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RESEARCH ARTICLE

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Sickness effects on social interactions depend on the type of behaviour and relationship

Sebastian Stockmaier[1,2] | Daniel I. Bolnick[1,3] | Rachel A. Page[2] | Gerald G. Carter[2,4]

[1]Department of Integrative Biology, University of Texas at Austin, Austin, TX, USA

[2]Smithsonian Tropical Research Institute, Balboa, Panama

[3]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

[4]Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH, USA

Correspondence
Sebastian Stockmaier
Email: sebastian.stockmaier@utexas.edu

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Alexander von Humboldt-Stiftung; University of Texas at Austin; Smithsonian Tropical Research Institute

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Abstract

1. Infections can change social behaviour in multiple ways, with profound impacts on pathogen transmission. However, these impacts might depend on the type of behaviour, how sociality as a biological trait is defined (e.g. network degree vs. mean edge strength) and the type of social relationship between the interacting individuals.
2. We used the highly social common vampire bat *Desmodus rotundus* to test how an immune challenge by lipopolysaccharide (LPS) injections affects two different social behaviours and three alternate measures of sociality, and whether the LPS effect differs by kinship relationship.
3. Effects of sickness should be lower for social behaviours that bestow greater benefits to inclusive fitness, such as food sharing. As predicted, immune-challenged bats experienced a greater reduction in allogrooming received than food sharing received.
4. Sickness effects might also depend on how a social interaction is defined (e.g. the number of grooming partners vs. the duration of grooming events). We predicted that sickness would impact both the number and duration of social encounters, but we only detected a decrease in the number of grooming partners.
5. Finally, sickness effects might vary with social relationship type. We predicted that sickness effects should be smaller for interactions among close kin. As expected, the immune challenge had smaller effects on mother–offspring interactions.
6. In conclusion, our results highlight the need to explicitly consider how the effects of sickness on social network structure can differ depending on the 'who, what, and how' of social interactions, because these factors are likely to influence how sickness behaviour alters pathogen transmission.

KEYWORDS

pathogen transmission, sickness behaviour, social behaviour, social network, vampire bat

1 | INTRODUCTION

Sickness can alter how animals behave and interact in several ways. Pathogens can manipulate hosts to *increase* rates of host social interaction in ways that favour their transmission (Klein, 2003; Klein, Zink, & Glass, 2004). In contrast, infections can *decrease* social interaction rates by inducing so-called 'sickness behaviour', a reduction in activity which diverts energy to immune responses or promotes host tolerance to infection (Hart, 1988; Kelley et al., 2003; Medzhitov, Schneider, & Soares, 2012). By reducing overall activity, sickness behaviour can decrease the rate of social encounters (Lopes, Block, & Konig, 2016; Van Kerckhove, Hens, Edmunds, & Eames, 2013), the

intensity of social behaviours like grooming (Stockmaier, Bolnick, Page, & Carter, 2018) and the amount of social exploration (Fishkin & Winslow, 1997). Healthy conspecifics might also avoid sick individuals (Behringer, Butler, & Shields, 2006; Boillat et al., 2015; Kiesecker, Skelly, Beard, & Preisser, 1999; Tobler & Schlupp, 2008), or sick individuals might cooperatively avoid groupmates or kin (Bos, Lefevre, Jensen, & d'Ettorre, 2012; Heinze & Walter, 2010; Stroeymeyt et al., 2018). It is important to consider the possibility of such effects in social network models of pathogen transmission because they can influence the spread of a pathogen (Bansal, Read, Pourbohloul, & Meyers, 2010; Silk et al., 2017).

In any empirical study, the estimated effects of sickness on social interactions could vary depending on how the interactions are measured and defined (e.g. automated association measures vs. observed interaction events), what behaviour is observed (e.g. mating vs. grooming) and what kinds of individuals are interacting (e.g. close kin or non-kin). Such differences could play a large and underappreciated role in how sickness behaviour alters pathogen transmission within social networks. To test for them, we used the highly social common vampire bat *Desmodus rotundus* and injections of the immunostimulant lipopolysaccharide (LPS). This study extends previous work that also used LPS to induce transient symptoms of a bacterial infection in vampire bats without using a pathogen, thereby isolating the role of sickness behaviour without any host manipulation (Stockmaier et al., 2018). Previously, Stockmaier et al. (2018) tested effects of LPS-induced sickness on social interactions among a few vampire bats in small cages, which experimentally controlled their association time and the number of association partners. Here, we instead tested the effects of sickness on social interactions among numerous freely associating bats in a larger flight cage. In this new context, sickness is able to change a greater array of social behaviours including the number and identity of interacting partners. Specifically, we assessed the sickness effects on three measures of sociality (the number of partners, the mean interaction rate per partner and total interaction rate), two social behaviours (social grooming and regurgitated food sharing) and two relationship types (close maternal kin and non-kin).

