Implementing network approaches to understand the socioecology of human-wildlife interactions.

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Abstract:

1. Human population expansion into nonhuman animals' habitats has increased interest in the behavioral ecology of human-wildlife interactions. To date, however, whether and how wild animals and their conspecifics form non-random associations in terms of when or where they interact with humans still remains unclear.
2. Here we adopt a comparative approach to address this gap, using social network analysis (SNA). SNA, increasingly implemented to determine human impact on wildlife spatial and social ecology, can be a powerful tool to understand how animal socioecology influences the spatiotemporal distribution of human-wildlife interactions.
3. For 10 groups of rhesus, long-tailed, and bonnet macaques (*Macaca* spp.) living in anthropogenically-impacted environments in Asia, we collected data on human-macaque interactions, animal demographics, and macaque-macaque agonistic and affiliative social interactions. We constructed 'human-interaction networks' based on associations between macaques that interacted with humans within the same time and spatial locations, and social networks based on macaque-macaque allogrooming behavior, affiliative behaviors of short duration (agonistic support, lip-smacking, silent bare-teeth displays, and non-sexual mounting), and proximity.
4. Pre-network permutation tests revealed that, for all macaque groups, human-interaction networks showed non-random structures. GLMMs revealed that individuals' connectedness within human-interaction networks were positively associated their connectedness within affiliation social networks, and social proximity networks although

this effect varied across species (bonnets > rhesus > long-tailed). Male macaques were more well-connected in human-interaction networks than females. Neither macaques' connectedness within grooming social networks nor their dominance ranks had an impact on human-interaction networks.

5. Our findings suggest that, in challenging, time-constraining anthropogenic environments, less time-consuming affiliative behaviors and additionally greater social tolerance (especially in less ecologically flexible species with a shorter history of exposure to human activity) may be key to animals' maintaining strong social connections. Subsets of these animals may also utilize greater exploratory tendencies and life-histories that are less energetically demanding in the long-term. Both of these strategies may contribute to animals' propensities to engage in joint risk-taking by being near and engaging with humans. From conservation and public health perspectives, human-interaction networks may inform interventions to mitigate zoonotic disease transmission and move human-wildlife interactions from conflict towards co-existence.

Key-words:

Behavioral ecology
Comparative studies
Conservation behavior
Human-wildlife interactions
Nonhuman primates
Social Network Analysis

Introduction:

An expanding human population has increased overlap and contact rates between humans and wildlife (Nyhus, 2016). The resulting human-wildlife interactions have visible, readily discernible outcomes on wildlife populations, but also subtler effects on animal ecology and behavior that remain less well-documented (Balasubramaniam et al., 2021). The sub-field of conservation behavior addresses this gap, and largely deals with how anthropogenic factors impact animal movement and (consequential) access to natural resources, interspecies ecosystem interactions with predators and competitors, and intraspecies spatial overlap and social interactions with their conspecifics (reviewed in Berger-Tal et al., 2016; Snijders et al., 2017). However, there exists comparatively less research on the inverse effect – that is, on how animal attributes that influence their life-history, or their interactions with socioecological components of their natural environment, might impact their behavior in anthropogenic environments (Balasubramaniam et al., 2021; Morrow et al., 2019). This is despite growing consensus that human-wildlife interactions generate coupled, bi-directional effects whereby they both affect, and are reciprocally affected by, wildlife ecology and behavior (Balasubramaniam et al., 2021; Carter et al., 2014; Lischka et al., 2018).

More recently, however, a handful of empirical studies have focused on how the socioecology of group-living wild animals can influence human-wildlife interactions. Specifically, these have revealed how wild animals' tendencies to engage in risk-taking behaviors within human-impacted environments are associated with a number of life-history and socioecological traits, such as animals' sex, dominance rank, spatial position within their groups, and connectedness within social networks (e.g. elephants, *Elephas maximus*: Chiyo et al., 2012;

black bears, *Ursus americanus*: Lischka et al., 2018; multiple species of macaques, *Macaca* spp.: Balasubramaniam et al., 2020a; Morrow et al., 2019). A common aspect of all these studies is that they have focused on the overall frequencies of human-wildlife interactions, or the overall degrees of exposure of individual wild animals to humans and anthropogenic factors. In comparison, less well-studied is whether and how animals form non-random associations in terms of when, where or how they interact with humans.

Understanding such patterns of associations in human-wildlife interactions is important for many reasons. First, capturing the dynamic, spatiotemporally variant socioecology of human-wildlife interactions could offer opportunities to study contemporary evolution, and animals' propensities to adaptively respond to rapidly changing environments (Wong & Candolin, 2015). Second, from a public health perspective, they could provide valuable information regarding whether or how some animals, by virtue of overlapping with humans and anthropogenic areas across time and space, may be the targets of interventions to mitigate the spread of zoonotic and emerging infectious diseases at human-wildlife interfaces (Cunningham et al., 2017; Townsend et al., 2020). Third, such animals may also be the targets of conservation efforts, interventions and policy making aimed at decreasing human-wildlife conflict while increasing mutual welfare and co-existence (Nyhus, 2016).

Network approaches offer exciting quantitative tools that may uniquely be able to address this gap in the literature. Beyond just rates or durations of interaction, networks allow for modeling the heterogeneity in relationships between entities (i.e. individual animals or humans; assigned as nodes) based on shared or interactive patterns of their association (assigned as edges) (Farine & Whitehead, 2015; Wey et al., 2008). In particular, social networks, which link animals based on their shared patterns of space-use associations or contact and non-contact social interactions (Farine & Whitehead, 2015), have found wide-ranging applications in animal behavioral ecology (Croft et al., 2008; Krause et al., 2014), including of late in conservation behavior (Snijders et al., 2017). For instance, epidemiological studies have used animal social networks to assess the vulnerability of wildlife populations to infectious disease outbreaks (Craft, 2015; Drewe & Perkins, 2015). More pertinently, an increasing number of studies have revealed how interactions with humans may decrease the connectedness of animal social networks (e.g. spotted hyenas, *Crocuta crocuta*: Belton et al., 2018; giraffes, *Giraffa camelopardalis*: Bond et al., 2020; bottlenose dolphins, *Tursiops aduncus*: Chilvers & Corkeron, 2001; moor macaques, *M. maura*: Morrow et al., 2019), and in extreme cases that involve the removal or relocation of individual animals, to the fragmentation of social networks (e.g. Killer whales, *Orcinus orca*: Williams & Lusseau, 2006). Such findings are of profound importance since decreased social network connectedness or fragmentation can strongly impact animal health and reproductive success (Nunn et al., 2015). Yet while most social network analysis has focused on space-use overlap or social interaction networks, little research has implemented network approaches to model human-wildlife interactions themselves, or even associations between wild animals that co-inhabit anthropogenic environments at the same time and space (Sosa et al., 2021a).

