Opportunistic evidence of the impact of bacterial infections on social integration in vampire bats

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Abstract

Social integration can affect an individual's susceptibility to infectious disease. Conversely, infectious disease can reduce an individual's social activity. Yet, it remains unclear to what extent short-term infections can inhibit aspects of long-term social integration (e.g., formation of new relationships). During a previous study on relationship formation, we captured female common vampire bats (*Desmodus rotundus*) from different wild populations and housed them together in captivity. Upon introduction, we observed an unplanned outbreak of bacterial infections that caused cutaneous lesions. After treating infected bats with an antibiotic, 5 bats recovered, but 4 others suffered lasting injuries. We analyzed how allogrooming rates changed over time among familiar and new pairs consisting of the 9 infected and 12 asymptomatic bats. Infected bats demonstrated lethargy and reduced social behavior. We found that more severely infected bats gave and received less allogrooming compared to asymptomatic bats, that this infection effect was initially larger for new pairs relative to familiar pairs, and that this effect decreased as infected bats recovered and new pairs became more familiar. These observed effects, although opportunistic and based on only

9 infected bats, were consistent with the hypothesis that short-term infections can impact relationship formation when new individuals join a group.

Introduction

Social integration, the quantity and quality of an individual's supportive social relationships, can affect that individual's susceptibility to infection (e.g.,1–4) and ability to tolerate the adverse effects of parasites (5,6). Conversely, infectious disease can often inhibit social behaviors of infected individuals (7–9) by diminishing their motivation to interact with others (e.g.,10–12), reducing their movement (e.g., in mice (13) and mongoose (14)), or causing others to avoid them (15–19). The effects of infection on social behavior vary across pathogens, hosts, levels of infection severity, and types of social relationships. For example, in vampire bats, sickness behavior reduces non-kin social grooming, but does not decrease maternal grooming of offspring (20). Similarly, mandrills avoid grooming parasite-infected non-kin but continue to groom infected close maternal kin (21). More generally, infections might reduce social interactions disproportionately more within new or weak social relationships compared to strong social bonds (22). For example, short-term infections are likely to have a bigger impact on mate choice (reviewed in 23) and on the process of pair bonding than on an existing pair bond (24). It remains unclear, however, to what extent infections impact same-sex social bond formation.

New social bonds form when new adults join a social community, which is also when individuals are exposed to new pathogens. Given that short-term events during relationship formation can have persistent long-term effects (25), the impacts of infections may have disproportionately greater long-term consequences on relationship formation than on existing relationships. To address this hypothesis, we report opportunistic evidence that an acute bacterial infection can reduce social integration in common vampire bats (*Desmodus rotundus*). In this species, social bond formation is observable as strangers transition from clustering to social grooming and regurgitated food sharing—a costly cooperative behavior (26). Allogrooming is the best measure of relationship formation, because it is a directed investment of time and energy that

also occurs frequently enough to track over time. During a previous 4-month study, we tracked changes in allogrooming among 21 female vampire bats before and after a week of forced proximity in which small groups of 3 bats from 3 distant sites were housed together for one week (25). Shortly after the 21 bats from different sites were first introduced in captivity, we observed an unplanned outbreak of a bacterial infection, which we treated with antibiotics (25). In this paper, we analyzed the social effect of these infections by tracking changes in allogrooming over time among pairs of 9 infected female bats and the 12 asymptomatic female bats that were previously familiar or unfamiliar with each other.

Methods

Study subjects

For an experiment testing the effects of forced proximity on relationship formation (25), we captured 8-9 common vampire bats from each of three sites in Panama that were 120-350 km apart. Upon capture, the bats (23 adult females, 2 juvenile males, and one juvenile female) appeared healthy with no pathological lesions. We housed the bats together in an outdoor flight cage (2.1 × 1.7 × 2.3 m) for approximately 4 months. During this time, five females gave birth to four males and one female pup (31 total bats). Details of the study colony can be found in (25,27).

