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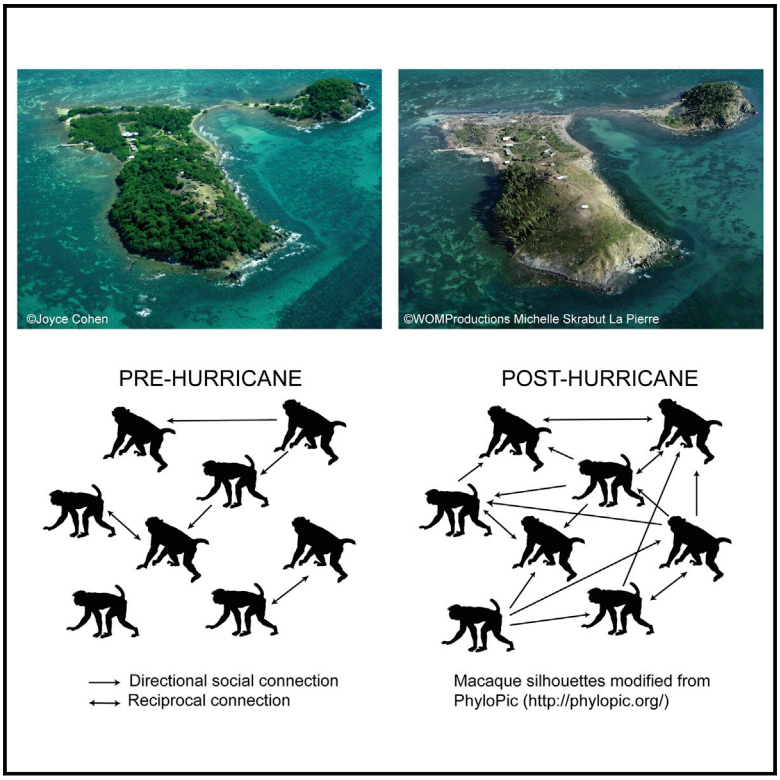
Rhesus macaques build new social connections after a natural disaster

Graphical abstract



Highlights

- After Hurricane Maria in 2017, macaques became more social
- Monkeys that were isolated before the storm increased social connections most after it
- Monkeys built new relationships rather than strengthened existing ones
- Monkeys adopted a "path of least resistance" approach to forming connections

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In brief

Testard et al. show that macaques became more tolerant of others and sought out new social connections after a devastating hurricane. Monkeys built new relationships rather than strengthened existing ones—suggesting the size of one's social network rather than the strength of one's relationships was critical in this context.

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Rhesus macaques build new social connections after a natural disaster

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SUMMARY

Climate change is increasing the frequency and intensity of weather-related disasters such as hurricanes, wildfires, floods, and droughts. Understanding resilience and vulnerability to these intense stressors and their aftermath could reveal adaptations to extreme environmental change. In 2017, Puerto Rico suffered its worst natural disaster, Hurricane Maria, which left 3,000 dead and provoked a mental health crisis. Cayo Santiago island, home to a population of rhesus macaques (*Macaca mulatta*), was devastated by the same storm. We compared social networks of two groups of macaques before and after the hurricane and found an increase in affiliative social connections, driven largely by monkeys most socially isolated before Hurricane Maria. Further analysis revealed monkeys invested in building new relationships rather than strengthening existing ones. Social adaptations to environmental instability might predispose rhesus macaques to success in rapidly changing anthropogenic environments.

INTRODUCTION

The quality and quantity of social relationships predicts morbidity and mortality in humans and other mammals.[1] Yet precisely how social relationships improve health and fitness outcomes remains poorly understood.[2] One model, the "Social Buffering Hypothesis,"[3] proposes that social relationships are critical mitigators of the negative consequences of exposure to adversity. In humans, the presence of strong social support predicts recovery from illness[4] and resilience to mental health disorders after terrorist attacks[5] or loss of a loved one.[6] Social relationships in non-human primates also play a critical role in weathering adversity. For example, compared with females with weaker bonds, female chacma baboons (*Papio ursinus*) with a network of strong and stable bonds showed attenuated physiological responses during periods of social instability.[7]

A tremendous source of instability for humans and other animals alike are natural disasters, such as earthquakes and tsunamis, and massive weather events, such as hurricanes.[8,9] Extreme weather can cause widespread destruction of the natural landscape, resources, and infrastructure,[10] all of which can disrupt the lives of humans and other animals.[11] With the intensifying climate crisis, devastating storms are expected to become less predictable[12] and increase in both frequency and force.[13,14] Understanding how individuals adjust and survive in severely transformed landscapes could inform species conservation and human adaptation to increasingly unstable environments by providing evidence regarding which factors promote resilience and survival.[15,16] According to the social buffering hypothesis, social relationships might be crucial for surviving extreme environmental challenges. Yet how societies re-organize and how individuals adjust their social relationships in response to catastrophic climatic events remains largely

