Vampire bats target their social grooming to hard-to-reach body parts

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1. Summary

Many group-living mammals and birds groom the fur (or preen the feathers) of their close associates, and this social grooming (or social preening) seems to build and maintain affiliative relationships. Female common vampire bats (*Desmodus rotundus*) lick each other in ways that appear to be responsive to cues of need, which suggests that this social grooming could be a low-cost form of helping in addition to being a social signal. If social grooming is a form of helping, then vampire bats should preferentially groom others in locations that are difficult to self-groom. We show that social grooming (n = 1515 events) did indeed occur most often on parts of the recipient's body where self-grooming (n = 1586 events) was least likely, often in locations where the recipient could not lick itself, like the back of the head. The finding that vampire bats preferentially groom each other in hard-to-reach locations provides further support for the hypothesis that social grooming is a low-cost form of help in vampire bats.

2. Introduction

In many group-living birds and mammals, and especially primates, individuals groom the fur (or preen the feathers) of group members or preferred close associates [1–4]. This 'allogrooming' or social grooming is likely to have evolutionary origins in the grooming of self and offspring, and like other forms of "social touch" [5], it can signal affiliative intentions. In addition to being a social signal, social grooming can also provide cleaning services that supplement self-grooming [6–10], which can include cleaning wounds [11], removing harmful ectoparasites [9,12–16], and smoothing out fur and feathers for shedding water and holding heat [8,17]. In these cases, social grooming can be considered not only a signal but a cooperative investment, especially if groomers spend substantial time or energy grooming others. Thus, social grooming appears to serve a "dual function" [9], acting as both a low-cost helping behavior and a signal of a groomer's willingness to cooperate or help in other ways, which can lead to longer-term cooperative returns including better access to food or social support [18–23].

Female common vampire bats (*Desmodus rotundus*) spend about 5% of their awake time grooming others by licking—a greater frequency than observed in any other bat species [24]. Previously unfamiliar and unrelated vampire bats use reciprocal social grooming to 'test the waters' while forming new reciprocal food-sharing relationships [19], in which partners regurgitate ingested food (blood) to feed each other when one has failed to feed [25,26]. Unlike food sharing in times of need, social grooming can be reciprocated immediately, making it a low-cost and low-risk way to immediately assess a cooperative relationship [19].

Although it is clear that social grooming has a social function in vampire bats, whether or not social grooming also serves as a form of helping (i.e. by cleaning the body) has not been established yet. If social grooming is truly a low-cost form of helping, then vampire bats should preferentially groom each other in locations that are difficult to self-groom. This pattern of grooming has been reported in a number of species (e.g. chimpanzees [3,10], bonobos [27], five lemur species [3,13,28], 24 other primate species [3,6,13,17,29–38], bird species from over 35 families [2,9,39], impala [12,40], cattle [7], mule deer [41], the European badger [42], and honey bees [43,44]) but has not yet been investigated in vampire bats. Here, we tested whether vampire bats preferentially groom each other in locations that are difficult to self-groom, by recording the locations on the body for both self-grooming and social grooming events and measuring the co-occurrence of self-grooming and social grooming across these locations.

3. Materials and Methods

To compare locations on the body for both self-grooming and social grooming events, we first sampled 1586 previously recorded social grooming events from 61 sampled hours across 17 days of recorded surveillance videos of interactions among common vampire bats (*Desmodus rotundus*) housed in a flight cage at the Smithsonian Tropical Research Institute in Gamboa, Panama (for details of the colony, see Razik et al. [45]). Sampled individuals included 26 adult females, 2 adult males, and 1 juvenile male. To avoid ambiguity, we only recorded social grooming events that were at least 5 seconds in duration. For each social grooming event, we labeled the location on the body that was being groomed for the most time during the event, with one of 11 categories: face, head, upper back, lower back, chest, belly, foot, arm, thumb, inside wing, and outside wing (Fig. 1). A 12th category, leg, was initially included but received only one self-grooming event and no social grooming events, and so was excluded from analysis.

