Social responses to a hurricane drive greater epidemic risk

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ABSTRACT

The increasing frequency and intensity of extreme weather events due to climate change has the potential to alter ecosystem dynamics and wildlife health. Here we show that increasing social connections in response to a hurricane enhanced disease transmission risk for years after the event in a population of rhesus macaques. Our findings reveal that behavioural responses to natural disasters can elevate epidemic risk, thereby threatening wildlife health, population viability, and spillover to humans.

MAIN TEXT

Natural disasters have devastating consequences for both man-made and natural landscapes, leading to casualties, displacement, and psychological distress [1,2]. These extreme events also impact the social structure of both human and other animal groups [3–6]. Following natural disasters, the social structure of affected human groups becomes more transitive[7] and cohesive[8]. In non-human animals, hurricanes have been shown to increase the modularity of dolphin groups[9] and to lead to more densely connected social networks in primates[5]. These observed changes in social structure can be caused by increased mortality following the disasters[4,10] or through group adjustments to new resource landscapes or ecological challenges[5]. Regardless of the cause, changes in the topography of relationships among group members can have important consequences for population viability.

Social structure plays a fundamental role in the dynamics of diffusion processes underlying the spread of innovations[11], intestinal microbes[12], and pathogens[13]. Of particular importance for the viability of populations is the influence that the social structure has on disease transmission. Modelling studies have revealed that the probability of an epidemic outbreak strongly depends on the social connectedness of a population, which can lead to faster pathogen spread[14]. Additionally, changes in social structure, such as modularity[13], lead to greater infection

prevalence in wild animals, which can pose an important danger for humans through zoonotic spillover[15]. Therefore, on the one hand, natural disasters affect the social structure of group-living species and, on the other, the topology of social contacts shapes disease dynamics. However, how and to what extent natural disasters affect disease risk via changes in sociality remains unknown. This knowledge-gap is likely due to the difficulty of obtaining empirical social networks before and after a natural disaster. Given the predicted increase in frequency and severity of extreme weather events with climate change, it is imperative that we evaluate the long-term effects of such disasters on epidemic risk in both animal and human populations. Here, we empirically address this knowledge-gap using an unprecedented data set of social interaction data from hundreds of free-ranging rhesus macaques (*Macaca mulatta*) collected from 5 years before until 5 years after a natural disaster, Hurricane Maria (**Figure S1** & **Table S1**).

On September 20th 2017, Hurricane Maria made landfall on Cayo Santiago, an island off the coast of Puerto Rico. This hurricane was the deadliest and most destructive natural disaster in Caribbean history. Within a few days, over 60% of Cayo Santiago's vegetation was destroyed[5] and five years later (Spring 2023) most of it still has not recovered. Severe deforestation greatly reduced shade availability, a fundamental resource for behavioural thermoregulation to the intense Caribbean heat[5,16]. As a result, monkeys concentrated in fewer, smaller shady areas, thus increasing the frequency of close-proximity contacts. In the year following Hurricane Maria, monkeys were three times more likely to sit close to each other (i.e., within 2m), and even five years after the storm, monkeys were still much more likely to be in proximity to conspecifics compared to before (**Figure S2**). Putatively by facilitating access to critical shade, social proximity strongly predicted individual survival (42% decrease in mortality risk after the storm)[16]. However, despite its adaptive value, hurricane-induced changes in social structure may have associated costs, including an increased rate of exposure to pathogen infections[17,18]. To estimate this cost, we used epidemiological simulations to evaluate how changes in social structure following Hurricane Maria influenced pathogen infection risk.

We simulated 1000 epidemics, sampling from social networks built from proximity data from seven macaque groups collected over a period of nine years (24 group-by-year replicates in total). In each simulation, we randomly assigned an infection probability drawn from a normal distribution with a mean of 0.15 and a standard deviation of 0.04, with values ranging from 0.000001 to 0.3 (see **Methods**). This distribution captures a wide range of airborne pathogen transmission risks, from very low to quite high (up to 30% probability of infection). Each simulation revealed the mean time step at which individuals in each group-year replicate became infected. We then fitted a mixed effects linear model including the probability of infection simulated, whether the simulation examined a pre- or a post-hurricane network, and a random effect of the group-by-year replicate to account for extraneous between-network differences. Our results show that, on average, following hurricane Maria individuals became infected 1.93 times faster (i.e., in roughly half the number of simulation time steps) than before the storm (95% CI 3.05-1.20; P=0.002, **Figure 1A**) due to their greater proximity to conspecifics. The hurricane's effect on the speed of pathogen transmission was equivalent to a 10% absolute increase in pathogen infectivity from 0.1 to 0.2, which led to 2.01-1.97 times

earlier infections (*P*<0.001; **Figure 1B**). These simulations reveal substantially higher epidemic risk after the hurricane, implying behavioural responses to natural disasters can strongly exacerbate population vulnerability to infectious disease outbreaks.

