Opportunistic evidence for impacts of *Staphylococcus* infection on social integration in vampire bats

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Abstract

Social integration affects an individual's susceptibility to infection, and conversely, infectious disease can reduce their social activity. It remains unclear, however, to what extent short-term infections might affect the formation of enduring social bonds. During a previous study on the formation of new allogrooming relationships among 21 common vampire bats (*Desmodus rotundus*), we used antibiotics to treat unplanned *Staphylococcus* infections in 9 bats, including 5 bats that recovered and 4 bats that suffered lasting injuries that prevented sustained flight. We compared the behaviors of the *Staphylococcus*-infected bats to healthy controls, and analyzed changes in allogrooming over time among infected and healthy bats that were familiar or unfamiliar. Relative to healthy bats, the 9 *Staphylococcus*-infected bats spent less time moving and allogrooming, and the 4 bats that suffered injuries received less grooming from new partners. These differences faded during 3 months of recovery. This pattern is consistent with the hypothesis that acute infections impact the development of social relationships. Our findings raise questions about how short-term infections might impact long-term social integration or partner choice.

Introduction

Social integration, the quantity and quality of beneficial social relationships, can affect an individual's susceptibility to infection (e.g.,1–4) or help individuals tolerate the adverse effects of parasites (5,6). Conversely, infectious disease can inhibit social behaviors of infected individuals (7–9) by reducing their motivation to interact with others (e.g.,10–12), reducing their movement (e.g., mice, (13) and mongoose (14), or causing others to avoid them (15–19). The effects of an infection on social behavior vary with many factors including the pathogen, the host, the infection severity, and the type of social relationship. For example, sickness behavior in a juvenile vampire bat can increase grooming received from its mother and reduce grooming received from other groupmates (20). Similarly, mandrills avoid grooming parasite-infected non-kin but continue to groom their infected close maternal kin (21). In general, one expects that infections might reduce social interactions disproportionately more within new or weak social relationships compared to strong social bonds (22). For example, 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 (see example of simulated infections in pair-bonded animals, 24). It remains unclear, however, to what extent infections impact same-sex social bond formation.

We expect new social bonds to form when new adults join a social network, which is also when individuals are exposed to new pathogens. Social bonds are relatively stable relationships, so events that influence relationship formation might have persistent long-term effects (25). If so, the impacts of infections on relationship formation may be greater and have disproportionately greater long-term consequences than the impacts on existing relationships. This begs the question: Can short-term sickness behaviors shape the long-term development of social bonds?

To help address this question, we report opportunistic evidence that bacterial infections appeared to reduce social bond formation 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 (26). 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 3 bats from 3 distant sites were housed together for one week (25). When the bats from different sites were first housed together, we observed an unplanned outbreak of *Staphylococcus* infections, which we treated with antibiotics (25). Here, we analyzed changes in allogrooming over time among the 9 *Staphylococcus*-infected bats and the 12 healthy bats that were familiar or unfamiliar with each other.

Methods

Behavior sampling

We captured 26 bats (8-9 bats from each of three sites in Panama that were 120-350 km apart) and housed them together in an outdoor flight cage. Four males and one female were born in captivity. Of these 31 bats, we used 21 females in a study testing the effects of forced proximity on relationship formation (25). We use the label 'unfamiliar' for pairs of bats that were introduced in captivity and 'familiar' for pairs that were captured from the same site (hollow tree or cave). We used three infrared surveillance cameras to sample social interactions among the individually marked bats. Over 114 days, we sampled 682 h of interactions, mostly bouts of allogrooming (>5 s in duration) and noted the actor and receiver. To estimate dyadic allogrooming rates, we averaged the seconds of allogrooming per hour across all hours in which the actor and receiver could interact. Details of the study colony can be found in (25,27).

