargic and engaged in less allogrooming than did asymptomatic bats. The negative effects of infection on allogrooming relationships were stronger for unfamiliar pairs than for pairs with existing allogrooming relationships. This observation of different impacts of an acute infection on developing and established relationships is consistent with evidence that the immediate and anticipated benefits of social interactions early in vampire bat relationships are relatively low compared with later stages of relationship development [49,76,77]. Moreover, the effects of infection on newly introduced pairs lasted several weeks after antibiotic treatment and recovery [72], consistent with the hypothesis that infection can influence future relationship development.

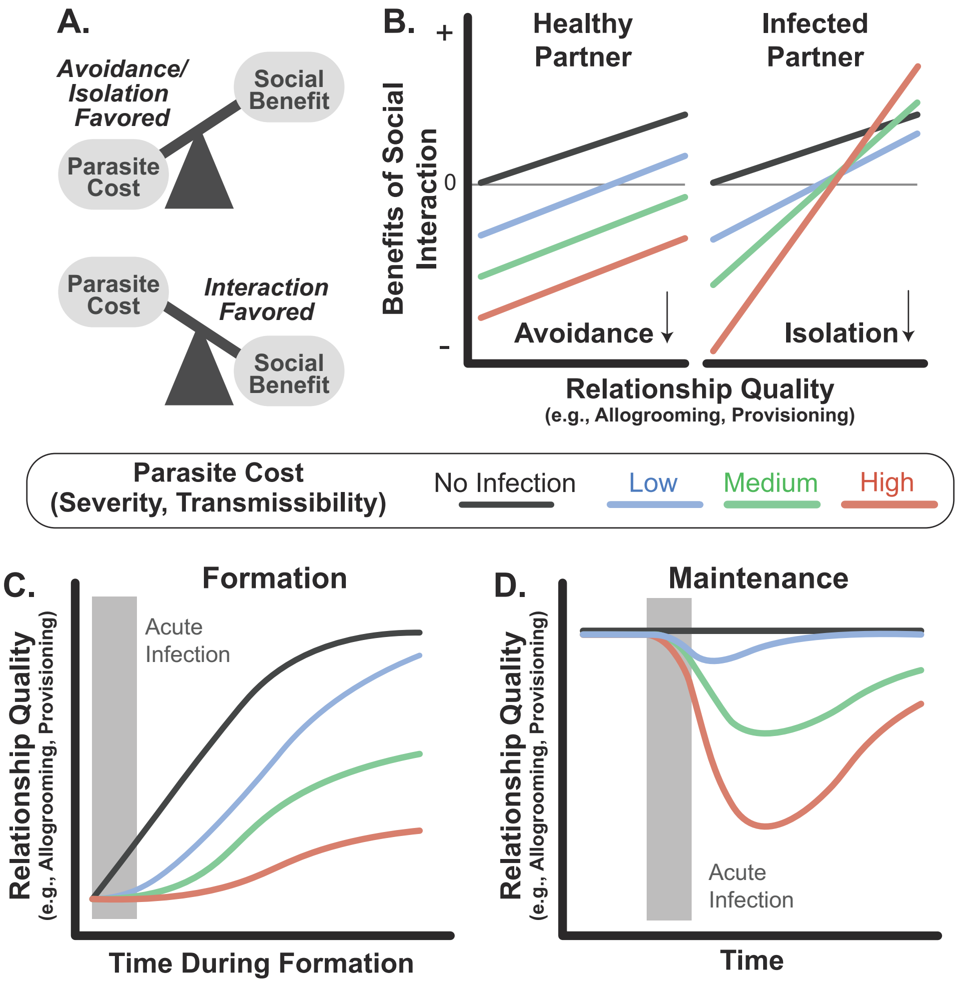

Figure 2. Trade-offs between social benefits and parasite costs shape investments in social relationships. (A) Individuals face a trade-off between the fitness benefits of social relationships and the fitness costs of infection. (B) This trade-off influences the optimal patterns of social interaction: more beneficial relationships (inferred from the rate of allogrooming, for instance) should increase the likelihood of interaction, and more severe or transmissible parasites should favour avoidance or isolation, but these effects may differ between uninfected and infected hosts. If this trade-off underlies changes in social interactions, then parasite severity and transmissibility could shape (C) relationship formation and (D) maintenance because delays in recovery will slow relationship formation or impair relationship maintenance (assuming recovery of the infected host).