Sickness should reduce certain social behaviours more than others, depending on the inclusive fitness costs and benefits of the behavioural change. Vampire bats engage in two well-studied cooperative behaviours, allogrooming and food sharing, which are both targeted to individuals in need but differ in their importance for survival (Narizano & Carter, 2019; Wilkinson, 1984). Allogrooming involves licking the recipient's body and is a frequent behaviour with low immediate benefits for receivers; in contrast, food sharing involves regurgitation of blood to bats in dire need and is a relatively rare behaviour with substantial benefits for receivers and relatively low costs for the donor (Wilkinson, 1984). We therefore predicted that mimicking bacterial infection by LPS would reduce the amount of allogrooming received more than it would reduce the amount of food received.

The observed social effects of sickness can also depend on how one quantifies social interaction rates. Animal interaction rates are often estimated from association rates, the frequency of being at the same place at the same time (Franks, Ruxton, & James, 2010; Whitehead & Dufault, 1999). However, association rates do not necessarily predict interaction rates in a linear or straightforward manner (Castles et al., 2014), especially for cooperative or mating behaviours. Testing the effect of sickness on both associations (Lopes et al., 2016) and interactions (e.g. mating, Lopes & König, 2016) allows one to disentangle these biologically distinct effects. Using focal observations of freely moving animals (unlike the confined partnerships in Stockmaier et al., 2018), we simultaneously measured both the time the subject spent grooming each bat and the number of different grooming partners each bat encountered. We tested whether LPS-induced sickness behaviour would decrease grooming interaction intensity (e.g. Stockmaier et al., 2018), the number of interaction partners (e.g. Lopes et al., 2016) or both.

Finally, social effects of sickness should vary depending on the actor–receiver relationship. For example, sexually transmitted pathogens are impacted by the mating network, not the association network. Maintaining close kin interactions despite a close relative's illness might increase a donor's inclusive fitness. In vampire bats, mothers and their offspring have among the strongest social bonds, because females are philopatric and mother–daughter bonds often continue into adulthood (Carter & Wilkinson, 2013, 2015; Wilkinson, 1985). Allogrooming rates between mothers and offspring are much higher than between non-kin (Carter & Wilkinson, 2013; Wilkinson, 1986). By injecting both mothers and their subadult offspring (1–2 years of age), we compared maternal interactions to the same bats' interactions with other groupmates (not close kin). We predicted that maternal allogrooming would be reduced less by the immune challenge compared to non-maternal grooming. We then used a simple model to illustrate how these kinship-based differences in sickness behaviour could affect pathogen transmission risk.

2 | MATERIALS AND METHODS

2.1 | Bat colony

We conducted experiments in a captive colony of 36 vampire bats, including 24 adult females captured from two distant sites in Panama, and their twelve captive-born offspring. This group structure of multiple matrilines and non-kin pairs matches the kinship structure of wild vampire bat colonies (Wilkinson, 1984). All bats were marked with unique combinations of forearm bands (for individual identification throughout the experiment) and housed together in a 1.7 × 2.1 × 2.3 m outdoor flight cage (hereafter 'colony cage') in Gamboa, Panama at the Smithsonian Tropical Research Institute. All bats except the fasted subjects (see below) were free to interact with others. Refrigerated or thawed cattle blood was provided in silo-style water dispensers (designed for birds) between sunset and sunrise, except during the time of the observation trial.

Our work was approved by the Smithsonian Tropical Research Institute Animal Care and Use Committee (#2015-0915-2018-A9 and #2016-0728-2019-A2, A3), the Animal Care and Use Committee of the University of Texas at Austin (AUP-2016-00124) and by the Panamanian Ministry of the Environment (Protocols: #SE/A-76-16 and #SE/A-64-17).