Staph infection

Soon after bats were housed together, 10 bats developed progressive symptoms of an infection (open, oozing lesions or inflamed tissue), which also infected their joints. Swab and tissue samples were sent to a veterinary doctor for bacterial cultures, which confirmed bacterial infection of *Staphylococcus aureus*. A Kirby-Bauer antibiotic test indicated strain susceptibility to the antibiotic Enrofloxacin, which we used to treat 9 infected bats. One bat died prior to receiving antibiotic treatment. Of the remaining 9 infected bats, five bats recovered without injury ("treated" bats), but four bats suffered lasting injuries that rendered them unable to fly for the remainder of the study ("injured" bats). We refer to the other 21 bats in the colony as "healthy".

Compared to the treated bats, injured bats were more impacted by the infection prior to the antibiotic treatment. The injured bats suffered from severe swelling with lesions on one or both wrists leading to tissue scarring and inability to sustain flight because of their infection. All injured bats were from a roost near La Chorrera, Panama. One treated bat, also from the La Chorrera roost, experienced minor swelling and injuries on both wrists, but healed without permanent tissue scarring and could sustain flight. Two treated bats from a different roost (a cave near Lake Bayano, Panama) had pus-filled lesions: on the lower abdomen and upper thigh for one bat, and on the lower back for the other bat. A third bat from Lake Bayano had minor swelling on 1-2 toes which disappeared after treatment with antibiotic. Finally, one treated bat from a hollow tree near Tolé, Panama had a large swollen knee, which was evident at the start of the study and did not change after antibiotic treatment. This bat displayed no other signs of infection and in retrospect may not have been infected with *Staphylococcus*.

To confirm that *Staphylococcus* infections caused sickness behavior, we compared behaviors of the 9 infected adult female bats with a control group of 9 healthy 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). For each of the 18 bats, an observer scored 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. Overall, we sampled six behaviors across all 18 bats 120 times on each of 14 days. To test if infection predicted the probability 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 grooming rates

In the previous study (25), a subset of 21 new pairs were forced into proximity together to induce social bonding. In this study, we excluded these pairs from our analysis to remove any effect of experimental forced proximity on relationship formation. However, including these pairs in the analysis does not change our conclusions about infection as a predictor of poor social integration. We considered *grooming received* as the best response measure of social integration, but we also tested how infection influenced grooming rates over time when the actor was infected (*grooming given*) and when either the actor or receiver was infected. To assess if dyadic rates of grooming for the 9 infected and 12 healthy bats changed over time, we fit three binomial mixed effect models (lme4 R package, 29) to test which factors predicted the presence or absence of allogrooming in sampled hours. In all models, actor and receiver identity were random intercepts. In the first model, fixed effects were prior familiarity of pair (true/false), infection status of either actor or receiver (true/false), time, and all interactions between those three fixed effects. To scale the β coefficients, we used 10 days as a unit of time. The second and third model were similar except that we defined 'infection status' based on the grooming *actor* (model 2) or grooming *receiver* (model 3).

In all models, we tested for a three-way interaction, and re-fit the model separately for familiar and unfamiliar pairs. In addition to Wald Test p-values, we report p-values from the likelihood ratio test (LRT p) for our three main predicted effects: (i) a three-way interaction between familiarity, infection status, and time, (ii) an interaction between infection status and time within unfamiliar dyads (infections have a large impact on how grooming changes over time), and (iii) a weaker interaction or no interaction between infection status and time within familiar dyads (infections have a smaller impact on how grooming changes over time).

Finally, we compared the post-recovery increases in grooming rates for bats that were healthy, treated, or injured. To do this, we first fit a binomial model for each bat to estimate its change in log odds of grooming per hour (change in grooming received). Then we used bootstrapping to estimate 95% CIs around the mean change in grooming received for healthy, treated, and injured bats. Due to our small sample sizes, caution must be taken when interpreting these CIs and p-values.

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, we found that the 9 *Staphylococcus*-infected bats spent less time moving and allogrooming, but these differences faded after 3 months of recovery (Figure 1). Before antibiotic treatment, infected bats spent 1.3% (95% CI = [0.6—2.1%]) of their time allogrooming versus 3.9% [2.3—5.6 %] in healthy bats, and infected bats spent 7.4% [4.8—9.9%] of their time moving around versus 17% [11—22%] in healthy bats. After recovery, however, the previously infected bats no longer showed clear differences from the healthy bats in resting or self-grooming (Figure 1). Further analysis suggested that the pre-treatment differences from the healthy bats in allogrooming and moving were greater in the 4 injured bats than the 5 treated bats (Figure S1).