We tracked the allogrooming relationships among 252 new and 126 familiar pairs of 21 adult females. We define ‘pairs’ as unique directed combinations of a groomer and receiver. We use the label ‘new’ for pairs that were introduced in captivity and ‘familiar’ for pairs that were captured from the same site (hollow tree or cave). We excluded from our analysis 42 pairs that were forced into proximity together to induce social bonding for the previous study; however, including these 42 pairs in the analysis does not change our conclusions.

Behavior sampling

We used three infrared surveillance cameras to sample social interactions among the individually marked bats (25). Over 114 days, we sampled 682 h of interactions, recording all visible

allogrooming and mouth-licking interactions (≥ 5 seconds in duration) as well as agonistic interactions (≥ 1 second in duration). For each interaction, we noted the actor, receiver, and duration. We used allogrooming to assess social integration because allogrooming was 94% of the 17,592 observed social interactions, while mouth-licking and aggression were only 6% and 0.3% of interactions, respectively. To estimate dyadic allogrooming rates, we averaged the seconds of allogrooming per hour across all hours in which the actor and receiver could interact. For further details, see (25).

Bacterial infection and treatment

Two to three weeks after the 26 wild-caught bats were first introduced, 10 female bats began to show progressive symptoms of a cutaneous infection (blisters or open lesions with pus, as well as inflamed tissue), which was often localized around joints. Symptoms progressed for approximately two weeks without signs of recovery. These infections were unexpected and to our knowledge have not previously been described in vampire bat colonies. The 10 infected bats varied in the severity of their symptoms. The most severe symptoms occurred in bats from a hollow tree near La Chorrera, Panama. The most severely infected bat developed large, pus-filled lesions on its back and had extreme inflammation around the wrists that led tissue to break apart and expose bone; we euthanized this bat before it received antibiotic treatment, and we did not include it in our analysis of social integration. Four other bats developed severe symptoms with ulcers and inflammation on one or both wrists, leading to tissue scarring and the inability to sustain flight. One bat from the same roost experienced only minor inflammation and ulcers on both wrists but healed without permanent tissue scarring and remained able to sustain flight. Three bats from a cave near Lake Bayano, Panama were also infected. Two bats developed pus-filled abscesses: on the lower abdomen and upper thigh for one bat, on the lower back for the other bat, and the third bat developed only minor inflammation on 1-2 toes. Finally, one bat from a hollow tree near Tolé, Panama had a large, round lesion on its knee, but this was evident at the start of the study and did not change over time. This

bat displayed no other signs of infection. With most cases having been observed in bats from either La Chorrera or Lake Bayano, it seems the bats from Tolé were most resistant to the pathogen.

Swab and tissue samples from skin lesions were cultured to isolate bacterial pathogens, which indicated the isolation of *Bacillus sp.* and *Staphylococcus aureus*. A Kirby-Bauer antibiogram indicated susceptibility of the isolated bacteria to the antibiotic Enrofloxacin. Given the urgency and results of the antibiogram, we immediately used Enrofloxacin antibiotic to treat the infected female bats (described above) over the course of seven days via daily subcutaneous injections. We did not perform additional testing to further identify the bacterial species or strain or test for other potentially infectious pathogens. After the antibiotic treatment, five bats recovered without injury (henceforth "treated"), but four bats suffered lasting injuries that rendered them unable to fly for the remainder of the study (henceforth "injured"). We refer to all other bats in the colony as "asymptomatic".

Confirming sickness behavior

To confirm that bacterial infections reduced individual activity and social behavior, i.e., 'sickness behavior', we compared the activity of 9 infected versus 9 asymptomatic adult female bats during a sample period of 1 week before the antibiotic treatment (pre-treatment week) and again during another 1 week about 11 weeks later near the end of study (post-treatment week). An observer scored videos using focal sampling for the presence or absence of 4 behavioral states: moving, resting (including sleeping), allogrooming (including mouth-licking), and self-grooming, following definitions in (12). These behaviors were scored every 30 seconds for 1 hour (starting one hour after sunset) per day for each bat. We sampled all 18 bats 120 times on each of 14 days. The observer could not be entirely blind to the condition because lesions were visible, but videos are available for confirmation. To test if infection predicted the frequency of these six behavioral states, we calculated the mean proportion of sampled times where each behavior occurred and estimated 95% confidence intervals (CIs) using bootstrapping with 5000 iterations (percentile method, boot package in R, 28).

