American Journal of Physical Anthropology

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Journal:	*American Journal of Physical Anthropology*
Manuscript ID	AJPA-2018-00005.R3
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	10-Sep-2018
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Key Words:	behavioral flexibility, vigilance, grooming reciprocity, survival analysis, habitat preservation
Subfield: Please select 2 subfields. Select the main subject first.:	Primate biology [behavior, ecology, physiology, anatomy], Non-primate animal models

Title

Rates of human-macaque interactions affect grooming behavior among urban-dwelling rhesus macaques (*Macaca mulatta*)

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Number of text pages: 39; **Number of Figures**: 6; **Number of Tables**: 1

Grant sponsorship: National Science Foundation (#1518555)

Abstract

Objectives

The impact of anthropogenic environmental changes may impose strong pressures on the behavioral flexibility of free-ranging animals. Here, we examine whether rates of interactions with humans had both a *direct* and *indirect* influence on the duration and distribution of social grooming in commensal rhesus macaques (*Macaca mulatta*).

Materials and Methods

Data were collected in two locations in the city of Shimla in Northern India: an urban setting and a temple area. We divided these two locations in a series of similar-sized physical blocks (N = 48) with varying rates of human-macaque interactions. We conducted focal observations on three free-ranging rhesus macaque groups, one in the urban area and two in the temple area.

Results

Our analysis shows that macaques engaged in shorter grooming bouts and were more vigilant while grooming in focal sessions during which they interacted with people more frequently, suggesting that humans directly affected grooming effort and vigilance behavior. Furthermore, we found that in blocks characterized by higher rates of human-macaque interactions grooming bouts were shorter, more frequently interrupted by vigilance behavior, and were less frequently reciprocated.

Discussion

Our work shows that the rates of human-macaque interaction had both a direct and indirect impact on grooming behavior and that macaques flexibly modified their grooming interactions in

relation to the rates of human-macaque interaction to which they were exposed. Because grooming has important social and hygienic functions in non-human primates, our work suggests that human presence can have important implications for animal health, social relationships and, ultimately, fitness. Our results point to the need of areas away from people even for highly adaptable species where they can engage in social interactions without human disruption.

Behavioral flexibility refers to individuals' ability to generate adaptive responses to rapid environmental changes (West-Eberhard, 1989; Lindshield, 2017). As human populations expand and transform wildlife habitats at a rapid rate, species that exhibit high degrees of behavioral flexibility are more likely to thrive in these emerging anthropogenic environments (Sih et al., 2011; Hockings et al., 2015). Assessing the links between anthropogenic factors and the extent to which animals show adaptive behavioral responses to such factors provides information about species' long-term survival and can better inform management practices and conservation efforts.

Examples of behavioral flexibility include urban-dwelling animals' ability to shift their activity patterns from diurnal to nocturnal (McClennen et al., 2001; Tigas et al., 2002; Riley et al., 2003; Gaynor et al., 2018) or change their movement patterns to avoid roads or areas with high human population density (Grover and Thompson, 1986; Brody and Pelton, 1989; Bryson-Morrison et al., 2017). Animals who live in urban environments may also alter their feeding habits, as urban areas can provide rich anthropogenic food resources, which can ultimately affect reproductive rates and population density (Fleischer Jr et al., 2003; Prange et al., 2004; Robbins, 2012). Further, birds and marine mammals who rely heavily on acoustic communication tend to modify their vocal frequencies to avoid their signals being masked by human noise (Rabin et al., 2003; Slabbekoorn and Peet, 2003).

Critically, a strong relationship between behavioral flexibility and relative brain size has been found in both mammals (Sol et al., 2008) and birds (Sol et al., 2005). This suggests that the ability to flexibly adapt to environmental changes requires high cognitive skills that are subserved by a cortex that typically scales up in volume as brains become larger. For this reason, studies on behavioral flexibility have particularly focused on non-human primates (hereafter NHPs). This is because NHPs have large brains both by absolute and relative measurements that are characterized by well-developed cortices, particularly in frontal areas that are critical for regulating complex cognitive behaviors (Finlay and Darlington, 1995; Reader and Laland, 2002; Dunbar and Shultz, 2007; Wise, 2008). As a result, an increasing number of studies have examined how NHPs flexibly respond to human-induced habitat alterations (reviewed in Nowak and Lee, 2013; Humle and Hill, 2016; McLennan et al., 2017; Sinha and Vijayakrishnan, 2017).

Studies on how NHPs flexibly adapt to an anthropogenic environment and human-NHP interactions, specifically, have increased in number especially over the last two decades, giving rise to the field of ethnoprimatology (Fuentes and Wolfe, 2002; Fuentes, 2006; Fuentes and Hockings, 2010; Radhakrishna et al., 2012; Dore et al., 2017; McLennan et al., 2017). Published studies, however, have largely focused on the exploitation of new feeding sources and modification of social organization. For instance, compared to individuals who live in areas of low anthropogenic impact, bonnet macaques (*Macaca radiata*) who inhabited a temple area and had access to anthropogenic food sources were more efficient at extracting food from experimental bottles (Mangalam and Singh, 2013). Luncz and colleagues (2017) recently showed

93 that a population of long-tailed macaques (*Macaca fascicularis*) living in Southern Thailand learned how to use stones to open oil palm nuts that had been introduced by people in the early 2000s. Regarding changes to social organization, Sinha (2005) reports the presence of species-atypical uni-male social groups of free-ranging bonnet macaques living in Bandipur National Park in Southern India. One reason suggested for this variation is that changes in anthropogenic food abundance and distribution lead females to form smaller groups that are easily monopolizable by a single male. Chimpanzees (*Pan troglodytes*) tend to modify their social organization by forming larger and more dense parties when foraging on crops to counter the high risks of retaliation from villagers (Wilson et al., 2007; Hockings et al., 2012). Despite the growing number of studies that have explored behavioral flexibility among NHPs (reviewed in Humle and Hill, 2016; McLennan et al., 2017), little is known about the influence of human presence on NHP affiliative behaviors, like social grooming. Understanding whether and how NHPs flexibly modify their social interactions to adapt to human presence can help us to better understand how interactions with humans may negatively affect NHP social relationships. This negative impact may have downstream consequences for group stability and individuals' health (Silk, 2007).

Social grooming is defined as a visual examination, search and manipulation of the skin or hair of a conspecific with either hands (in the case of apes and monkeys) or a toothcomb (in the case of strepsirrhines). It is the most common affiliative behavior in primates, occupying up to 20% of individual's daily time budget (Henzi and Barrett, 1999). Grooming clearly benefits the recipient, as it removes harmful ectoparasites (Tanaka and Takefushi, 1993; Zamma, 2002; Akinyi et al., 2013) and decreases stress levels (Aureli et al., 1999; Shutt et al., 2007). Furthermore, social grooming promotes the release of pleasure-inducing β-endorphins (Keverne et al., 1989) and plays a key role in establishing and maintaining social relationships, which can ultimately increase individuals' fitness (Silk et al., 2003; Silk et al., 2009; Silk et al., 2010).