Effects of infection on dyadic grooming rates

Overall, we found evidence that infected bats engaged in less allogrooming compared to healthy bats, that this difference decreased with time, and that this difference was even larger for new relationships and for bats that were injured. We found no evidence that infection decreased allogrooming symmetry: allogrooming is often mutual and highly symmetrical within pairs (26,31,32), and pairwise allogrooming was bidirectional within the hour in 84% of cases with an infected bat and in 81% of cases with two healthy bats. This confirms our expectation that any sickness effects on grooming given and grooming received are causally linked.

For pairs of bats with either an infected groomer or receiver, we found a three-way interaction between familiarity, infection status, and time ($\beta = 0.041$, SE = 0.014, LRT $p = 0.003$). In familiar pairs, infection did not predict how allogrooming changed over time ($\beta = 0.009$, SE = 0.011, LRT $p = 0.412$), and familiar allogrooming did not clearly change with time ($\beta = -0.005$, SE = 0.009, Z = -0.522, $p = 0.601$) or differ by infection ($\beta = 0.086$, SE = 0.133, Z = 0.645, $p = 0.519$). In new (unfamiliar) pairs, however, allogrooming did increase over time ($\beta = 0.019$, SE = 0.007, Z = 2.731, $p = 0.006$) and infection predicted both less grooming ($\beta = -1.106$, SE = 0.086, Z = -12.855, $p < 0.001$) and a larger increase in grooming with time ($\beta = 0.059$, SE = 0.009, LRT $p < 0.001$, Table S2).

The pattern was similar when testing the allogrooming effects of an infected actor. We found a trend suggesting the same three-way interaction ($\beta = 0.027$, SE = 0.014, LRT $p = 0.051$). In familiar pairs, infection in the actor did not predict how much grooming changed over time ($\beta = 0.02$, SE = 0.011, LRT $p = 0.068$) but in new pairs, infection in the actor did influence how grooming changed with time ($\beta = 0.043$, SE = 0.009, LRT $p < 0.001$, Table S1).

When testing the allogrooming effects of an infected receiver, we did not detect a three-way interaction ($\beta = 0.009$, SE = 0.014, LRT $p = 0.498$). In both familiar and new pairs, infected receivers had initially lower levels of allogrooming received leading to greater increases in grooming received over time compared to healthy receivers (familiar: $\beta = 0.028$, SE = 0.011, LRT $p = 0.009$; unfamiliar: $\beta = 0.034$, SE = 0.009, LRT $p < 0.001$, Table S1; Figure 2).