Effects of infection on dyadic allogrooming rates

To assess how dyadic rates of allogrooming changed over time among familiar or new pairs of bats that were either infected or asymptomatic, we fit a logistic mixed effect model (lme4 R package, 29). The response was the presence or absence of allogrooming for each groomer-receiver pair and hour. Fixed effects were prior familiarity of the pair (true/false), infection severity of the actor (0 = asymptotic, 1 = infected, 2 = injured), infection severity of the receiver (same scale), time (unit was 10 days), interactions between time and other fixed effects, interactions between familiarity and infection severity, and two three-way interactions between groomer/receiver infection severity, familiarity, and time. Groomer and receiver identity were random intercepts. We converted each model coefficient to an odds ratio (OR) and used the profile likelihood method to estimate 95% confidence intervals around ORs. When estimating confidence intervals via bootstrapping, the 95% CIs were very similar and the conclusions were the same..

We predicted a three-way interaction between familiarity, time, and infection severity (for both groomers and receivers), because we expected that the impact of infection on the slope of allogrooming rates over time would differ between familiar pairs and new pairs. We expected infections to have a greater impact on allogrooming rates in new pairs relative to familiar pairs. In new pairs, we predicted an interaction between infection severity and time as predictors of allogrooming, because infections should cause allogrooming rates to be initially lower during relationship formation and then allogrooming rates of infected and asymptotic bats should converge over time as the infected bats recovered. In familiar pairs, we expected this interaction to be weaker because relationships were already formed, so infections should have a smaller impact on how allogrooming changes over time in more established relationships.

Ethics

This work was approved by the Smithsonian Tropical Research Institute Animal Care and Use Committee (no. 2015-0501-2022) and the Panamanian Ministry of the Environment (no. SEX/A-67-2019).

Data accessibility

Data and R code are available on Figshare (30).

Results

Confirming sickness behavior

Consistent with sickness behavior and recovery, the 9 infected bats spent less time moving and allogrooming, but these differences faded with time (Fig. 1). Before antibiotic treatment, infected bats spent 1.3% of their time allogrooming, 95% CI = [0.6, 2.1%], versus 3.9% [2.3, 5.6%] in asymptomatic bats. Infected bats spent 7.4% [4.8, 9.9%] of their time moving versus 17% [11, 22%] in asymptomatic bats. After recovery, however, the previously infected bats no longer showed clear differences from the asymptomatic bats in allogrooming or movement (Fig. 1). The pre-treatment differences from the asymptomatic bats in allogrooming and moving were also greater in the 4 injured bats than in the 5 treated bats (Fig. S1). We did not detect clear effects of infection on resting or self-grooming (Fig. 1).

