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

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Abstract:

1. Human population expansion into wildlife habitats has increased interest in the behavioral ecology of human-wildlife interactions. To date, however, the socio-ecological factors that determine whether, when or where wild animals take risks by interacting with humans and anthropogenic factors still remains unclear.
2. We adopt a comparative approach to address this gap, using social network analysis (SNA). SNA, increasingly implemented to determine human impact on wildlife 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 co-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, within all macaque groups, specific individuals jointly took risks by repeatedly, consistently co-interacting with humans within and across time and space. GLMMs revealed that macaques' tendencies to co-interact with humans was positively predicted by their tendencies to engage in short-duration affiliative interactions and tolerance of conspecifics, although the latter varied across species (bonnets>rhesus>long-tailed). Male macaques were more likely to co-

interact with humans than females. Neither macaques' grooming relationships nor their dominance ranks predicted their tendencies to co-interact with humans.

5. Our findings suggest that, in challenging anthropogenic environments, less (compared to more) time-consuming forms of affiliation, and additionally greater social tolerance in less ecologically flexible species with a shorter history of exposure to humans, may be key to animals' joint propensities to take risks to gain access to resources. For males, greater exploratory tendencies and less energetically demanding long-term life-history strategies (compared to females), may also influence such joint risk-taking. From conservation and public health perspectives, wildlife connectedness within such co-interaction networks may inform interventions to mitigate zoonosis, 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; Carter et al., 2014; Lischka et al., 2018). The sub-field of conservation behavior addresses this gap, and largely deals with the impact of anthropogenic factors and human-wildlife interactions on wildlife socioecology, i.e. 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 how wildlife socioecology, for instance animals' life-history strategies and their interactions with their conspecifics, might in turn impact animals' navigation of anthropogenic environments and tendencies to interact with humans (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).

To-date, only 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 with conspecifics in terms of when, where or how they interact with humans.

Understanding such patterns of associations between conspecifics among free ranging animals in the context of human-wildlife interactions is important from both evolutionary and conservation perspectives. First, capturing the dynamic, spatiotemporally variable 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). For socioecologically flexible wildlife species, navigating anthropogenic environments entails taking risks to procure high-energy human foods, that may increase wild animals' exposure to anthropogenic factors and their interactions with people (Balasubramaniam et al., 2020a; Chiyo et al., 2012; Lischka et al., 2018; Marty et al., 2020; Morrow et al., 2019). So, assessing patterns of spatiotemporal associations between conspecifics in human-wildlife interactions could offer insights into whether wild animals and their conspecifics attempt to navigate these environments through joint risk-taking behavior, for instance by consistently and repeatedly co-engaging with humans across time and space to procure anthropogenic foods. From a public health perspective, such research 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). Such animals may also be the targets of other conservation efforts, interventions and policy making aimed at moving human-wildlife interactions from conflict towards 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 interactions, 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 network analysis (SNA) 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 to the fragmentation of social networks (e.g. the simulated removal of nodes in networks of Killer whales, *Orcinus orca*: Williams & Lusseau, 2006). Such findings are of profound importance since decreased social network connectedness or fragmentation can impact animal health and reproductive success (Nunn et al., 2015). Yet while most SNA studies have focused on space-use overlap or social interaction networks, little research has implemented SNA to model human-wildlife interactions themselves. A recent, exceptional study on feral dogs used SNA to show that dog-dog social interactions were mediated by interactions between dogs and humans (Bhattacharjee & Bhadra, 2021). However, SNA is yet to be used to examine associations between free-ranging animals that co-inhabit anthropogenic components of their environment, or jointly take risks by co-interacting with humans, at the same time and space (Sosa et al., 2021a).

In this study, we address the above gaps in our current understanding of the ecology of human-wildlife interactions. We do so by implementing comparative, network-based approaches to understand whether free-ranging nonhuman primates engage in joint risk-taking behavior in anthropogenic environments by co-interacting with humans. We also ask whether such co-interactions are influenced by animals' socioecology, and their sociodemographic characteristics related to their evolutionary history and life-history strategies. 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 variable 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 both competitive (i.e. aggression, submissive status signaling) and cooperative (e.g. grooming, tolerance through proximity, other forms of affiliation such as lip-smacking and coalitionary support during conflicts) social interactions and (consequently) social network connectedness with their conspecifics. Such variation in macaques' social networks has previously been 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 this study.

We constructed ‘human co-interaction networks’ for ten groups of three macaque species living in anthropogenic environments in India and Malaysia. These networks linked individual, pre-identified macaques and their group conspecifics based on their tendencies to co-interact with humans within the same time and space. To determine whether macaques were prone to jointly take risks by consistently and repeatedly co-interacting with humans within and across time and space, we first tested whether (1) the connectedness of macaques within their human co-interaction networks was significantly greater than expected by chance. Second, we examined whether (2) macaques’ tendencies to jointly take risks were also influenced by aspects of their socioecology and sociodemography. Specifically, we tested whether macaques that were more well-connected to others, i.e. more central within their social networks of grooming, tolerance or (hereafter) proximity, and affiliative interactions of shorter durations, were also more well-connected or central within their human co-interaction networks. Furthermore, we tested whether males and higher-ranking individuals of both sexes, given their relatively greater exploratory tendencies and energetic demands compared to females and lower-ranking macaques (Balasubramaniam et al., 2020a; Marty et al., 2020; Morrow et al., 2019), were more prone to joint risk-taking through being more well-connected in their co-interaction networks. As a cross-species comparative component, we also explored whether the above-predicted associations between macaques’ human co-interaction network connectedness and social network connectedness varied across different macaque species.

Materials and Methods:

Study sites and subjects: We collected demographic and behavioral data 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 in the city center (one group) 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).

Supplementary Table 1 provides details on the duration and periods of data collection, study groups, and subjects. We collected data for a period of 16-18 months (July 2016 – May 2018) for rhesus macaques in Northern India and long-tailed macaques in Malaysia, and for a period of 11 months (July 2017 – May 2018) for bonnet macaques in Southern India. Despite these cross-site differences in observation period, all groups were observed for substantial amounts of time, that were also closer to each other than expected since we observed just two bonnet macaque groups compared to four groups each of rhesus and long-tailed macaques (Supplementary Table 1). In any case, we accounted for differences in observation times in our network constructions and analyses (see details below). Although seasonal differences may have impacted intraspecific variation in macaque ecology and behavior, more in-depth longitudinal assessments of such variation were beyond the scope of this study (see Discussion). As such, the data analyzed in this study spanned the entire duration of data collection and therefore the breath of both seasons and times of the day (9:00 am – 5:00 pm: see below).

