Abstract

Humans and their associated anthropogenic factors may strongly affect the demographics, activity, and fragmentation of wild animal populations. Yet, the degree and nature of such impact on indicators of animals’ social relationships remain largely under-investigated, despite the well-documented importance of strong social ties for an individuals’ health and fitness. Here, we examined whether interactions with humans may affect core aspects of social life in a primate species, by constraining the time available for individuals to engage in social interactions. Specifically, we predicted that individuals who spent more time monitoring or interacting with humans reduce their time socializing with conspecifics (i.e., the time constraints hypothesis). Alternatively, human presence may result in increased levels of stress, leading to an increase in social behaviours which serve as a coping mechanism (i.e., the social stress hypothesis). We collected data between September 2016 and September 2017 on four groups of long-tailed macaques in Malaysia at two sites with differing levels of human impact. In support of the time constraints hypothesis, we found that at the site with moderate human impact, monkeys who monitored human activity more frequently engaged less often in grooming. In contrast, at the site with high human impact, we found evidence supporting the social stress hypothesis, as indicators of stress were positively associated with social interactions, although we could not link them to the presence of humans. Our results suggest that the nature of human impact on macaques’ social behaviour is dependent upon the intensity of human activity and interaction with the macaques. These findings therefore provide insights into how humans may influence individual fitness and group social structure in animals living in an anthropogenic environment. More broadly, our results may lead to a better
understanding of animal behaviour in anthropogenic environments, implementing conservation and population management strategies, and mitigating human-wildlife conflict.

Keywords: time constraints, human-wildlife interactions, social interactions, stress, anthropogenic environment, nonhuman primates

Introduction

The recent global expansion of human populations and resulting expansion of anthropogenic landscapes generate novel, spatiotemporally dynamic environments for animal populations (e.g., ungulates: Grover and Thompson, 1986; carnivores: Riley et al., 2003; nonhuman primates: Bryson-Morrison et al., 2017). Yet, the extent to which life in such anthropogenic landscapes fundamentally changes animals’ social lives is understudied. In the current study, we investigated the impact of human presence on the social behaviour of a social mammal living in an anthropogenic environment. We ask whether components of anthropogenic environments, such as the presence of humans and high numbers of human-wildlife interactions, shift how individual animals spend their time, specifically constraining the time available for individuals to engage in social activity (Dunbar, 1992).

At any given moment in time, animals can only engage in a single behaviour and thus their time is constrained. Time constraints inevitably lead to trade-offs as time engaging in one behaviour precludes time spent in another behaviour. How time is shifted between activities can be impacted by either intrinsic (e.g., increased energy demand during pregnancy/lactation: Hamel & Coté, 2008, Dunbar & Dunbar 1988) or extrinsic factors (e.g., increased vigilance when
predation risk is high: Brown & Kotler, 2004; Creel et al., 2014; Laundré et al., 2001). Time constraints may be particularly impactful in socially living animals, as they need to dedicate a significant proportion of the time budget to social interactions (for a review see Dunbar et al., 2009). Social interactions between group members are essential to maintain social stability and relationship and group cohesiveness (e.g., Silk, 2007; Hinde, 1976), and time engaging in social interactions has been observed to be preserved rather than engaging in other behaviours (e.g., resting) even when time is constrained (Dunbar & Dunbar, 1988). Yet, if extrinsic (e.g., widely spread natural resources, low quality food) or intrinsic (e.g., high energetic demands due to lactation) factors force individuals to engage more in non-social behaviours (e.g., foraging), their opportunity to engage in social interactions is reduced, potentially affecting social relationships within a group (Dunbar & Dunbar, 1988).