One reason for this may be that researchers may face logistical and ethical challenges while attempting to construct human-wildlife interaction networks. For instance, the inclusion of humans or anthropogenic features as node(s) in human-wildlife ‘bimodal’ or ‘multimodal’ networks would require that researchers identify and track the behavior of individual people, specific human sociodemographic communities, and/or other features of anthropogenic landscapes that come into contact with wildlife (e.g. livestock, feral mammals: Bhattacharjee & Bhadra, 2020). Collecting such data is not always feasible, in light of the considerable geospatial and sociocultural variation that researchers face while sampling human demographics, experiences, and behavior (Barua et al., 2013; Dickman, 2010; Karanth et al., 2018). A more feasible approach may be to record interactions between humans and pre-identified wild animals across time and overlapping space, and ‘project’ these interspecies interactions into what are effectively unimodal ‘social’ networks in which wild animals are linked based on their interactions with shared features of their ecology (here, humans)**.** Such projections have been constructed before for other ecological networks, for instance the conversion of a primate-parasite bimodal network into a unimodal ‘social’ network that linked nonhuman primate species (nodes) based on the parasites they shared (edges) (Gomez et al., 2013). In the context of human-wildlife interactions, such constructions would provide useful opportunities to determine whether animals interact with humans in non-random ways across time and space, and the socioecological determinants of such associations.

In this study, we implement a network approach to capture heterogeneity in associations between humans and group-living wild nonhuman primates across time and space, for multiple human-primate interfaces in Asia. We address the above gaps in our current understanding of the ecology of human-wildlife interactions, by asking whether wild macaques (*Macaca* spp.) living in human-impacted environments (1) associate in non-random ways based on when or where they interact with humans, that are also (2) influenced by their demographic and behavioral characteristics linked to their life-history and socioecology. Aside from sharing close evolutionary histories with humans (Hasegawa et al., 1985; Roos & Zinner, 2018), wild primates are also increasingly sharing ecological space and resource-use overlap with humans (Fuentes, 2012; Mckinney, 2015). Anthropogenic factors may present (in evolutionary time-scales) relatively novel, socioecological constraints on wild primates, with individuals having to continuously adjust their behavior to adapt to human activities and behavior (Mckinney, 2015). Among the most ecologically and behaviorally flexible of all nonhuman primates, many species of macaque, particularly rhesus macaques (*M. mulatta*), long-tailed macaques (*M. fascicularis*), and bonnet macaques (*M. radiata*), are considered ‘edge’ wildlife species that overlap and experience spatiotemporally variant contact-rates and interactions with humans (Gumert, 2011; Priston & McLennan, 2013; Radhakrishna & Sinha, 2011). At the same time, they also show marked inter- and intra-specific variation in social interactions and (consequently) social network connectedness with their conspecifics, which has been strongly linked to differences in their evolutionary or phylogenetic relationships (Balasubramaniam et al., 2012; Thierry, 2007), exposure to socioecological factors (Sterck et al, 1997), and exposure to anthropogenic impact (Balasubramaniam et al., 2020b; Kaburu et al., 2019b; Marty et al., 2019). For these reasons, they are well-suited model systems for implementing network approaches to understand associations of human-wildlife interactions and their links to animal socioecology and behavior.

‘Human-interaction networks’ were constructed for ten groups of three macaque species living in anthropogenic environments. These networks linked individual, pre-identified macaques based on their tendencies to interact with humans within the same time and space. To determine whether macaques were associated in terms of their tendencies to interact with humans in non-random ways across time and space, we first tested whether (p1) the patterning and distribution of individuals’ connectedness within their human-interaction networks would be significantly different from random. Second, we examined whether macaques’ human-interaction networks were associated with their social networks. For this, we tested whether (p2) the node centrality of individuals within their human-interaction networks was positively associated with their centrality within their social grooming, proximity, and/or short-duration affiliation networks. We also explored the effects of individuals' sociodemographic factors, i.e. their sex, dominance rank, and species, on their connectedness/centrality within their human-interaction networks. As a cross-species comparison, we also determined whether the above-predicted associations between human-interaction network centrality and social network centrality varied across different macaque species.

Materials and Methods:

Study sites and subjects: Demographic and behavioral data were collected on ten groups of macaques living in urban and peri-urban environments ranging from temperate areas in Northern India, to tropical environments in Southern India and Malaysia. The groups were as follows: four groups of rhesus macaques at a Hindu temple and the surrounding forested area (three groups) and a town mall area (one group) in the city of Shimla in Northern India (31.05 N, 77.1 E); four groups of long-tailed macaques at a Hindu temple (two groups) and a recreational park (two groups) in the outskirts of Kuala Lumpur in Malaysia (3.3 N, 101 E); and two groups of bonnet macaques at a recreational area in the outskirts of the rural town of Thenmala within the state of Kerala in Southern India (8.90 N, 77.10 E) (Balasubramaniam et al., 2020b; Marty et al., 2020). Subjects were pre-identified, adult male and female macaques. At all three locations, macaque home ranges overlapped with humans and anthropogenic landscape features. However, there were systematic inter- and intraspecific differences in macaques' degrees of exposure to humans, and indeed the frequency and types of interactions that they engaged/experienced with humans, which informed our expectation of detecting both within- and between-site differences or heterogeneity in human-interaction patterns. Supplementary Table 1 provides details on the study groups and subjects of the study. More details regarding the similarities and differences between the study sites may be found in our previous publications (Balasubramaniam et al., 2020b; Marty et al., 2020).

Data collection: Data were collected following a standardized protocol that was implemented across all three field-sites, with inter-observer reliability being reached both within and across sites (details in Kaburu et al., 2019a). All data were collected for five days a week, between 9:00 am and 5:00 pm. Given the susceptibility of social network analysis to sampling methods and sampling bias (Farine, 2017; Farine & Whitehead, 2015), particularly to the inter-dependencies of data used to construct multiple types of networks, we used different sampling approaches to collect data on human-macaque interactions and macaque-macaque social behavior.

To record human-macaque interactions, we used an ‘event sampling’ approach (Altmann, 1974; Beisner & McCowan, 2013; Kaburu et al., 2019a). For each macaque group and site, we divided their home-range that overlapped with anthropogenic settlements into a series of spatial blocks of roughly equal sizes, within which human-macaque interactions were most likely to occur (see Kaburu et al., 2019a for details). Choices of block numbers and locations differed across groups, and were assigned during a preliminary ‘training’ phase (of ~2 months) during the groups’ home-ranges were determined. However, block numbers and locations changed during the course of data collection in accordance with any shifts we saw in macaques’ home ranges that resulted in our adding or dropping event sampling at some blocks. Critically, block sizes were uniformly similar within and across study sites, and were set such that observers could potentially view and record all macaques and humans that were present within the block at a given time. To record human-macaque interactions, observers visited these blocks in a pre-determined, randomized order on each day. From a pre-assigned, fixed location within each block that maximized their visual field, observers recorded all human-macaque interactions that involved pre-identified macaques that were present within the block for a ten-minute duration, before moving on to the next block. We followed such a randomized block sampling approach to avoid over-sampling of human-macaque interactions in more (versus less) densely populated areas of macaques' home-ranges, which can result in sampling bias (Farine, 2017; Farine & Whitehead, 2015).