Similar to affiliative relationships, infections should impact initial mate choice more than continued investment in pair bonds that enhance parental care. Parasites are known to shape mate choice [67,78]: female rock doves (*Columba livia*), for example, strongly avoided males infected with lice [79], and female mice (*Mus musculus*) exposed to parasite cues prefer familiar males over unfamiliar males, even though unfamiliar males are normally preferred [73]. However, when longer term reproductive relationships are established, particularly in pair bonds where the fitness of infected and healthy mates is strongly interdependent, infections should have weaker (or positive) effects on relationships (figure 3A). For instance, pair-bonded zebra finches remained in close proximity despite immune challenges [80], and pair-bonded prairie voles more strongly preferred their bonded mate than an unfamiliar conspecific after an immune challenge [81]. In mating systems where partnerships are continually assessed, the impact of infections can change as the balance between parasite costs and anticipated reproductive benefits shifts. For example, female western lowland gorillas (*Gorilla gorilla gorilla*) are more likely to leave ageing males, and this tendency is even stronger when males are infected with a skin disease [82]. This raises questions about whether infections could accelerate the dissolution of reproductive relationships by tipping the balance between parasite costs and benefits.

Infections should have minimal effects on parent–offspring relationships (figure 3C). Still, as offspring become increasingly independent, the effect of parasite costs on parent–offspring relationships should increase (figure 3C). This prediction is supported by observations that nematode-infected female European shag (*Phalacrocorax aristotelis*) provision their newly hatched chicks at similar rates to nematode-free mothers; however, as chicks age, nematode-infected mothers invest comparatively less in care than nematode-free mothers [74]. While this result supports the idea that parasites have different effects on early and late parent–offspring relationships, it remains unclear to what extent parasite-driven differences in parental care shape longer term parent–offspring relationships.

Competitive and dominance relationships are also influenced by social history and may therefore differentially respond to parasites over time. Most group-living animals form dominance hierarchies structured by a combination of phenotypic differences (e.g. body size), individual experiences (winner–loser effects) and pairwise interaction history [83–85]. Because dominance relationships are built from cumulative interactions, early infections may disrupt hierarchies, while established hierarchies may be robust to infections (figure 3D). Supporting this hypothesis, male mice infected with the tapeworm *Taenia*

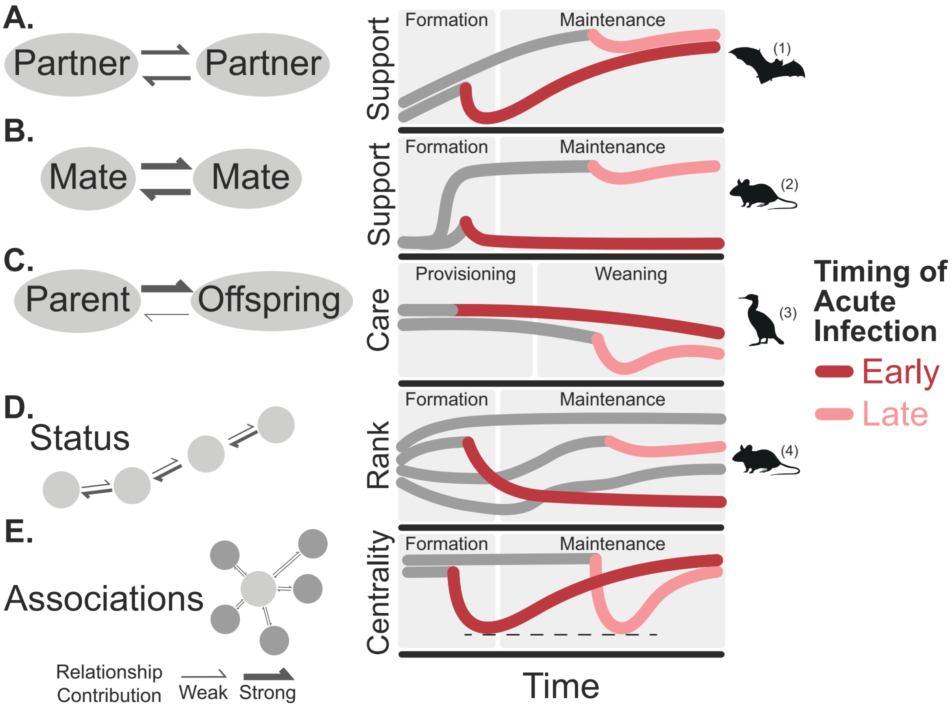

Figure 3. Acute infection effects on long-term social relationships might vary with relationship type and duration. Various social relationships, from enduring (A) same-sex affiliative relationships, (B) reproductive relationships, (C) parent–offspring relationships, (D) dominance relationships based on competition and status and (E) associations based on by-product benefits can have stages of investment or development (shaded regions). As fitness interdependence changes during relationship formation, relationships may respond differently to acute infections depending on whether they occur early (red lines) or late (pink lines). Icons represent systems where temporal changes in relationships are linked to different effects of parasites on relationships: (1) [72], (2) [73], (3) [74] and (4) [75]. Animal icons were sourced from PhyloPic.org.