In the Anthropocene, many if not all animal populations are affected by expanding human populations to a certain degree (e.g., Sih, Ferrari, & Harris, 2011). In response to human encroachment, animals commonly alter their behaviour to avoid humans or to utilise anthropogenic food resources (e.g., ungulates: Grover and Thompson, 1986; carnivores: Prange et al., 2004; Riley et al., 2003; non-human primates: Gumert et al., 2011; Ruppert et al. 2018; Bryson-Morrison et al., 2017). Factors such as these may affect animal’s social behaviour. Indeed, changes in social behaviour in response to anthropogenic influences are known in multiple taxa (e.g., fish: Bruintjes & Radford, 2013; reptiles: Lacy & Martins, 2003; mammals: Lusseau, 2003), potentially as a consequence of time constraints. The impact of anthropogenic factors on animal social behaviour can have downstream consequences on their social networks (Hyenas; Crocuta crocuta, Belton, Cameron, & Dalerum, 2018), social structure
Changes to social interaction patterns are potentially most important in species where they affect individual fitness and group cohesion. Non-human primates (hereafter NHPs) are the best-studied taxon with respect to the importance of social interactions. In NHPs, social interactions are used to establish and maintain long-term social bonds (Schülke et al., 2010; Silk et al., 2009; Silk et al., 2010; Silk, 2014) as well as to maintain group cohesion and social stability (Dunbar, 1992; Kappeler & van Schaik, 2002), all of which may impact health and survival (e.g., Kappeler et al. 2015; Silk 2014). Further, high versus low human disturbance has been found to differentially impact social interaction patterns in some NHP populations living in anthropogenic environments (Barbary macaques: Majolo et al., 2013; hamadryas baboons, Papio hamadryas: Kamal et al., 1997, rhesus macaques, Macaca mulatta: Kaburu et al. 2018).

Thus, NHPs are a good taxon for examining time constraints because allocation of time away from social interactions (in favor of monitoring or engaging with humans) is likely to have consequences on both group stability and fitness.

When time constraints decrease the time available for social interactions, individuals can reduce the number of social partners, while maintaining relationships only with preferred individuals such as close kin (Berman & Thierry, 2010; Dunbar & Dunbar, 1988) and, or, decrease the frequency of social interactions with all social partners. According to this time constraints hypothesis, if human presence and, or, interactions with humans limits the amount
of time available for animals to engage in social interactions, we expect individuals that interact more with people to interact with fewer social partners or to interact less frequently with conspecifics.

While human presence and, or, interactions with humans might reduce social interactions via the time constraints framework, an alternative mechanism could lead to an increase in social interactions with conspecifics. Exposure to human activity has been associated with greater stress levels in NHPs (e.g., Maréchal et al., 2011) and other taxa (e.g., birds: Müllner et al., 2004; Viblanc et al., 2012), either because people may disrupt animals’ daily activities, or because the highly clumped nature of anthropogenic food increases within-group competition (Sinha & Mukhopadhyay, 2013; Hsu, Kao & Agoramoorthy, 2009). In response to increased stress, NHPs often engage in stress-reducing (coping) behaviours such as allogrooming (hereafter grooming) (de Waal, 1984; de Waal & Luttrell, 1985; Judge & De Waal, 1997; Schino et al., 1988, Aureli et al. 1989; Aureli & Yates, 2010), including when this stress is caused by the presence of humans (Matheson et al. 2006; Maréchal et al. 2016). Thus, according to this social stress hypothesis, if humans stress animals and, as a result, animals engage in coping behaviours such as grooming, then animals are expected to increase, rather than decrease, their number of social partners or frequency of social interactions.

While changes in social behaviours in undisturbed groups could be attributed to time constraints imposed by large groups (high number of social partners), or widely spread natural resources (increased need for foraging time)(e.g., Berman et al. 2008; Berman and Thierry, 2010; Dunbar et al., 1992, 2009; Korstjens et al., 2010), observed changes in individuals’ social behaviour within and across different anthropogenic contexts are rarely linked to time budget
constraints or trade-offs. Within-context effects refer to inter-individual differences in social behaviour that are observed entirely within the same type of anthropogenic environment. Across context effects refer to inter-individual differences in social behaviour that are observed in animals that use a mix of anthropogenic and natural environments (e.g., high-disturbance areas such as temples and low-disturbance areas such as forested parklands) and whose social behaviour is summarized across these different environments. In the present study, we investigated whether the frequency of interactions with humans in an anthropogenic environment imposes time constraints on social behavior patterns between conspecifics. In comparison to previous studies which focus on group-level differences between contexts (e.g., fewer social interactions in areas with high versus low human impact, or disturbance), we investigated inter-individual differences in monkeys' behaviour toward humans and their social interactions with conspecifics within and across contexts. The stronger the effect of time constraints or social stress is for the individual, the more likely we will detect them across-context. Such across-context patterns are also most likely to have downstream effects on an individual's health and fitness.