Subjects were all adult males and females within each group. All subjects were pre-identified using facial and other physical features during a ~2 month preliminary phase prior to the commencement of data collection at each site. 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 co-interaction patterns. 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: We collected data 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. Moreover, 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 the preliminary phase (see above) during which 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).

We defined a 'human-macaque interaction' 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).

We used ‘focal animal sampling’ (Altmann, 1974) to record macaque-macaque social interactions and social proximity with conspecifics. On each day, and in each location, we followed individual macaques 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 co-interaction networks and social networks: For each macaque group, we constructed weighted, undirected ‘human co-interaction networks’ based on the spatiotemporal similarity of monkeys’ interactions with humans (Fig. 1a). That is, we assigned 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. Such reconstructions enable determining whether macaques were associated by way of their consistent and repeated tendencies to jointly take risks by co-interacting with humans within the same time and anthropogenic space, and (ultimately) the factors that influence such associations. Edge-weights were calculated and assigned to these human co-interaction networks, as the ratio between the total number of such occasions in which pairs of macaques ‘co-interacted’ with humans within the same block and time-period, to the total duration of event sampling sessions conducted during the course of their overlapping tenure within their group. This approach accounted for the observability of each pair of macaques within a particular group, although not necessarily for their propensities to co-occur at these blocks at the same time and (thereby) their opportunities to interact with humans (we provide an alternative approach to account for the latter in the data analysis described below; see also Discussion).

For each macaque group, we also constructed three types of weighted, undirected ‘social 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. We used the conservative criterion of animals within body-length (as opposed to more liberal criteria of proximity within 3 meters) to better capture and distinguish social tolerance of conspecifics from aggregations of animals that simply overlap or share the same space (Adams et al., 2012; Albery et al., 2020; Pawley & McArdle, 2018; more details in the Discussion).

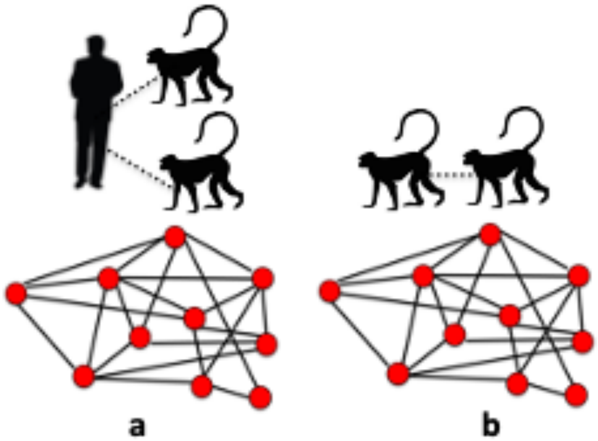


Figure 1: Macaque (a) co-interaction networks (dotted line inter-linking two macaques via their joint interactions with humans) and (b) social networks (dotted line directly inter-linking two macaques that share a social interaction).

Calculations of dominance rank and social network centrality: 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). Perc is a network-based ranking method that combines information from direct dominance interactions with information from multiple indirect dominance pathways (via common third parties) to quantify dyadic dominance relationships, and uses these to generate ordinal ranks (Fujii et al., 2015). Perc has been implemented in several of our previous studies to estimate rank orders of macaque groups (e.g. Balasubramaniam et al., 2016; Marty et al., 2019; Vandeleest et al., 2016). Moreover, the method has been shown to yield rank orders that are consistent with those yielded by other, popularly used methods by behavioral ecologists such as David's score, I&SI ranks, and Elorating (Funkhouser et al., 2018). 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. Our choices of which centrality measures to calculate were informed by their biological relevance, using the decision-trees provided in Sosa et al. (2021b). In the context of our human co-interaction networks, we were interested in the extent to which individual macaques co-engaged with humans at the same time and space as others. To determine this, we calculated each macaque's direct co-engagement with humans with other macaques, i.e. their *weighted degree* or (hereafter) *strength centrality*, as the sum of all the edge-weights of edges directly connected to an individual (Croft et al., 2008; Newman, 2003). Moreover, we were also interested in determining 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. To this end, we also calculated *eigenvector centrality*, 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). In summary, we anticipated that these two measures of individuals' connectedness would be the most biologically relevant to understanding the socioecological underpinnings of macaques' joint propensities to co-engage in risk-taking behaviors to access anthropogenic foods (this study), as well as 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 (see Discussion). 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 obtain percentile scores, i.e. to lie between 0 (lowest score) and 1 (highest score). Centrality measures were calculated using the 'Igraph' package in R (Csardi & Nepusz, 2006).

Data analysis: To assess whether macaques consistently and repeatedly engaged or co-interacted with humans within and across time and space (1), we used 'null-model' pre-network randomization tests (Farine, 2017; Farine & Carter, 2020). For each human co-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 permuted networks. These permuted networks were constructed after randomly swapping the identities of interactants from the raw data that was used to construct the original network. Thus, permuted networks retained some key characteristics of the original network the number of nodes (individuals) and the total number of edges (Farine, 2017). They were, therefore, useful in determining whether, for a given network size and total number of connections, the observed connectedness of macaques within their human co-interaction networks was significantly greater than expected by chance. Recent studies have shown that pre-network randomizations are more reliable than post-network randomization tests (i.e. node-swapping: Farine, 2017) to test 'null' hypotheses pertaining to the (non)randomness of network connectedness (Puga-Gonzalez et al., 2020).

To test whether macaques that were more well-connected or central within their social networks were also more central within their human co-interaction networks (2), we ran Generalized Linear Mixed-effects Models (GLMMs) with a Beta error structure, using the 'glmmtmb' package in R (Magnusson et al., 2019). We selected a Beta error structure since our outcome variables ranged between 0 and 1. For an effective sample size of 338 macaques (after removing one influential case: see below) across ten groups, we ran two sets of GLMMs, one for each of two outcome variables of macaques' human co-interaction network centrality measures, i.e. strength centrality and eigenvector centrality (Supplementary Tables 2 and 3). Each model-set consisted of seven models. We implemented a corrected Akaike Information Criterion (AICc) to select and interpret the best-fit model from each set, using the MuMIn package in R (Burnham & Anderson, 2002; Burnham et al. 2011).