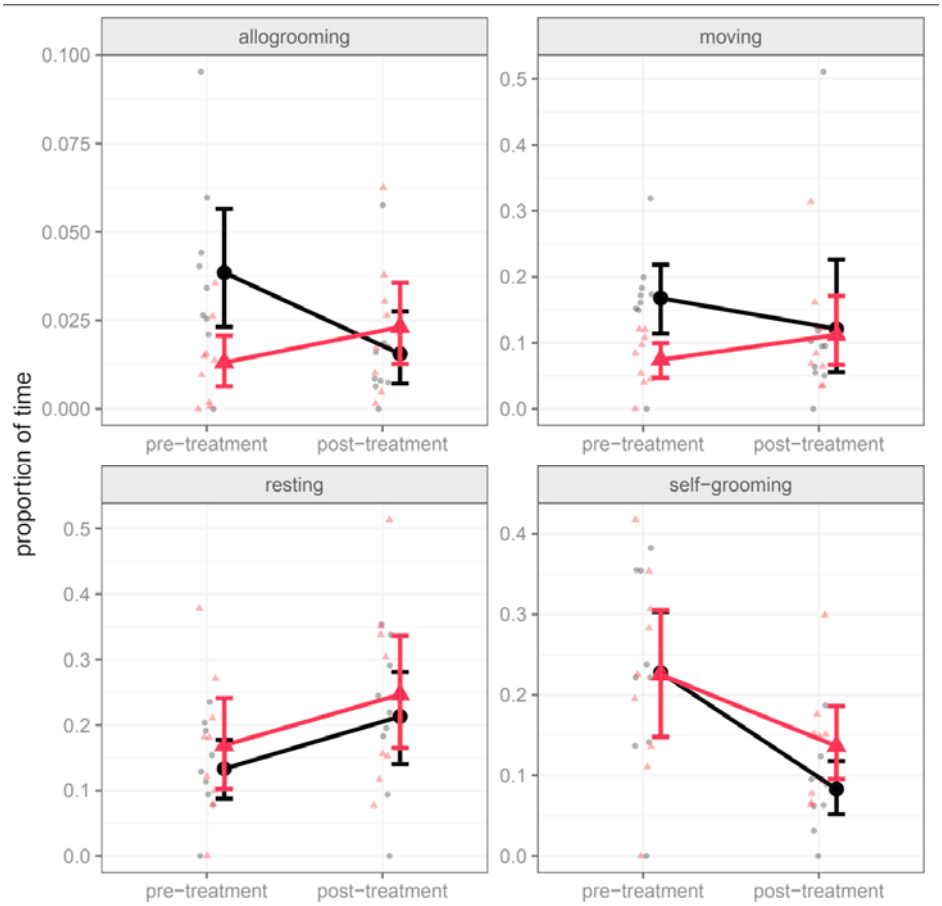

Figure 1. Bats with bacterial infections spent less time allogrooming and moving pre-treatment but not post-treatment. Dots and error bars show mean proportions of time doing each behavior ± bootstrapped 95% CIs for infected bats (red triangle) and asymptomatic bats (black circle) female bats during the outbreak (pre-treatment) and after they had recovered (post-treatment). Resting and self-grooming did not clearly differ by infection. Fig. S1 shows a version of this plot with infected bats divided into 'treated' and 'injured' bats.

Effects of infection on dyadic allogrooming rates

In vampire bats, allogrooming is often mutual and highly symmetrical within pairs over time (26,31,32). We found no evidence that infection removed allogrooming symmetry: pairwise allogrooming was bidirectional within the hour in 84% of cases with an infected bat and in 81% of

cases with two asymptomatic bats. This confirms our expectation that any sickness effects on allogrooming given and allogrooming received will be causally linked (i.e., grooming given causes grooming received), and that the behavior of both bats should influence the dyadic allogrooming rate. This justifies our decision to include infection severity of both groomers and receivers as simultaneous predictors with additive effects in our statistical model. After detecting a three-way interaction between infection severity, familiarity, and time for both allogrooming given and received (given: OR = 1.04, 95% CI = [1.03, 1.06], $p < 0.0001$; received: OR = 1.03 [1.01, 1.05], $p = 0.002$), we fit separate models for new and familiar pairs to compare coefficients (Fig. 2).

In new pairs, an interaction between infection severity and time showed that infections affected how allogrooming rates changed over time (interaction effect on grooming given: OR = 1.06 [1.05, 1.07], $p < 0.001$; on grooming received: OR = 1.05 [1.04, 1.06], $p < 0.001$). Specifically, infections initially reduced allogrooming rates during relationship formation, then the allogrooming rates of infected and asymptomatic bats converged over time as the infected bats recovered (Fig. 3). Overall, allogrooming rates in new pairs were reduced by infections (grooming given: OR = 0.45 [0.25, 0.83], $p = 0.007$; grooming received: OR = 0.49 [0.26, 0.92], $p = 0.019$).