While grooming provides significant advantages to the recipient, it can also impose costs to the groomer. Individuals who spend more time grooming conspecifics, for instance, spend less time resting (Dunbar, 1988) or engaging in vigilance behaviors directed towards detecting predators (Cords, 1995; Mooring and Hart, 1995). In other words, individuals who are focused on grooming a partner have fewer opportunities to engage in other activities. Moreover, social grooming entails proximity to a potentially dangerous group member (Kaburu et al., 2013; Schino and Alessandrini, 2015) and can increase the risk of exposure to parasite infection (MacIntosh et al., 2012).

Given such cost-benefit trade-offs associated with grooming, a breadth of studies has examined the socio-ecological factors driving an individual's economic decisions when investing in grooming interactions. Such trade-offs result in variation in grooming effort that is related to group stability (McCowan et al., 2008; Wittig et al., 2008; Kaburu and Newton-Fisher, 2013), group size (Dunbar, 1991; Lehmann et al., 2007), dominance rank (Schino, 2001), and the presence of other group members in proximity to the grooming dyad (Kaburu and Newton-Fisher, 2016; Newton-Fisher and Kaburu, 2017). However, there is still only limited information on the influence of human disturbance on social grooming, and the studies conducted thus far paint an unclear picture of the relationship. In free-ranging pygmy marmosets (*Cebuella pygmaea*), for example, tourist pressure was found to disrupt social play but not social grooming (De la Torre et al., 2000). Studies on commensal macaque and baboon populations have shown that provisioned and urban groups tend to spend less time foraging and more time resting and grooming compared to groups living in more rural areas (Forthman-Quick and Demment, 1988;

Malik and Southwick, 1988; Marriott, 1988; Riley, 2007; Fuentes et al., 2011; El Alami et al., 2012; Jaman and Huffman, 2013; Lute et al., 2014; Koirala et al., 2017). In contrast, among male Barbary macaques (*Macaca sylvanus*), monkeys were shown to spend less time grooming when tourists were in closer proximity (Majolo et al., 2013), and a population of Hamadryas baboons (*Papio hamadryas*) living in Western Saudi Arabia was found to engage in more grooming activity outside than inside a provisioning area (Kamal et al., 1997). Finally, among Tibetan macaques (*Macaca thibetana*), Balasubramaniam et al. (2011) speculate that one reason for the detection of consistently strong reciprocity in grooming among females might be the increased tourist impact, which can lead to elevating stress levels and a consequent increasing demand for grooming.

Studies investigating behavioral flexibility to date have only investigated a single social group or context, which may be one reason why the results from previous studies are inconsistent. Examining multiple social groups across different contexts characterized by varying levels of human impact, however, is critical to establish a strong mechanistic understanding of how humans affect social grooming in NHPs. Furthermore, most previous studies have largely focused on the indirect effect of human pressures on social grooming, by examining differences in primate grooming activity in areas with categorically high vs low human impact (e.g., Kamal et al., 1997; Jaman and Huffman, 2013). In contrast, whether actual (i.e., direct) interactions with people influence grooming interactions has received little attention. Addressing this is important because humans may engage in a diverse array of interactions with commensal primates. The present study explores whether macaques flexibly modify their grooming behavior in relation to both direct forms of interactions with people as well as the possibility of interacting with people (i.e., grooming in a space characterized by frequent human-macaque interaction). In other words, we examine whether rates of human-macaque interaction have both *direct* and *indirect* impact on social grooming in three groups of rhesus macaques (*Macaca mulatta*) living in the city of Shimla, the capital city of the Northern Indian state Himachal Pradesh. Rhesus macaques are an ideal species to study behavioral flexibility because they are the most socio-ecologically and behaviorally flexible and the most geographically widespread species among all NHPs (Fooden, 2000; Brandon-Jones et al., 2004; Kumar et al., 2011; Southwick and Siddiqi, 2011). They inhabit a variety of anthropogenic contexts ranging from agricultural areas, to cities, temples, roads and canal banks (Pirta et al., 1997; Southwick and Siddiqi, 2011). This flexibility and their vast ranges have led some to label rhesus macaques a "weed species" much like humans (Richard et al., 1989).

In India, the relationship between people and rhesus macaques can take both negative and positive forms. On the one hand, people are aggressive towards macaques, because they consume and damage crops in agricultural areas, damage buildings, snatch food and objects from people and occasionally physically harm them (Pirta et al., 1997; Chauhan and Pirta, 2010a; Singh and Thakur, 2012). On the other hand, Hindu people have a positive relationship with macaques as they worship and feed them (Pirta et al., 1997; Singh and Thakur, 2012). Despite efforts from the government to control the macaque population through sterilization, translocation, or culling (Saraswat et al., 2015), rhesus macaque populations are exponentially increasing (Singh and Thakur, 2012), further aggravating the negative interactions between humans and macaques.

We tested a *direct* effect of human-macaque interactions on the social grooming behavior of commensally living groups of rhesus macaques. More specifically, we predicted that more vigilance behavior during grooming bouts would reduce the duration of grooming bouts, and would make the bout less frequently reciprocated if macaques engaged in more interactions with

185 people. Therefore, we examined whether during focal observations in which macaques interacted
186 with people more frequently, they engaged in shorter, less frequently reciprocated grooming
187 bouts that contained more instances of vigilance behavior. We predicted less frequently
188 reciprocated grooming bouts in observations in which the focal animal interacted with people
189 more frequently because if individuals need to reduce the duration of their grooming interactions
190 due to increased opportunities to interact with people, they should have fewer opportunities to
191 reciprocate grooming immediately. We did not expect macaques to compensate for such
192 interruptions to grooming bouts (and lost opportunities to reciprocate) by engaging in mutual
193 grooming because monkeys do not commonly groom each other simultaneously. Rather,
194 grooming reciprocity in monkeys is commonly achieved by alternating grooming bouts, whereby
195 individuals switch between the roles of groomer and groomee (Barrett et al., 1999; Manson et al.,
196 2004). This reciprocity is thought to be a strategy that individuals use to balance the amount (and
197 thus the benefits) of grooming given with the amount received (Schino and Aureli, 2008).

198 Furthermore, we hypothesized that rates of human-macaque interactions might have an
199 *indirect* impact on macaque grooming interactions, if monkeys modify their grooming behavior
200 in relation to the location where the grooming occurs. More specifically, by examining a number
201 of areas characterized by varying levels of human-macaque interactions, we predicted that in
202 areas with higher frequencies of human-macaque interaction, grooming bouts should be shorter,
203 with more vigilance, and less frequently reciprocated compared to areas with lower rates of
204 human-macaque interactions. In other words, we tested whether the *possibility* of interacting
205 with people can influence grooming behavior and pattern in our commensal rhesus macaque
206 groups. Similar to the way in which people who are about to cross a street look in both directions
207 for the possible presence of cars (regardless of the actual presence of cars), macaques who are

grooming in a location characterized by frequent human-macaque interactions may frequently stop or look up from their grooming bouts, regardless of whether they actual interact with humans.