Rather than testing multiple combinations of predictor variables and risking Type-I errors, our model sets were composed of seven, carefully constructed models that were informed by the hypotheses we were testing (Burnham et al., 2011). In all models, we included macaques' sociodemographic attributes (i.e. sex, dominance rank, species) as main effects, and group ID as a random effect. To control for the time spent by macaques at the interface areas (blocks), and their overall exposure or opportunities to interact with people which may influence their connectedness within human co-interaction networks, we also included macaques' overall proximity to humans (proportions of time spent within three meters of one or more humans) as a main effect in all the models. In each model set, the first model (model 1 of Supplementary Tables 2 and 3) was effectively the 'null' or 'control' model that did not include any social network centrality measures as main effects. Models 2 and 3 included measures of macaques' centrality within their grooming and short-duration affiliation networks (model 2), and proximity and short-duration affiliation networks (model 3) respectively. This was because grooming and proximity network centrality measures (but not short-duration affiliation networks) were collinear, and so could not be included in the same model. Finally, models 4 to 7 were more complex versions of models 3 and 4, as they included interaction terms between species and each social network centrality measure to explore cross-species differences in the effects of social network centrality on human co-interaction network centrality.

From each model set, we shortlisted and interpreted model summary parameters from a single, best-fit model that had the lowest AICc score, that was also < 8 AICc points from the next best-fit model (Burnham et al., 2018; Harrison et al., 2018). Such a large difference of AICc points is a more conservative criterion than a difference of 2 points that is otherwise accepted (Burnham et al., 2011), and has been suggested as being more appropriate for model selection under many circumstances as it further minimizes the likelihood of Type-I errors (Burnham et al., 2011; Harrison et al., 2018). To account for inter-dependencies in human co-interaction network measures examined as outcome variables, we used a post-network 'node-swapping' randomization procedure to calculate permuted p (p_{perm}) values for the observed model coefficients for predictor variables that showed significant effects in each candidate model (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 co-interaction centrality scores through randomly swapping the nodes of each human co-interaction network. We preferred post-network randomizations to pre-network randomizations in this case, since this approach is less susceptible than the latter to type-II errors while testing regression-based null hypotheses (Weiss et al., 2020).

We used the *influence_mixed* and *infIndexPlot* functions to check the presence of influential observations. This revealed a single influential case, which was subsequently omitted from the analyses. We confirmed that all GLMMs met the necessary assumptions of model validity (i.e., distribution of residuals, residuals plotted against fitted values: Quinn & Keough, 2002). All statistical tests were two-tailed, and we set the p values to attain statistical significance to be < 0.05.

Results:

(1) Macaques' joint engagement or co-interactions with humans:

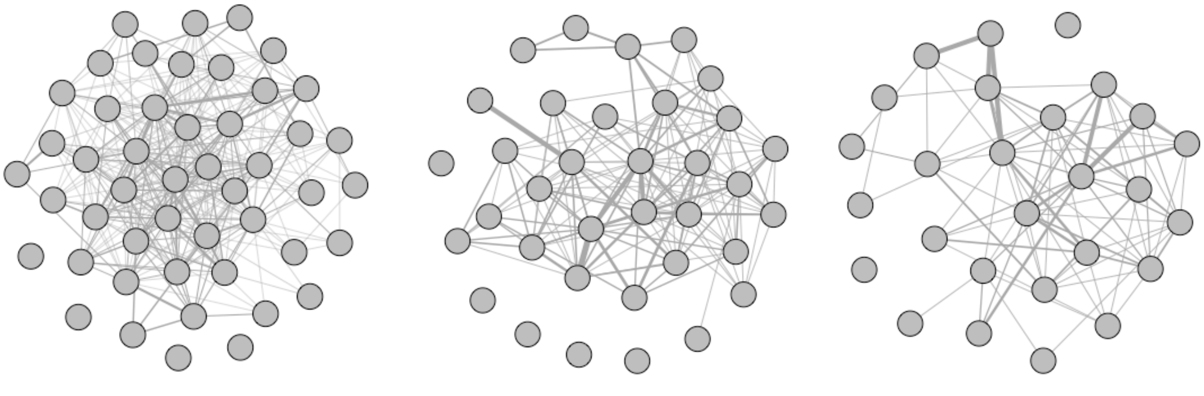
Across macaque groups and species, we found evidence to suggest that macaques took joint risks by co-interacting with humans. For all ten macaque groups, human co-interaction networks were more well-connected than expected by chance (examples in Fig. 2a-c). Table 1 summarizes the attributes and characteristics of each network. The majority of human co-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 co-interaction strength of individuals (Table 1). Despite these features, pre-network randomization tests 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 networks generated by swapping the identities of the individuals from the original edge-list. That is, all networks deviated significantly from the null hypothesis of random connectedness, suggesting that specific macaques consistently, repeatedly co-interacted with humans within and across time and space.

Table 1: Summary of attributes of macaques' human co-interaction networks. For mean strength, p values are based on pre-network randomization tests (see Methods)

Species (group)	**Network (group) Size**	**Males**	**Females**	**Edges or links**	**Unconnected individuals**	**Strength[1] (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**

**$p < 0.01$

[1] Values were calculated from raw strength scores calculated for each macaque as the sum of its edge-weights that factored in co-interactions with humans within the same time and space per unit observation effort during their shared tenure within the group



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

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

(2) Effects of macaques' social networks and sociodemography on their human co-interaction networks:

We found that aspects of macaques' social network centrality (specifically short-duration affiliation centrality and proximity centrality) and sociodemography (specifically species and sex) influenced their tendencies to co-interact with humans.