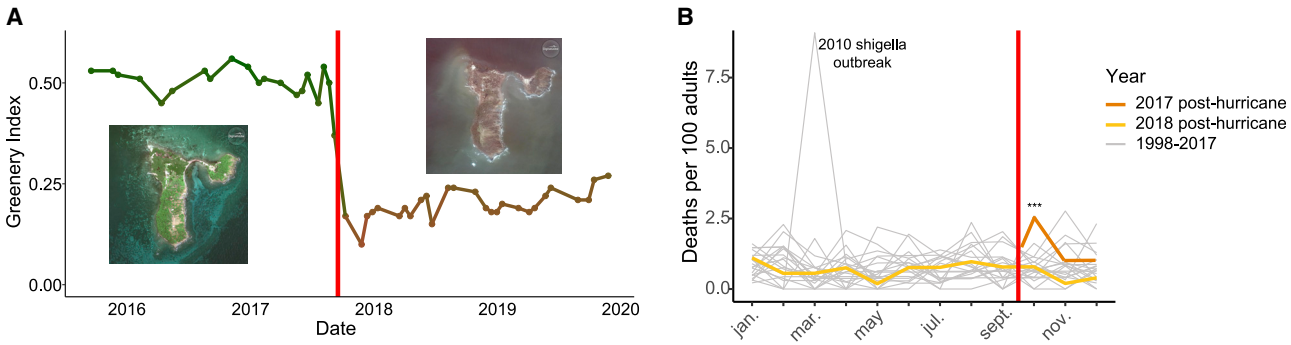

Figure 1. Hurricane Maria's effect on vegetation and mortality

(A) Foliage cover from Cayo Santiago Island, as measured by greenness, decreased by 63% after Maria (t test, $p = 3.7 \times 10^{-25}$). Images are Digital Globe aerial photos of Cayo Santiago island, Puerto Rico, before Hurricane Maria (left) and after (right). See Figure S1 for details on the damage to each group's home range. (B) The death rate per 100 adults per month, from 1998 to 2018. We plot adult death rates because the exact date of death of infants and juveniles had an estimated error margin of up to 8 months due to the difficulty in individually recognizing and tracking young animals who had not yet received their unique ID tattoos. Color code: 2017 post-hurricane in dark orange and 2018 in yellow. Grey lines are years 1998 to 2017 pre-hurricane. The October 2017 death rate was more than triple the rate expected based on October months in previous years (> upper bound for 99.99% CI, $p < 0.0001$). The peak in March corresponds to a Shigella outbreak in 2010. The red vertical lines indicate the date when Hurricane Maria made landfall on Cayo Santiago. See Data S1A for comparison of mortality rates after natural disasters in previous studies.

unexplored. This is, in part, due to the unpredictable character of natural disasters and the rarity of having longitudinal data collected on individuals both before and after these events.

Here, we examined changes in social relationships after a natural disaster within a population of free-ranging rhesus macaques on Cayo Santiago island, Puerto Rico. On September 20, 2017 Hurricane Maria, then a category 4 hurricane, made landfall on Puerto Rico and caused widespread physical and environmental destruction. The human death toll from the hurricane in Puerto Rico numbers in the thousands,[17] making it among the deadliest storms on record. A surge in mental health disorders, including depression and anxiety, attests to the lingering effects of physical, financial, and social devastation.[18] Cayo Santiago also suffered catastrophic damage. After the hurricane, green vegetation declined by 63% (t test, $p = 3.7 \times 10^{-25}$) (Figure 1A) and nearly all research and husbandry infrastructure was destroyed by the storm. Although the adult death rate peaked in the month after the hurricane (more than triple the expected death rate based on October months in previous years, >99.99% confidence interval [CI] or $p < 0.001$), it returned to expected numbers in subsequent months when compared to previous years (Figure 1B). Furthermore, the population of rhesus macaques experienced relatively few deaths due to the storm itself, compared with previously studied animal populations after natural disasters[19–24] (2% of the Cayo population died immediately after the hurricane and 7% in the six following months, compared to 30%–65% mortality in prior studies; see Data S1A). This is consistent with a recent study showing no overall increase in mortality after major hurricanes compared with that in non-hurricane years for the past decades in this population (Hurricanes Hugo in 1989, Georges in 1998, and Maria in 2017).[25] Food and water provisioning ensured that monkeys' basic nutritional needs were generally met before and after these disasters.

Our study uses rarely available data to investigate how a non-human primate population, that has a similar physiology and behavior to humans,[26,27] adapted socially to an environmental catastrophe and its lingering effect in the absence of mass mortality. Mass mortality precludes the ability to assess social network changes outside of the direct consequences of group size reduction.[19,28] That relatively few monkeys were killed in the aftermath of Hurricane Maria is an unusual circumstance that allows us to draw parallels with human responses to disasters in which whole communities have their homes and livelihoods destroyed but relatively few individuals are killed directly by the events themselves (e.g., Hurricane Harvey[29]). Furthermore, because the monkeys live on an island, their behavioral responses to the hurricane could inform predictions of behavioral responses by humans who are unable or unwilling to move after a disaster, as well as the behavioral responses of animal populations living in protected habitat "islands" without migration corridors.

We investigated whether and how monkeys adjusted their investment in social relationships in response to Hurricane Maria, drawing on a detailed dataset that encompasses behavioral observations occurring 3 years prior to, and 1 year immediately after, Hurricane Maria. Our study had five main questions: (1) we tested whether individuals changed their probabilities of engaging in affiliative (pro-social) behaviors after the hurricane compared with before. We predicted that rhesus macaques would show an increase in affiliative behavior, consistent with the social buffering hypothesis. (2) We investigated inter-individual differences in social responses to the hurricane. Specifically, we asked whether pre- to post-hurricane changes in probabilities of affiliative behaviors were similar for all monkeys and, if not, whether inter-individual differences were predicted by gregariousness prior to the hurricane,[30] the loss of a grooming partner as a result of the storm,[31] or clustering around newly scarce resources like shade.[11,32] In prior studies, gregariousness and loss of a partner influenced individual social responses to a mass predation event in wild mice[30] and female chacma baboons.[33] (3) We explored which social strategies individual