Materials and Methods

Study site and subjects

Observational protocols were approved by the Institutional Animal Care and Use Committee of the University of California, Davis. These protocols were designed in consultation with the Himachal Pradesh Forest Department and complied with the legal requirements of India.

We collected data over a one-year period between July 2016 and July 2017 in the city of Shimla (31° 05’ N- 077° 10’ E) at two sites located at a distance of approximately 1.5 km from each other: Mall Road and Jakhoo (Figure 1). Mall Road is the main road of Shimla characterized by both commercial and residential buildings, while Jakhoo is located on the highest peak of Shimla at 2,455 m above sea level and comprises a Hindu temple and a surrounding forested area. The temple area includes the temple itself and the paved temple grounds (i.e., a small garden encircled by a sidewalk; cement stairs that lead up to a cement apron that surrounds a 30-meter-tall statue of Hanuman) where visitors rest and vendors sell food and goods (Figure 1). The temple area is commonly used by 4-5 different macaque groups, and the macaques that use the temple area use also the surrounding forested area. We collected data on adult males and females from three groups of rhesus macaques, one in Mall Road (hereafter Mall group, *MG*) and two in Jakhoo (Ripped-ear’s group, *RG*, and Hook’s group, *HG*). MG’s home range revolves around the Bharat Sanchar Nigam Limited (BNSL) office (an Indian telecommunication company), while RG’s and HG’s home ranges are near Jakhoo temple.

[Figure 1 here]

Macaques in Mall Road and at Jakhoo temple engage in substantially different types of interactions with humans. Although human density is high at both Mall Road and Jakhoo temple, people in Mall Road tend to avoid macaques, show aggressive behavior towards them, or ignore them. In contrast, rhesus groups at Jakhoo temple experience a higher diversity of interactions with people, including aggressive interactions, humans providing food to the macaques, and macaques snatching items from people (Chauhan and Pirta, 2010a; Chauhan and Pirta, 2010b).

At the beginning of the study, there were a total of 79 focal animals: 21 from MG (5 males and 16 females), 23 from HG (6 males and 17 females) and 35 from RG (9 males and 26 females). Group composition changed slightly during the study period either due to new male immigrants, animals disappearing, or juveniles reaching sexual maturity. The number of focal animals per month ranged between 78 and 84 (mean ± SD = 81.8 ± 2 per month).

Behavioral data collection

In order to measure rates of human-macaque interaction, we divided the areas in Mall Road and Jakhoo (both temple and forest) where humans and macaques could potentially interact into a series of spatial blocks within which human-macaque interactions were most frequent. During the initial training phase at the field site between May and July 2016, we estimated macaque home ranges by documenting areas that the macaques were using. We used those data to establish the initial set of spatial blocks. However, as data collection continued throughout the year, the macaques were recorded using new areas, and we added or dropped blocks accordingly. Although spatial blocks covered much of the groups' home ranges, not all areas of a group's home range were sampled using this block-sampling method. We identified a total of 18 blocks at Mall Road, and 30 blocks at Jakhoo (15 at the temple and 15 in the forest) of similar size ($259m^2 \pm 150m^2$). We used such a "block-sampling" approach in order to systematically collect data on human-macaque interaction and avoid sampling bias (e.g., over-sampling densely populated areas). Observers followed a pre-determined, randomized list of blocks to sample. The observer would record all human-macaque interactions observed in the selected block for 10 minutes (even those involving non-focal animals including macaques from other groups or juveniles), following a specific ethogram (see Supplementary Material). Demographic scans were conducted immediately before and after the 10-min session, counting the number of people and macaques present in the block.

We define a human-macaque interaction as a series of events linked to each other temporally and through common participants, such as multiple events involving either the same dyad (e.g., a macaque approaches a person who avoids the macaque; then the person threatens the macaque, who avoids the person) or multiple inter-connected dyads (e.g., a macaque approaches a person who avoids, and a second person threatens the macaque in support of the first person). We conducted a total of 1245 human-macaque sampling sessions in the Mall and 1868 at Jakhoo (1385 at the temple and 483 in the surrounding forest).

Data on grooming interactions were collected by conducting focal animal sampling (Altmann, 1974) five days per week between 9:00 am and 5:00 pm by four observers (reliability, Cohen's $k > 0.85$). Data were entered into Samsung Galaxy Tablets using customized data forms created in HanDBase® (DDH software). Focal samples were 10 minutes in duration, and each day focal animals were selected using a pre-determined random list. We aimed to collect focal observations twice a week per animal, once in the morning and once in the afternoon. If the focal animal went out of sight for more than 3 minutes during an observation, the observation was considered aborted. Data from that aborted observation were maintained in the database and used for the data analysis but observers attempted to re-do a complete focal sample on that animal at the next available opportunity. A total of 1107.8h of observations were collected: 322.0h from MG, 487.7h from RG, and 298.1 from HG. We recorded a total of 6916 focal samples: 2086 from MG, 3007 from RG, and 1823 from HG.

During focal observations, we recorded grooming behavior and vigilance. We defined vigilance as instances in which an individual raised his or her head to look up in the middle of a grooming bout. During grooming interactions, observers recorded information on the identity of groomer and groomee, as well as the time when the grooming started and ended and the number of instances of vigilance. A grooming bout was considered terminated when the groomer stopped grooming by taking both his or her hands off the groomee for more than 10s. During grooming interactions, we also recorded the spatial block (see above) in which the grooming occurred. Finally, every two minutes we recorded the id of the monkeys in proximity of the focal animal.

Since grooming bout length and reciprocity can be affected by dominance steepness (a measure of the distance between ranks: De Vries et al., 2006) and/or social stability (Stevens et al., 2005; McCowan et al., 2008; Balasubramaniam et al., 2011; Kaburu and Newton-Fisher, 2013; Kaburu and Newton-Fisher, 2015), we recorded dominance interactions both during the focal and *ad libitum* sampling (Altmann, 1974). Dominance interactions included both aggressive behaviors (e.g., chase, bite, slap), displacements and submissive signals (e.g., silent bared teeth; de Waal and Luttrell, 1985).

Data analysis

Dominance steepness was calculated from a winner-loser matrix that contained decided dyadic dominance interactions using the R function *steeptest* within the package 'steepness' (Leiva and De Vries, 2014). The steepness index ranges between 0 (shallow) and 1 (steep), with shallow steepness indicating dominance ranks that are close to each other. We also used the David's scores (David, 1963) generated by the *steeptest* function to obtain macaques' dominance ranks. We employed the *stab.elo* function in the 'EloRating' package to calculate rank stability (Neumann and Kulik, 2014), whose index ranges between 0 (unstable) and 1 (stable). This index reflects to what extent individuals change their rank position over consecutive days.