We studied long-tailed macaques (*Macaca fascicularis*), a species known for their ability to adapt readily to anthropogenic environments and to engage in a wide range of interactions with humans (Fuentes et al., 2008, 2011; Gumert et al., 2011; Riley & Fuentes, 2011; Sha et al., 2009). More importantly, long-tailed macaques show a high inter-individual variability in the degree of human-macaque interactions, a precondition to study time constraints on an individual level (e.g., Fuentes et al. 2005).
In NHPs and other mammals, social grooming brings many proximate and ultimate benefits, including reduced stress levels (Brent et al. 2010; Young et al. 2014), and the establishment and maintenance of long-term social bonds and group social cohesion (reviewed in Henzi & Barrett, 1999). Yet given that grooming for long durations may form a significant proportion of the activity budget of primates, the patterning and distribution of grooming may be (and has been previously shown to be) impacted by time constraints (Berman & Thierry 2010; Dunbar et al. 2009). Hence, we predict that human-related behaviours, particularly those with a long duration such as macaque monitoring of human activity (e.g., in search of potential food or to anticipate potential threats from humans) compared to those that are shorter in duration (e.g., direct aggression, receiving food provisions), are more likely to impose time constraints on social grooming behaviour. In two populations of long-tailed macaques living in environments that were characterized by different levels of human presence, we examined whether and how interactions with humans affected their grooming behaviour. Related to this, we conducted four analyses to test our predictions:

1) **Site specific differences**: We first tested for differences between the two sites in the overall rates of human-macaque interactions

2) **Grooming diversity and frequency**: Second, we tested our predictions related to the time constraints hypothesis and the social stress hypothesis by analysing each of two grooming variables (grooming partner diversity and grooming frequency) for evidence of either time constraints or social stress.

   a) Grooming partner diversity: For monkeys with high levels of monitoring or interaction with humans, the *time constraints hypothesis* predicts a reduction in grooming diversity
as individuals focus on fewer grooming partners to maintain strong social bonds, whereas the social stress hypothesis predicts an increase in the diversity of grooming partners to reduce tension.

b) Grooming frequency: Following the same logic, grooming frequency may decrease under time constraints, but it may increase in individuals under stress as a coping mechanism.

3) Determinants of monitoring and self-scratch: Finally, to better understand the potential drivers of time constraints and social stress in anthropogenic environments, we also investigated whether specific types of human-related behaviours lead to either increased monitoring rates or other signs of stress (Figure 1).
Figure 1: The time constraints hypothesis (A) predicts that monitoring human behaviour imposes time constraints on relevant social interactions leading to a reduction in an individual’s grooming diversity and grooming frequency. Alternatively, the social stress hypothesis (B) predicts that monitoring humans would lead to stress-induced coping behaviours, resulting in an increase in social interactions.

2. Materials and Methods

2.1 Study subjects and study site

Research protocols were approved by the institutional animal care and use committee at the University of California (#20593), Davis, and met the legal requirements of Malaysia.