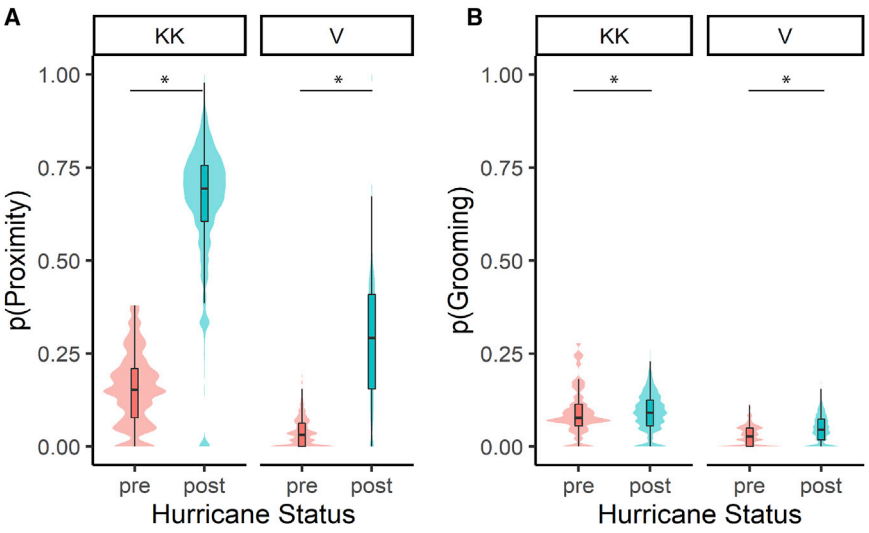

Figure 2. Rhesus macaques showed higher probabilities of affiliative behaviors after Hurricane Maria

(A and B) Distribution of the probability of being in proximity (A) and grooming (B) pre- (red) and post-hurricane (blue) for study groups V and KK. Pre-hurricane violin plots summarize multiple years of data collection (2015–2017). 2017 data only includes observations up to Hurricane Maria (September 20, 2017). Stars indicate statistical significance (95% CIs of model estimates do not include the null value, i.e., $p < 0.05$) (Table S1).

monkeys adopted. In particular, we asked whether individual monkeys increased their number of social partners or strengthened their existing connections (or both), two strategies that potentially provide different benefits after catastrophic events.[7,22,30]

Our results confirmed that rhesus macaques engaged more in affiliative interactions after the storm and that this effect was driven by an increase in their number of partners rather than intensifying existing relationships. These findings motivated us to explore the final two of our five questions: (4) because partner selection might provide critical insights into the function of social relationships,[34–36] we asked which partners monkeys associated with after the disaster. We predicted that monkeys would preferentially invest in relationships with kin and high-ranked individuals, which might be best placed to help them cope with the physical challenges and potentially increased competition for resources unleashed by the hurricane and its aftermath (i.e., vegetation-based food or shade) (Figure 1A).[7,37] (5) We asked whether simple association heuristics (reciprocity and closure of triangles) and shared space use (i.e., proximity) predicted formation of new relationships.

RESULTS

We focused our investigation on adult males and females in two study groups (KK and V) for which we had behavioral data both before and after Hurricane Maria (KK, n = 66 and V, n = 93). Group V ranged alone on "Small Cayo," an area that was severed from the main island ("Big Cayo") after the hurricane (Figure S1) and which was the least defoliated. By contrast, group KK ranged on Big Cayo with other groups, mostly on the eastern part of the island, which was the most defoliated after the hurricane. The groups also had divergent demographic characteristics: the male to female ratio was 1:2 in group KK and almost 1:1 in group V. These two important differences could lead to divergent responses to the hurricane and its aftermath. Furthermore, three out of five of the statistical analyses we used did not permit the inclusion of group membership as a covariate (see STAR Methods). Therefore, in order to assess the potential differences in social response to the hurricane between groups while maintaining analytical consistency, we analyzed all our results separately by group. We also focused our investigation on affiliative behaviors and excluded aggressive behaviors because of differences in how aggression was recorded before and after the hurricane (see STAR Methods).

Probability of affiliative interactions increased after the hurricane

To evaluate the influence of Hurricane Maria on rhesus macaques' probability of exhibiting affiliative behavior, we focused on two measures commonly used to quantify affiliation among non-human primates:[38] sitting within two meters of another monkey[39,40] (henceforth "proximity") and grooming each other's fur (henceforth "grooming"). We used a sub-sampling procedure to account for differences in the way data were collected before and after the hurricane (see STAR Methods). This procedure allowed us to match pre- and post-hurricane observations across individuals, time of year, and time of day. We found that macaques were more than four times more likely to be found in proximity to another monkey after the hurricane than before (binomial general linear mixed-effects model [GLMM], group KK proximity odds ratio (OR) = 5.71, 95% CI = {4.74, 6.90}; group V proximity OR = 6.49, 95% CI = {5.84, 7.19}) (Table S1; Figure 2A). They were also >50% more likely to be found grooming after the hurricane than before (binomial GLMM, group KK grooming OR = 2.01, 95% CI = {1.52, 2.63}; group V grooming OR = 1.46, 95% CI = {1.22, 1.75}) (Table S1; Figure 2B).