A 'human-macaque interaction' was defined as any contact or non-contact behavior that was initiated by a macaque towards a human (e.g. approach, aggression, begging for food), or by a human towards a macaque (e.g. approach, aggression, provisioning with food), that elicited a reaction behavior (e.g. submissive avoidance, fleeing, or screaming, counter-aggression, acquiring and feeding on human foods) from the initial recipient. We defined an "event" as either a single such interaction, or a series of such sequentially occurring interactions that were linked to each other temporally and/or through common/multiple participants (more details and definitions in Kaburu et al., 2019a).

'Focal animal sampling' (Altmann, 1974) was used to record macaque-macaque social interactions and social proximity with conspecifics. On each day, and in each location, individual macaques were followed in a pre-determined, randomized sequence for ten-minute durations. In each session, we recorded events of dyadic agonistic interactions (aggressive and submissive behaviors), social or allogrooming, and other forms of dyadic affiliation that were of shorter durations than grooming (i.e. coalitionary support during social conflicts, lip-smacking, non-sexual mounting, or silent bare-teeth displays in non-agonistic or peaceful contexts), that involved the focal animal as either the initiator or the recipient. Once every two minutes within a focal session, we temporarily ceased recording data in a continuous manner to conduct a point-time scan of the focal, to record the identities of all group conspecifics that were within body-length proximity of the focal. More details on the definitions of behaviors may be found in Kaburu et al., 2019a.

Construction of human-interaction networks and social networks: For each macaque group, undirected ‘human-interaction networks’ based on the spatiotemporal similarity of monkeys’ interactions with humans (Fig. 1a) were constructed. That is, links between all macaque subjects in a given group that engaged in human-macaque interactions within the same ten-minute event sampling session and within the same block were assigned. Such reconstructions enable determining whether macaques associated in non-random ways in terms of their tendencies to interact with humans across time and anthropogenic space, and if so what socioecological factors influence such associations. Edge-weights were calculated and assigned to these human-interaction networks, as the ratio between the total number of such occasions in which pairs of macaques spatiotemporally ‘co-interacted’ with humans, to the total duration of event sampling sessions conducted during the course of their overlapping tenure within their group, thereby accounting for their observability.

For each macaque group, we also constructed three types of weighted, undirected ‘social contact networks’ based on our recordings of social macaque-macaque interactions of grooming, short-duration affiliative behaviors, and social proximity (Fig. 1b). In grooming and short-duration affiliation networks, nodes were individual macaques, and edge-weights were calculated as the frequency of behaviors (given or received) between each pair of animals divided by the total focal observation time of each member of that pair during the course of their overlapping tenure within their group (details in Balasubramaniam et al., 2020a). In proximity networks, edge-weights were calculated as the number of point-time samples in which a pair of individuals was seen within body-length of each other, divided by the total number of point-time samples collected for each member of the pair during the course of their overlapping tenure within their group.

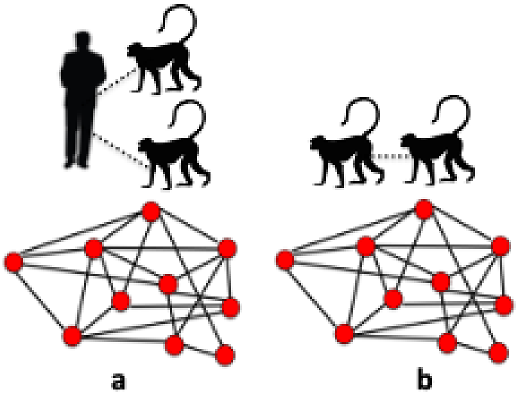


Figure 1: Macaque (a) human-interaction networks and (b) social networks

Calculations of dominance rank and social network centrality measures: Using data on male-male and female-female dyadic aggressive interactions that elicited a submissive response from the recipient, we constructed dominance hierarchies separately for males and females for each group. Using these, we calculated the dominance rank of each macaque in each group, using the 'Perc' package in R (Fujii et al., 2015). To account for cross-group variation in group size, we standardized ordinal ranks to create a rank index ranging between zero (lowest-ranking macaque) and one (highest-ranking macaque) (Kaburu et al., 2019b). For each individual macaque within each type of network, we calculated weighted, undirected measures of their connectedness or centrality, both based on just their direct connections and by considering their secondary connections. First, we calculated *weighted degree* or (hereafter) *strength* as the sum of all the edge-weights of edges directly connected to an individual, i.e. the number and strength of an individuals' direct connections (Croft et al., 2008; Newman, 2003). Second, we calculated *eigenvector* as the number and strength of an individuals' direct and secondary connections, i.e. the reach of an individuals' connectedness or social ties (Bonacich, 2007; Brent, 2015).

There is broad consensus among behavioral ecologists that these centrality measures are among the most biologically relevant (Sosa et al., 2021b). In the context of our human-interaction networks, these measures would indicate the extent to which individual macaques engaged with humans at the same time and space as others (strength). By taking into account secondary connections, eigenvector, on the other hand, represents the extent to which individuals interacted more with humans alongside group members who themselves interacted more with humans while alongside other monkeys within the same time and space. In other words, we anticipate that these measures of their connectedness would be relevant to understanding (i) the socioecological underpinnings of macaques' risk-taking behaviors in anthropogenic environments, and (ii) whether some individuals, due to their greater connectedness in one or both types of networks, may serve as targets for interventions to manage human-wildlife interactions and the risk of zoonotic transmission. To account for differences in group size (and hence the number of nodes or available partners within a network), we re-scaled the values calculated for each network measure within each group to sum up to one. Centrality measures were calculated using the 'Igraph' package in R (Csardi & Nepusz, 2006).

Data analysis: To determine whether human-interaction networks showed non-random structures (p1), we implemented a 'null' model pre-network randomization procedure (Farine, 2017; Farine & Carter, 2020). For each human-interaction network, we calculated the mean strength centrality of all individuals, and compared this 'observed' mean to a distribution of mean strength centrality scores calculated from each of 1000 permutations of the network generated by randomly swapping its edges. This approach has been shown to be more reliable than other, post-network permutation-based null model approaches, i.e. node-swapping, to test the 'null' hypothesis of random network structure (Puga-Gonzalez et al., 2020). To test whether the structure of macaques' connectedness within their human-interaction networks were associated with their connectedness within social networks (p2), we ran General Linear Mixed-effects Models (GLMMs) implementing a corrected Akaike Information Criterion (AICc) based model-selection and interpretation approach, using the 'Lme4' R package (Burnham & Anderson, 2002; Burnham et al., 2011).