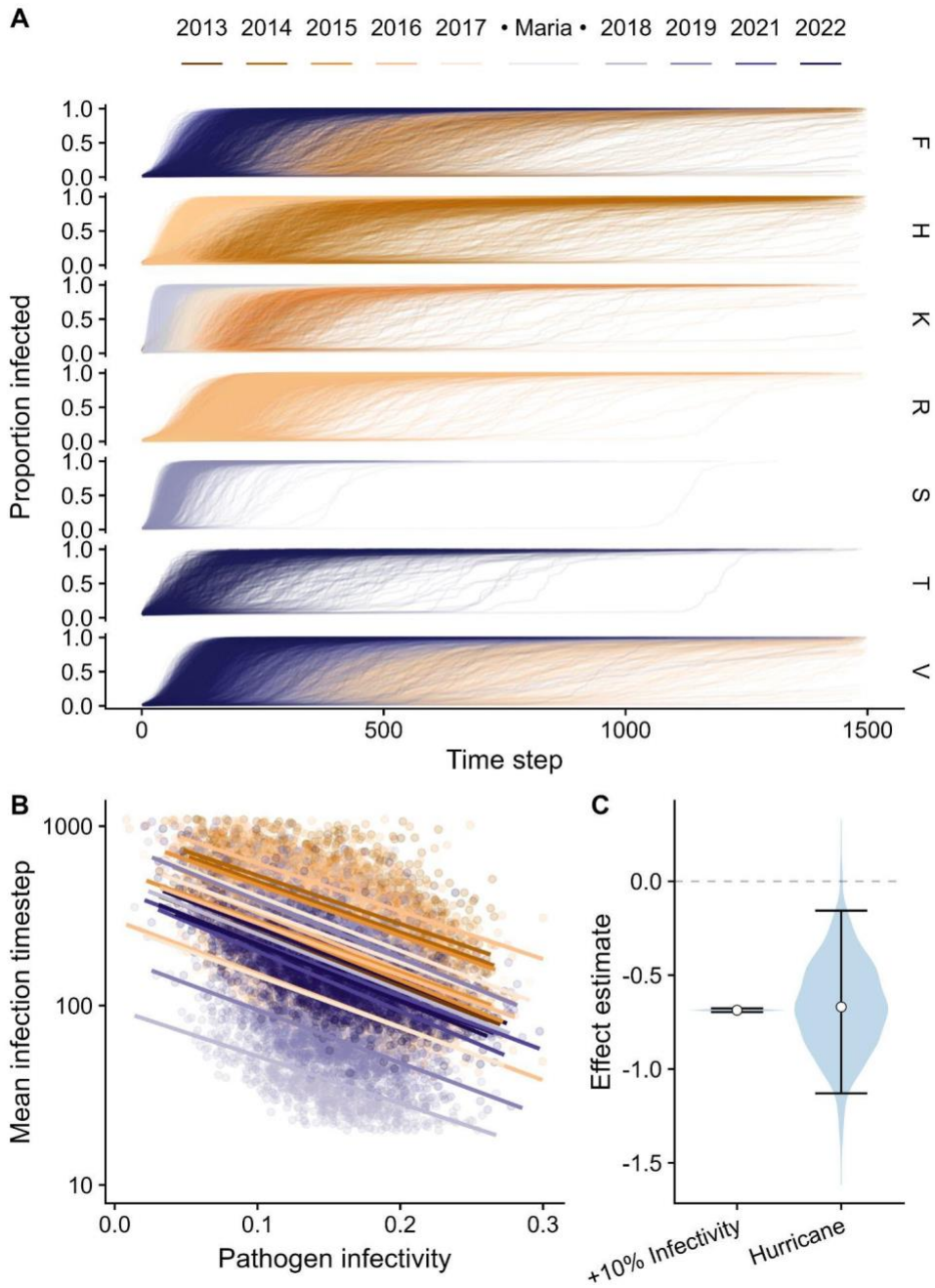

Figure 1: Simulated epidemic dynamics as a function of year, pathogen infectivity and group the macaques belong to. Simulation outputs are grouped into year and group replicates. Each year is represented by a different colour, with oranges indicating pre-hurricane years and purples post-hurricane years. In Panel A, each line represents one of 1000 simulations carried out on each group-year replicate (N=24,000), depicting the proportion of infected individuals at each simulation timestep. Post-hurricane years (purples) reached higher proportions of infected individuals markedly faster than pre-hurricane years (oranges). Each social group is a different row; the group name is on the right of

each row. In Panel B, each point represents the mean simulation time step at which individuals become infected in a given simulation (N=24,000) as a function of pathogen infectivity. Solid lines represent models fitted to each group-year replicate, coloured by year as in Panel A. Pathogen infectivity was associated with substantially earlier mean infection timestep on a $\log_{10}$-scale. In Panel C, the effect estimate for a 10% increase in infectivity is given next to the estimate for the effect of the hurricane. The blue violins represent the probability distribution of the posterior effect estimate; the error bars the 95% credibility interval and the points the mean.

While the direct impacts of natural disasters on human health are relatively well understood[19,20], their influence on the long-term resilience of animal populations remains understudied. If a pathogen invades a population after a natural disaster and reduces host survival or reproduction, this process could disproportionately decrease its viability, posing an important conservation threat additional to the short-term, direct effects of the natural disaster. The magnitude of the indirect effects of Hurricane Maria on the risk of infection in macaques demonstrates the importance of considering the long-term consequences of natural disasters, and of habitat disturbance more generally, for the health and survival of wild gregarious species.

In addition to impacting population viability, greater pathogen prevalence among wildlife makes it more likely that humans will encounter infected animals or pathogens in the environment. This in turn increases the probability of zoonotic spillover[21], which has become progressively more frequent in the last century[22]. The threat of spillover could be exacerbated following natural disasters due to infrastructure damage – e.g. to water systems[23]– and increased population density in safe areas[22]. Similarly, if the epidemic erodes social structure and causes animals to behave differently or disperse, the probability of zoonotic spillover may further increase, posing an important public health risk.