Monkeys that were socially isolated before the hurricane showed the greatest increase in affiliation after it

Although on average monkeys were more affiliative in the year after the hurricane, there was variability in the extent to which individuals changed their probability of grooming (mean change in probability of grooming = 0.014, std. = 0.06) (Figure S2A) and proximity (mean = 0.357, std. = 0.163) (Figure S2B.). Some monkeys increased their probability of affiliation more than others, and some monkeys decreased their probability. We evaluated three potential factors that might explain this variation: (1) group members' level of integration before the hurricane, defined as overall time spent grooming (seconds per hour observed) and

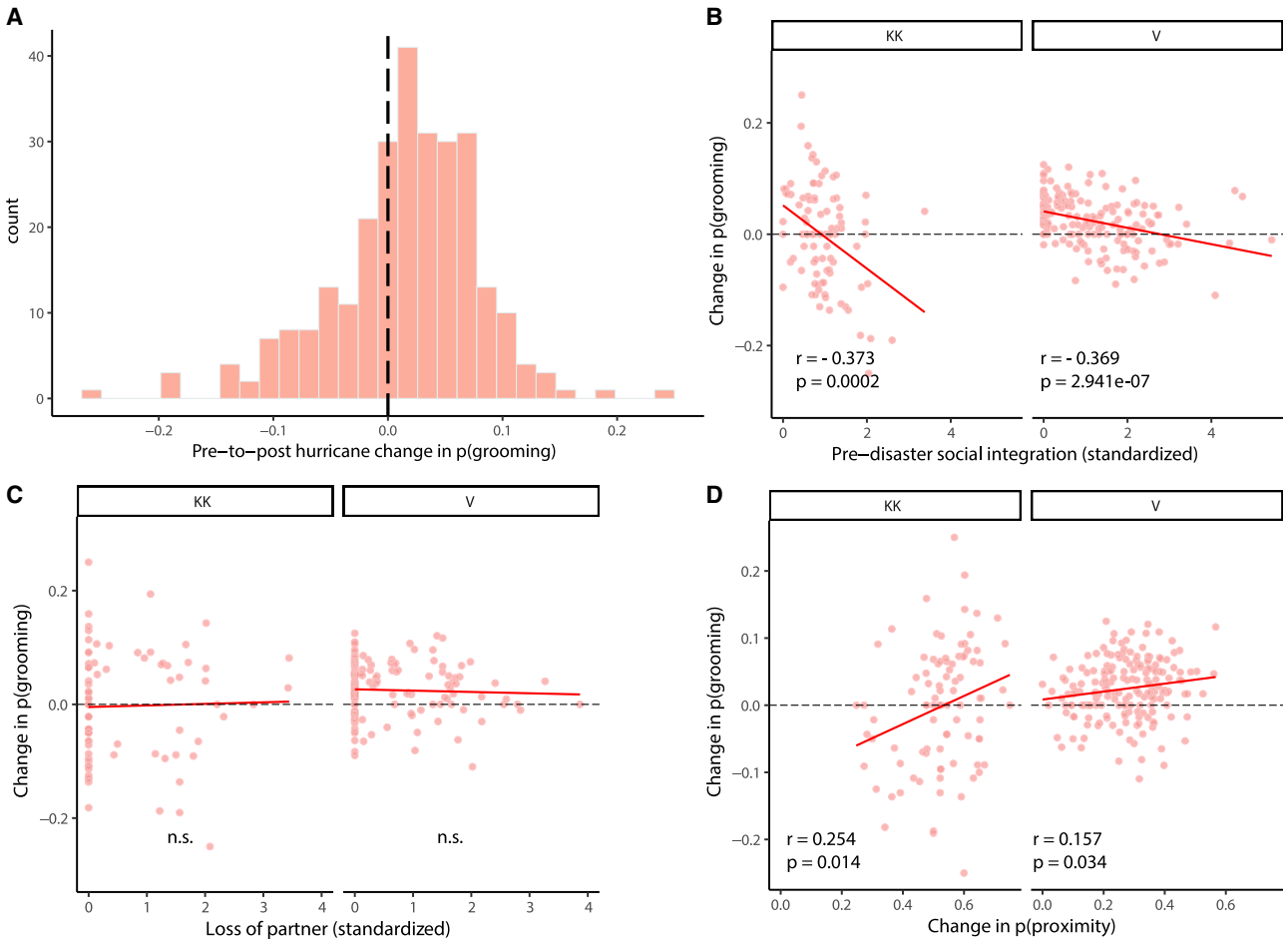

Figure 3. Pre-disaster social integration, but not loss of a partner, predicted changes in the probability of engaging in grooming after Hurricane Maria

(A) Distribution of pre- to post-hurricane changes in an individual's probability of grooming (for one sub-sampling iteration, see Figure S2 for all 500 subsampling iterations).

(B–D) Pre- to post-hurricane change in an individual's probability of grooming (based on one sub-sampling iteration) as a function of: (B) pre-disaster levels of individual social integration (measured by time spent grooming); (C) standardized strength of relationship to lost partners (measured by pre-disaster time spent grooming lost partners); (D) the change in an individual's probability of being in proximity to others after the hurricane compared with before. Red lines in (B), (C), and (D) are regression lines using ggplot geom_smooth in R. correlation coefficients (r) and p values are computed by using cor.test in R. n.s., non-significant. See Table S2 for GLMM results across all subsampling iterations.

the frequency of proximity events (frequency per hour)—referred to as "gregariousness" in STAR Methods. (2) Whether individuals lost members of their pre-hurricane social network (i.e., a pre-storm grooming partner who died within 6 months after the hurricane).[30,31,33] Although the island did not suffer from mass mortality as a result of the storm, the death rate was higher in the month after the hurricane (October 2017) than in this month in previous years (Figure 1B), which might affect probabilities of affiliation beyond what was expected from normal demographic processes.[31] (3) For the grooming probability model only, whether increased grooming reflected increased use of shared space (i.e., proximity to others) after the disaster.