For a sample size of 339 macaques across ten groups, we ran two sets of negative-binomial models, one for each of two outcome variables of macaques' human-interaction network centrality measures, i.e. strength and eigenvector (Supplementary Tables 2 and 3). Each model-set consisted of seven models. In each model set, the first model included only sociodemographic attributes (i.e. sex, dominance rank, species) and was effectively the 'null' or 'control' model. Models 2 and 3 included sociodemographic attributes plus a single measure of macaques' corresponding centrality (e.g. strength centrality as a predictor of human-interaction strength centrality) in the grooming, short-duration affiliation, and proximity networks. Centrality measures from the grooming and proximity networks (but not short-duration affiliation networks) were strongly collinear and were not included in the same model. Finally, models 4 to 7 included interaction terms between species and each social network centrality measure to explore cross-species differences in associations.

From each model set, we shortlisted and interpreted model summary parameters from one or more 'candidate' models that had the lowest AICc scores that were within an AICc of 2 points from each other, and < 2 points from the next best-fit model. To account for inter-dependencies in human-interaction network measures examined as outcome variables, we re-calculated the p values for the observed model coefficients for predictor variables that showed significant effects in each candidate model, using a post-network node-swapping randomization procedure (Farine, 2017; Farine & Carter, 2020). In these, we compared observed model coefficients to a distribution of coefficients generated by re-running the candidate GLMM following the re-assignment of human-interaction centrality scores through randomly swapping the nodes of each human-interaction network. Node-swapping is less susceptible (than pre-network randomizations or edge-swapping) to type-II errors while testing regression-based null hypotheses (Weiss et al., 2020).

We conducted various diagnostics of model validity and stability (Cook's distance, dfBetas, and Variance Inflation Factors; distribution of residuals, residuals plotted against fitted values) for all candidate models. These revealed no influential cases, strong collinearity among our predictor variables, or obvious deviations from the assumptions of normality and homogeneity of residuals (Quinn & Keough, 2002). All statistical tests were two-tailed, and we set the p values to attain statistical significance to be < 0.05.

Results:

(P1) The structure of human-interaction networks:

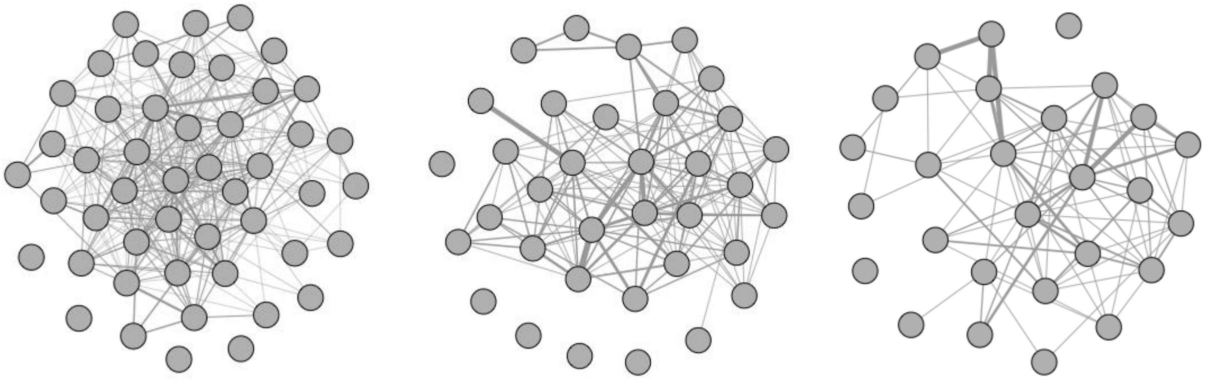
For all ten macaque groups, human-interaction networks were well-connected and exhibited significant structure (examples in Fig. 2a-c). Table 1 summarizes the attributes and characteristics of each network. The majority of human-interaction networks (7/10) were somewhat fragmented, insofar as they had one or up to a few individuals that remained disconnected from the main network fragment (a minimum of one individual in a bonnet macaque group: BM_G2; a maximum of 7 individuals in a rhesus macaque group: RM_G4).

There was also marked inter-network variation in the average human-interaction strength centrality of individuals (Table 1). Despite these features, pre-network randomization tests performed by randomly swapping network edges revealed that, for each network, the observed mean strength centrality of individuals was significantly greater than the distribution of strength centralities calculated following 1000 permuted 'edge-swapped' networks. That is, all networks deviated significantly from the null hypothesis of random network structure.

Table 1: Summary of attributes of macaque human-interaction networks. For mean strength, p values are based on a pre-network randomization procedure (see Methods)

Species (group)	**Network (group) Size**	**Males**	**Females**	**Edges or links**	**Unconnected individuals**	**Strength (mean ± sd)**
Bonnet (BM_G1)	48	26	22	318	4	0.10 ± 0.07**
Bonnet (BM_G2)	28	10	18	115	1	0.09 ± 0.06**
Long-tailed (LM_G1)	35	11	24	144	5	0.10 ± 0.08**
Long-tailed (LM_G2)	19	7	12	122	0	0.30 ± 0.16**
Long-tailed (LM_G3)	34	15	19	91	6	0.20 ± 0.24**
Long-tailed (LM_G4)	24	5	19	178	0	0.23 ± 0.14**
Rhesus (RM_G1)	27	9	18	87	2	0.08 ± 0.06**
Rhesus (RM_G2)	24	7	17	173	0	0.10 ± 0.05**
Rhesus (RM_G3)	41	13	28	342	2	0.05 ± 0.03**
Rhesus (RM_G4)	59	14	45	238	7	0.05 ± 0.03**

$^{**}p < 0.01$



(a) **(b)** **(c)**

Figure 2: Examples of weighted, undirected human-interaction networks constructed for groups of (a) bonnet macaques (BM_G1), (b) long-tailed macaques (LM_G1), and (c) rhesus macaques (RM_G1).

(P2) Associations between macaques' human-interaction networks and social networks:

We found strong evidence to suggest that the connectedness/centrality of individual macaques within their social networks strongly influenced their connectedness/centrality within their human-interaction networks.

For strength centrality, our AICc selection criterion led to the short-listing and interpretation of two candidate GLMMs. The first candidate model (Table 2A: model 3 of Supplementary Table 2) showed a significant positive effect of both short-duration affiliation strength centrality (Fig. 3a) and proximity strength centrality on human-interaction strength centrality. The second candidate model (Table 2B: model 6 of Supplementary Table 2) further showed a significant interaction between proximity strength centrality and species, which revealed that the effect of proximity was most pronounced among bonnet macaques, moderate among rhesus macaques, and least pronounced (did not reach significance) among long-tailed macaques. Neither candidate model included grooming centrality measures: proximity and short-duration affiliation strength centrality had a greater impact than grooming strength centrality on human-interaction network centrality. Macaque sex had a significant impact on human-interaction network strength centrality, with males showing greater values than females (Table 2A, B; Fig. 3b). However, dominance rank had no effect (Table 2A, B). Across species, we found that the average strength centrality of individuals was the highest among long-tailed macaques, and the lowest among rhesus macaques, with bonnet macaques falling in between (Table 2A).