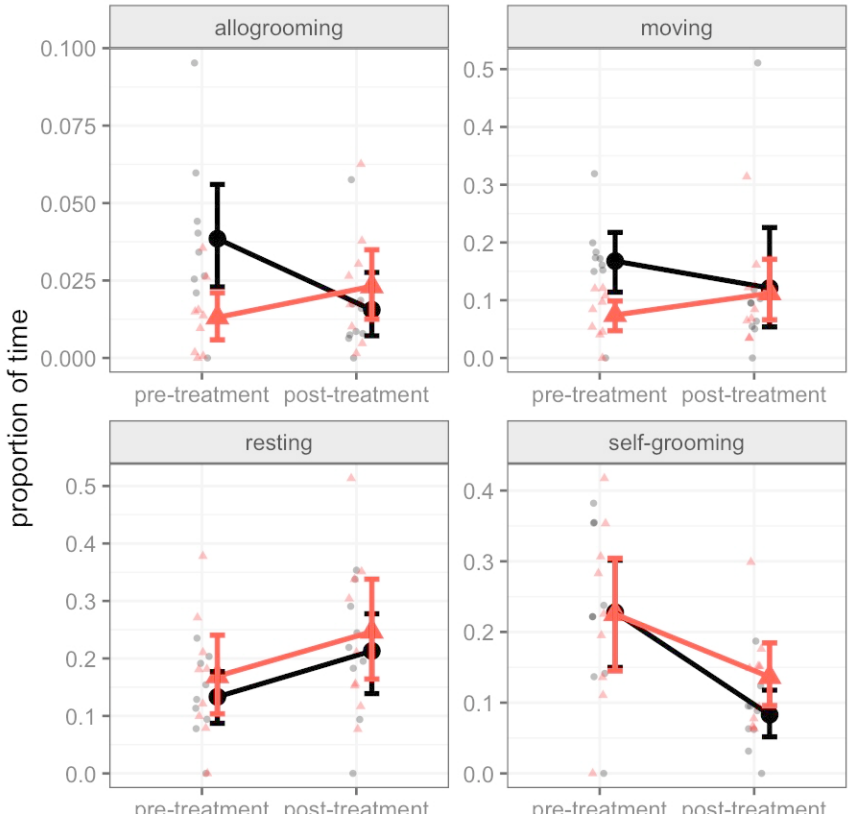

Figure 1. Sickness behavior: bats with *Staphylococcus* infections spent less time allogrooming and moving. Plots show mean proportions ± bootstrapped 95% CIs for behaviors of infected (red triangle) and healthy (black circle) female bats during the outbreak (pre-treatment) and after they had recovered (post-treatment). We did not detect effects of infection on resting or self-grooming either before or after antibiotic treatment. Figure S1 shows this plot with infected bats divided into 'treated' and 'injured' bats.