We studied four groups of wild long-tailed macaques in anthropogenic environments around Kuala Lumpur, Malaysia, from September 2016 until September 2017. Two groups (Pirate’s and Lip’s group) were studied at Batu Caves (hereafter BC), a Hindu temple and major tourist attraction in Malaysia (3°14′14"N, 101°41′02″E). The groups at BC experienced constant high levels of human impact at the temple area (3,500-4,000 visitors per day). When not present at the temple area, the groups spent time at the cliffs surrounding the temple where humans and observers have no access. This circumstance allowed us to test only for individual within-context time constraints in BC, as we could not test whether individuals compensate for missed social opportunities when they were away from the human-macaque interface. The other two groups were studied at Templer Park (Taman Eco Rimba Kancing; 3°17′58″N, 101°37′08″E), a recreational park in the rainforest north of Kuala Lumpur, where the human impact is moderate (around 150 visitors per day). The groups (Entrance group and Hulk’s group) spent most of their days in the forest or near the forest edge where observers could follow
them. Thus, the groups at TP were observed across context with humans present and absent as well as in areas where humans had no access (i.e., forested areas). By observing their behaviour across these different contexts, we were more likely to detect time constraints that have downstream effects on an individual’s health and fitness. Data from across context will allow us to get a representative time budget as different behavioural patterns are expected between contexts (e.g., rate of human-primate interactions). The group sizes in BC ranged from 24 adult individuals in Pirate’s group (18 females, 6 males) to 32 in Lip’s group (19/13). In Templer Park (TP), group sizes ranged from 18 (Hulk’s group, 12/6) to 35 adult individuals (Entrance group, 24/11). All four groups were fully habituated to the presence of humans.

2.2. Behavioural data collection

PM and five other observers collected behavioural data on adult individuals of each group for two to three days a week, using ten-minute focal animal sampling sessions (Altmann, 1974). We conducted regular focal animal sampling between 9am and 5pm. The team collected a total of 1023 hours of focal observations on 109 individual long-tailed macaques. Inter-observer reliability ranged between 0.85 and 0.98 as assessed by Cohen’s kappa (Martin & Bateson, 1993). The order of the sampled focal animals was predetermined and randomized every day before data collection started. We recorded all social interactions between macaques and between the focal animal and humans. We instantaneously recorded the activity of the focal individual every 2 minutes (i.e., feeding, resting, grooming, locomotion, socializing, as well as whether the focal animal was, or was not monitoring human activity, i.e., looking directly at people. As a proxy for stress, we recorded all occurrences of self-scratching during the focal
observations, a self-directed behaviour that is generally considered a reliable indicator of stress in NHPs (e.g., Maestripieri et al., 1992) particularly in long-tailed macaques (Aureli et al. 1989).

A self-scratch bout was defined as uninterrupted (with no break) scratching of the body and could include multiple body parts.

To calculate dominance ranks (in order to account for potential rank differences in social interactions), we recorded all displacements (approach/leave interactions), submissions, and agonistic dyadic aggressive interactions between individuals with a clear winner/loser outcome during focal sampling and ad libitum in between. Human-macaque interactions were analysed on the level of events which comprise a single interaction (e.g., food provisioning) or multiple connected interactions (e.g., approach/beg/provision). We counted each event once independent of complexity. We entered all the data using the HanDBase® application (DDH software) on Samsung tablets (Samsung Tab3/Tab4).

2.3 Site specific differences

The two different sites (BC and TP) were analysed separately because there were significant between-site differences in the nature and frequency of human interactions with macaques and the because data collection at BC was limited to within-context whereas TP had no context-dependent limitations to observation and data could therefore be collected across-context. By doing so, we facilitate interpretation of the results and avoid complex 3-way interactions. To statistically verify between-site differences in human-macaque interactions, we used Wilcoxon rank sum tests to determine whether rates of (i) macaques monitoring humans,
(ii) human-macaque interaction events or (iii) grooming frequencies were significantly different between the sites.

2.4 Grooming diversity and frequency

For grooming partner diversity, a measure of the variety of partners with whom each individual groomed, we counted the number of grooming partners a specific individual had during all combined focal observation and divided this number by the total time the individual was observed. Grooming frequency was calculated by using the number of grooming observations during the instantaneous recordings every two minutes, divided by the total number of instantaneous recordings for each focal animal.

2.5 Statistical analyses

We determined dominance rank from dyadic dominance interactions with clear winner/loser outcomes using the package Perc in R (Fujii et al., 2016). We then standardized ordinal ranks to account for group size and created a rank index ranging between zero and one, indicating the top and bottom ranking macaque, respectively.