Table 2: Candidate GLMMs (models 3 and 6 of Supplementary Table 2) examining the effects of individuals' sociodemographic attributes (sex, dominance rank, species), and social network strength centrality (grooming, proximity, and affiliation) by species, on their human-interaction network strength centrality. P_{perm} indicate p values from permuted networks that were estimated using the post-network randomizations or 'node-swapping' algorithm (see Methods).

Model 3

Predictor	**B**	**SE**	**Z**	**P**	**P_{perm}**
(Intercept)	1.74	0.19	9.21	<0.01**	
Sex (males vs females)	0.30	0.11	2.67	0.01*	<0.01**
Rank Index	-0.10	0.17	-0.61	0.54	
Species (long-tailed vs bonnet)	0.57	0.19	2.98	<0.01**	<0.01**
Species (rhesus vs bonnet)	-0.35	0.19	-1.88	0.06(*)	
Species (long-tailed vs rhesus)	0.92	0.16	5.78	<0.01**	<0.01**

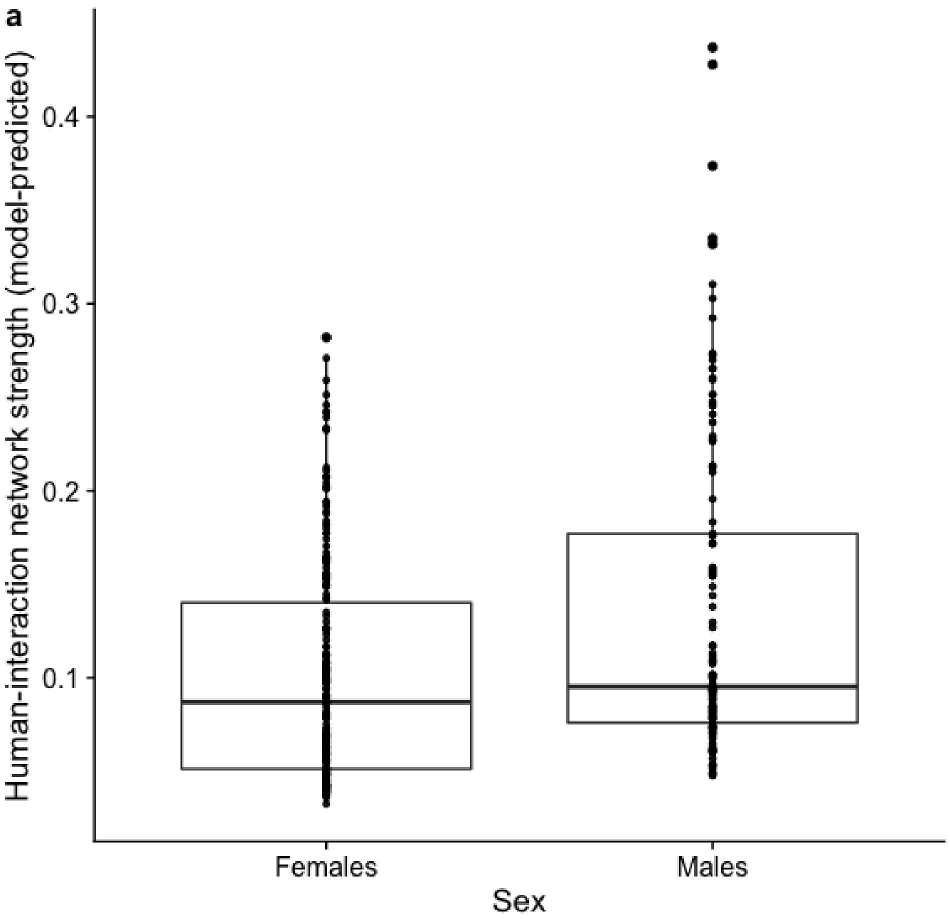
Proximity Strength	8.30	3.35	2.47	<0.01**	0.03*
Affiliation Strength	7.34	2.81	2.61	<0.01**	<0.01**

**$p < 0.01$; *$p < 0.05$; (*)$0.05 < p < 0.10$

Model 6

Predictor	**B**	**SE**	**Z**	**P**	**P_{perm}**
(Intercept)	1.20	0.33	3.61	<0.01**	
Sex (males vs females)	0.40	0.12	3.42	<0.01**	<0.01**
Rank Index	-0.07	0.16	-0.43	0.67	
Species (long-tailed vs bonnet)	1.30	0.37	3.51	<0.01**	<0.01**
Species (rhesus vs bonnet)	-0.01	0.37	-0.04	0.97	
Species (long-tailed vs rhesus)	1.32	0.27	4.92	<0.01**	<0.01**
Affiliation strength	4.59	2.94	1.57	0.12	
Proximity strength (bonnets)	27.71	9.74	2.85	<0.01**	<0.01**
Proximity strength (long-tailed)	4.14	3.64	1.14	0.25	0.18
Proximity strength (rhesus)	16.48	5.85	2.82	<0.01**	<0.01**
Proximity strength (long-tailed vs bonnets)	-23.56	9.97	-2.36	0.02*	<0.01**
Proximity strength (rhesus vs bonnets)	-11.22	10.45	-1.07	0.28	
Proximity strength (long-tailed vs rhesus)	-12.34	6.28	-1.96	0.04*	0.04*

**$p < 0.01$; *$p < 0.05$


a
Human-interaction network strength (model-predicted)
0.4
0.3
0.2
0.1
Females
Males
Sex