We found that both the amount of time spent grooming and the frequency at which individuals were in proximity to others before the hurricane predicted the extent to which an individual increased their engagement in affiliative behaviors after the hurricane. Specifically, the less time monkeys spent grooming or in proximity to other monkeys before the hurricane, the greater the increase in their probability of engaging in grooming and proximity afterward (linear mixed model [LMM], proximity model, group KK = −0.105, 95% CI = {−0.134, −0.074}; group V = −0.023, 95% CI = {−0.033, −0.012}; grooming model, group KK = −0.051, 95% CI = {−0.064, −0.037}, group V = −0.016, 95% CI = {−0.02, −0.012}) (Figure 3B; Table S2). This effect was stronger than what would be expected by regression to the mean alone (Pitman t test, $p < 0.0001$). An individual's pre-storm strength of connections (measured by time spent grooming) to monkeys who died after the hurricane did not predict their hurricane-related changes in affiliation (LMM, proximity model, group KK = 0.006, 95% CI = {−0.007, 0.018}; group V = 0.000, 95% CI = {−0.009, 0.008}; grooming model, group KK = −0.006, 95% CI = {−0.014, 0.003}; group V = −0.002, 95%

CI = {−0.006, 0.002}) (Figure 3C; Table S2). Monkeys who increased their probability of being in proximity after the storm, in relation to their pre-storm baseline, also displayed a pre- to post-disaster increase in grooming behavior (LMM, group KK = 0.074, 95% CI = {0.016, 0.134}; group V = 0.08, 95% CI = {0.034, 0.138}) (Figure 3D; Table S2).

Monkeys increased the quantity but not intensity of their social relationships after the hurricane

Monkeys might be observed to engage in affiliative behaviors at higher probabilities either because they have more partners, or because they spend more time with specific partners, or both. To test whether monkeys formed new connections, or strengthened the ones they already had, we examined connections at the dyadic level. We focused on grooming because, unlike proximity where many individuals can sit near one another because of mutual attraction to a third party or a common resource, grooming interactions are almost exclusively dyadic in the rhesus macaque[41] and partner choice is active and clear.

We examined network density, the proportion of unique pairwise connections observed over all possible pairwise connections.[42] We found that grooming networks were denser after the hurricane in both groups (sub-sampling-based grooming networks; mean pre- to post-hurricane difference in network density = 0.008, 95% CI = {0.003, 0.012}; see Table S3 for statistics by year). As such, macaques had a greater number of unique grooming partners after the hurricane (Figure 4; see Figure S3 for all groups and years). In contrast, there was no evidence that pairwise grooming relationships were stronger after the hurricane (LMMs: group KK estimate = −0.039, 95% CI = {−0.088, 0.012}; group V estimate = −0.036, 95% CI = {−0.088, 0.015}) (Table S4). Even relationships to familiar partners, i.e., partners that monkeys interacted with at least once in the years preceding the hurricane, were not strengthened after the hurricane, and actually became weaker in group V (LMMs: group KK estimate = 0.018, 95% CI = {−0.20, 0.29}; group V estimate = −0.175, 95% CI = {−0.33, −0.013}) (Table S4).

Individuals interacted with different types of partners after the hurricane

Partner selection might provide insights into the function of social relationships. We investigated how grooming within a group was distributed among specific partner types after Hurricane Maria. Dyads were categorized according to kinship, sex, gregariousness, and social status (see STAR Methods). "Gregariousness" here represents how sociable an individual was compared with their group in a given year pre-hurricane and does not necessarily indicate a stable personality trait.

We found that monkeys were less likely to groom kin after the hurricane than they were before in group V, and group KK showed a non-significant result in the same direction (group V mean pre- to post-hurricane difference in proportion of time spent grooming kin = −0.13, 95% CI = {−0.30, −0.003}) (Table S5; Figure 5) (group KK, mean difference = −0.045, 95% CI = {−0.14, 0.04}). Females from both groups were more likely to groom males after the hurricane (group KK mean difference = 0.143, 95% CI = {0.08, 0.21}; group V mean difference = 0.13, 95% CI = {0.06, 0.24}) (Table S5; Figure 5). Males from group KK, but not group V, were less likely to groom females after the hurricane than before (group KK mean difference = −0.087, 95% CI = {−0.16, −0.02}). In group V but not KK, "less gregarious" individuals (i.e., who groomed or were groomed relatively less before the storm) had a higher likelihood of grooming each other after the hurricane than they did before, whereas "more gregarious" individuals had a lower likelihood of grooming each other (less gregarious to less gregarious: group KK mean difference = 0.125, 95% CI = {−0.02, 0.26}; group V mean difference = 0.21, 95% CI = {0.002, 0.42}; more gregarious to more gregarious: group KK mean difference = −0.02, 95% CI = {−0.05, 0.01}; group V mean difference = −0.11, 95% CI = {−0.19, −0.003}) (Table S5; Figure 5). Finally, we found no evidence for increased likelihood of grooming from low- to high-ranking individuals after the hurricane (group KK mean difference = 0.043, 95% CI = {−0.02, 0.04}; group V mean difference = −0.02, 95%CI = {−0.11, 0.06}) (Table S5; Figure 5).