Although previous studies suggested a link between natural disasters and disease prevalence caused by increased contact rates in non-human animals[24], empirical demonstrations of this phenomenon were lacking in both humans and other animals. Our results empirically demonstrate how natural disasters can alter infection disease dynamics via changes in social organisation and therefore represent compound threats to both animal and human health, even years after the disaster itself. The clear impact of adaptive behavioural responses to altered resource availability (i.e. shade) on disease risk illustrates the indirect and unexpected ways in which natural disasters can impact the survival of animal populations. The increasing frequency and severity of extreme weather events due to climate change forecasts growing disease risks for both wildlife and humans, which must be grappled with through more robust, better-informed conservation efforts and public health measures.

METHODS

1. Study system

We studied a semi free-ranging population of rhesus macaques living on Cayo Santiago Island, Puerto Rico (1809 N, 65 44 W). Rhesus macaques live in multi-male multi-female groups with

a polygynandrous mating system. Male rhesus macaques disperse from their natal group around sexual maturity, but females typically remain in their natal group for their entire lives, such that social groups are stably composed of matrilines[25,26]. Rhesus macaques are notable for their high frequency and severity of aggression and absence of reconciliation between conspecifics when compared to other macaque species, which leads to a social organisation that can be described as both highly "despotic and nepotistic"[26,27].

The population of rhesus macaques used for this study has been continuously monitored since it was established in 1938 following the release of 409 animals originally captured in India. Cayo Santiago is managed by the Caribbean Primate Research Center (CPRC), which supplies food to the population daily and water *ad libitum*. There is no contraceptive use and no medical intervention aside from tetanus inoculation when animals are weaned yearlings. Animals are free to aggregate into social units as they would in the wild and there are no natural predators on the island.