429

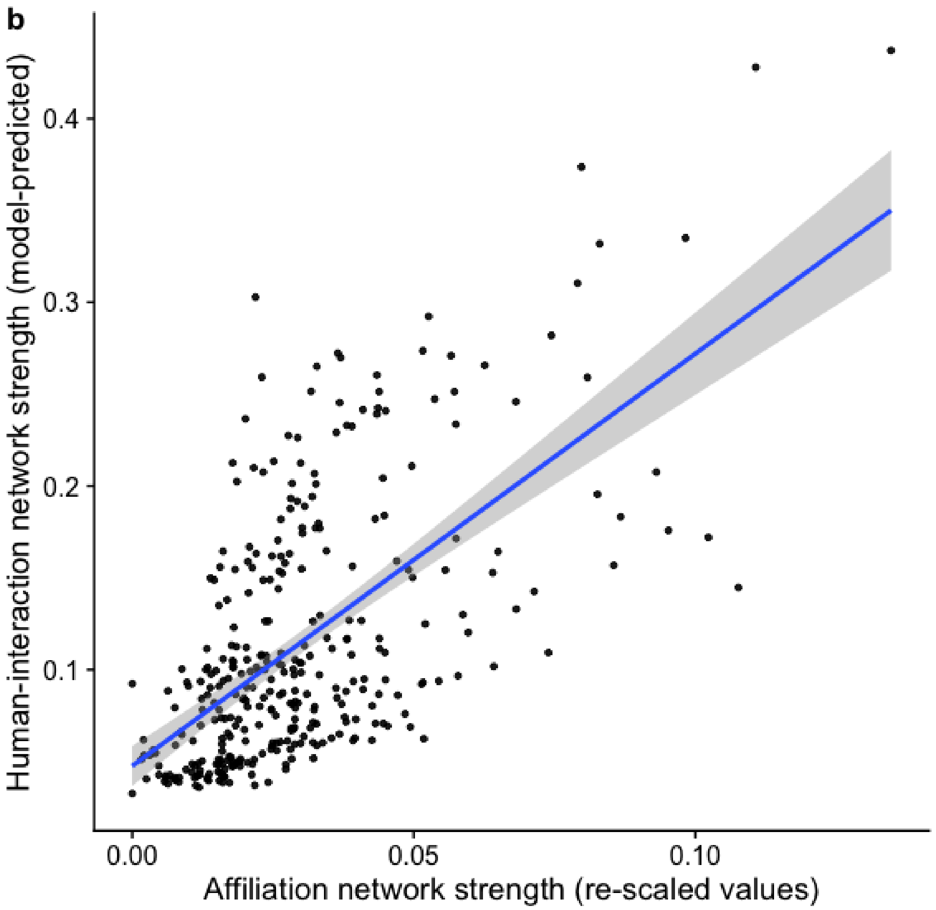


Figure 3: Effect of (a) sex and (b) affiliation strength centrality on the outcome of human-interaction network strength centrality

For eigenvector centrality, results were largely consistent. The first candidate model (Table 3A: model 3 of Supplementary Table 3) showed a significant positive effect of both short-duration affiliation eigenvector centrality (Fig. 4a) and proximity eigenvector centrality on human-interaction eigenvector centrality. The second candidate model (Table 3B: model 6 of Supplementary Table 3) further showed a significant interaction between proximity eigenvector centrality and species, which revealed that the effect of proximity was the strongest among bonnet macaques, moderately strong among rhesus macaques, and least strong (did not reach significance) among long-tailed macaques (Fig. 4b). Neither candidate model included grooming centrality measures, i.e. proximity and short-duration affiliation network centrality had a stronger (compared to grooming network centrality) impact on human-interaction network centrality. Macaque sex, but not dominance rank, had a significant impact on human-interaction network eigenvector centrality, with males showing greater values than females (Table 3A, B). However, unlike for strength centrality, there were no cross-species differences in mean human-interaction eigenvector centrality measures (Table 3A).

Table 3: Candidate GLMMs (models 3 and 6 of Supplementary Table 3) examining the effects of individuals' sociodemographic attributes (sex, dominance rank, species), and social network eigenvector centrality (grooming, proximity, and affiliation) by species, on their human-interaction network eigenvector centrality. P_{perm} indicate p values from permuted networks that were estimated using the post-network randomizations or 'node-swapping' algorithm (see Methods).

Model 3

Predictor	**B**	**SE**	**Z**	**P**	**P_{perm}**
(Intercept)	2.12	0.14	14.77	<0.01**	
Sex (males vs females)	0.18	0.11	1.61	0.01*	0.02*
Rank Index	-0.06	0.18	-0.33	0.74	
Species (long-tailed vs bonnet)	-0.07	0.13	-0.53	0.60	
Species (rhesus vs bonnet)	0.01	0.12	0.05	0.96	
Species (long-tailed vs rhesus)	-0.07	0.11	-0.67	0.50	
Proximity eigenvector	7.81	2.87	2.72	0.01*	0.01*

Affiliation eigenvector	6.94	2.58	2.69	0.01*	0.03*

456 **p < 0.01; *p < 0.05

457 Model 6

Predictor	**B**	**SE**	**Z**	**P**	**P_{perm}**
(Intercept)	1.71	0.25	6.93	<0.01**	
Sex (males vs females)	0.27	0.12	2.24	0.03*	<0.01**
Rank Index	-0.04	0.18	-0.20	0.84	
Species (long-tailed vs bonnet)	0.41	0.26	1.54	0.12	
Species (rhesus vs bonnet)	0.40	0.25	1.62	0.10	
Species (long-tailed vs rhesus)	0.00	0.18	0.02	0.98	
Affiliation eigenvector	5.52	2.69	2.05	0.04*	0.15
Proximity eigenvector (bonnets)	22.09	7.66	2.88	<0.01**	<0.01**
Proximity eigenvector (long-tailed)	6.22	3.40	1.83	0.07(*)	<0.01**
Proximity eigenvector (rhesus)	8.39	4.00	2.10	0.04*	<0.01**
Proximity eigenvector (long-tailed vs bonnets)	-15.87	7.80	-2.03	0.04*	<0.01**
Proximity eigenvector (rhesus vs bonnets)	-13.70	7.80	-1.76	0.08(*)	<0.01**
Proximity eigenvector (long-tailed vs rhesus)	-2.17	4.69	-0.46	0.64	0.15