2.2 | Experimental design, statistical analysis and transmission model

To induce food sharing, we conducted two types of fasting trials (LPS and control trials). Each fasting trial simulates a bat returning to the roost after missing a night of foraging (Carter & Wilkinson, 2013; Wilkinson, 1984). Each bat (n = 35, one bat was excluded because it accidentally received the wrong treatment in one trial) was tested in one LPS and one control trial in random order (15 bats received LPS first) and exposed to the same potential interaction partners during both trials. For each trial, we removed the focal bat from the colony cage, fasted it in isolation for 26–28 hr, then weighed it and returned it to the colony cage during the night. In LPS trials, fasted subjects were injected subcutaneously with LPS (L2630 Sigma Aldrich; dose: 5 mg/kg body mass; range of injected volume: 60–98 μl) in phosphate-buffered saline (PBS) 5 hr before reintroduction to the colony cage. In control trials, fasted subjects were injected with an equivalent volume of only PBS (Stockmaier et al., 2018). We injected bats 5 hr prior to observation because we previously detected symptoms for at least 6 hr post-injection (Stockmaier et al., 2018). After reintroduction to the cage, we immediately video-recorded the focal bat's allogrooming and food-sharing interactions with other bats by closely following and recording it continuously for 1 hr using an infrared (IR) light and an IR-sensitive Sony Nightshot camcorder through a clear-sided plastic wall of the cage. After this 1-hr trial was concluded, we removed the focal bat from the colony cage and weighed it again to assess its mass gain from food sharing. The fasting trials in this study were part of an ongoing series of trials to induce and measure food-sharing and social-grooming rates between the bats over 22 months in captivity (Carter et al., 2019). The time between LPS and PBS trials for each bat ranged from 14 to 16 days. Additionally, an injected bat had at least 29 hr to recover before it could be an actor in another bat's trial on the following day, which was a sufficient recovery time based on previous work (Stockmaier et al., 2018). We also used the body mass before the injection and the body mass before reintroduction (5 hr) to verify that LPS injections caused weight loss and therefore had physiological effects.

To score behaviours, observers watched videos of the trials and scored the identity of the actor and receiver bats, and the onset and duration of all food-sharing and allogrooming events involving the focal subject. Observers were blind to the injection treatment. Allogrooming involves a bat chewing or licking another bat's body, and food sharing involves a recipient bat licking a donor's mouth. For allogrooming and food sharing, observers only measured bouts 5 s or longer and recorded two separate events when two consecutive bouts were at least 5 s apart (following Carter & Wilkinson, 2013, 2015).

Allogrooming and food-sharing durations from an actor to a receiver within a trial were log-normal, so we transformed them using natural log(x + 1). To measure the standardized effect of LPS (proportional change) for each bat, we used:

$$\frac{Y_{LPS} - Y_{PBS}}{Y_{LPS} + Y_{PBS}},$$

where Y_{LPS} and Y_{PBS} are the measures during the LPS and PBS trial of the individual bat respectively. We removed cases with zero denominators (non-interacting bats), but our conclusions did not change when we included those bats in our analysis as observations of zero change. Overall, this index allows for comparisons while controlling for unit and amount of grooming per bat. For instance, when quantifying the effect of LPS on maternal grooming, an LPS-injected mother would have an LPS effect index of 1 if she only groomed her offspring during the LPS trial, an index of 0 if she groomed her offspring equal amounts in each trial and an index of −1 if she only groomed her offspring during the PBS trial.

To test the null hypotheses of no LPS effect, we used a permuted paired t-test because of the non-normal and non-independent nature of our dyadic data. This nonparametric test randomly swaps the PBS and LPS trial data within each bat to calculate a distribution of t-statistics expected under the null hypothesis and then compares the observed t-statistic to this distribution to obtain a two-sided p-value. To estimate 95% confidence intervals (CI) for LPS effect sizes, we used nonparametric bootstrapping using accelerated bias-corrected percentile limits (Puth, Neuhäuser, & Ruxton, 2015). We used 5,000 iterations for both methods.

We calculated the mean and bootstrapped 95% CI for the LPS effect on three measures of network degree centrality (number of food donors or 'food sharing indegree', number of groomers or 'allogrooming indegree' and number of bats groomed or 'allogrooming outdegree'), on three measures of node strength (total food received from groupmates, total grooming received from groupmates and total grooming given to groupmates), and three measures of interaction intensity (mean food received per donor, mean grooming received per groomer and mean grooming given to recipients that were groomed). We only injected the fasted focal bats, so we did not test LPS effects on food given to other bats.