We fitted Generalized Linear Mixed-Models (GLMM) to examine whether in focal samples where macaques interacted more frequently with people they also engaged in shorter grooming bouts, showed less frequent reciprocation of grooming and more instances of vigilance. We set grooming bout duration, rates of vigilance (count/second), and whether a grooming bout was reciprocated or not as outcome variables in different models with either negative binomial (family model for bout duration and vigilance) or binomial (family model for grooming reciprocity) distribution. In all the models we included as fixed effects rates of human-macaque interactions (number of human-macaque interactions divided by minutes of observation) as well as the presence/absence of monkeys in proximity during the grooming interaction, and groomer's standardized dominance rank. We included whether there were monkeys in proximity to the grooming dyad because the presence of conspecifics can potentially affect grooming duration and reciprocity (Kaburu and Newton-Fisher, 2016; Kaburu and Newton-Fisher, 2017), as well as vigilance behavior (Maestripieri, 1993). We included groomer's dominance rank because rank strongly influences grooming effort both in rhesus macaques (Snyder-Mackler et al., 2016) and other NHP species (Schino, 2001), with the majority of grooming effort directed from subordinates to dominants than in the opposite direction and between close-ranking individuals. In order to control for group size, we standardized dominance rank as follows:

$$\frac{(Rank - 1)}{(N - 1)}$$

Where *N* represents the number of focal animals in the group. Standardized dominance rank values range between 0 (top-ranking animal) and 1 (bottom-ranking animal). Finally, we included the identities of focal animal as random effect in all models to control for dependency in the data involving the same individuals. For the models in which the number of vigilance behaviors was the outcome, we set grooming bout duration as an exposure variable, since there is more opportunity to be vigilant during longer grooming bouts. Negative binomial and binomial GLMMs were run in R using, respectively, the *glmer.nb* or *glmer* functions in the package *lme4* (Bates et al., 2014).

A visual representation of the rates of human-macaque interactions (number of human-macaque interactions/min of observation) per block shows a gradient of variation in the frequencies of interactions between humans and macaques across the blocks (Figure 2). Therefore, to test whether grooming bouts performed in blocks with higher rates of human-macaque interactions were shorter, less frequently reciprocated, and contained more instances of vigilance compared to grooming performed in blocks with lower rates of human-macaque interactions, we first took the mean of grooming duration, vigilance and reciprocity across the grooming interactions recorded in each block. We then fitted a GLM using the function *glm* in the R package *MASS*, in which mean grooming duration, vigilance rates and reciprocity frequency (number of reciprocated bouts/total number of grooming bouts) were set as outcome variables in separate models. The models with grooming vigilance and reciprocity were fitted with a Poisson distribution, while the model with grooming duration was fitted with a negative binomial distribution due to overdispersion. Fixed effects included rates of human-macaque interactions, field site ID (Mall vs Jakhoo) and the size of the spatial block, because larger blocks might be more likely to have more people and, hence, more human-macaque interactions. For the models in which grooming vigilance and reciprocity were included as outcome variables, we set mean grooming duration and total number of grooming bouts, respectively, as exposure variables. Since the goal of this analysis was to assess whether features of the blocks (i.e., rates of human-macaque interaction) impact grooming interactions, we excluded blocks in which grooming interactions were never recorded , giving a final sample size of 33 blocks.

[Figure 2 here]

In order to calculate the time frame within which a grooming bout is more likely to be reciprocated, we followed Schino and colleagues' approach (Schino et al., 2009; Schino and Pellegrini, 2009) and employed survival analysis using the R function *bshazard*. This type of analysis is particularly suited for observations with a pre-determined observation time (10 minutes in our case) in which observations are concluded before reciprocation can be observed (i.e., 'censored' observations). We did this to circumvent the arbitrariness of the selection of a time frame for immediate reciprocation. We used survival analysis to estimate the rate at which individuals reciprocated grooming in relation to the time elapsed from the end of the grooming they had received. We then compared this rate (and its 95% confidence interval) with the baseline grooming rate calculated by taking the weighted average grooming frequency per dyad. Weights represented the number of times a dyad was present in the data set. This weighting is necessary to make sure that the baseline is comparable to the data obtained from the survival analysis (Schino et al., 2009; Schino and Pellegrini, 2009).

Results

We recorded a total of 6252 grooming interactions during focal observations: 1731 from MG, 2553 from RG, and 1943 from HG. RG experienced higher rates of interactions with people (3.14 interactions/hr) than both MG (1.96 interactions/hr) and HG (1.74 interactions/hr). Mean grooming duration was shorter with higher vigilance rates in RG (mean grooming duration = 124.4 s; mean vigilance rate = 0.03/second of grooming) than in HG (mean grooming duration =130.2 s; mean vigilance rate = 0.02/second of grooming) and MG (mean grooming duration =146.7 s; mean vigilance rate = 0.02/second of grooming). Finally, RG showed a frequency of grooming reciprocity of 0.17 reciprocated bouts per total number of grooming bouts while both MG and HG displayed a frequency of grooming reciprocity of 0.19.

Dominance steepness and social stability

We collected a total of 6203 dominance interactions: 1577 from MG, 3220 from RG, and 1406 from HG. Groups showed similar values in dominance steepness (MG = 0.5042, RG = 0.4731, HG = 0.471), and all study groups displayed stability indices that were very close to 1 (MG = 0.9945, RG = 0.9922, HG = 0.9911), suggesting highly stable dominance hierarchies.

Time frame of grooming reciprocity

Figure 3 shows the results of the survival analysis. After receiving grooming, rhesus macaques were more likely to reciprocate partner's grooming compared to the baseline, and this probability remained higher for the first 50s after the end of the previous grooming. We therefore used this analysis to consider immediate reciprocation if an individual reciprocated grooming within 50s after he or she had received grooming from the partner.

[Figure 3 here]

Direct impact of human-macaque interactions on macaque grooming behavior

Our analysis of the focal observations showed that rates of human-macaque interactions recorded during focal observations significantly influenced focal animals' grooming duration and vigilance rates (Table 1). More specifically, in support of our hypothesis, we found that during focal samples in which macaques interacted with people more frequently, they engaged in shorter grooming bouts ($\beta \pm SE = -2.82 \pm 0.28$, $z = -10$, $p < 0.001$) and more frequent vigilance behavior ($\beta \pm SE = 1.24 \pm 0.33$, $z = 3.8$, $p < 0.001$). However, contrary to our prediction, we did not find any significant impact of the rates of human-macaque interactions on the likelihood of grooming reciprocation ($\beta \pm SE = 0.56 \pm 0.82$, $z = 0.7$, $p = 0.490$). Moreover, grooming bouts performed in proximity to other macaques were more likely to be shorter ($\beta \pm SE = -0.22 \pm 0.03$, $z = -6.5$, $p < 0.001$) and less likely to be reciprocated ($\beta \pm SE = -0.27 \pm 0.10$, $z = -2.6$, $p =0.009$). Finally, grooming bouts were longer in duration when groomers were lower ranking ($\beta \pm SE = 0.15 \pm 0.06$, $z = 2.5$, $p =0.012$).