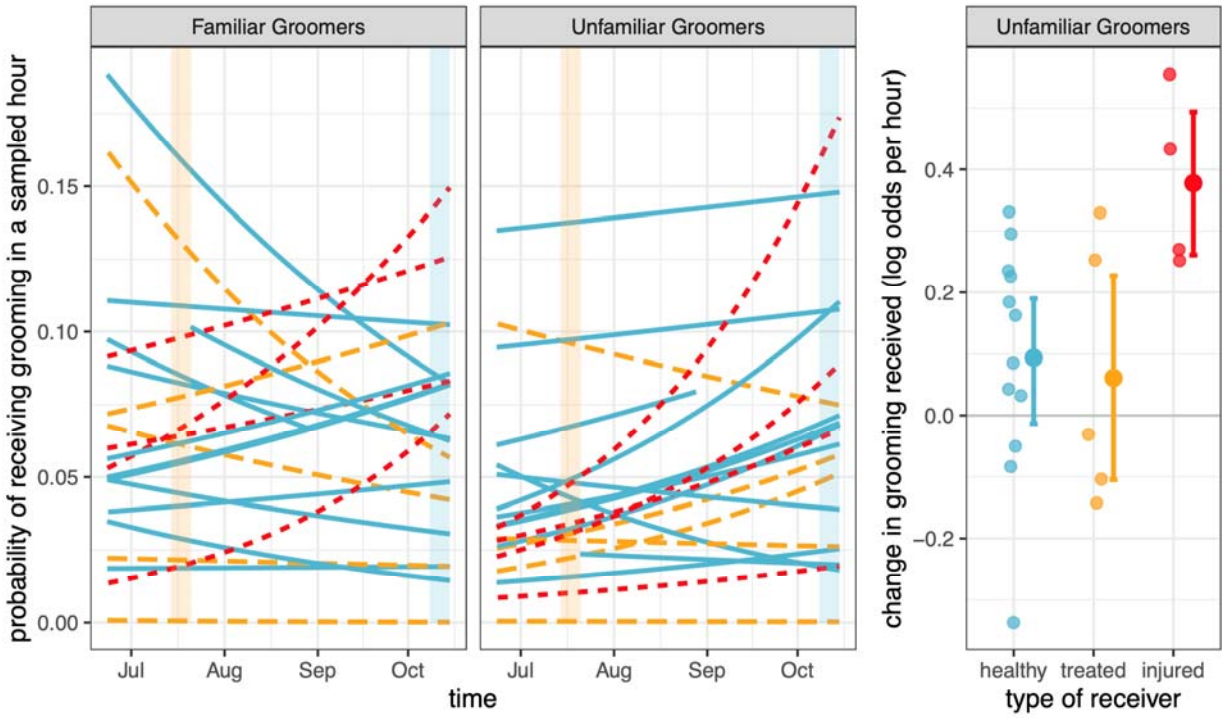

Figure 2. Evidence for effects of infection on social integration. Left panel shows changes in the probability of receiving grooming over time from a familiar groomer to a receiver bat that was healthy (solid cyan), treated (dashed orange), or injured (dotted red). Middle panel shows the same plot but for new (unfamiliar) pairs of bats. In both left and middle panels, 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). Right panel shows the change in log odds (from middle panel) for each type of receiver. Large points with error bars are means and bootstrapped 95% CIs.

Discussion

This study presents opportunistic and observational evidence for reduced social integration in infected bats. Our results should be treated with caution due to the impossibility of estimating effect sizes precisely with small sample sizes (9 infected bats with varying levels of infection severity). However, while several studies have quantified social interactions when animals are infected with, or exposed to pathogens (14,16–18,33–38), to our knowledge, no studies have focused on the impact of infections on social bond formation. Our findings and effect size estimates could therefore be valuable for informing future studies that test this hypothesis in more detail.

We found that, relative to healthy bats, the 9 bats initially infected with *Staphylococcus* (and the 4 injured bats in particular) exhibited sickness behavior; they spent less time moving and allogrooming. As expected from an infectious pathogen, infections were biased based on the bat's origin. The top five most severely infected bats and all 4 injured bats were from the same population.

Several results are consistent with the hypothesis that acute infections impacted the development of social relationships. Infected bats gave and received less allogrooming with new

partners. Infection did not predict reduced allogrooming as much in 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 (Figure 2).

A possible alternative explanation is the reverse causal relationship: bats with worse social integration had weakened immune systems and therefore suffered worse infections because of their social traits. However, this hypothesis does not explain why severe infections only occurred in bats from the same population or why the gap in social integration disappeared over time after antibiotic treatment. If the infected bats were already less social or less healthy for other reasons besides the infection, then we would expect their social integration to be worse overall and not just during the outbreak.

The sickness behavior we observed was similar to the responses of vampire bats to simulated infections with injections of lipopolysaccharide, LPS (12,20). We quantified sickness behaviors in response to a naturally-infecting pathogen, which is less often done for vertebrates (but see 33,35,39,40) compared to studies on sickness behavior using an immune challenge (e.g., (8,10–12,15,20,24,31,41–43). The use of immune challenges, like LPS, 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 *Staphylococcus*-infected bats did not**,** possibly because *Staphylococcus* causes skin lesions. Similarly, little brown bats (*Myotis lucifugus*) infected with *Pseudogymnoascus destructans* (white-nose syndrome), a fungal skin disease, showed increased self-grooming (39).

Our findings raise several questions about how short-term infections might impact relationship formation and long-term social integration. When might vampire bats or other animals suppress their infection-induced behavioral symptoms to continue social interactions and integration (20,41,42,44–46)? 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 (42,47). Immune challenges like LPS could also be used to test at what stage of relationship formation sickness behaviors have the strongest effects, and for how long they would have to last for lingering effects on social integration. Immune challenges can be used to control the duration and precise onset times of symptomatic periods.

In conclusion, social integration benefits health, immune function, and susceptibility to disease (1–4). Conversely, however, infections might also reduce social integration in several ways. Sickness behavior can cause individuals to be less socially active. Cues of infection have clear impacts on mate choice (reviewed in 23) and there may be similar effects on choice of other kinds of social partners (e.g., same-sex social bonds). If there are critical periods of social integration, then infections during this time might have long-term social consequences. Consistent with this possibility, we presented opportunistic and observational evidence for reduced social integration in vampire bats after an outbreak of a naturally infecting pathogen. While our sample sizes are small and do not allow us to estimate precise effect sizes, 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.

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