To examine the effect of relationship type, we calculated the mean and 95% CI for the LPS effect on allogrooming for (a) mothers grooming offspring, (b) mothers grooming non-offspring groupmates, (c) offspring grooming mothers, and (d) offspring grooming non-mother groupmates. In each case, we tested the effect of LPS on both the actor and receiver. We report unadjusted p-values for each test, and in Table S1, we report which adjusted p values were <0.05 when using a sequential Bonferroni approach for multiple comparisons (Holm, 1979).

Finally, to illustrate how sickness behaviour could impact pathogen transmission from mothers to offspring versus from mothers to non-offspring, we calculated the probability of pathogen transmission from one individual to another, as:

$$P(\text{transmission}) = 1 - (1 - p)^{t}.$$

For various values of p (infectivity, i.e. probability of pathogen transmission per second of allogrooming), we examined how much the observed LPS-induced shift of the allogrooming interaction rate t in our study could affect the probability of pathogen transmission from one individual to another. Importantly, although contact network models using duration of social interactions can better predict transmission (Aiello et al., 2016; Clay, Lehmer, Previtali, St Jeor, & Dearing, 2009), the exact relationship between duration of a social interaction (e.g. grooming) and transmission is challenging to measure. Therefore, for simplicity, we assume a linear relationship between contact duration and transmission probability.

3 | RESULTS

Vampire bats showed the expected physiological response to LPS. Compared to control injections, LPS injections caused the same bats to lose on average 0.21 g more body mass during the 5-hr period from the injection to reintroduction into the colony cage (2.76% average LPS-induced body mass loss, 2.09% average body mass loss after PBS injections, Figure S1).

Immune-challenged bats had fewer grooming partners. On average, LPS-injected bats groomed one fewer bat (allogrooming outdegree, $n = 30$, $p < 0.002$, Figure 1a), and were groomed by one fewer groomer (allogrooming indegree, $n = 35$, $p = 0.020$, Figure 1a), which led to them spending 3 min less time grooming others (84.5% decrease caused by LPS, $n = 30$, $p < 0.002$, Figure 1a) and receiving 1.6 min less grooming from others (18.7% decrease caused by LPS, $n = 35$, $p = 0.019$, Figure 1a). However, we did not detect changes in per-partner intensity of grooming given ($n = 13$, $p = 0.728$, Figure 1a) or received ($n = 31$, $p = 0.657$, Figure 1a). We observed an average of 9.9 min of allogrooming per 1-hr trial.

In contrast, we observed no clear effect of LPS on food sharing. Food sharing in a trial predicted mass gain during both trial types (Figure S2), but we did not detect an LPS effect on the number of food donors (food sharing indegree, $n = 29$, $p = 0.643$, Figure 1a) or the total food received ($n = 29$, $p = 0.573$, Figure 1a). We observed an average of 4.4 min of food sharing per 1-hr trial.

We found evidence that the LPS effects on allogrooming varied by relationship type (Figure 1b). LPS-injected bats groomed their non-kin partners less (a decrease in 22 out of 24 cases, $n = 24$, $p < 0.002$, Figure 1b). Non-injected bats also decreased grooming of LPS-injected bats that were not close kin (22 out of 33 cases, $n = 33$,