Subjects for this study were adult males and females (at least 6 years old), individually recognizable by tattoos, ear notches, and facial features. We used 7 social groups, TT, F, KK, V, R, HH and S, for which there was behavioural data either before and/or after Hurricane Maria, between 2013 and 2022. Our dataset included 790 unique adult individuals. We used multiple available years of observational data (HH: 2014, 2016; R: 2015, 2016; F: 2013, 2014, 2015, 2016, 2017; KK: 2013, 2015, 2017, 2018; V: 2015, 2016, 2017) to characterise social networks before the hurricane (''pre-hurricane''). Post-hurricane, our sample included observational data from 2018, 2019, 2021 and 2022 (S: 2019; TT: 2022; F: 2021, 2022; V: 2018, 2019, 2021, 2022; KK: 2018). See **Figure S1** and **Table S1** for details on sample size within each group and year.

2. Behavioural data collection

In all years of data collection except 2018 (year immediately following Hurricane Maria) and three social groups in 2016, 2017 and 2019 (HH, KK and S respectively), behavioural data were collected with 10-min focal animal samples. At the 0-, 5-, and 10-min marks of the focal follow, we collected instantaneous scan samples during which we recorded the identity of all adults within two metres (i.e., in proximity). For groups HH in 2016, KK in 2017 and S in 2019, we collected 5-min focal animal samples with instantaneous scan samples at the beginning and end of the focal follow, the data collection protocol was otherwise identical to other non-hurricane years. We balanced data collection on individuals across time of day and across months to account for temporal variation in behaviours. Data-collection hours were from 6am to 2:30pm due to CPRC operating hours. To collect behavioural data before 2020 we used Teklogic Psion WorkAbout Pro handheld computers with Noldus Observer software. After 2020, we used the Animal Observer App on Apple iPads.

In the year following Hurricane Maria (from November 2017 to September 2018), damage resulting in inconsistent access to electricity in Puerto Rico imposed the adoption of a downgraded means of recording data using basic tablets. We recorded group-wide instantaneous scan samples at 10-min intervals. For all animals in view of an observer, we

recorded the identity of all adults within two meters (i.e., in proximity)–similarly to instantaneous scans recorded during focal follows prior to the hurricane. Observers were given 15 mins to complete a group-wide scan session, were required to stand a minimum of 4 m from monkeys and, because of very good visibility of these terrestrial animals, were able to identify them at distances upward of 30 m.

Our subjects were observed over a mean (SD) of 2.61 (1.70) years, and did not have to be observed both before and after the hurricane to be considered. In other words we did not conduct within-individual comparisons as in[5]. In non-hurricane Maria years, we included on average 84.32 (36.96) scan observations embedded within focal follows per individual per year, and 533.36 (127.41) scans per individual in the post-hurricane year (November 2017 - September 2018). Note that because of storms and Hurricane Maria, data collection stopped on August 31, 2017 and didn't resume until November 2nd, 2017.

3. Bayesian estimating of social networks using BISoN

For each group and year separately, we estimated social networks based on proximity interactions captured during scan samples.

Networks are usually constructed by taking a normalized measure of sociality, such as the proportion of sampling periods each pair spends engaged in a social behavior (e.g. the Simple Ratio Index; SRI). These normalized measures ensure that pairs that are observed for longer are not erroneously determined to be more social[28]. This is important because observing social events can be challenging and uniform sampling over all pairs is not always possible[29]. Though normalized measures of sociality will not be biased by sampling time, they will be accompanied by varying levels of certainty. For example, edge weights will be treated as a certain 0.5 for both a case where individuals have been seen together once and apart once, and equally where individuals have been together 100 times and apart 100 times. Despite there being considerably more certainty around the values of the latter example than the former, methods to estimate and propagate uncertainty through social network analyses remain largely unused.

In this study, we generated weighted Bayesian networks using the BISoN framework and bisonR package[30]. This framework allowed us to account for uncertainty in the edges connecting individuals in the network based on how often they were sampled and, more importantly, propagate this uncertainty to subsequent analyses. Proximity networks were estimated based on data collected through scan sampling[31] across all groups and years. Edges in the networks represented the number of times a pair of individuals were observed in proximity or grooming relative to the total observation effort for the dyad (i.e., total scans individual A + total scans individual B), or the probability of interaction. Given that the observed interaction data was binary (i.e. for every observation sample, was the focal animal in proximity to another monkey? Y/N) we modeled the uncertainty around the edges using as prior a beta distribution with alpha = 0.1 and beta = 0.1. Proximity networks were undirected.