In familiar pairs, by contrast, the interaction between infection severity and time was weaker (interaction effect on grooming given: OR = 1.02 [95% CI: 1.00, 1.03], $p = 0.02$; on grooming received: OR = 1.03 [1.01, 1.04], $p = 0.001$; Fig. 2). Relative to infections in new pairs, infections in familiar pairs had a smaller impact on how allogrooming rates changed over time (Fig. 3). Unlike the new pairs, we did not detect a clear overall effect of infections on allogrooming given or received (grooming given: OR = 0.80 [0.37, 1.82], $p = 0.57$; received: OR = 0.80 [0.38, 1.78], $p = 0.55$).In sum, we found evidence that bacterial infections decreased allogrooming given and received, that this effect of sickness behavior was greater for new pairs relative to familiar pairs, and that it also decreased with time as infected bats recovered (Fig. 2).

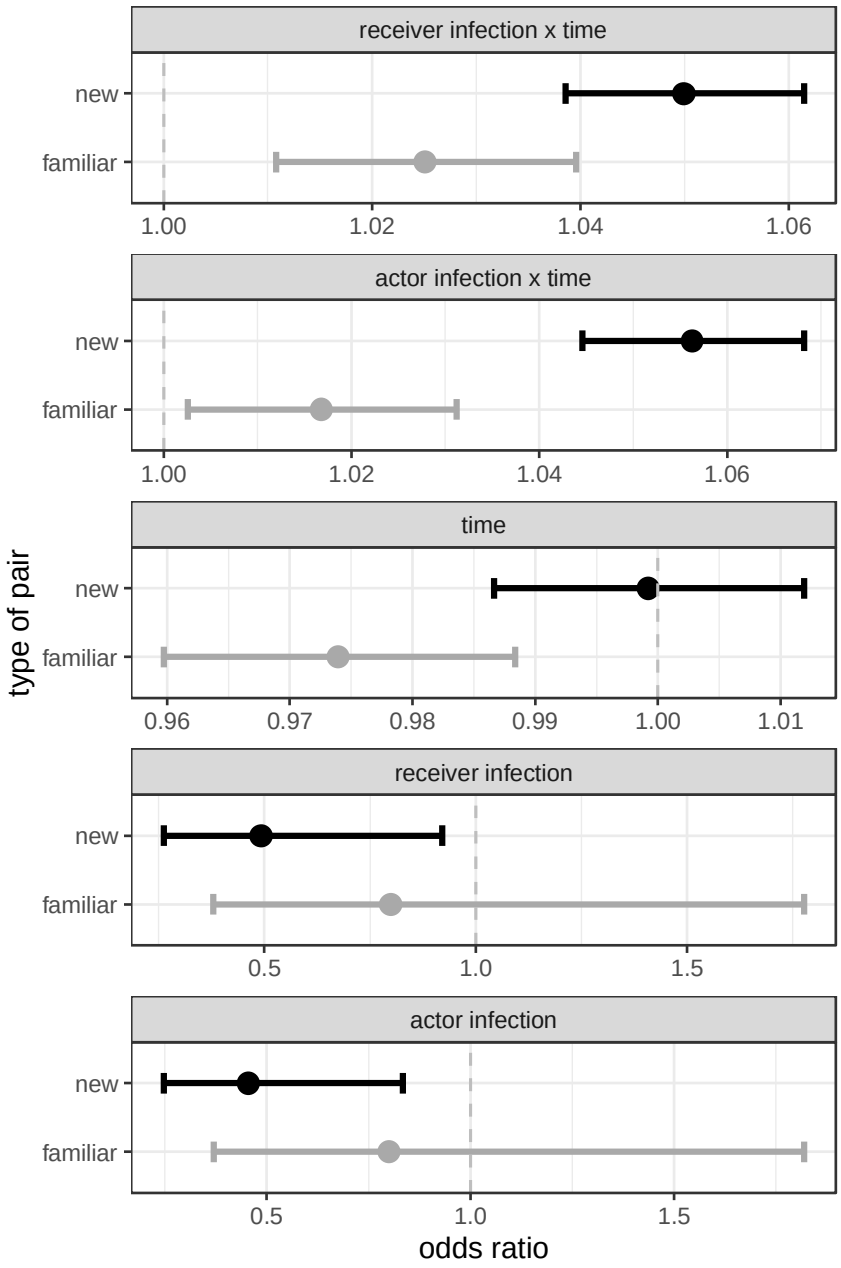

Figure 2. The effect of infection severity on allogrooming over time differed between new and familiar pairs. Points show odds ratios, and profile likelihood 95% CIs, from generalized linear mixed effect models fit for both new pairs and unfamiliar pairs.