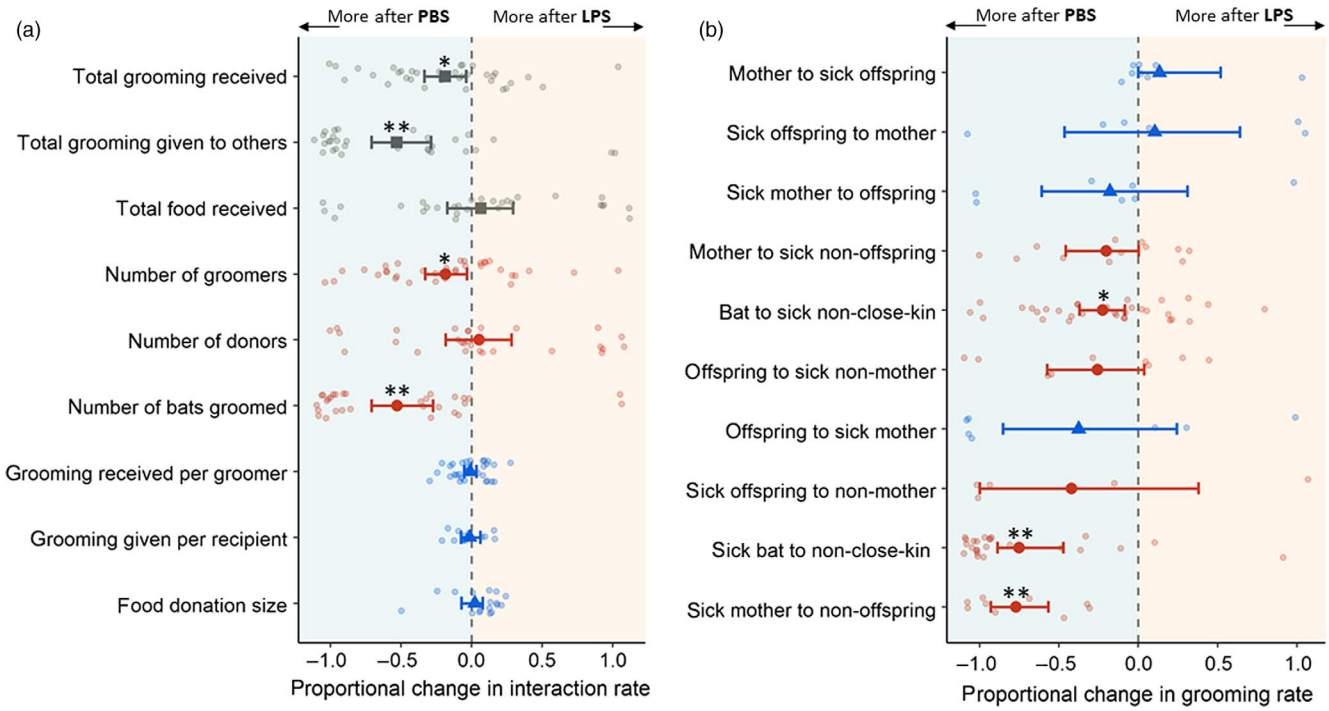

FIGURE 1 Effect of the mimicked bacterial infection on different network response measures and relationship types. All plots show mean standardized lipopolysaccharide (LPS)-effects ± bootstrapped 95% confidence intervals (see Table S1) and data points. (a) LPS effect sizes on three measures of node strength (grey, squares), three degree-centrality measures (red, circles) and three measures of interaction intensity (blue, triangles). (b) LPS effect sizes on allogrooming between different relationship types. Data colours distinguish between maternal (blue, triangles) and non-maternal (red, circles) relationship types. One asterisk indicates $p < 0.05$ and two asterisks indicate p-values that remain <0.05 after a sequential Bonferroni correction

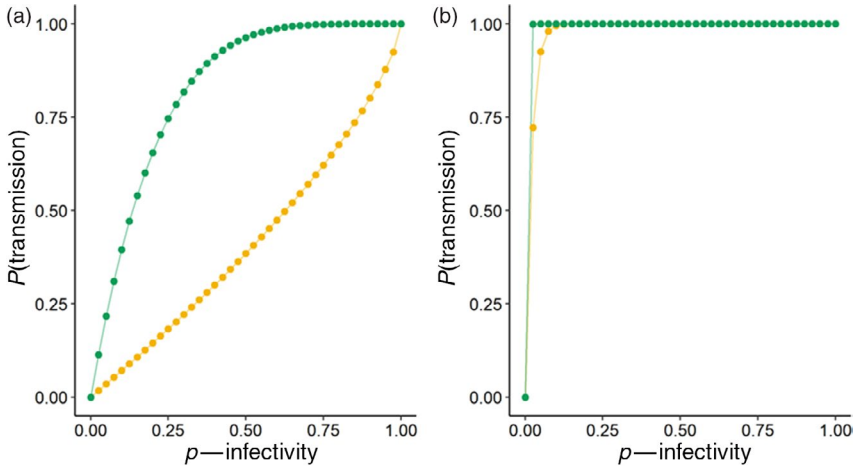

FIGURE 2 Model of how sickness could reduce the probability of pathogen transmission from sick mothers to non-offspring but not to offspring. Estimated probability of transmission from the mother to non-offspring (a) and to offspring (b) after both, lipopolysaccharide (yellow) and phosphate-buffered saline (green) injections