For each of the social grooming events we sampled, we attempted to find a paired observation of self-grooming by that bat or any other visible bat (the first self-grooming event to be observed later in time) and we labeled the self-groomed body location using the same criteria, leading to 1515 observations of self-grooming. We used this sampling design to ensure social grooming and self-grooming events were sampled at the same times of day. To assess which body locations were less accessible to be self-licked, we also recorded whether 1128 of the self-grooming events were performed by either licking or scratching.

We used a permutation test to determine whether the distributions of self-grooming and social grooming were more convergent or divergent across the body than expected by chance. As our observed "divergence" statistic, we calculated the absolute difference between the proportion of total self-grooming that occurred on a given body part and the proportion of total social grooming that occurred on that same body part, then averaged these differences across all 11 body parts. We then compared the observed value to the distribution of 5000 expected

divergence values generated by repeatedly shuffling the locations across all grooming events (preserving the frequency of locations but removing any association with type of grooming). We then calculated the p-value as the percentage of the expected values that were more extreme than the observed statistic.

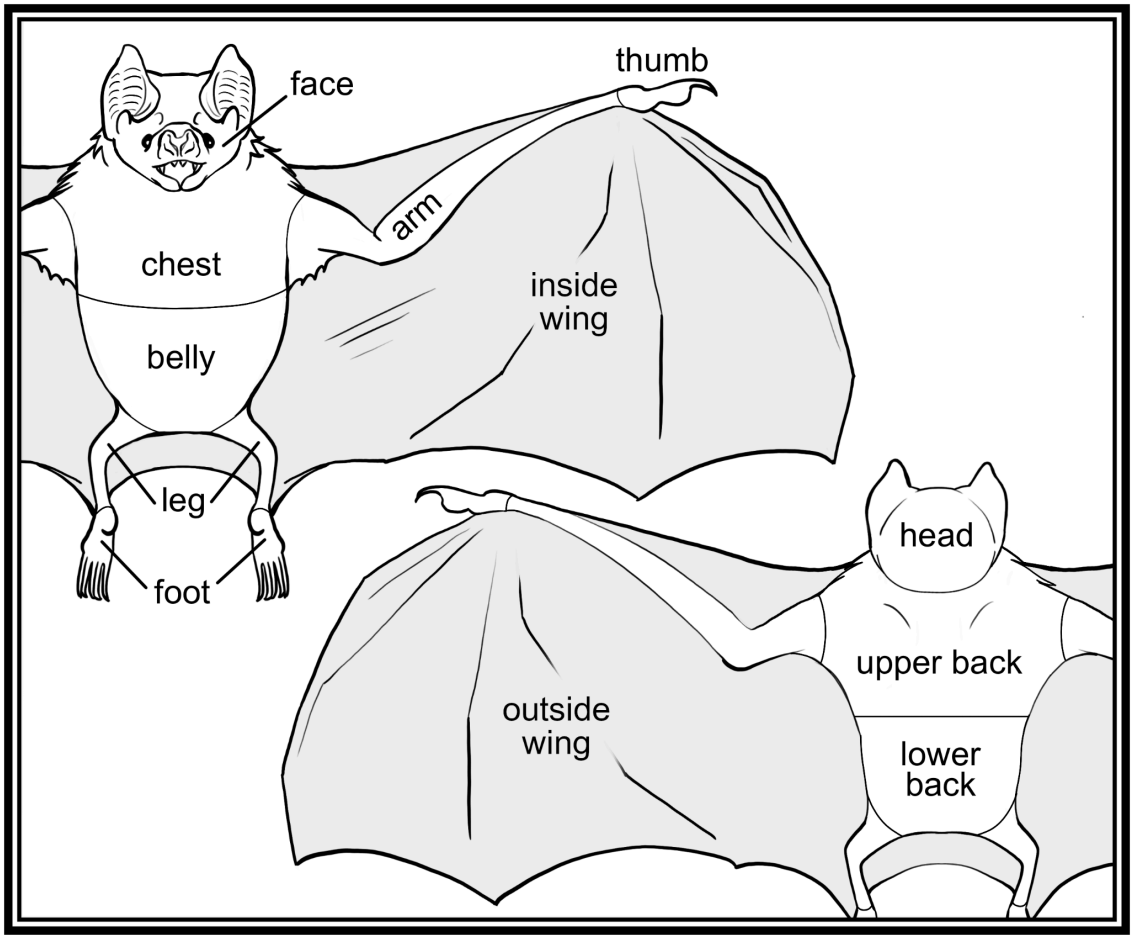

Fig 1. Categorical locations for self-grooming and social grooming events. Illustration by Tobias Nguyen.

4. Results

Social grooming occurred most often on parts of the recipient's body that were the least likely to be self-groomed (Fig. 2), and this difference was much greater than expected from chance (observed divergence = 12.5% , 95% quantiles of expected values = [0.4, 1.2 %], $p < 0.0002$, Fig. 3). For each body part, self-grooming occurred entirely or almost entirely as either licking or scratching but not a mix of both (Fig. 4). The bats used almost exclusively licking to groom their inside wing, foot, thumb, and arm, and they used scratching (with their foot) to clean their belly, lower back, chest, upper back, head, and face. Based on their apparent range of movement, a bat's face, back of head, back, and chest could only be self-groomed by scratching, and these were also the locations most targeted by allogroomers (Fig. 2).

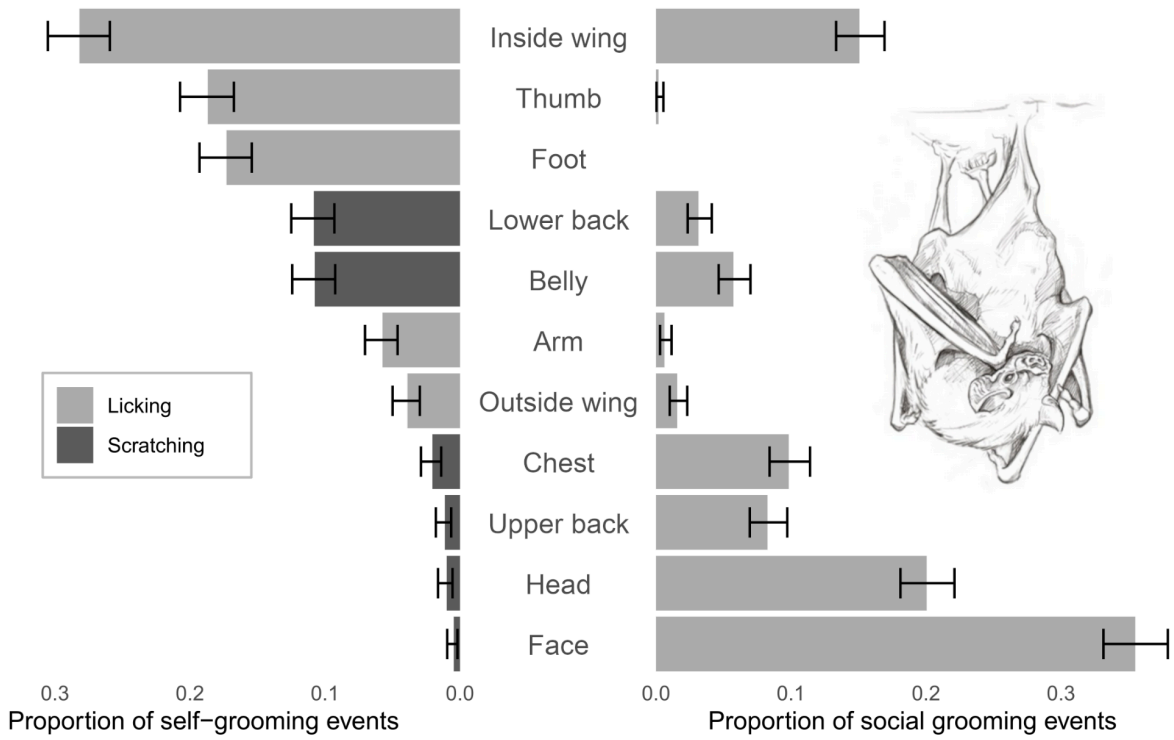

Figure 2. Self-grooming and social grooming are targeted to different body locations. Locations on the body (y-axis) are listed in order of self-grooming frequency. Error bars show 95% confidence intervals from a binomial test. Bat illustration by Javier Lazaro.