Indirect impact of human-macaque interactions on macaque grooming behavior

Our GLM analysis revealed that rates of human-macaque interactions negatively predicted grooming duration ($\beta \pm SE = -2.49 \pm 0.64$, $z = -3.9$, $p < 0.001$, Figure 4) and positively predicted vigilance rates ($\beta \pm SE = 3.86 \pm 1.27$, $z = 3.05$, $p = 0.002$, Figure 5). In other words, in blocks where human-macaque interactions were more frequent, macaques engaged in significantly shorter grooming bouts and more vigilance. Finally, we found a strong negative trend between rates of human-macaque interactions and rates of reciprocated bouts: grooming interactions were less frequently reciprocated in blocks where human-macaque interactions were more frequent ($\beta \pm SE = -3.13 \pm 1.76$, $z = -1.78$, $p = 0.07$, Figure 6).

[Figures 4, 5 & 6 here]

Discussion

Our results demonstrated that rhesus macaques flexibly modify their grooming behavior in response to the rates of human-macaque interaction to which they are exposed. Specifically, we found that during focal samples with more frequent human-macaque interactions, grooming bouts were shorter in duration with more frequent vigilance. Additionally, our work shows that macaques adjust their grooming behavior not only when they are directly involved in interactions with people, but also when they are grooming in areas characterized by high rates of human-macaque interactions, suggesting an indirect influence of human-macaque interactions on macaque grooming behavior. In particular, we found that in blocks that tend to have higher rates of human-macaque interaction, macaques engage in shorter grooming bouts that contain more vigilance and are less frequently reciprocated.

To date, a growing body of literature in ethnoprimatology has begun to reveal how NHPs exhibit the ability to flexibly adjust their behavior in an anthropogenic environment, by modifying, for instance, their diet, activity budget and social organization in response to human pressure (reviewed in McLennan et al., 2017). The present results build on this body of literature by demonstrating that NHPs also flexibly modify their social grooming behavior in relation to human presence. Perhaps most importantly, our study highlights the indirect impact that humans have on macaque social interactions – macaques' grooming behavior was influenced by features of the space in which they groomed (i.e., the typical rate of human-macaque interaction in that spatial block), regardless of whether macaques actually interacted with humans. These findings are consistent with the hypothesis that macaques might be more likely to interrupt (by increasing vigilance rates) or shorten grooming bouts to increase their opportunity to monitor human activity.

Previous studies have indicated that grooming may impose costs to the groomer by reducing their opportunities to be vigilant towards either predators or conspecifics (Maestripieri, 1993; Cords, 1995; Mooring and Hart, 1995). Our findings are consistent with this literature insofar as urban macaques grooming can potentially reduce opportunities to monitor human activity. Alternatively, it is possible that it is human activity that imposes costs to the macaques by reducing their opportunities to engage in grooming interactions. Future studies will be needed to test these two alternative hypotheses. Either way, our data suggest that even highly adaptable 'weed' species such as rhesus macaques might need areas away from people to engage in long, uninterrupted social activities such as grooming. Further, if such quiet spaces are not available to commensal macaque groups, social relationships, and thus potentially social cohesion, may suffer.

Studies on social grooming have shown that grooming duration and reciprocity can be affected by a variety of factors, such as group size (Lehmann et al., 2007), social stability (McCowan et al., 2008; Wittig et al., 2008; Kaburu and Newton-Fisher, 2013), kinship (Silk, 1982), bystander presence (Kaburu and Newton-Fisher, 2016; Newton-Fisher and Kaburu, 2017), dominance rank and/or its influence on the supply-and-demand of other rank-related benefits (Schino, 2001; Schino and Aureli, 2008). While these factors can explain some of the variation in grooming bout length, reciprocity and vigilance in our study, we examined grooming behavior in groups that were similar in size and dominance steepness and did not show signs of dominance instability. Therefore, human-macaque interactions can shape grooming behavior in a nepotistic, despotic primate species (Thierry, 2007; Balasubramaniam et al., 2012), even in groups where dominance ranking is very clear.

Previous work on commensal macaques and baboons demonstrate that urban, compared to rural, populations spend less time foraging and more time resting and grooming (Forthman-Quick and Demment, 1988; Malik and Southwick, 1988; Marriott, 1988; Riley, 2007; Fuentes et al., 2011; El Alami et al., 2012; Jaman and Huffman, 2013; Lute et al., 2014; Koirala et al., 2017). One explanation for these patterns is that these urban-dwelling populations have the opportunity to forage on high-calorie anthropogenic food, which, in some areas, is regularly provided by government authorities (cfr. Jaman and Huffman, 2013). Such urban populations can therefore meet their energetic requirements more quickly and thus afford to spend more time resting or in social activities (Jaman and Huffman, 2013; Koirala et al., 2017). Our study population, in contrast, has only opportunistic (i.e., unpredictable) access to human food and their ability to access human food depends on people's willingness to provide food to the macaques (given the lack of regular feeding sessions). Their access to human food is also influenced by whether they steal the food or other valuable items (e.g., glasses or scarfs) carried by people into the temple and trade these items for food via bartering (a behavior commonly observed at Jakhoo temple and described also in other sites and species, such as in Balinese long-tailed macaques: Brotcorne et al., 2017). Additionally, the temple area in Jakhoo is commonly used by a total of 4-5 different macaque groups, likely generating strong inter- and intra-group competition over food-providing resources (cfr. Southwick et al., 1976). This competition between macaques to access human food might explain why grooming bouts were shorter and less likely to be reciprocated when there were other macaques within three meters. We therefore suggest that both the unpredictability of access to anthropogenic foods, and the high levels of intra- and inter-group competition over food explain macaques' tendency to engage in shorter grooming bouts with more vigilance when they are in proximity to locations with high levels of human-macaque interaction.