p = 0.006, Figure 1b), but mothers did not decrease their grooming towards their LPS-injected offspring (n = 8, p = 0.267, Figure 1b). LPS-injected mothers did not clearly decrease grooming towards their offspring (n = 7, p = 0.442, Figure 1b), but they did clearly decrease grooming towards non-offspring (nine out of nine observed mothers, n = 9, p < 0.002, Figure 1b). This observed change in the behaviour of immune-challenged mothers would lead to lower pathogen transmission towards non-kin (Figure 2a), but not towards their offspring (Figure 2b). Treatment order had no effect on mass change or behaviour (Table S1) and Table S2 shows all mean LPS effect sizes, bootstrapped confidence intervals and sample sizes. Including bats with no observed social interactions in our analysis does not change the conclusions (Table S3).

4 | DISCUSSION

Sickness behaviour can reshape social networks in ways that alter the epidemiology of infectious disease (Lopes et al., 2016; Stroeymeyt et al., 2018; Van Kerckhove et al., 2013). In such cases, effective modelling of epidemiology will need to account for the effects of sickness on social behaviour. However, the effects of sickness behaviour on social network measures can vary depending on the specific behaviour that is sampled, who is sampled, and how. We demonstrate this in vampire bats, a socially complex species that engages in multiple types of social interactions and harbours several pathogens including *Bartonella* (Becker et al., 2018), haemoplasmas (Volokhov et al., 2017) and rabies (Aguilar-Setien et al., 2005). Specifically, we find that LPS-induced sickness behaviours affected social interactions and depended on the type of behaviour (grooming vs. food sharing), the composition of the interacting pair or group of animals (non-kin vs. mother–offspring pairs), the metric of social connectedness (association vs. interaction) and the social environment (larger vs. smaller groups, compare to Stockmaier et al., 2018).

Immune-challenged vampire bats were involved in less allogrooming, and this effect was driven by fewer grooming recipients (reduced network degree centrality) rather than by lower interaction intensity per recipient (reduced network edge weights). LPS effects on grooming intensity per partner should be harder to detect because grooming bout durations vary greatly between and within dyads. Interestingly, when the same bats were forced into close proximity, LPS did decrease grooming intensity per recipient (Stockmaier et al., 2018). In this study, however, when we allowed the bats to freely associate as in a larger roost, the decrease in grooming occurred due to a reduction in the number of grooming partners rather than a decrease in grooming duration. Put differently, although sickness behaviour can influence both the number of partners and the grooming time per partner, the latter effect was stronger for bats in constant close association (Stockmaier et al., 2018).

The observed effects of sickness behaviour can result from either a change in the rate of encountering others, a change in the interaction time with each partner, or both. Consequently, the size of sickness effects may differ between social networks based on association (e.g. 'gambit of the group', Franks et al., 2010; Whitehead & Dufault, 1999) and social networks based on directed, weighted interactions like allogrooming. This point highlights the importance of studying the social effects of sickness—and its potential effects on pathogen transmission—under ecologically relevant conditions (Lopes et al., 2016), in addition to the more common approach of testing these effects in controlled spaces (e.g. Fishkin & Winslow, 1997; Stockmaier et al., 2018). If sickness-induced lethargy influences encounter rates more than it influences per-partner interaction time, then sickness behaviour might have a disproportionately larger effect on reducing pathogen transmission between clusters of individuals (Lopes et al., 2016) compared to the effect within a single site or cluster.

We also found evidence that immune-challenged bats were groomed by fewer bats causing them to also receive less grooming overall, but we did not detect a change in the mean grooming intensity per partner. This reduction in grooming received is likely explained by the fact that much allogrooming is mutual and possibly reciprocal (Carter & Wilkinson, 2013; Wilkinson, 1986). Therefore, sick bats might have received less allogrooming because they were less active, encountered fewer bats and groomed them less. Sickness may have also reduced encounter rates by decreasing contact calling which attracts other bats (Carter, Logsdon, Arnold, Menchaca, & Medellin, 2012; Carter & Wilkinson, 2016).