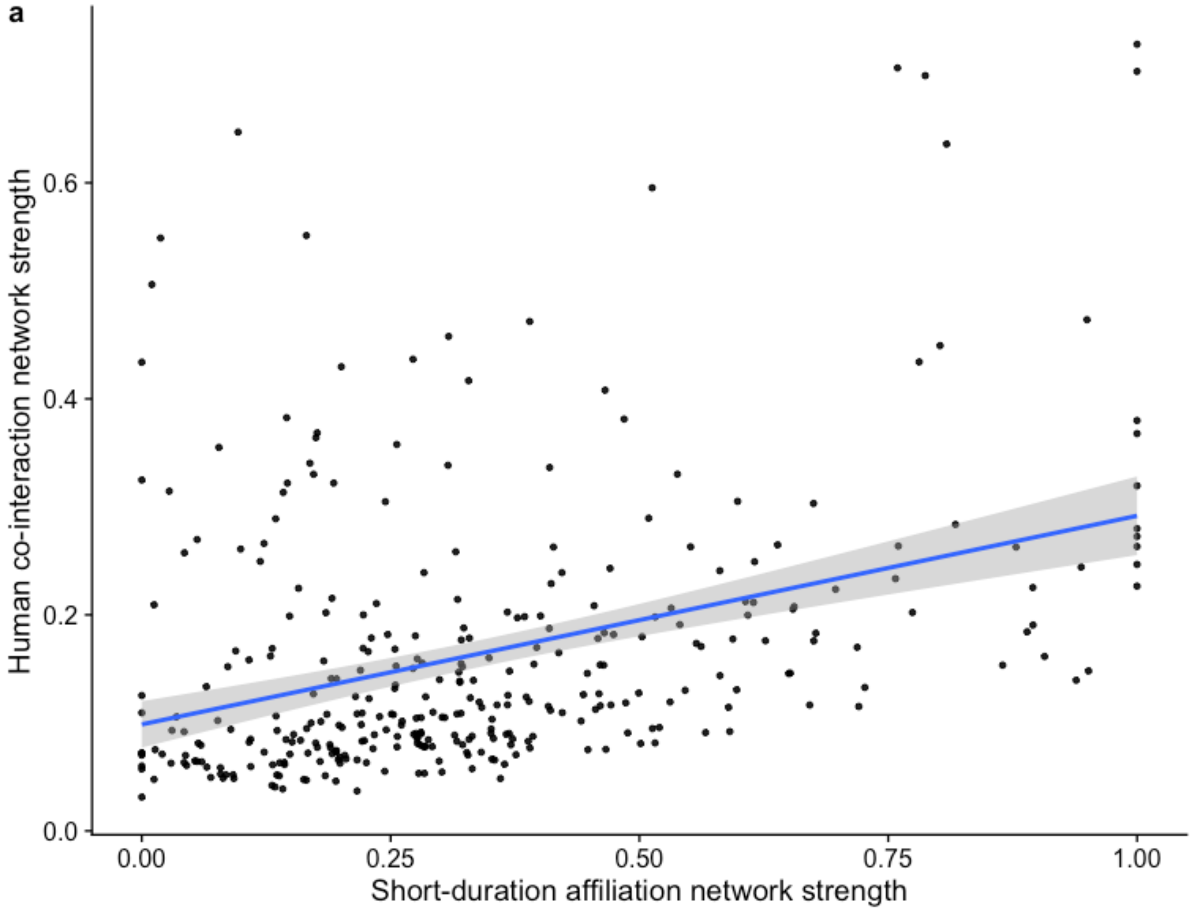
For macaques' strength centrality within their human co-interaction networks, the best-fit model (model 6 from Supplementary Table 2: dAICc of < 8 from the next best-fit model) included short-duration affiliation centrality and proximity centrality, but not grooming centrality (Table 2). Specifically, this model showed a significant positive effect of short-duration affiliation strength centrality on human co-interaction strength centrality (Table 2; Fig. 3a). There was also a significant interaction between proximity strength centrality and species, which revealed that the effect of proximity strength centrality on human co-interaction strength centrality was most pronounced among bonnet macaques, moderate but still significant among rhesus macaques, and least pronounced (did not reach significance) among long-tailed macaques (Table 2; Fig. 3b). Macaque sex had a significant impact on human co-interaction strength centrality, with males showing greater values than females (Table 2; Fig. 3c). However, dominance rank had no effect on human co-interaction strength centrality (Table 2).

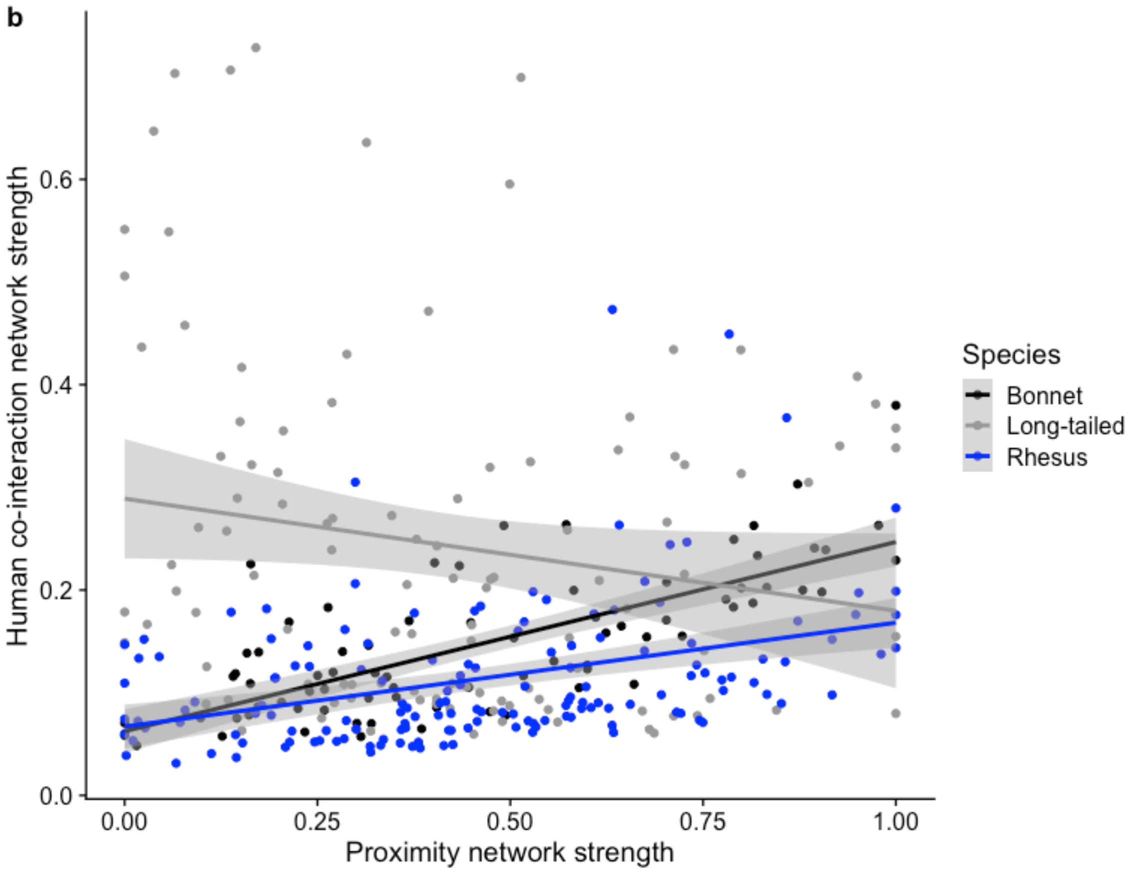
Table 2: Candidate GLMM (model 6 of Supplementary Table 3) examining the effects of individuals' sociodemographic attributes (sex, dominance rank, species), and social network strength centrality (short-duration affiliation, and proximity by species), on their human co-interaction network strength centrality. Macaques' overall proximity to humans, i.e. an indicator of their presence at the interfaces and thereby their opportunities to interact with humans, was included as a 'control' predictor variable. P_{perm} indicate p values from permuted networks that were estimated using the post-network randomizations or 'node-swapping' algorithm (see Methods).