Most studies examining the effect of anthropogenic factors on wildlife have looked at their effect on animal health or non-social activities. For example, some studies have evaluated how anthropogenic factors can impact animal stress levels (by increasing, for instance, animals' chronic levels of glucocorticoids: Fourie et al., 2015), disrupt their feeding time (Lott and McCoy, 1995; Barbara, 1999), and change their ranging pattern to avoid human-populated areas (Klein et al., 1995). Research on how human presence or anthropogenic factors influence animal social behaviors is less common, with the few previous efforts having generally focused on aggressive interactions. These studies report higher rates of intra-group aggression in anthropogenic areas, as a result of increased population density and the consequent competition over human food (Southwick et al., 1976; Sol et al., 1998; Lacy and Martins, 2003; Richter et al., 2009; Jaman and Huffman, 2013; Sinha and Mukhopadhyay, 2013). All of these factors have also been shown to have long-term effects on a species' reproductive success, and ultimately, survival in both primate and non-primate species (Klein et al., 1995; Bejder et al., 2006). In contrast to previous work, our research explores the influence of human presence on affiliative behaviors. In addition to its hygienic and stress-relief benefits (Tanaka and Takefushi, 1993;

Aureli et al., 1999; Zamma, 2002; Shutt et al., 2007; Akinyi et al., 2013; Wooddell et al., 2017), grooming can be used by low-ranking individuals as a means to reduce aggression (Xia et al., 2012; Xia et al., 2013), receive agonistic support when facing conflict and aggression (Hemelrijk, 1994; Koyama et al., 2006; Kaburu and Newton-Fisher, 2015) or be tolerated around feeding sources by dominant individuals (Carne et al., 2011; Tiddi et al., 2011). Work on both yellow (*Papio cynocephalus*) and chacma (*P. ursinus*) baboons has shown how balanced grooming interactions can improve females' fitness by enhancing infant survival (Silk et al., 2003; Silk et al., 2009) and increasing their longevity (Silk et al., 2010).

Our work suggests that by disrupting or affecting macaques' grooming behavior, human disturbance can yield downstream negative effects on macaque health and social life. For instance, Sánchez-Villagra et al. (1998) showed that, among red howler macaques (*Alouatta seniculus*), higher ectoparasite infestation was found in groups that displayed the lowest grooming rates, and two solitary individuals showed the most severe cases of parasite infestation. Yellow baboons who received the highest amount of grooming were shown to exhibit the lowest number of ticks and these individuals were in better health than individuals who received less grooming, further confirming the important hygienic role of grooming (Akinyi et al., 2013). Similarly, individuals who are more socially isolated or more peripheral exhibit higher levels of stress hormones in the presence of social and environmental stressors and suffer higher levels of parasite infestation than individuals who are more socially integrated into a group (Kikusui et al., 2006; Young et al., 2014; Balasubramaniam et al., 2016). Future work, however, will be needed to more closely link the negative influence of human disturbance on social grooming with health outcomes and effects on social relationships and fitness in commensal NHPs. The extent to which human presence, in combination with attributes such as sex, dominance rank, or personality of the macaques impacts inter-individual differences in grooming strategies remains unclear. In this regard, some of our preliminary findings from long-tailed macaques in Malaysia provide convergent evidence that macaques who interact more with people tend to spend less time grooming (Marty et al., under review.). Whether or not such findings are species-typical or may be generalized to other commensally-living macaque groups and/or species remains unclear.

Rhesus macaques have a wide distribution from temperate to sub-tropical areas in South Asia, warranting the category of 'least concern species' in the IUCN classification (Timmins et al., 2008). Their wide distribution is mainly due to this species' ability to adapt to different contexts and diets. However, our results show that, despite rhesus macaques' high adaptability to an urban setting, they still may need an area far from people where they can engage in social interactions without human disturbance, highlighting the importance of preserving forested areas even for this highly adaptable species. While future work will need to examine the impact of humans and anthropogenic factors on inter-individual, -group, or -species differences in grooming and vigilance behavior across a wider variety of contexts, socioecological factors (e.g., dominance rank, seasonality, fluctuations in people density), and longitudinal time frames, our study shows that humans can impose time constraints on macaque social behavior, which can have potential long-term consequences on macaque social life and health.

Acknowledgments

This work was funded by the National Science Foundation (#1518555) to Brenda McCowan. We thank the Himachal Pradesh Forest Department for giving us permission to conduct our research in Shimla. We are also grateful to Eduardo Saczek, Taniya Gill, Bidisha Chakraborty and Benjamin Sipes for their assistance with data collection, to Santosh Thakur for assisting with the logistics during field work, and to two anonymous reviewers for providing constructive comments on a previous draft of the manuscript.

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Table 1. Results of the GLMM models examining whether during focals rates of human-macaque interactions, groomer's rank and the presence/absence of monkeys in proximity significantly predicted grooming duration, vigilance and reciprocity.

Outcome	***Predictor***	***Estimate***	***SE***	***z-value***	***P***
Grooming duration	Intercept	5.04	0.05	110.0	< 0.001
	Human-macaque interaction rates	**-2.82**	**0.28**	**-10.0**	**< 0.001**
	Groomer's rank	**0.15**	**0.06**	**2.5**	**0.012**
	Monkey in proximity	**-0.22**	**0.03**	**-6.5**	**< 0.001**
Grooming vigilance	Intercept	-3.94	0.05	-75.7	< 0.001
	Human-macaque interaction rates	**1.24**	**0.33**	**3.8**	**< 0.001**
	Groomer's rank	0.10	0.06	1.6	0.110
	Monkey in proximity	0.03	0.03	0.9	0.367
Grooming reciprocity	Intercept	-1.72	0.14	-12.4	< 0.001
	Human-macaque interaction rates	0.56	0.82	0.7	0.490
	Groomer's rank	0.19	0.20	1.0	0.341
	Monkey in proximity	**-0.27**	**0.10**	**-2.6**	**0.009**

Figure captions

Figure 1. Map of the study site showing the two study locations, Mall Road and Jakhoo with relative pictures (© Google Earth). The home range of the Mall group revolved around Bharat Sanchar Nigam Limited (BNSL) office on the north of the study site. Jakhoo comprised a Hindu temple and a forested area surrounding the temple.

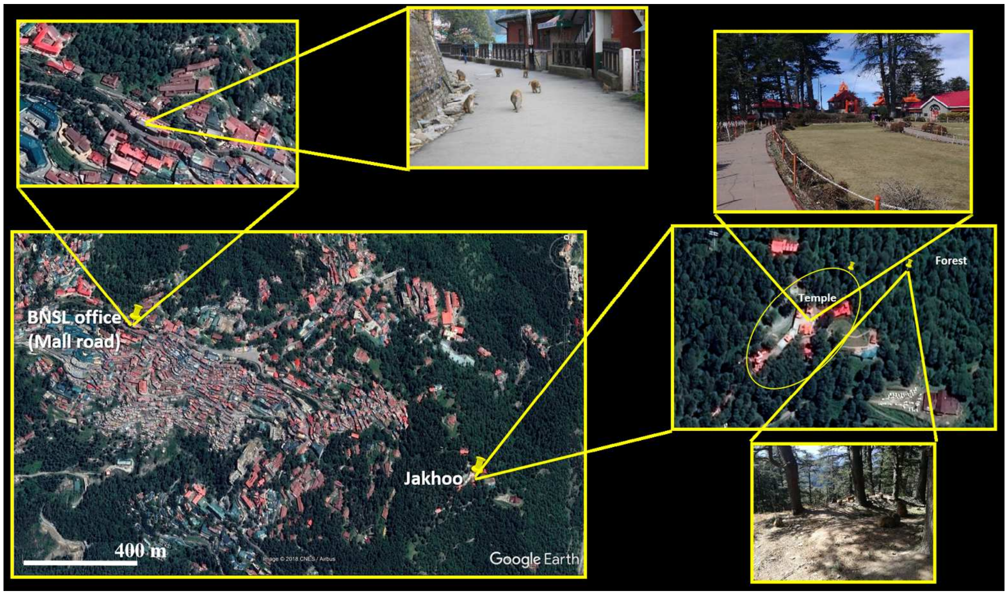
Figure 2. Rates of human-macaque interaction (number/min of observation) for each block in both Jakhoo (black) and Mall Road (grey).