Bats did not reduce food sharing towards immune-challenged individuals. This observation is consistent with previous findings that sickness-induced changes to social behaviour are context-specific (Yee & Prendergast, 2010). Food donations are need-based (Wilkinson, 1984), and the LPS-injected individuals were fasted prior to injections to induce a need for food. Once a donor bat had approached a fasted bat in need, the regurgitations are often triggered by the receiver licking the donor's mouth (begging). The fact that the regurgitations remain unchanged suggests that immune-challenged receivers did not refuse to beg and that donors did not avoid them.

In general, our results indicate that sick conspecifics were not actively avoided, nor did they isolate themselves. Instead, our observations were most consistent with the simplest explanation that reduced social interactions resulted from LPS-injected bats being lethargic. Studies on banded mongoose (Fairbanks, Hawley, & Alexander, 2015) and rhesus monkeys (Willette, Lubach, & Coe, 2007) also found no evidence for avoidance of sick conspecifics. In these species and the vampire bats, the overall benefits of social interactions might outweigh the benefits of avoiding sick individuals, especially in highly connected groups where indirect transmission is almost inevitable (Loehle, 1995). Altruistic self-isolation following pathogenic infections could evolve through kin selection (Shakhar & Shakhar, 2015), as seen for instance in pathogen-exposed ants that spend more time outside the nest and away from the brood (Bos et al., 2012; Heinze & Walter, 2010; Stroeymeyt et al., 2018). In vampire bats, however, the direct and indirect fitness benefits of social interactions (Carter & Wilkinson, 2013, 2015; Wilkinson, 1984) likely outweigh the indirect fitness benefits of potentially preventing infections to related groupmates.

The mimicked bacterial infection reduced grooming towards non-close-kin, but it did not reduce maternal care. Mothers did not groom their offspring less when either the mother or their offspring were immune-challenged. Allogrooming rates from mothers to their offspring were about four times higher than non-maternal grooming rates, as seen previously in this species (Carter & Wilkinson, 2013; Wilkinson, 1986). Given this extensive maternal investment (Carter, Wilkinson, & Page, 2017; Delpietro & Russo, 2002) and the fact that a mother is often the primary food donor for each female bat (Carter & Wilkinson, 2013; Wilkinson, 1984), it is likely that reducing maternal care is more costly to fitness than the physiological risks posed interacting with an infected bat (Lopes, 2014). Several other experiments also suggest that the need for maternal care can partially overcome sickness behaviour (Aubert, Goodall, Dantzer, & Gheusi, 1997; Weil, Bowers, Dow, & Nelson, 2006) or pathogen avoidance (Poirotte & Charpentier, 2020). Transmission probabilities based on interaction rates could remain unchanged between a sick mother and her offspring but decrease between the same bat and non-closely related groupmates (Figure 2). Therefore, when modelling the effects of sickness on pathogen spread using social networks, it could be beneficial to account for variation in relationship types.

Sickness effects are pathogen-specific. For example, rabies virus in vampire bats will change interactions in different ways than what we observed here. Rabid bats found in the field are often covered in bites, potentially because of increased aggressive interactions (Delpietro, Russo, Carter, Lord, & Delpietro, 2017). Our results cannot be extrapolated to all live pathogens and are best viewed as isolating the effect of reduced activity, a common symptom of infections.

In summary, infections can change social behaviour, and ultimately, pathogen transmission (Colman, Spies, & Bansal, 2018; Funk, Salathé, & Jansen, 2010; Lopes, 2014; Rizzo, Frasca, & Porfiri, 2014; Stroeymeyt et al., 2018; Van Kerckhove et al., 2013). Our results highlight that such effects can differ depending on the 'who, what, and how' of social interactions within animal groups, which should be considered when designing and interpreting studies of pathogen transmission based on networks.

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AUTHORS' CONTRIBUTIONS

S.S. and G.G.C. designed the study and carried out the experiments and husbandry; G.G.C. captured the bats and established the captive colony; G.G.C., D.I.B. and R.A.P. coordinated the study and provided valuable resources and lab space. All authors contributed to draft the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R scripts to repeat our analysis are publicly available on figshare: https://doi.org/10.6084/m9.figshare.7726256.v7 (Stockmaier, 2019).

ORCID

Sebastian Stockmaier https://orcid.org/0000-0001-8280-8086
Daniel I. Bolnick https://orcid.org/0000-0003-3148-6296
Rachel A. Page https://orcid.org/0000-0001-7072-0669
Gerald G. Carter https://orcid.org/0000-0001-6933-5501

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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