Reciprocity and closure of triads drove the formation of new network edges from pre- to post-hurricane networks

Finally, we tested whether new grooming-based relationships were driven by simple association heuristics (closure of triads and reciprocity) or shared use of space (i.e., probability of being in proximity). Note that in macaques, grooming relationships are not necessarily reciprocal and can be instead a "commodity" exchanged for agonistic support or tolerance while feeding.[44,45] We used a temporal exponential random graph model (TERGM).[46] These models are designed to test hypotheses related to how and why social interactions occur.[47] TERGMs can directly test the role of emergent network properties, like transitivity, in structuring interactions, which is not possible with other modeling frameworks.[47] Including closure of triads as a predictor enabled us to ask whether monkey A was more or less likely to become connected to monkey B if both shared a common partner.[48] Reciprocity allowed us to test whether A was more likely to groom B after the hurricane if B groomed A before the event. Finally, including proximity as a factor permitted us to test whether the probability of A and B to be in proximity after the hurricane rendered grooming between them more likely. Importantly, contrary to our previous analysis of predictors of changes in individual probability of grooming, our test of the role of shared space use in relationship formation here is at the dyadic level. Previously, we tested whether individuals who had a higher probability of being in proximity to other monkeys also had a higher probability of grooming after the hurricane. Here, we specifically test whether proximity to a partner renders grooming more likely with that specific partner. We also controlled for network density, which could drive triadic closure or reciprocity effects.[47]

We found that reciprocity and triadic closure had strong positive effects on the likelihood of relationship formation after the hurricane (sub-sampling-based TERGM: group KK triad closure estimate = 0.38, 95% CI = {0.092, 0.632}, reciprocity estimate = 1.35, 95% CI = {0.746, 1.933}; group V triad closure estimate = 0.66, 95% CI = {0.338, 0.994}, reciprocity estimate = 2.41, 95% CI = {1.61, 2.99}) (Figure 6.). In other words, network edges were more likely to form if they closed a triangle or reciprocated a pre-storm edge. By contrast, probability of being in proximity between dyads did not predict grooming relationship formation