Figure 3. Rates of grooming reciprocation in relation to the time elapsed from the end of the previous grooming. Smoothed line represents the hazard estimate, while the dashed lines represent the 95% confidence interval. The bold horizontal dashed line represents the baseline rates of grooming and the bold vertical dashed line marks the time after receiving grooming within which monkeys were more likely to reciprocate partner's grooming bout compared to the baseline.

Figure 4. Relationship between mean grooming bout (s) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.

Figure 5. Relationship between mean vigilance rates (number/seconds of grooming) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.

Figure 6. Relationship between mean frequency of reciprocity (number/tot number of bouts) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.



Map of the study site showing the two study locations, Mall Road and Jakhoo with relative pictures (© Google Earth). The home range of the Mall group revolved around Bharat Sanchar Nigam Limited (BNSL) office on the north of the study site. Jakhoo comprised a Hindu temple and a forested area surrounding the temple.

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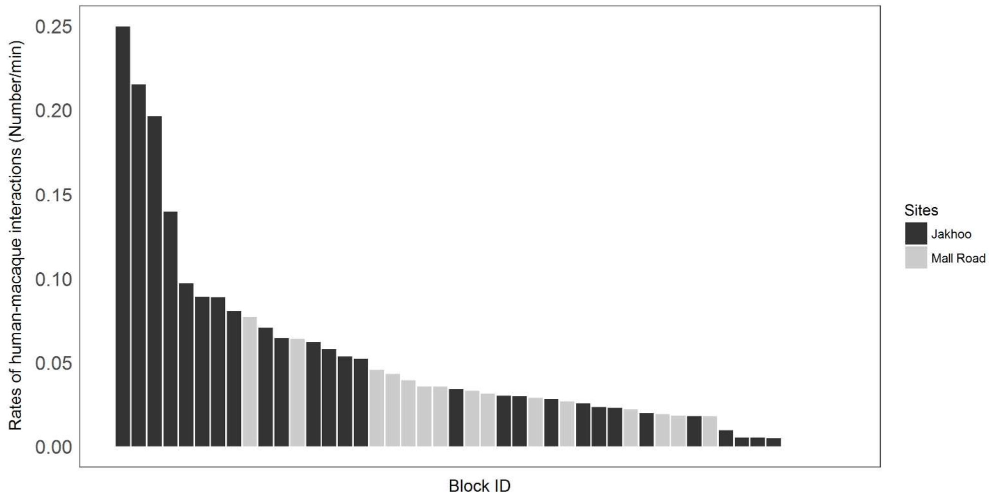

Rates of human-macaque interaction (number/min of observation) for each block in both Jakhoo (black) and Mall Road (grey).

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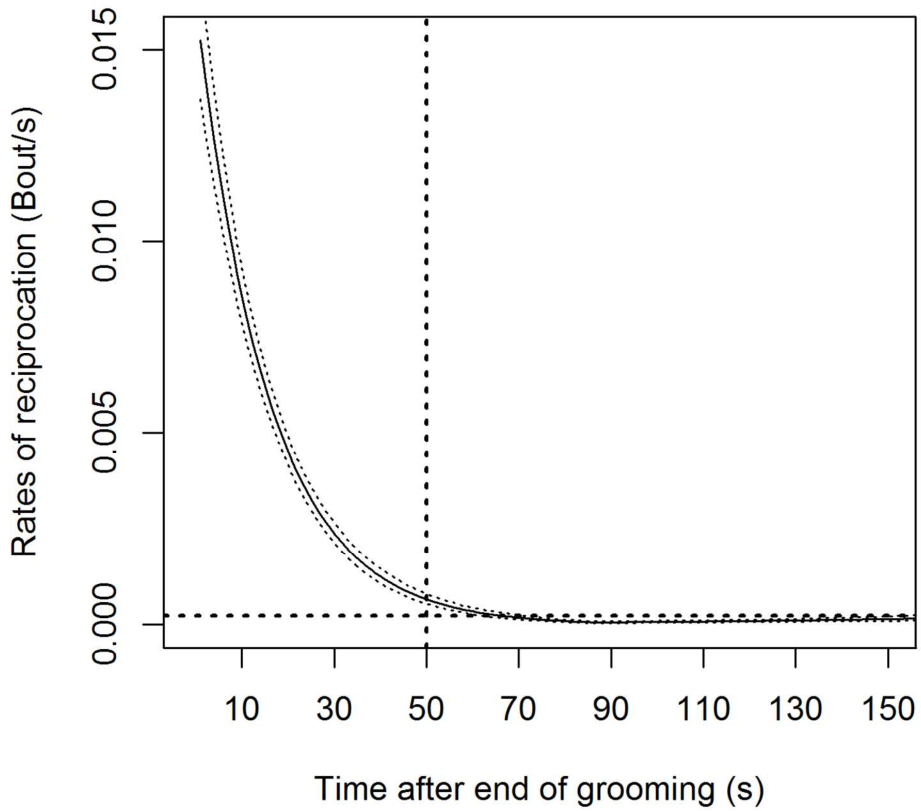
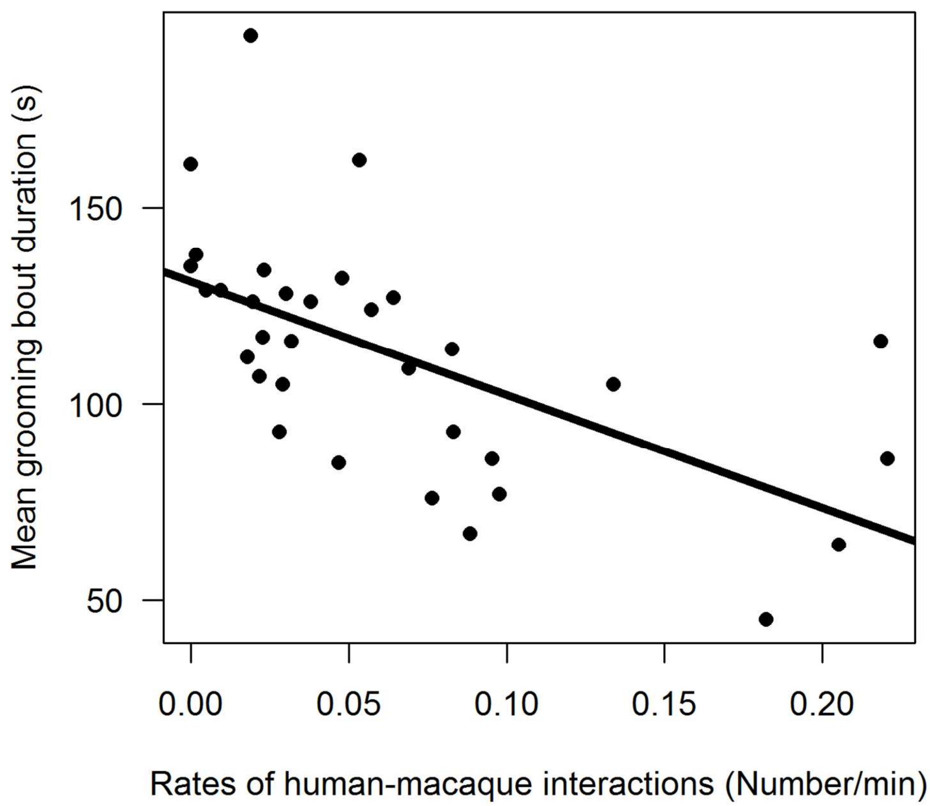