Predictor	**B**	**SE**	**Z**	**P**	P_{perm}
(Intercept)	-3.83	0.49	-7.87	<0.01**	
Sex (males vs females)	0.60	0.15	4.01	<0.01**	<0.01**
Rank Index	0.23	0.20	1.14	0.25	
Species (long-tailed vs bonnet)	1.83	0.56	3.27	<0.01**	<0.01**
Species (rhesus vs bonnet)	0.39	0.56	0.69	0.49	
Species (long-tailed vs rhesus)	1.44	0.45	3.18	<0.01**	<0.01**
Human proximity	1.06	0.23	4.64	<0.01**	<0.01**
Short-duration affiliation strength centrality	0.67	0.27	2.45	0.01*	
Proximity strength centrality (bonnets)	2.06	0.46	4.50	<0.01**	<0.01**
Proximity strength centrality (long-tailed)	-0.40	0.34	-1.17	0.24	0.18
Proximity strength centrality (rhesus)	0.98	0.35	2.78	0.01*	<0.01**
Proximity strength centrality (long-tailed vs bonnets)	-2.45	0.52	-4.69	<0.01**	<0.01**

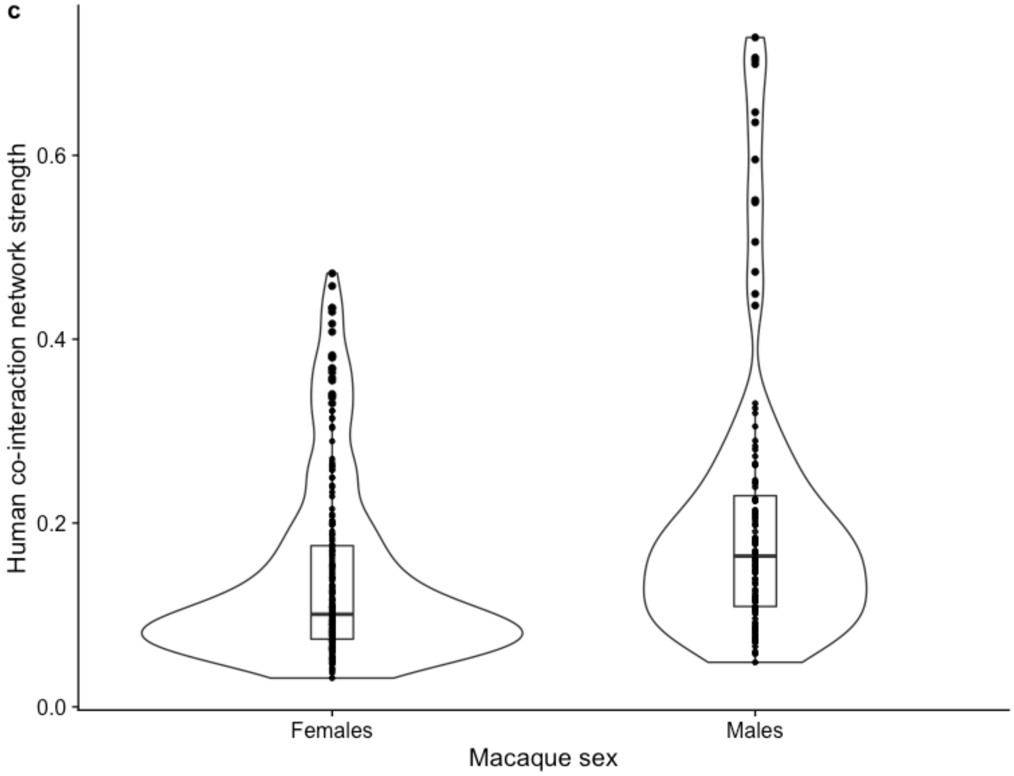
Proximity strength centrality (rhesus vs bonnets)	-1.08	0.51	-2.10	0.04*	
Proximity strength centrality (long-tailed vs rhesus)	-1.37	0.44	-3.10	<0.01**	0.04*

**p < 0.01; *p < 0.05




b
Human co-interaction network strength
0.0
0.2
0.4
0.6
0.00
0.25
0.50
0.75
1.00
Proximity network strength
Species
Bonnet
Long-tailed
Rhesus

486


c
Human co-interaction network strength
0.0
0.2
0.4
0.6
Females
Males
Macaque sex

487

Figure 3: Effect of macaques' (a) short-duration affiliation strength, (b) proximity strength by species, and (c) sex, on their human co-interaction network strength. For the effect of sex (c), the box-and-violin plot indicates the median (horizontal line in the middle of each box), the inter-quartile ranges (boxes), data-points including outliers (whiskers), and the probability density of the data at different values (violins).