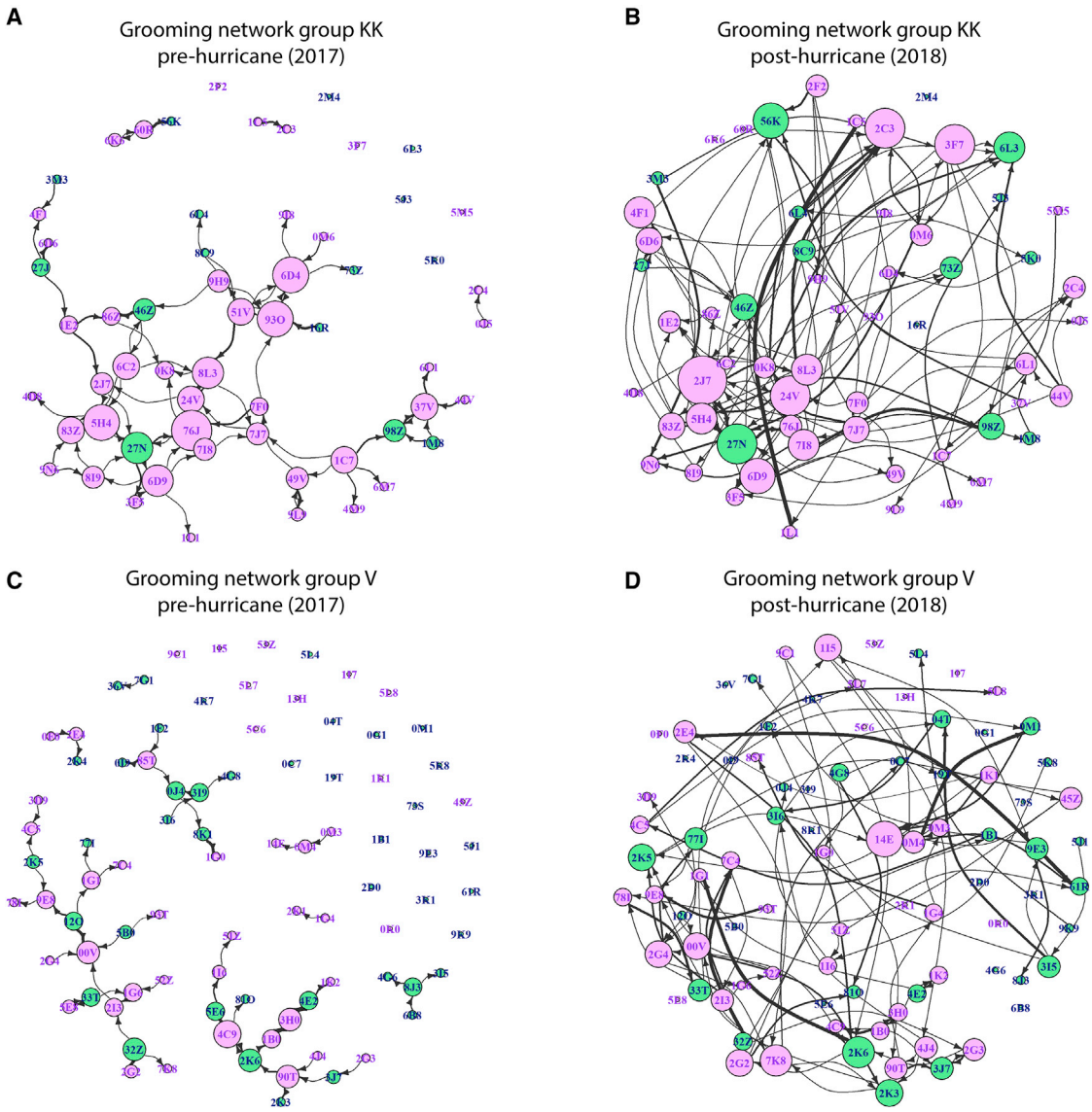

Figure 4. Grooming networks were denser after Hurricane Maria

(A–D) Example grooming networks based on one sub-sampling iteration for group KK before the hurricane in 2017 (A) and after in 2018 (B); group V in 2017 (C) and in 2018 (D). 2017 networks include data up to Hurricane Maria (Sept 20, 2017). See Figure S3 for all groups and years. Note: network plots have average values of connectedness and are representative of other sub-sampling iterations. Each node is an individual. Color coding is as follows: males, green; females, purple. Edges indicate a grooming relationship, and arrows indicate the direction of grooming. Edge thickness indicates relationship strength based on proportion of grooming (number of scans a pair was observed grooming to total number of scans featuring animals from that pair). Node size scales with the number of unique partners. Network layout was held constant for pre- and post-hurricane periods to make the comparison clearer. Note, we estimated the precision of our pre-hurricane grooming networks based on Whitehead[43] (see STAR Methods for details). This method estimates the correlation between the observed and true interactions probabilities between dyads within a network. Correlations >0.4 are generally considered to indicate useful representations of the underlying social structure.[43] In our networks, correlation estimates for all groups and years range between 0.714 and 0.862 (Data S1C). See Tables S3 and S4 for hurricane effect on network density and relationship strength respectively in groups V and KK.

after the hurricane (sub-sampling-based TERGM: group KK proximity estimate = −0.3, 95% CI = {−0.54, 0.32}; group V estimate = −012, 95% CI = {−1.51, 0.83}) (Figure 6). In other words, sharing space with an individual, due to limited edible vegetation or shade in a hurricane-disrupted tropical climate, did not wholly explain grooming relationship formation at the dyadic level.

DISCUSSION

Our findings are consistent with the social buffering hypothesis. Adult monkeys became more affiliative and actively sought social contact after a natural disaster.[7,49] Increases in social relationships, however, were not distributed uniformly across the population. Instead, monkeys that were socially isolated before