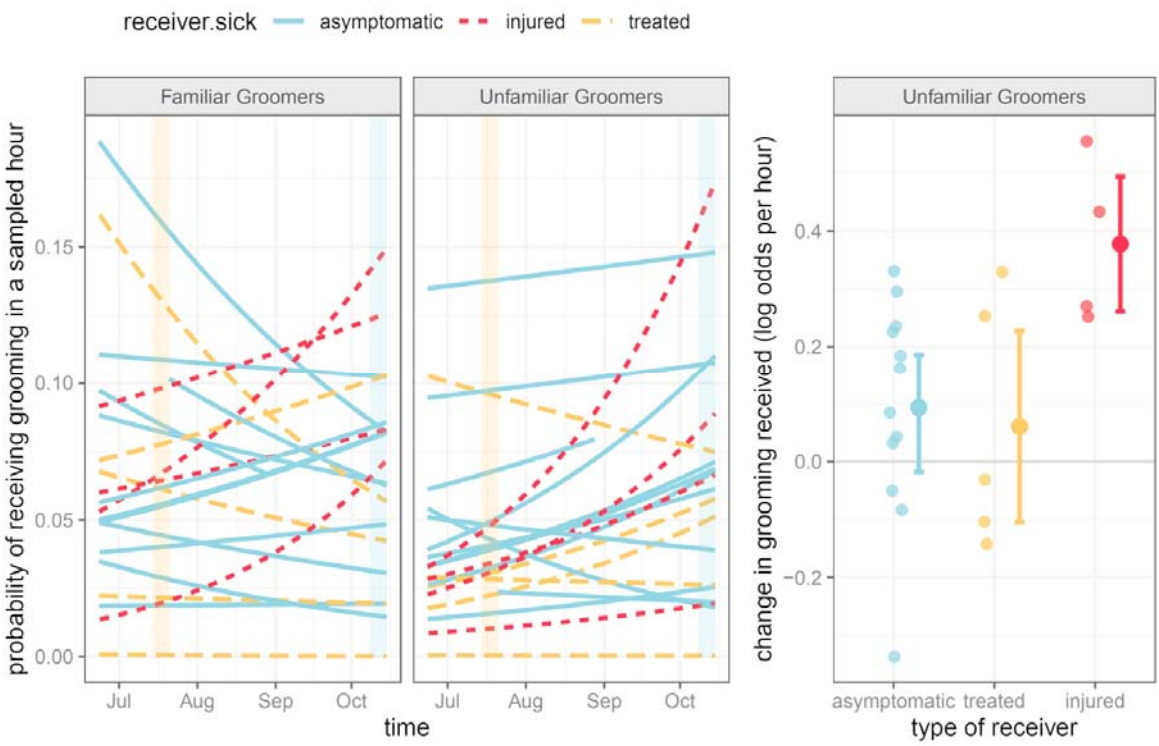

Figure 3. Social integration by infection status. Left panel shows changes in the probability of receiving allogrooming over time from a familiar groomer when the receiver was asymptomatic (solid cyan), treated (dashed orange), or injured (dotted red). Yellow shaded region indicates the week prior to antibiotic treatment (pre-treatment) and blue shaded region indicates one week at the end of the experiment (post-treatment). Middle panel shows the same plot but for previously unfamiliar groomers (new pairs). The probability of receiving allogrooming prior to the antibiotic treatment was reduced in infected bats, and especially the injured bats. Right panel shows the change in log odds (pre-treatment vs post-treatment) of allogrooming received for each type of receiver. Large points with error bars are means and bootstrapped 95% CIs. Effects on allogrooming given and received are causally linked through reciprocity. These plots assess social integration through allogrooming *received*; results for allogrooming *given* are even more dramatic (Fig. 2).