crassiceps were less likely to become dominant during initial interactions, but infection had no clear effect on established hierarchies [75]. Infections may also affect competitive relationships by directly altering traits that influence competitive outcomes. In bighorn sheep (*Ovis canadensis*), for example, acute pneumonia infections, particularly during early development, can impair horn growth [86], which determines reproductive contests [87]. This suggests that early-life infections may therefore have lasting effects on competitive outcomes well into adulthood (figure 3D).

Unlike previously considered social relationships, some social associations are formed for short-term by-product benefits, like huddling for warmth or risk dilution. Because social history does not shape these by-product benefits, infections should have a similar magnitude of effect on these social associations, no matter the time of group formation (figure 3E). Instead, the trade-off is simply between the immediate by-product benefits and the parasite costs. For example, in the absence of predators, rainbow trout (*Oncorhynchus mykiss*) groups infected with an eye fluke form smaller shoals, but both uninfected and infected groups respond to predator cues by forming larger shoals [88]. This leads to the hypothesis that, for by-product associations, the duration of an association does not significantly alter parasite-driven behaviour, though to our knowledge, this remains to be explicitly tested.

2. Conclusion

The feedback between social interactions and parasitism has largely been studied with an epidemiological focus on contact rates [28,89–92]. However, different types of social relationships pose different costs and benefits for infected and uninfected hosts, likely shaping how infection alters social behaviour. And these changes might, in turn, shape long-term dynamics of relationships. This trade-off between social benefits and parasite costs can be context-dependent, dynamic and often asymmetric within dyads, leading individuals to have diverse social motivations in the face of parasitism. In turn, even short-term parasite-induced changes in social interactions might have long-term social consequences. The effect of infection on social relationships is likely to depend on the severity and timing of infection and the type of social relationship.

Testing cost–benefit trade-offs across social relationships requires integration of theory and experiments. Game theoretic models [93] and dynamic network models [7] that incorporate asymmetric costs and benefits for infected and uninfected partners could yield new insights into both behaviour and epidemic dynamics. Experiments that track changes in relationship formation in response to infection or immune challenge can measure how short-term physiological responses translate to long-term social dynamics (e.g. [80,81,94]). Operant choice tests can reveal relationship-specific motivations for infected and uninfected hosts that are difficult to detect in the wild (e.g. [81]). Although translating these approaches to natural systems is challenging because longitudinal sampling of both infection and relationship dynamics is difficult, field manipulations of infection status (e.g. anthelmintic interventions [74]) offer promising alternatives. Finally, new generative models of social networks [95,96] or the dynamics of social interactions [97] will be essential for disentangling infection effects on directed social behaviour from individual tendencies, dyadic interdependence and confounding factors such as space and time.

Animal behaviourists and disease ecologists have long appreciated that (i) social networks can shape parasite transmission [2,3,98,99], (ii) parasite-induced sickness behaviour or avoidance influences social networks [28,89–91], and (iii) social relationships are important determinants of fitness, particularly in the face of parasitism [35,100]. A critical challenge remains to more fully address the role social relationships play in behavioural and physiological responses central to epidemic dynamics. A particularly promising direction is to explore how such dynamics affect the persistence of diseases within social networks [7]. For instance, if parasites causing severe disease most strongly disrupt the formation of new relationships, the result may be the severing of 'weak ties' that bridge social clusters and facilitate population-wide transmission [3]. As a consequence, infection may lead to more fragmented, modular social networks and slow-burning epidemics rather than explosive outbreaks [13–15]. We suggest that modelling feedbacks between parasites and long-term social relationships is a challenging but worthwhile step towards predicting both the fitness consequences for individual hosts and the outcomes of epidemics.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. W.R.: conceptualization, visualization, writing—original draft; V.O.E.: supervision, writing—review and editing; G.G.C.: conceptualization, writing—original draft; S.S.: conceptualization, writing—original draft.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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