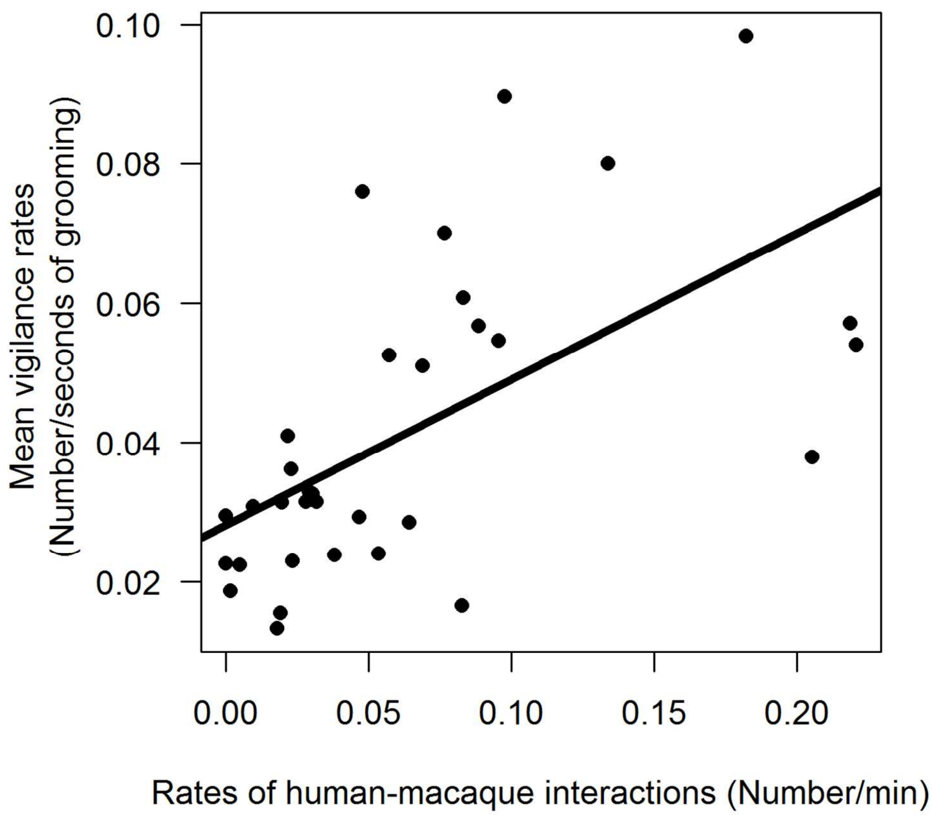
Rates of grooming reciprocation in relation to the time elapsed from the end of the previous grooming. Smoothed line represents the hazard estimate, while the dashed lines represent the 95% confidence interval. The bold horizontal dashed line represents the baseline rates of grooming and the bold vertical dashed line marks the time after receiving grooming within which monkeys were more likely to reciprocate partner’s grooming bout compared to the baseline.

127x127mm (300 x 300 DPI)



Relationship between mean grooming bout (s) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.

127x127mm (300 x 300 DPI)



Relationship between mean vigilance rates (number/seconds of grooming) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.

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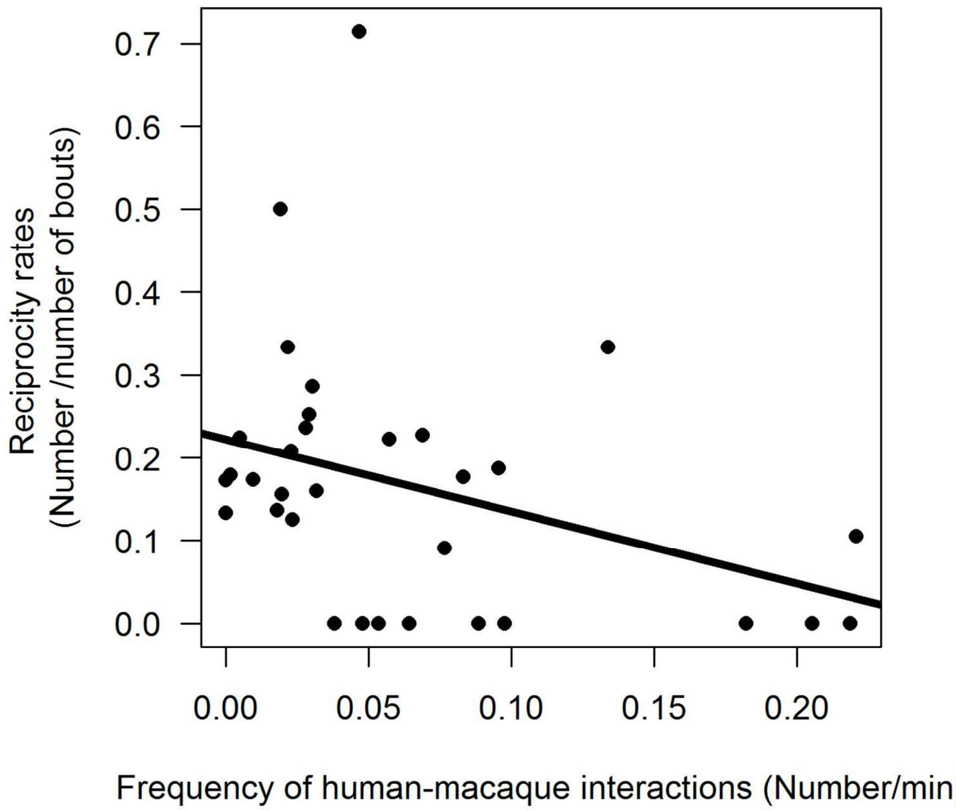

Relationship between mean frequency of reciprocity (number/tot number of bouts) and rates of human-macaque interactions (number/min) in the human-macaque blocks. Each dot represents a block. Line represents the best fit line.

127x127mm (300 x 300 DPI)