Due to substantial differences between sites in the ability to observe the macaques, we fitted generalized linear mixed models (GLMM) for each location separately. We treated grooming partner diversity (number of different grooming partners), grooming frequencies (% of scans in which animals were grooming), monitoring humans, and self-scratch as count data and accordingly fitted negative binomial models (models 1-5) with the total observation time for each individual as an offset. All significance levels were set to two-tailed p-values < 0.05.
Using the *MuMIn* and *lme4* packages in R, we applied the AIC model selection criterion approach (Burnham, Anderson, & Huyvaert, 2011; Grueber et al., 2011). Grooming partner diversity (number of grooming partners divided by observation time) and grooming frequency (percentage of grooming during the 2 min instantaneous records) were set as response variables whereas monitoring (time constraints hypothesis) and self-scratching rates (social stress hypothesis) were set as predictors. The model set included different combinations of predictors including sex, rank, and interactions between monitoring/self-scratch and sex and monitoring/self-scratch and rank (see supplementary material). In case monitoring or self-scratch turned out to be a significant predictor of any response variable in Model 1-3, we ran additional negative binomial models to test the predictors of monitoring and/or self-scratching counts as outcome variables. When monitoring was the response variable, we included human to monkey aggression, provisioning rates, submissions to humans, average humans within three meters, rates of feeding on anthropogenic food (subcategory of feeding in the activity budget recorded during the instantaneous records), and rates of human-macaque events as predictors (model 4). When self-scratching rates was the response variable, we entered human to monkey aggression, the total number of human-macaque events, the average number of humans within three meters (measured during the instantaneous recordings), and the rate of aggressions received from conspecifics as predictors (model 5). As in Models 1-3, we included combinations of sex and rank in the models. We used AIC scores to choose a candidate set of models (Burnham and Anderson 2002), and following the concept of parsimony, we removed models from the candidate set if there was a simpler model with better AIC (Richards 2008). We report in the Results the models in the candidate set with dAIC <2, as models within 2 AIC points of
each other are considered equally good (Burnham and Anderson 2002; Burnham, Anderson, Huyvaert 2011). As a consequence of the AIC approach, the best models may not include the predictor of interest if it did not improve model fit.

For each best-fit model, we checked various diagnostics of model validity and stability (Cook's distance, DFBetas, DFFits, and Variance Inflation Factors; distribution of residuals, residuals plotted against fitted values). None of these indicated obvious influential cases, or any obvious deviations from the assumptions of normality and homogeneity of residuals (Field, 2005; Quinn and Keough, 2002). Further, we also checked all negative binomial models for over-dispersion. We analysed the data in R (R Development Core Team, 2009) using the lme4 and glmmADMB packages.

3. Results

3.1 Site specific differences

Monitoring rates between sites differed significantly with higher rates in BC than in TP ($w=2958$, $N_{BC}=56$, $N_{TP}=53$, $p<0.001$; Figure 2A). Similarly, individuals at BC engaged in more human-macaque events ($w=-2919$, $N=109$, $p<0.001$; Figure 2B) and in less grooming than individuals in TP ($w=81$, $N=109$, $p<0.001$, median TP=0.079, BC=0.008). In addition, both outcome variables (grooming frequency and groom diversity) were differentially distributed between sites (see Supplementary Material). These findings established a clear premise for expecting between-site heterogeneity in our data, hence justifying our separate analyses of the groups at BC versus at TP.
Figure 2: Monitoring rates (A) and human-macaque event rates (B) in the TP groups (in white: entrance/hulk) and the BC groups (in grey: lip/pirate) with group level mean values (underneath the group name). Solid horizontal lines represent the medians, while box height corresponds to the interquartile range. Whiskers indicate the maximum and minimum values. Dots represent outliers. Asterisks indicate a p-value < 0.001.

3.2a Grooming partner diversity

The best-fit models did not show a significant influence of monitoring on grooming partner diversity at either field site (Table 1A &1B). However, grooming partner diversity was associated with self-scratch rates in BC. Individuals that self-scratched more frequently had a more diverse grooming network than other animals (Table 1B).

Table 1:
Model 1: Results of the best fit GLMM testing the influence of monitoring and self-scratch behaviour on grooming partner diversity in TP (A) and BC (B). Significant p-values are indicated in bold.