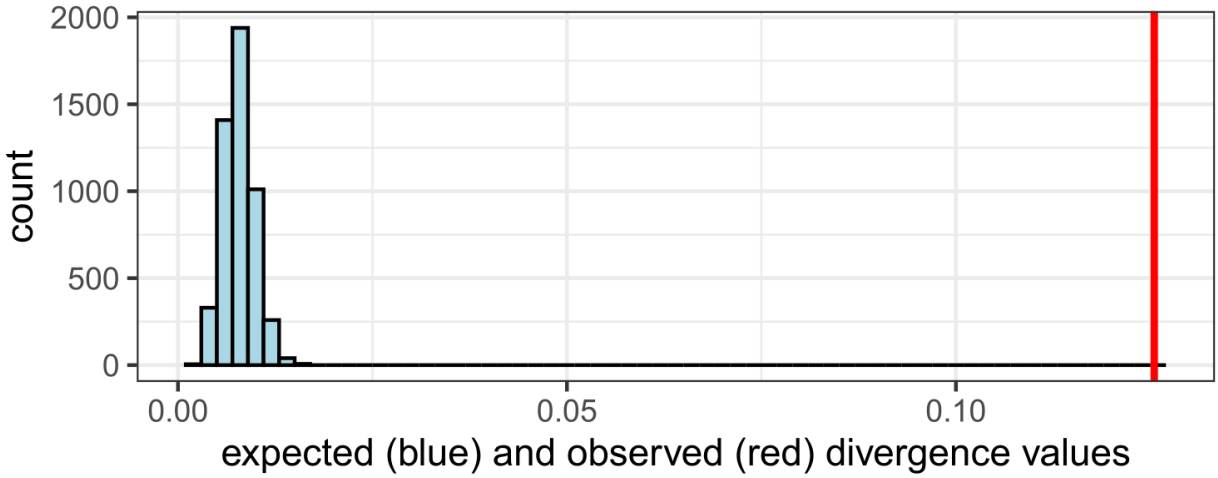

Figure 3. Divergences between self-grooming and social grooming are far greater than expected from randomized grooming. Blue histogram shows 5000 expected divergence values with no association between type of grooming and location on body. Red line is the observed divergence value.