The results were consistent for eigenvector centrality. Once again, the best-fit model (model 6 from Supplementary Table 3: dAICc of < 8 from the next best-fit model) was one that included short-duration affiliation eigenvector centrality and proximity eigenvector centrality, but not grooming eigenvector centrality (Table 3). Individuals' short-duration affiliation eigenvector centrality showed a non-significant trend to be positively associated with their human co-interaction network centrality (Table 3). As with the strength model, there was a significant interaction between proximity eigenvector centrality and species, which revealed that the effect of proximity eigenvector centrality on co-interaction eigenvector centrality was most pronounced among bonnet macaques, moderate but still significant among rhesus macaques, and least pronounced (did not reach significance) among long-tailed macaques (Table 3; Fig. 4). As with strength centrality, there was also a significant effect of macaques' sex - males showed greater co-interaction eigenvector centrality than females (Table 3). Finally, dominance rank had no effect on human co-interaction network eigenvector centrality (Table 3).

Table 3: Candidate GLMM (model 6 of Supplementary Table 3) examining the effects of individuals' sociodemographic attributes (sex, dominance rank, species), and social network eigenvector centrality (short-duration affiliation, and proximity by species), on

their human co-interaction network eigenvector centrality. Macaques' overall proximity to humans, i.e. an indicator of their presence at the interfaces and thereby their opportunities to interact with humans, was included as a 'control' predictor variable. P_{perm} indicate p values from permuted networks that were estimated using the post-network randomizations or 'node-swapping' algorithm (see Methods).

Predictor	**B**	**SE**	**Z**	**P**	**P_{perm}**
(Intercept)	-2.98	0.48	-6.15	<0.01**	
Sex (males vs females)	0.64	0.16	3.96	<0.01**	<0.01**
Rank Index	0.31	0.22	1.40	0.16	
Species (long-tailed vs bonnet)	0.91	0.57	1.60	0.11	
Species (rhesus vs bonnet)	0.62	0.56	1.11	0.27	
Species (long-tailed vs rhesus)	0.29	0.47	0.61	0.54	
Human proximity	0.89	0.26	3.42	<0.01**	<0.01**
Short-duration affiliation eigenvector centrality	0.46	0.28	1.64	0.10	0.09(*)
Proximity eigenvector centrality (bonnets)	2.24	0.45	5.03	<0.01**	<0.01**
Proximity eigenvector centrality (long-tailed)	0.25	0.38	0.67	0.50	0.58
Proximity eigenvector centrality (rhesus)	0.90	0.39	2.30	0.02*	<0.01**
Proximity eigenvector centrality (long-tailed vs bonnets)	-1.99	0.53	-3.73	<0.01**	<0.01**
Proximity eigenvector centrality (rhesus vs bonnets)	-1.34	0.52	-2.56	0.01*	<0.01**

Proximity eigenvector centrality (long-tailed vs rhesus)	-0.65	0.50	-1.30	0.19	0.15

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

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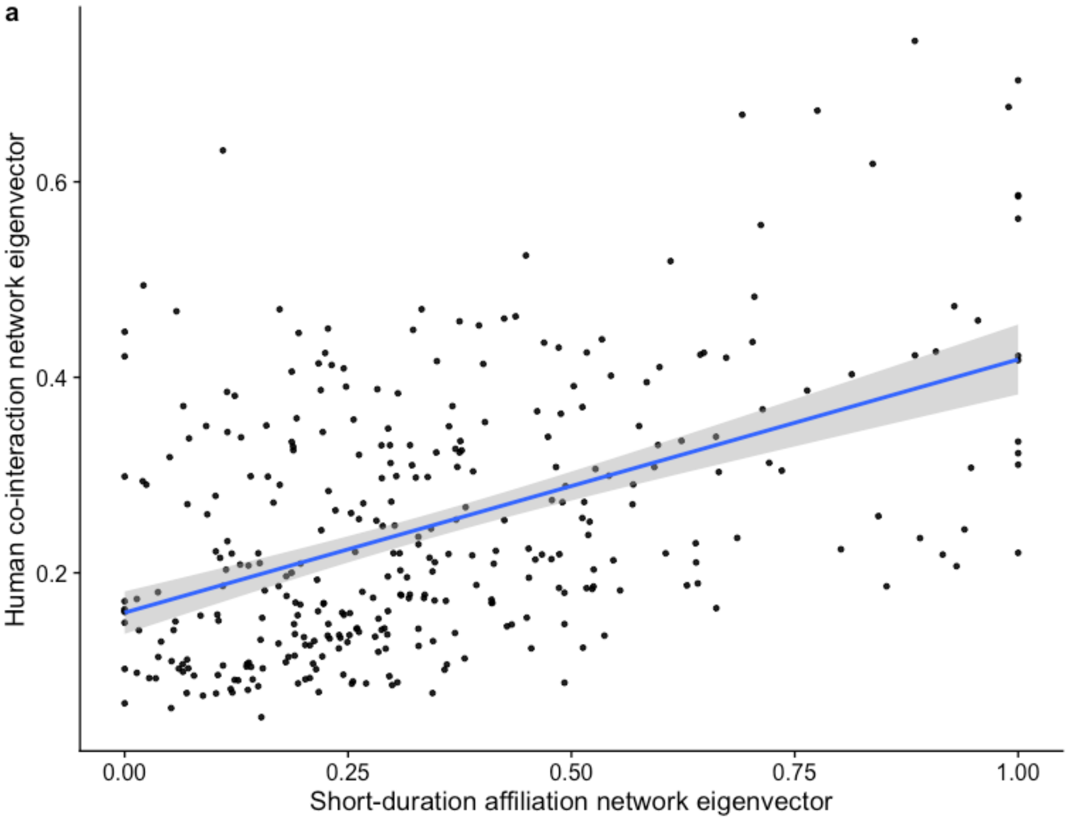