(A)

<table>
<thead>
<tr>
<th>Grooming Partner Diversity TP</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.98</td>
<td>0.11</td>
<td>-37.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sex (Males)</td>
<td>-0.36</td>
<td>0.11</td>
<td>-3.41</td>
<td>&lt;0.001</td>
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<tr>
<td>Rank</td>
<td>-0.34</td>
<td>0.15</td>
<td>-2.31</td>
<td>0.021</td>
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</table>

(B)

<table>
<thead>
<tr>
<th>Grooming Partner Diversity BC</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-5.67</td>
<td>0.37</td>
<td>-15.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sex (Males)</td>
<td>-0.65</td>
<td>0.21</td>
<td>-3.1</td>
<td>0.002</td>
</tr>
<tr>
<td>Rank</td>
<td>-0.2</td>
<td>0.28</td>
<td>-0.71</td>
<td>0.476</td>
</tr>
<tr>
<td>Self-Scratch rate</td>
<td>4.85</td>
<td>1.48</td>
<td>3.28</td>
<td>0.001</td>
</tr>
</tbody>
</table>

3.2b Grooming frequency

Monitoring human activity did not significantly predict grooming frequencies at BC (Table 2B). Yet, we found a significant relationship between monitoring and grooming frequencies at TP (Table 2A). Specifically, individuals who exhibited greater rates of monitoring human activity had significantly lower grooming frequencies than individuals who monitored less (Figure 3). For BC, we present two models as they performed equally good and had an AIC score within 2. Self-scratch rate was positively correlated with grooming frequency (Table 3B), and one of the two best-fit models suggests that the impact of self-scratch rate depends on rank. While model B1 (AICc = 296.76) included a non-significant interaction term of self-scratch rate and rank, model B2 (AICc = 297.24) revealed a significant relationship between grooming frequency and
self-scratch rate. Increased self-scratch rates were associated with higher grooming frequencies, regardless of rank.

Table 2:

Model 2: Results of the best-fit GLMM testing the influence of monitoring and self-scratch behaviour on grooming frequency in TP (A) and BC (B). Significant p-values are indicated in bold.

(A)

<table>
<thead>
<tr>
<th>Grooming Frequency TP</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.83</td>
<td>0.3</td>
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<tr>
<td>Sex (males)</td>
<td>-0.48</td>
<td>0.11</td>
<td>-4.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rank</td>
<td>-0.51</td>
<td>0.15</td>
<td>-3.33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Monitoring rate</td>
<td>-5.57</td>
<td>1.95</td>
<td>-2.85</td>
<td>0.004</td>
</tr>
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</table>

(B1)

<table>
<thead>
<tr>
<th>Groom Frequency BC</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.63</td>
<td>0.54</td>
<td>-6.69</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sex (Males)</td>
<td>-1.04</td>
<td>0.22</td>
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<td>Rank</td>
<td>-1.85</td>
<td>0.89</td>
<td>-2.07</td>
<td>0.038</td>
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<tr>
<td>Self-Scratch rate</td>
<td>2.24</td>
<td>3.19</td>
<td>0.7</td>
<td>0.483</td>
</tr>
<tr>
<td>Self-Scratch rate*Rank</td>
<td>9.55</td>
<td>5.95</td>
<td>1.6</td>
<td>0.108</td>
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</table>

(B2)

<table>
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<tr>
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<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-4.26</td>
<td>0.39</td>
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<td>Sex (Males)</td>
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<td>-4.34</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rank</td>
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<td>0.32</td>
<td>-1.54</td>
<td>0.123</td>
</tr>
<tr>
<td>Self-Scratch rate</td>
<td>6.59</td>
<td>2.01</td>
<td>3.27</td>
<td>0.001</td>
</tr>
</tbody>
</table>

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3.3. Determinants of monitoring frequency and self-scratch frequency

Monitoring frequency in TP was not associated with aggression received from humans, provisioning behaviour, submission to humans, non-aggressive events with humans, frequency of consuming anthropogenic food, and the rate of human-macaque events. None of the models performed better than the empty model. Similarly, self-scratching rates in BC were not predicted by any of the selected independent variables. None of the candidate models performed better than the empty model (see Supplementary Material).
4. Discussion