Discussion

While several studies have quantified the effect of pathogens on host social behavior (14,16–18,46–51), it is unclear to what extent short-term infections can impact long-term social bond formation. We present opportunistic observational evidence that acute symptoms of bacterial infection can limit allogrooming relationship formation in vampire bats. Relative to asymptomatic bats, the initially infected bats (and the injured bats in particular) spent less time moving and allogrooming. Infected bats gave and received less allogrooming with new partners, but we did not detect that infection severity predicted less allogrooming with familiar partners. These differences faded during 3 months of recovery, suggesting they were caused by short-term sickness behavior rather than by permanent injuries that reduced movement. These observations, albeit opportunistic and sparse, are valuable for informing future experiments with greater power and control.

Because we did not randomly and experimentally infect the bats, a possible alternative explanation is the reverse causal path: bats with worse social integration (or worse social competence) had weaker immune systems and therefore suffered worse infections. However, this hypothesis does not explain why the gap in social integration disappeared over time after antibiotic treatment. If the infected bats were already less social or less healthy for reasons besides the infection, then we would expect their social integration to be worse overall, not just during the outbreak. If variation in the severity of infection was based on dominance or social competence, we would expect variation in infection severity within each group. Instead, infection severity was almost perfectly correlated with capture population, suggesting that infections were a cause, not a consequence, of how bats formed new relationships.

The sickness behavior we observed was largely similar to the responses of vampire bats to simulated infections from injections of lipopolysaccharide, LPS (12,20). In vertebrates, quantifying sickness behaviors in response to a naturally-infecting pathogen is less common (but see 45,47,52,53) compared to sickness behaviors caused by an immune challenge like LPS (8,10–12,15,20,24,31,54–56). The use of immune challenges allows for controlled experiments on the connection between the inflammatory and the behavioral response to infection, but naturally infecting pathogens can have different, pathogen-specific effects**.** For instance, LPS-injected

vampire bats reduced their self-grooming (12), but these infected bats did not**,** probably because the bacterial pathogens caused skin lesions. Another pathogen that infects the skin, the fungus *Pseudogymnoascus destructans* (which causes 'white-nose syndrome' in North American bats) also leads to increased self-grooming (52).

The skin ulcers, abscesses, and inflammation we observed in common vampire bats were due to an acute bacterial infection. Samples collected from symptomatic bats' lesions indicated the presence of *Bacillus sp.* and *Staphylococcus aureus*. There are several *Bacillus* species (e.g., *Bacillus anthracis, Bacillus cereus,* and *Bacillus pumilus*) that may infect the skin or colonize wounds, but these infections are uncommon and often present with classic symptoms (e.g. black eschars and necrosis, 33–36) that we did not observe in our colony. Alternatively, several species within the *S. aureus* complex, including *Staphylococcus schweitzeri* and *Staphylococcus argenteus,* among others (37–39), typically infect the skin and cause symptoms that are consistent with what we observed. *S. aureus* complex has also been isolated from the feces of Old-World fruit bats (40–43) and the common vampire bat (44,45).

We view our results as a starting point for future studies that address the effect of infections on long-term social integration and relationship formation. Our findings raise several questions. When might vampire bats or other animals suppress their infection-induced behavioral symptoms to continue social interactions and integration (54,55,57–59)? At what stages of relationship formation do sickness behaviors have the strongest effect on social interactions? How long must sickness behavior last for it to cause lingering social effects? To test for potential trade-offs between the severity of behavioral symptoms and continued social interactions, researchers could use immune challenges that are dose-dependent (55,60). Immune challenges like LPS could be used to measure how long sickness behavior would have to last for lingering effects on social integration, to control the duration and precise onset times of symptomatic periods, and to test what stage of relationship formation is most impacted by sickness behaviors.

In conclusion, we found opportunistic observational evidence for reduced social integration in infected vampire bats after an outbreak of a naturally infecting pathogen. Sickness behavior and

other cues of infection can reduce social activity and mate attraction (reviewed in 23), and there may be similar effects on choice and formation of same-sex social bonds. If there are critical periods of relationship formation, then infections during this time might have long-term social consequences.

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Visualization: IR, SS, GC

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