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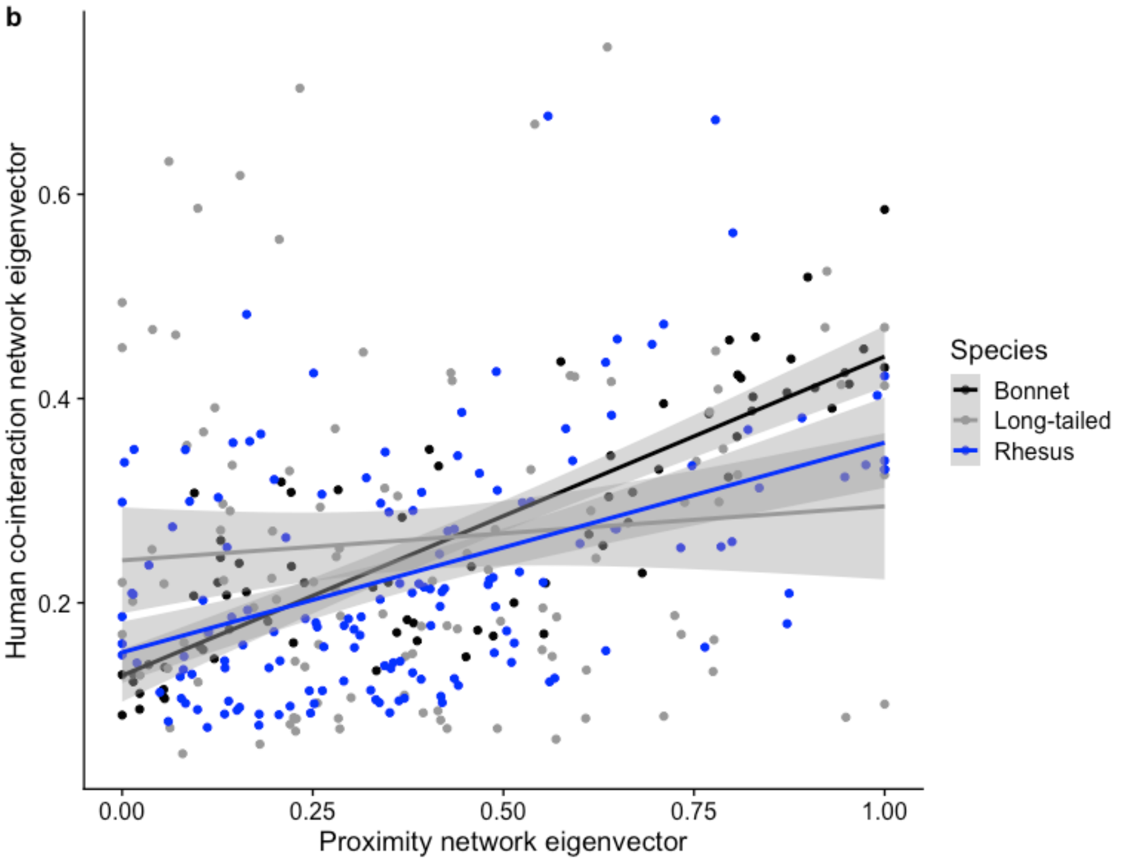
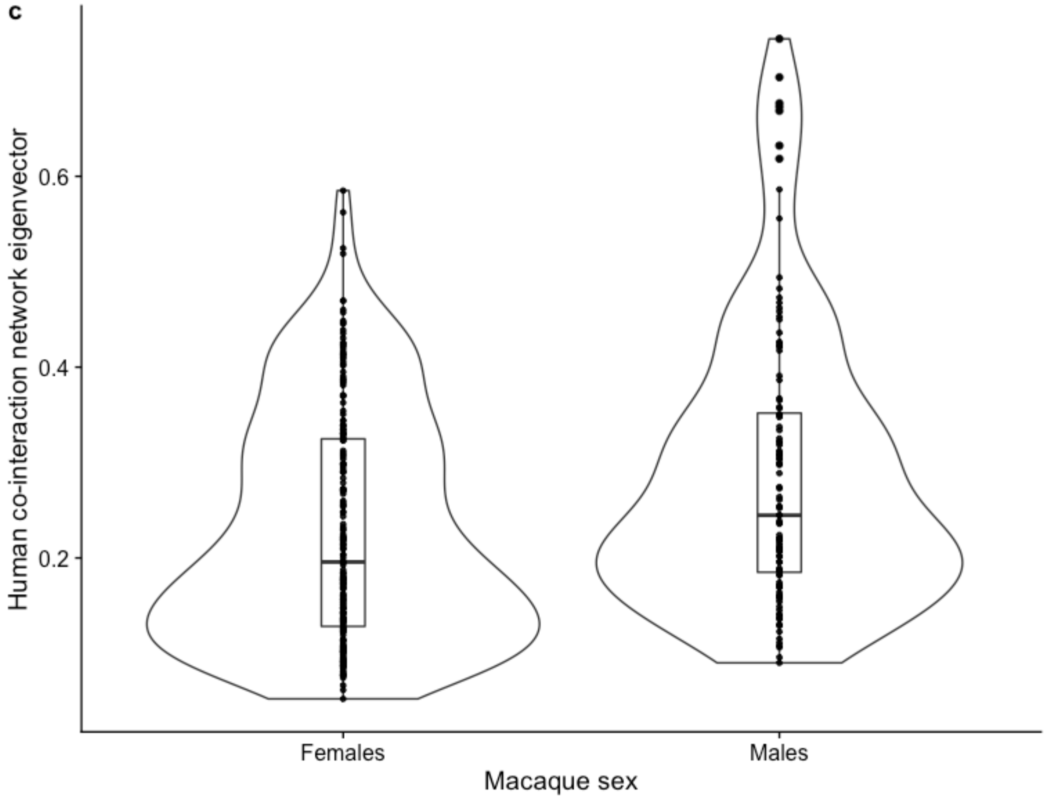

b
Human co-interaction network eigenvector
0.2
0.4
0.6
0.00
0.25
0.50
0.75
1.00
Proximity network eigenvector
Species
Bonnet
Long-tailed
Rhesus

519


c
Human co-interaction network eigenvector
0.2
0.4
0.6
Females
Males
Macaque sex

520

Figure 4: Effects of macaques' (a) short-duration affiliation eigenvector centrality, (b) proximity eigenvector centrality by species, and (c) sex on their human co-interaction network eigenvector centrality. For the effect of sex (c), the box-and-violin plot indicates the median (horizontal line in the middle of each box), the inter-quartile ranges (boxes), data-points including outliers (whiskers), and the probability density of the data at different values (violins).