4. Pathogen spread simulation

To quantify how the hurricane's behavioural impacts influenced infectious disease risk, we simulated epidemics of a hypothetical pathogen through the annual networks of each macaque group. We used 1000 Bayesian networks (BISoN package[30]) of each group-year combination as simulation replicates in order to account for the uncertainty of dyadic weight estimates in the observed proximity networks. For each simulation we generated a new pathogen infectivity $(P)_I$, drawn randomly from a normal distribution (Mean=0.15, SD=0.04, range=0.000001-0.3). In each simulation, we chose a random individual at timestep 0 to be infected with the hypothetical pathogen. As such, there were three sources of random variation at the initiation of each simulation: the structure of the network (drawn from the Bayesian model posterior), the first infected individual, and the infectivity of the pathogen. In each simulation timestep, each infected individual transmitted the pathogen to its contacts with probability A*B, where A equals the probability that two individuals interact (i.e., the weight of the dyadic connection in the network) and B equals a binomial coin flip with probability P_I. Each simulation continued until either all individuals were infected or 10,000 timesteps elapsed.

We fitted a linear mixed model (LMM) to our simulations' outputs to determine the size and significance of the hurricane's effect. For this model, each data point was a simulation result (N=24000, comprising 1000 simulations across each of 24 year:group combinations) and the response variable was the mean timestep at which individuals in that replicate were infected. The explanatory variables included in the model were: i) the P_I value of the pathogen in the simulation; ii) a binary factor denoting whether the simulation included a network from before or after Hurricane Maria and iii) a random effect of the group-by-year combination. This model formulation was conservative in its ability to detect a hurricane effect, as there was incomplete mixing between the group:year random effect and the hurricane effect. To put the hurricane effect's magnitude in context, we compared its estimate from the linear model with the estimate for the P_I value's effect (Figure 2C). All analyses were carried out in R (Version 4.2.3).

Acknowledgements: We thank the Caribbean Primate Research Center staff for their important roles in data collection and in the maintenance of Cayo Santiago.

Funding: Support for this research was provided by the National Institutes of Health (R01MH118203, U01MH121260, R01MH096875, P40OD012217, R01AG060931, R00AG051764, R56AG071023), a RAPID award from the National Science Foundation (1800558) and a Royal Society Research Grant (RGS/R1/191182). Cayo Santiago is supported by grant 8-P40 OD012217-25 from the National Center for Research Resources (NCRR) and the Office of Research Infrastructure Programs (ORIP) of the National Institutes of Health. GFA was supported by NSF grant number DEB-2211287.

Author contributions: CT, AMR and GA conceptualized the study; CT, AMR and GA analysed the data; JN and DP; NSM, JH, MM, MLP, LJNB secured funding for this work; CT and LJNB drafted the manuscript with input from all authors; LJNB supervised this work. All authors read and approved the manuscript.

Competing interests: MLP is a scientific advisory board member, consultant, and/or co-founder of Blue Horizons International, NeuroFlow, Amplio, Cogwear Technologies, Burgeon Labs, and Glassview, and receives research funding from AIIR Consulting, the SEB Group, Mars Inc, Slalom Inc, the Lefkort Family Research Foundation, Sisu Capital, and Benjamin Franklin Technology Partners. All other authors declare no competing interests.

Data and materials availability: Upon publication, data will be available on Open Science Framework platform and code GitHub at https://github.com/camilletestard/Cayo-Maria-Disease-Modeling