458 **p < 0.01; *p < 0.05

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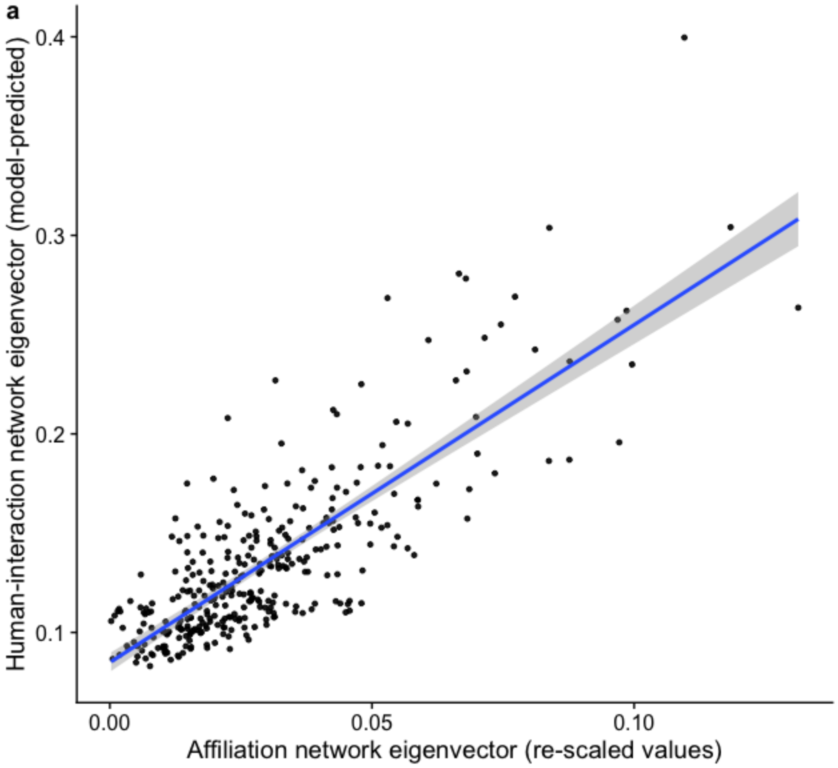
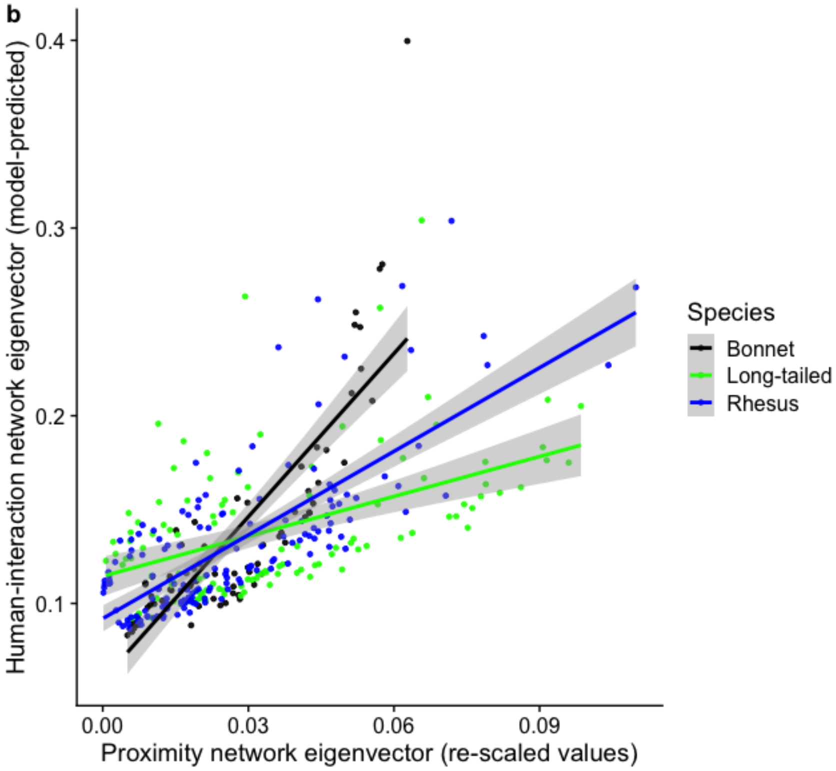

a
Human-interaction network eigenvector (model-predicted)
0.4
0.3
0.2
0.1
0.00
0.05
0.10
Affiliation network eigenvector (re-scaled values)

463


b
Human-interaction network eigenvector (model-predicted)
0.4
0.3
0.2
0.1
0.00
0.03
0.06
0.09
Proximity network eigenvector (re-scaled values)
Species
Bonnet
Long-tailed
Rhesus

464

Figure 4: Effects of (a) affiliation eigenvector centrality and (b) proximity eigenvector centrality by species on human-interaction network eigenvector centrality.

Discussion:

For multiple groups of wild macaques living in anthropogenic environments, we used a network-approach to reveal non-random patterns of associations in human-wildlife interactions. Moreover, we revealed that macaques' connectedness within their human-interaction networks were strongly influenced by aspects of their behavioral ecology. Below we discuss our findings, and their implications for understanding the behavioral ecology of human-wildlife interactions from both evolutionary and conservation perspectives.

For all macaque groups, human-interaction networks showed a non-random structure, confirming that macaques showed heterogeneous, non-random patterns of using anthropogenic features of their home range and engaging with humans across time and space. This finding provides an important pretext to conducting assessments of whether/how these non-random spatiotemporal associations of wild macaques and humans, are influenced by animal ecology and behavior (as we do in this study). This has important implications both for understanding animals' adaptive responses to dynamic anthropogenic environments, and for conservation- and public health-related initiatives (discussed below). In constructing human-interaction networks, we advanced previous studies that have focused on specific types of human-wildlife interactions (e.g. encounter rates, avoidance, contact-behaviors like aggression and food provisioning), or their overall frequencies of occurrence (reviewed in Balasubramaniam et al. 2020a), to focusing on patterns of human-wildlife associations as revealed by network connectedness. Researchers have been increasingly implementing social network analysis to understand human impact on animal-animal spatial and social behavior, but not necessarily to model human-wildlife interactions themselves (Snijders et al., 2017; Sosa et al., 2021a). Our construction of human-interaction networks addressed this gap. Indeed, approaches similar to ours may be used to construct other human-wildlife interaction networks in which terrestrial, group-living wildlife populations that overlap with anthropogenic environments (e.g. wild ungulates, elephants, other nonhuman primates like baboons and chimpanzees) may be inter-linked based on their shared spatiotemporal overlap and/or interspecies interactions with humans, livestock, or feral mammals.

Macaques' human contact networks were strongly associated with some aspects of their behavioral ecology, but not so with others. For instance, the connectedness of macaques within their human contact networks were strongly associated with their connectedness within networks of affiliative social interactions of short duration, but not so their grooming networks. In group-living primates, affiliative interactions bring proximate benefits such as the reduction of stress levels (Aureli et al., 1999; Shutt et al., 2007), underlie strong alliances between kin and friends (van Hoof & van Schaik, 1992), and are key to the establishment and maintenance of strong long-term social bonds (Silk et al. 2003; Young et al., 2014). Our previous work on these populations revealed how monitoring human activity reduced the time available for macaques to engage in grooming (rhesus macaques: Kaburu et al., 2019b; longtailed macaques: Marty et al., 2019; bonnet macaques: Balasubramaniam et al., 2020b), but not necessarily for other short-duration affiliative interactions like coalitionary support, lip-smacking, and silent bare-teeth displays in non-aggressive contexts which remained unaffected (bonnet macaques: Balasubramaniam et al., 2020b).

One of the primary motivations for monkeys to interact with humans is to obtain anthropogenic foods (Marty et al., 2020). The benefits of within-group social cohesion and tolerance may, at least in part, help offset the potential physiological and health-related costs or risks involved in gaining access to these foods. Thus, we speculate that in anthropogenic environments in which wild primates may routinely face time-constraints, animals may rely more than usual on short-duration affiliative interactions, which may be especially key to maintaining group cohesion and strong ties of social support when animals have to compromise on their grooming time. Such ties of short-duration affiliative interactions may also encourage collective (and perhaps even cooperative) risk-taking as indicated by animals' co-engagement with humans at the same time and space to procure anthropogenic foods. Our finding of strong, consistent (across multiple groups and three species) associations between macaques' connectedness within their short-duration affiliative social networks and their human-interaction networks supports this argument.