Discussion:

For all macaque groups, we found that animals were significantly more well-connected within their human co-interaction networks than expected by chance. That is, wild animals were actively involved in joint risk-taking behavior with their conspecifics, by consistently and repeatedly co-engaging with humans within and across time and anthropogenic space. This finding provides an important pretext to conducting assessments of whether or how such patterns of joint risk-taking by wild animals in anthropogenic environments may be influenced by their life-history and socioecological strategies, which we tested in the second part of this study. Such evidence of joint risk-taking also 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 co-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 the overall frequencies of human-wildlife interactions (reviewed in Balasubramaniam et al. 2020a; Morrow et al., 2019), to reveal clear spatiotemporal patterns of associations to these interactions as revealed by our SNA approach. Researchers have been increasingly implementing SNA 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 co-interaction networks addressed this gap. Indeed, approaches similar to ours may be used to construct other human-wildlife co-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 co-occurrence or overlap with anthropogenic landscapes, or interspecies co-interactions with humans, livestock, or feral mammals.

We found evidence for some (but not other) aspects of macaque socioecology and demography to influence their co-interactions with humans. First, macaques' centrality within their short-duration affiliation networks positively predicted their centrality within human co-interaction networks. In group-living primates, affiliative interactions like grooming, coalitionary support, and lip-smacking may reduce animals' short- and long-term stress levels (Aureli et al., 1999; Shutt et al., 2007), and are key to the establishment and maintenance of strong long-term social bonds (Silk et al. 2003; Young et al., 2014). One of the primary motivations for wild primates to interact with humans is to obtain anthropogenic foods (Marty et al., 2020). The benefits of possessing within-group social alliances and strong social bonds may, at least in part, help offset the potential physiological and health-related costs of risking interactions with humans to gain such foods. More generally, we speculate that in challenging, potentially unpredictable anthropogenic environments that also reduce the time available for grooming (discussed further below), animals may rely more than usual on short-duration affiliative interactions to maintain strong social bonds. In other words, these forms of affiliative relationships may particularly underlie or encourage animals' collective (or we speculate perhaps even cooperative) tendencies to take risks through co-interacting with humans.

Human co-interaction networks were also positively influenced by proximity networks of social tolerance, with the effect sizes being somewhat 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 of each other (Balasubramaniam et al., 2012; Thierry, 2007), have a more restricted range, are 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 or less ecological flexibility (e.g. bonnet macaques compared to rhesus and long-tailed macaques), being near familiar individuals such as close kin or conspecifics may encourage greater propensities among individual animals to jointly take risks in anthropogenic environments.

Alternatively, these cross-species differences in the effects of proximity networks on co-interaction networks may in fact be an outcome of cross-site, or indeed even within-site differences in the distribution and density of anthropogenic factors and (consequently) human-macaque (co-)interactions. 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 centrality within human co-interaction networks: males were more central or well-connected than females. Sex-biased 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 joint risk-taking behavior among social allies may all explain why males are more central in human co-interaction networks than females (Balasubramaniam et al., 2020a; Morrow et al., 2019).

Unlike short-duration affiliation and proximity, macaques' grooming networks had no effect on their human co-interaction networks. One reason for this may be because anthropogenic factors may influence primate grooming patterns in different, sometimes contrasting ways. For instance, our previous work on these populations revealed how increased monitoring of human activity led to a systematic reduction in the time invested by macaques in grooming, but less so to a reduction in the number of partners individuals chose to groom (rhesus macaques: Kaburu et al., 2019b; longtailed macaques: Marty et al., 2019; bonnet macaques: Balasubramaniam et al., 2020b). Moreover, in two out of the four groups of long-tailed macaques that were exposed to an exceptionally high density of humans, interactions with humans led to an increase (rather than to a decrease) in rates of grooming, presumably as means to cope with anthropogenic stressors (Marty et al., 2019). Such contrasting findings within species suggest that it may be necessary to examine intraspecific variation (cross-group, but also within-group differences) in macaque socioecology to better understand how grooming networks influence co-interaction networks.

One potential limitation of this study concerned the lack of information on macaques' co-occurrence or space-use overlap, which may influence their social interactions (Adams et al., 2012; Albery et al., 2020; Pawley & McArdle, 2018). Lacking data on GPS coordinates, we were unable to construct animals' space-use sharing or co-occurrence networks. Despite this, it is unlikely that our networks, findings and interpretations may simply be explained as a by-product of macaques' aggregation or space-use overlap, for the following reasons. First, the results of our pre-network randomization tests suggest that human co-interaction networks, rather than being by-products of simple aggregations or co-occurrence of animals, were an outcome of specific animals actively choosing to consistently and repeatedly co-interact with humans. Second, in group-living animals like nonhuman primates that show complex social systems, social interactions like grooming and other forms of affiliation are selectively and heterogeneously distributed in spite of animals that overlap in space. Moreover, our conservative criterion for defining ‘proximity’ (animals within body-length of each other) is more likely to capture selective social tolerance of conspecifics, rather than capturing animals that simply overlap in space. Third, our results were independent of macaques’ overall occurrence (if not co-occurrence) in anthropogenic areas, as indicated by our inclusion of their times’ spent in proximity to humans as a predictor of their centrality within human co-interaction networks. A second potential limitation concerns the lack of more precise information on the (GPS) locations of human-wildlife 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 co-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 geospatial data on both macaque space-use overlap and human-macaque interactions would be vital next steps. Finally, implementing multi-level approaches (Finn et al., 2019) to capture potential heterogeneity in human co-interaction patterns across different spatial (blocks) and temporal (observation windows) layers was also beyond the scope of this study, but another important next step.

Our study has important implications for the conservation and management of human-wildlife interfaces. Macaques that are more central in their human co-interaction networks, because of their coming into contact with more people across time and space, may be targets of interventions that move these human-wildlife 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 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 co-interaction networks may be social-ecological ‘superspreaders’ of disease, i.e. both within wildlife systems and across human-wildlife interfaces. We reckon that these animals would be particularly important targets of disease intervention or control strategies like vaccination and antibiotic treatment (Rushmore et al., 2014). Indeed, our finding of a lack of association between macaques’ human co-interaction networks and grooming networks suggests that these 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 both conservation and public health perspectives.

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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.

Graphical Abstract Caption:

Long-tailed macaques co-interacting with a human who is provisioning them, in Kuala Lumpur Malaysia (Picture Credits: Dr. Pascal R. Marty).

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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