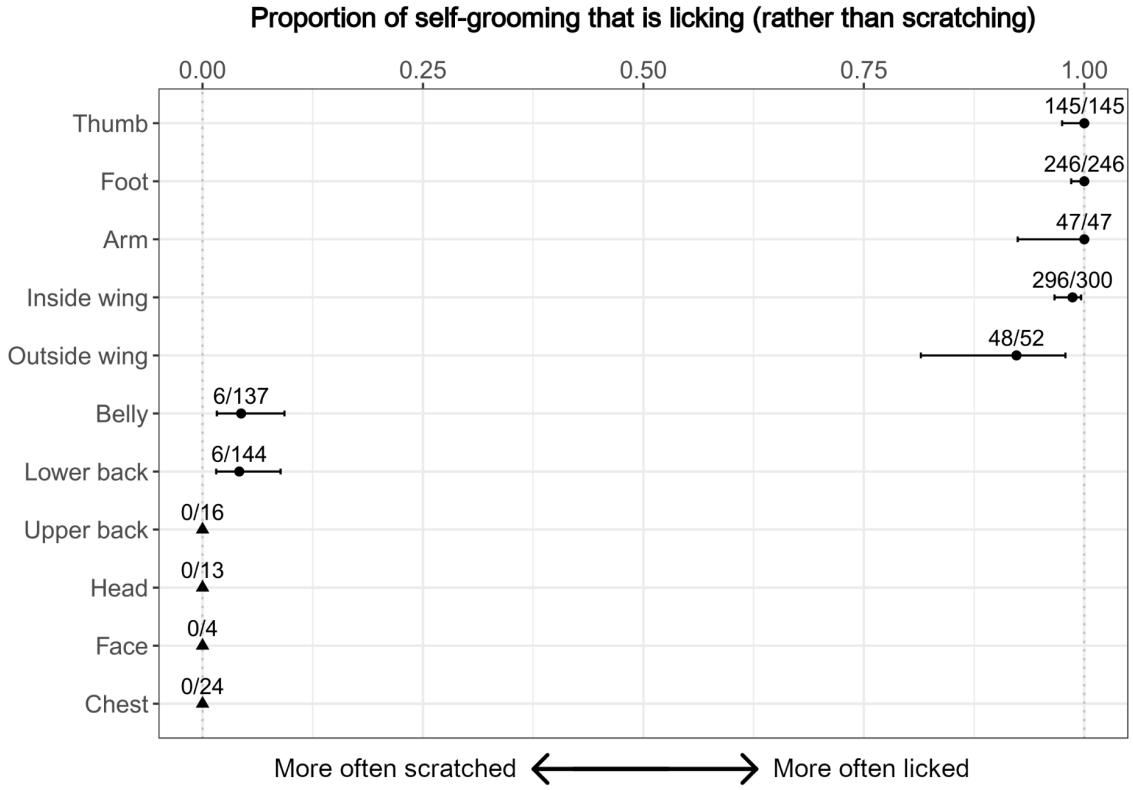

Figure 4. Vampire bats groomed body parts by either licking or scratching but not both. Points are proportions of a sample of self-grooming events that were licking for each body location (0 is 100% scratching and 1 is 100% licking). Numbers show counts of licking out of total cases. Error bars are 95% confidence intervals from a binomial test, except for locations where self-licking is impossible (triangles).

5. Discussion

Female vampire bats preferentially groom (lick) each other on body locations that are the least self-groomed and that appear difficult or impossible for the recipients to lick by themselves, such as the back of the head, face, and upper back. We have previously observed that vampire bats are sensitive to others' cues of need for grooming, such as wet/disturbed fur or self-grooming [46], and that they target foreign objects like metal bands on the forearm. Considering those observations together with the present study, it seems that vampire bats target social grooming towards areas that require cleaning, supporting the hypothesis that social grooming is a form of helping, rather than simply being a signal of motivation to affiliate or cooperate.

Many body parts that are hard to self-groom also happen to be highly accessible to the groomer when hanging face-to-face. Could the distribution of social grooming we observed result from a groomer simply licking whichever area is closest to its mouth? Two lines of evidence contradict this hypothesis and suggest that the grooming site is determined more by

what is less accessible to the recipient (and therefore needs cleaning) than by what is more accessible to the social groomer. First, the amount of social grooming on ventral body parts (chest, belly) was only slightly more than their respective dorsal counterparts (upper and lower back), even though the ventral side is more accessible to the social groomer. Second, there was very little social grooming on the thumbs, which are highly accessible to social groomers. Vampire bats have large, specialized thumbs that they use to jump, land, walk, and run [47–50]. The only obvious reason the thumbs would not be socially groomed is that they receive frequent self-grooming; in other words, the sites of social grooming are influenced by the sites of self-grooming.

The inner wing was frequently groomed during both self- and social grooming, making it the only exception to our finding that social grooming occurs where self-grooming is rare. This exception cannot be explained solely by the large surface area of the inner wing, because the outside wing membrane has the same surface area and received little grooming from either party. It also cannot be fully explained by accessibility to the groomer, because then we would expect much more frequent grooming of the chest and belly as well. Instead, the inner wing may be socially significant or require extra grooming for reasons we do not yet understand.