Human-interaction networks were also influenced by social proximity networks, with the effect sizes being different across species. They were the strongest for bonnet macaques and the weakest for long-tailed macaques, with rhesus macaques falling in-between. Species-typical differences in behavior that is also linked to differences in evolutionary history may at least partly explain these patterns. In comparison to rhesus macaques and long-tailed macaques, bonnet macaques are considered to be more socially tolerant (Balasubramaniam et al. 2012; Thierry, 2007), are less widely distributed and less ecologically flexible (Gumert, 2011; Priston & McLennan, 2013; Radhakrishna & Sinha, 2011), and have had a shorter (in evolutionary time-scales) history of exposure to changing, anthropogenically impacted environments (Gumert, 2011; Priston & McLennan, 2013; Radhakrishna & Sinha, 2011). More generally, these patterns across macaques suggest that in group-living wildlife characterized by more tolerant social systems and/or less ecological flexibility (e.g. bonnet macaques compared to rhesus and long-tails), being near familiar individuals such as close kin or conspecifics may encourage greater propensities among individual animals to take risks in anthropogenic environments. On the other hand, cross-site, or indeed even within-site differences in the distribution and density of anthropogenic factors and (consequently) human-macaque interactions, may also underlie these observed cross-species. For instance, bonnet macaques experienced the overall lowest densities of humans, and their interactions with humans were also more concentrated when the groups were within specific areas (blocks) of their home-range (McCowan, *Unpublished Data*). In comparison, rhesus and (especially) long-tailed macaques were exposed to higher densities of humans, and their interactions with humans were also more widely distributed across the groups' home-ranges (McCowan, *Unpublished Data*). It is therefore likely that rhesus and long-tailed macaques, more so than bonnet macaques, engaged with humans both preferentially while being near their conspecifics, as well as opportunistically when they were not near their conspecifics. More comprehensive tests of these explanations await future research that quantitatively evaluates, rather than controls for (as was done in this study), intraspecific variation within and across groups of the same species.

Macaques' sex also had an effect on their connectedness within human-interaction networks: males were more well-connected than females. Sex-based differences may also reflect differences in life-history requirements and the socioecological roles of males and females. While philopatric females usually form the core of macaque social networks, dispersing males tend to be more exploratory, stay in the group periphery, and (consequently) experience more frequent interactions (Balasubramaniam et al., 2020a; Morrow et al., 2019). Moreover, across group-living mammals, males face high long-term energetic demands pertaining to their life-history requirements of maintaining large body sizes and other physical features (e.g. horns, antlers, canines) that render competitive and reproductive advantages (Clutton-Brock, 2017). Thus, a combination of their exploratory behavior, movement and dispersal, and life-history requirements that may entail greater risk-taking (Balasubramaniam et al., 2020a; Morrow et al., 2019), may explain why males are more central or well-connected within human-interaction networks than females.

One methodological limitation in our construction of human-interaction networks concerned the lack of more precise information on these interactions. Although we contained the assignment of links based on interactions within the same block and time-frame, the construction of more conservative, albeit more sparsely-connected, human-interaction networks may have been possible if we had restricted links to interactions that occurred between macaques and the same human(s), and at the same precise GPS location. Collecting more precise geospatial data on human-macaque interactions would be a vital next step. Moreover, implementing multi-level approaches (Finn et al., 2019) to capture potential heterogeneity in human-interaction patterns across different spatial (blocks) and temporal (observation windows) layers was also beyond the scope of this study, but another important next step. Finally, our results may have been impacted by spatiotemporal variation in human density, which, through affecting the overall frequencies of human-macaque interactions, may also impact the connectedness of macaques within their human-interaction networks. We will assess this possibility in a future assessment of intraspecific variation in these networks.

Our study has important implications for the conservation and management of human-wildlife interfaces. Macaques that are more well-connected within their human-interaction networks, because of their coming into contact with more people across time and space, may be targets of interventions that move human-primate interactions from conflict towards coexistence (Nyhus, 2016). Human-wildlife interfaces, now more so than ever before, are also widely recognized as 'hotspots' for the transmission of zoonotic and emerging infectious disease, including SARS-CoV-2 (Cunningham et al., 2017; Townsend et al., 2020). From an epidemiological perspective, it is now well-established that animals that are central within their contact social networks may function as within-group 'superspreaders' of infectious agents (Craft, 2015; Drewe & Perkins, 2015). Similarly, it is likely that macaques that are central within human-interaction networks may be disease 'superspreaders' both within wildlife systems and across human-wildlife interfaces, making these animals particularly important targets of disease intervention strategies like vaccination and antibiotic treatment (Rushmore et al., 2014). Indeed, our finding of a lack of association between macaques' human-interaction networks and contact social grooming networks suggests that human-interaction and social contact networks may offer somewhat independent socioecological pathways for disease spread. Assessing the vulnerability versus resistance of both types of networks to zoonotic transmission and disease outbreaks would therefore be vital from conservation and public health perspectives.

Acknowledgements:

We thank various organizations, specifically the Himachal Pradesh Forest Department (HPFD), Economic Planning Unit Malaysia, the Forestry Department of Peninsular Malaysia, the Department of Wildlife and National Parks Peninsular Malaysia, Tourism Selangor, and the Kerala Forest and Wildlife Department, for giving us permission and logistical support to conduct research in India and Malaysia. We thank several research assistants - Shelby Samartino, Balasubramaniam et al. Mohammed Ismail, Taniya Gill, Alvaro Sobrino, Rajarshi Saha, Camille Luccisano, Eduardo Saczek, Silvia La Gala, Nur Atiqua Tahir, Rachael Hume, Kawaljit Kaur, Bidisha Chakraborty, Benjamin Sipes, Nalina Aiempichitkijkarn, Pooja Dongre, and Menno van Berkel - for their assistance with data collection, processing, and storage in the field. The authors were supported by the U.S. National Science Foundation (Grant no. 1518555) awarded to PI McCowan.

Author Contributions:

K.N.B (first- and corresponding-author), under the supervision of B.M. (last-author), took the lead in in the study design, supervision of data collection, and the conductance of data analysis and manuscript writing. B.A.B. and E.B.M. were involved in the study design and manuscript writing. P.M., S.S.K., and M.A. all helped design the study, supervised data collection, and participated in manuscript writing. N.R., A.I., S.A.M.S., L.M., S.R., and U.K. helped formulate and implement data collection protocols in India and Malaysia, and participated in manuscript writing as co-authors. B.M. supervised the entire study.

Data Availability:

The data used for this manuscript is available with the corresponding-author, and will be made available to reviewers upon request. It will be made publicly available through an online repository if or when the manuscript is accepted for publication.

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