The present study takes an important step forward in understanding the impact of humans on social behaviours in animals living in an anthropogenic environment. In this study, we tested two hypothetical frameworks through which overall human activity and, or, interactions with humans may affect social behaviour of non-human primates in contrasting ways. Our results provide support for the time constraints hypothesis and partial support for the social stress hypothesis. Evidence from Templer Park (TP), where the human impact is comparably lower, supports the time constraints hypothesis: individuals that monitored human activity more frequently were engaged less often in grooming with conspecifics. In contrast, evidence from Batu Caves (BC), where the level of human impact is greater, partially supports the social stress hypothesis: increased self-scratch rates (a behavioural proxy for stress) were associated with increased grooming partner diversity and frequency, presumably acting as a coping mechanism. Our results suggest that the nature of human impact on macaques’ social behaviour is dependent upon both the intensity of human activity, and direct interactions between humans and macaques.

4.1 Time Constraints Hypothesis

Grooming frequency (but not grooming partner diversity) was strongly affected by monitoring human activity at the site with less human impact (TP). Animals that visually monitored human activity more often, spent less time grooming but preserved their number of grooming partners (grooming diversity). This observation stands in contrast to previously
described effects of time constraints on grooming behaviour in NHPs where grooming partner
diversity was reduced under time constraints (Berman & Thierry, 2010; Dunbar & Dunbar,
1988). The degree to which individuals alter their grooming network under time constraints is
likely to be influenced by a variety of factors such as group size, hierarchical group stability,
intensity of time constraints, availability of grooming partners, kin biased grooming patterns,
and ultimately species differences (e.g. Berman & Thierry, 2010; Dunbar, 1992; Dunbar &
Dunbar, 1988; Wittig et al., 2008). In addition, the importance of strong social bonds (high
frequency of grooming) versus weak social bonds on an individual’s fitness is debated. In some
primate populations, weak social bonds can significantly contribute to an individual’s fitness
(chacma baboons, *Papio ursinus*; McFarland et al., 2017) whereas they do not in others (yellow
baboons, *Papio cynocephalus*; Silk, Seyfarth, & Cheney, 2018). The pattern observed in this
study indicating that long-tailed macaques under time constraints may choose to preserve the
diversity of their grooming connections while compromising on the strength of connections,
suggesting that weak bonds may play a key role in fitness for this species.

In TP, where animals were followed across context (in areas where humans were
present and outside of those areas), we expect that the observed time constraints are
presumably stronger and therefore more likely to have downstream effect on health and
fitness.

The apparent lack of time constraints in BC was surprising because we expected the site
with the higher rate of human-macaque interaction to show the strongest impact of human
presence. Indeed, almost all individuals in BC showed monitoring frequencies well above the
level observed to impose time constraints in TP, indicating that time constraints affected all
individuals. If time constraints act on a group rather than on an individual level (affecting all individuals equally), our individual-based, within-context approach would not have detected them. Our group level measurements of grooming frequency strongly suggest that the groups at BC experience time constraints as mean grooming rates in BC were significantly lower than in TP. Yet, to conclusively test the effect of time constraints on a group level, a larger number of groups observed across different contexts under varying levels of human-macaque interactions would be needed.