Our findings were similar to those reported in several other species, particularly those which groom with their mouths. Those species tended to target social grooming to locations close to the head which are difficult to self-lick (e.g. lemurs [3,13,28], impala [12,40], cattle [7], mule deer [41], and many birds [2,9,39]). Some oral groomers use the hind legs to scratch these areas, just as we observed in vampire bats. Interestingly, scratching seems to occur less frequently in species or individuals that allogroom versus those that do not. A study of four antelope species found that all species scratched with their hind legs, but this behavior was less frequent in the impala [12], a species which engages in regular allogrooming of the head and neck [40,51]. In rockhopper and macaroni penguins, social grooming mainly occurred between mated pairs; accordingly, unpaired individuals hosted more ticks and more frequently scratched their heads with their feet [52]. These examples suggest that allogrooming serves some cleaning function and that oral grooming is in some way preferable to scratching [12]. This idea is consistent with our interpretation that vampire bats scratch certain body parts only because they cannot be licked, not because scratching is better suited to that body part.

Multiple factors besides accessibility influence where animals receive grooming. Some sites require more cleaning, due to longer hair [6,31], being more frequently soiled [3], wounds [11], or ectoparasites [15]. The recipient can exert control over the site of social grooming by moving to expose different parts of its body [6,29,43,51,53–56]. This behavior can highlight hard-to-reach areas, but sometimes serves other purposes. In vervet monkeys, the recipient presents new body parts possibly to prolong the grooming session [57]. In three species of macaque, the groomer apparently switches to grooming the back, tail, or upper leg to communicate the end of the social interaction [6,58]. Anecdotally, in vampire bats, the recipient seems to move to facilitate social grooming—for example, the inside and outside wing can only be groomed if the recipient opens its wing.

Groomers and recipients may also position themselves defensively, rather than in a way that maximizes cleaning. In primates, grooming face-to-back rather than face-to-face is thought to prevent eye contact, protect the groomer from biting, and protect the recipient's vulnerable ventral side [27,30,34,53,59,60]. For this reason, the back and tail may receive more frequent

grooming when the risk of aggression is increased, such as when there is a difference in rank (e.g. rhesus macaques [53], long-tailed macaques [60], mandrills [59], bonobos [27], and the langur *Semnopithecus entellus* [30]), when the groomer is male [27,60], when the recipient is carrying an infant [53], or when agonistic behavior preceded the grooming bout [34,53]. Bonobos more frequently groomed face-to-face than chimpanzees, which are thought to be more aggressive [61], and the same pattern was found with bonnet macaques versus the more aggressive pigtail macaques [6]. Given that our study focused on female vampire bats, and male vampire bats are more likely to compete aggressively, future work should consider comparing grooming locations for females vs male vampire bats.

Finally, body parts that serve special functions may receive disproportionate social grooming. In primates, it has been suggested that the face receives frequent social grooming in part because of its role in communication and individual recognition [38,60,62]. In our study, the most socially groomed body part was the face. It is possible that some small amount of grooming on the face was due to mouth licking, which serves as a means to share food, a signal of intent to share or receive food, and possibly for gathering information or sharing microbiota [63]. However, the bats in our study were not fasted and mouth licking among non-fasted bats is very infrequent [63].

In conclusion, we found evidence that vampire bats direct social grooming (licking) to parts of the recipient's body where self-grooming was least likely, and where a bat cannot lick itself. This finding corroborates several other lines of evidence [19,46] that vampire bats use social grooming not only as a social signal, but also as a form of relatively low-cost helping.

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Ethical Statement

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).

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Data Accessibility

Data and R scripts are attached as supplementary material.

Competing Interests

We have no competing interests.

Authors' Contributions

CC: data curation, formal analysis, writing—review and editing; TN: formal analysis, writing—original draft, writing—review and editing; MM: data curation, writing—review and editing; GC: conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, writing—original draft, and writing—review and editing.

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

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