SUPPLEMENTARY INFORMATION

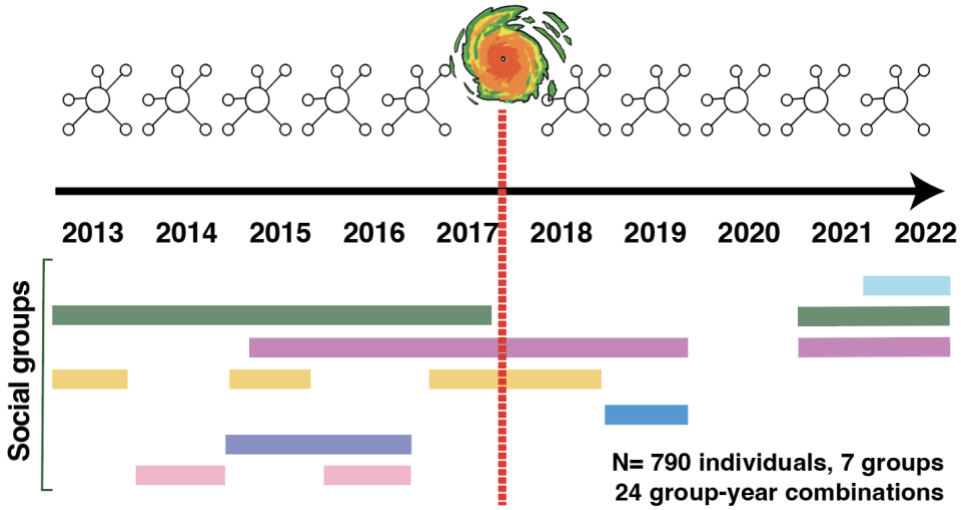

Figure S1. **Coverage of data collection across social groups and years**. Adapted from *Testard et al. 2023* [16]

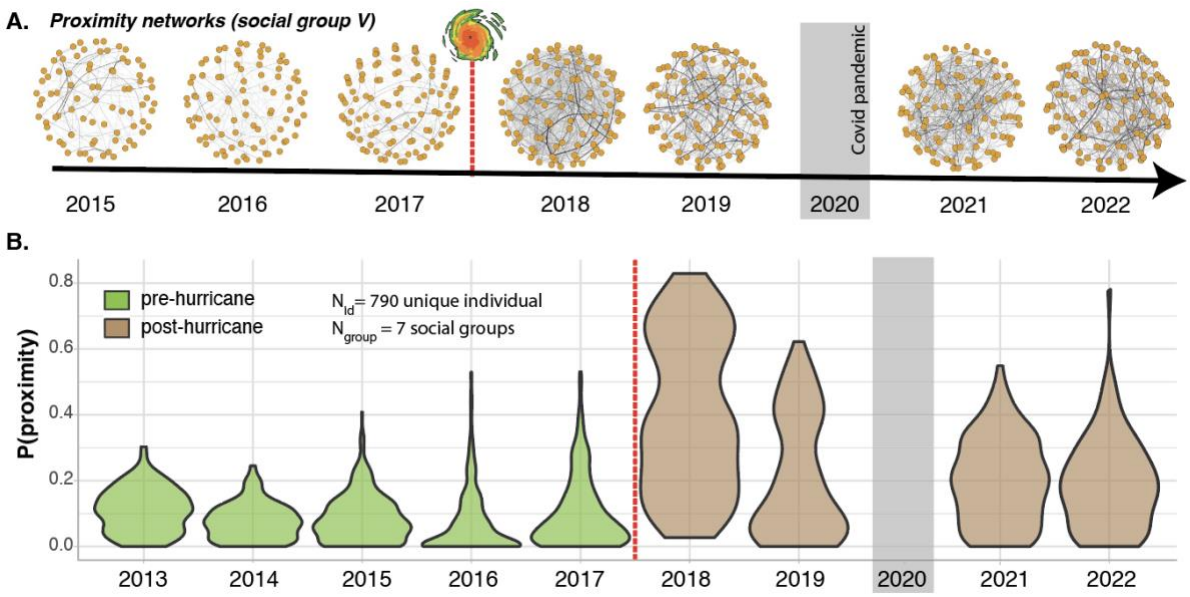

Figure S2. Cayo Santiago macaques exhibit a persistent increase in social tolerance after Hurricane Maria. (**A**) Proximity networks for social group V from 2013 to 2022, excluding 2020 due to the COVID19 crisis are shown as example networks. Each node represents an individual and edges represent the probability for two individuals to be in proximity to one another. The thicker the line the higher the probability of proximity. Red dotted line marks Hurricane Maria. (**B**) Probability of being observed in proximity to another monkey from 2013 to 2022, across 790 individuals in 6 social groups, 24 group-year combinations. Adapted from *Testard et al. 2023* [16]

	2013	2014	2015	2016	2017	2018
F	100	106	103	123	113	0
HH	0	45	0	69	0	0
KK	30	0	54	0	61	63
R	0	0	94	125	0	0
S	0	0	0	0	0	0
TT	0	0	0	0	0	0
V	0	0	80	90	102	67

Table S1. Sample sizes by group and year. Note that an individual can be sampled in multiple years.

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