Previous studies have mainly tested the time constraints hypothesis in the context of group size (e.g. Berman et al. 2008; Berman & Thierry, 2010; Dunbar et al., 2009) or temporal changes in energetic demands (Dunbar & Dunbar, 1988). In this study, we showed that human-imposed time constraints affect certain individuals independently of context, signifying their potential impact on an individual’s fitness by affecting social bonds (e.g., Silk et al. 2010; Silk et al. 2009). Yet, monitoring human activity can also be associated with some substantial benefits. Individuals living in an anthropogenic environment are likely to face a trade-off between preserving time for social interactions to maintain social relationships and investing time to increase access to anthropogenic food resources (as a main benefit for animals living in an anthropogenic environment, Whittaker and Knight, 1998; Oro et al. 2013). However, we did not find an association between the frequency of monitoring and provisioning or on the intake of anthropogenic food. Increased monitoring rates in our population thus seem to be more likely associated with negative (reduced social interactions) rather than positive consequences for the individual (increased anthropogenic food intake). We acknowledge that on a group level, the advantages of living in an anthropogenic environment with access to human food (e.g.,
shorter interbirth interval: Strum, 2010; Koganezawa & Imaki, 1999) are likely to outweigh the disadvantages in many species. However, our results indicate that time constraints may be maladaptive for certain individuals. In addition, as we were not able to directly relate monitoring behaviour to certain human-macaque interactions, we assume that inter-individual differences in intrinsic (e.g., personality, experience) or extrinsic factors (e.g., demographics of humans) may lead to variations in the frequency of monitoring human activity. This relationship may ultimately affect an individual’s fitness by weakening social bonds through the process of time constraints. As a next step, long-term data on an individual’s reproductive success would be needed to conclusively show that time constraints imposed by human presence may adversely affect fitness by reducing the strength of social bonds. In addition, a more holistic approach incorporating other activities (e.g., resting, feeding) would potentially reveal additional insights into the process of time constraints on animals living in an anthropogenic environment.

4.2 Social Stress Hypothesis

As predicted by the social stress hypothesis, shared human-macaque interfaces can lead to stress in macaques (e.g., Maréchal et al., 2011). Indeed, some individuals in our groups at BC showed signs of stress (self-scratching) and these affected individuals participated more in social interactions, showing increased grooming frequency and increased number of grooming partners. Potential explanations for increased signs of stress include both direct human-macaque interactions as well as indirect human-inflicted changes in social behaviours between individuals (increased within group aggression: Hsu et al., 2009; Ram et al., 2003; Sinha &
Mukhopadhyay, 2013). Even though our results presumably support the social stress hypothesis, we recommend caution in this interpretation, as we could not find a direct link between self-scratching behaviours and any human-monkey interaction nor with sex or rank. Similarly, aggression received by other macaques, as one of the foremost causes of social stress (e.g., Ostner, Heistermann, & Schülke, 2008) did not predict self-scratching rates in the population at BC. Further investigation potentially using additional methods to measure stress levels (e.g., glucocorticoid measures: Marty et al. 2017), and incorporating individual specific attributes such as personality, is likely to provide further insight.

4.3 Conclusion

To our knowledge, this study is the first to reveal empirical evidence for how human-related behaviours may impose time constraints across context (human vs non-human) on animals’ social interactions, which have been shown to directly affect individual fitness. Ultimately, such changes in social behaviour can also affect the social dynamics in a group by reducing group cohesion and stability, leading to species atypical social structures (e.g., Sinha et al., 2005) or group fission (Henzi et al., 1997a; Henzi et al., 1997b). Changes in behaviour in the presence of humans may be temporally or spatially apparent in a variety of species, affecting social (e.g., dolphins: Lusseau, 2003) and other behaviours such as feeding (e.g., rhinos: Lott & McCoy, 1995). Yet, whether such context-dependant behavioural adjustments are a consequence of time constraints and translate into context independent changes in behaviour patterns potentially affecting an individual’s fitness or group stability remains largely unknown. Due to the potential impact on an individuals’ fitness, the human-wildlife interface is of
increasing importance not only for NHP research (McKinney & Dore, 2018) but also for the
study of animal behaviour in general (reviewed in Wong and Candolin, 2015). Still, our
knowledge of the ecological and evolutionary consequences of long-term behavioural changes
in response to human disturbance is still rudimentary. Studying the effects of both direct and
indirect human-wildlife interactions on behavioural changes, group dynamics, demographics,
and their effect on individual and population health and fitness will substantially contribute to a
better understanding of the shared human-wildlife interface. Ultimately, while further study
will aid in the development of efficient and culturally appropriate interventions to relieve
human-wildlife conflict, we think this work provides an important step in understanding how
specific features of the anthropogenic environment influence dynamics of macaque social
groups.

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