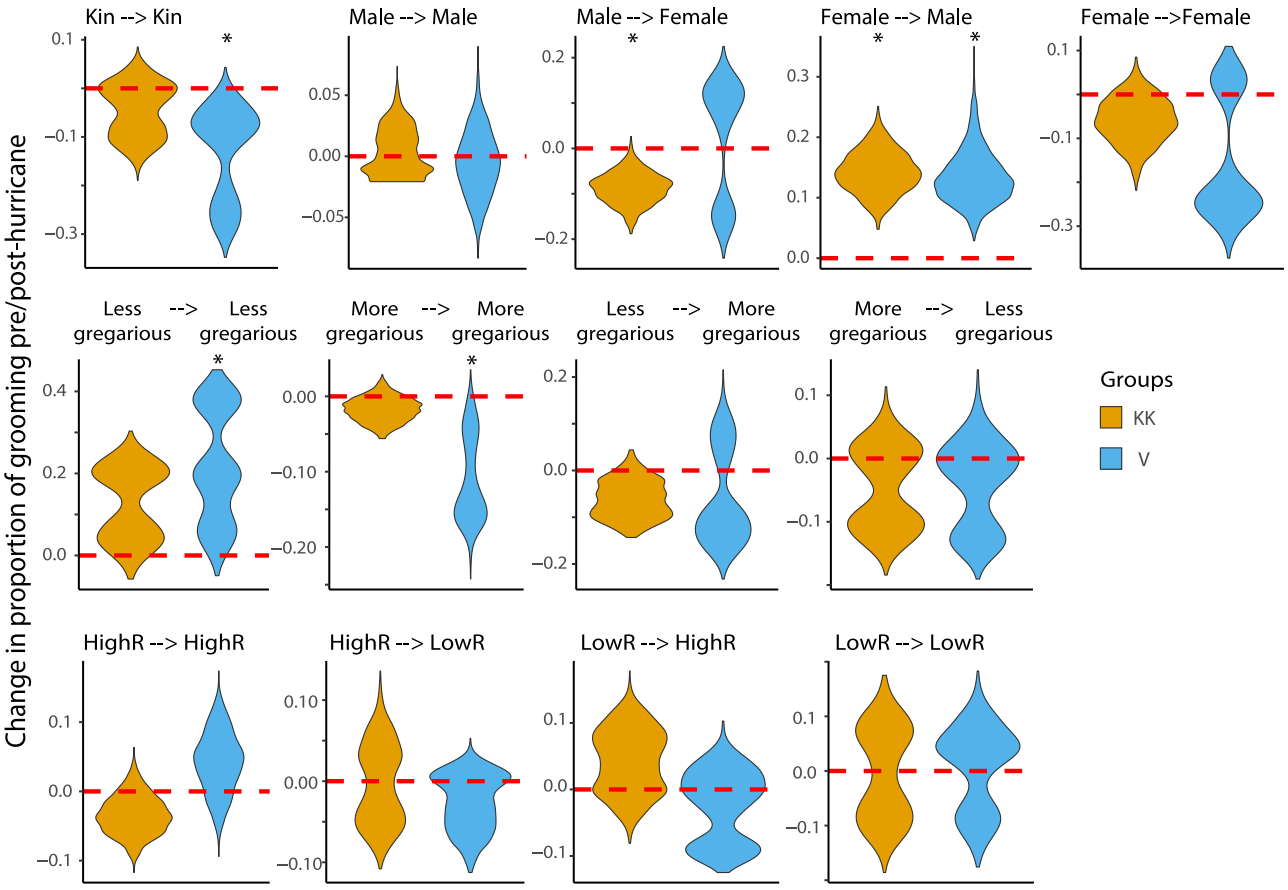

Figure 5. Monkeys groomed different types of partners after Hurricane Maria

Violin plots summarize changes in proportion of grooming directed from one type of partner to another pre- to post-hurricane for individuals in group KK (orange) and group V (blue). Dotted red lines mark the "no change" limit. Stars indicate a significant change (95% CI does not include 0; $p < 0.05$) in proportion of grooming from before the hurricane to after (Table S5). "Male → Female" indicates grooming from males to females. Abbreviations are as follows: HighR, high-ranking; LowR, low-ranking. Note: the bi- or tri-modal shape of the violin plots reflect the pre-hurricane year used for comparison (2 for KK and 3 for V). We plotted all years together to facilitate presentation of results. Only differences robust to the pre-hurricane year used for comparison are ultimately detected as statistically significant.

the hurricane showed the greatest increases in affiliation after it. On the basis of these findings, we postulate that individuals more peripheral to their social network had the biggest drive to invest in social relationships during periods of instability, consistent with a previous study in wild mice after a mass predation event.[30] There were strong sex differences in the drivers of these changes. Specifically, females groomed males more, thereby making males more connected. This finding is consistent with the role of females in promoting group cohesion in some animal societies.[50,51] These results also suggest monkeys that were already highly connected before the hurricane did not derive additional benefits from being more affiliative.[52] Together, we take these findings as strong evidence for flexibility in the ability of rhesus macaques to negotiate their social landscape in the aftermath of a natural disaster.

We also found that macaques widened their social networks to include more partners but did not strengthen the quality of their relationships. Monkeys did not exhibit enhanced efforts to interact with familiar partners, kin, or higher-ranking individuals after the hurricane. These findings are consistent with a strategy to gain social tolerance and support from the greatest number of individuals, and to benefit from broader social integration, rather than focusing on reinforcing relationships to "key" partners. Extended ego-networks can enhance individuals' integration into communities.[53] By contrast, strong ties that increase local cohesion might lead to fragmentation of the larger group because of formation of multiple smaller cliques.[53] To broaden their social networks, macaques tended to adopt a "path of least resistance" approach in forming new relationships, by closing triads and reciprocating grooming. Closure of triads—that is, becoming friends with the friends of your friends—is a frequent mechanism for bond formation across the animal kingdom,[48] including humans.[54] Overall, these results are consistent with a group-level response to an extreme life event of Hurricane Maria's magnitude, in which individuals become more tolerant of one another and seek contact with unfamiliar partners or non-kin, a pattern observed in humans after catastrophic events that affect whole populations.[55–57] One potential driver of this social response is the formation of a large pool of partners that is mobilizable when needed, to reduce one's vulnerability during

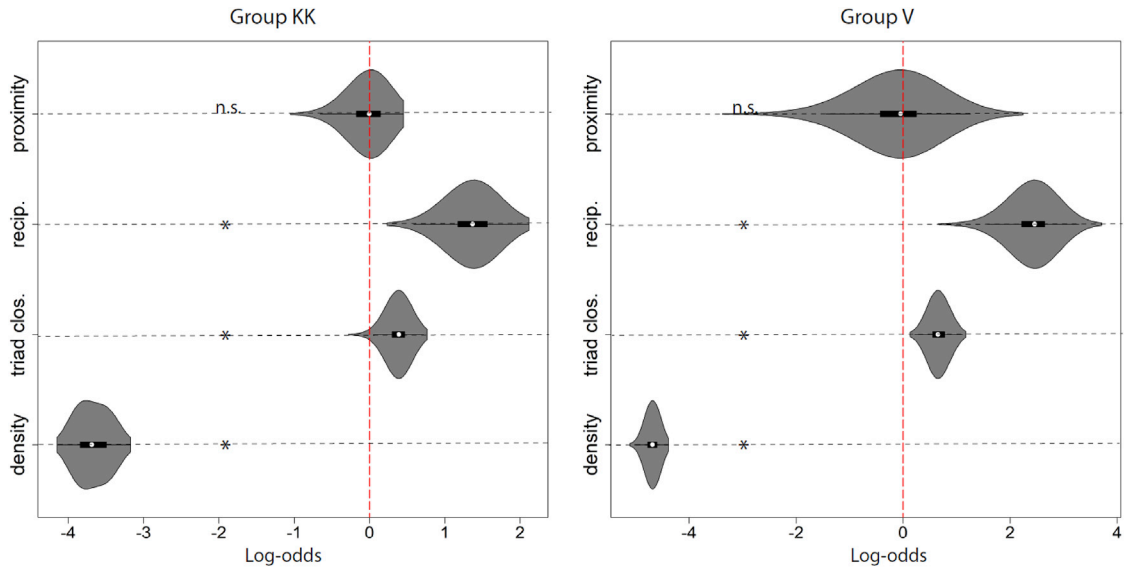

Figure 6. Reciprocity and closure of triads, but not probability of being in proximity, increased the likelihood of grooming between dyads after the hurricane

Violin plots summarizing the distribution of TERGM formation model log-odds for group KK (left) and V (right). Labels from top to bottom: proximity, reciprocity, triadic closure and network density (a control term). We plot the full distribution of log-odds over all 500 modeling iterations. Stars indicate a significant effect on relationship formation (95% CI of parameter estimate does not include 0; $p < 0.05$; see Table S5 for statistics). Positive log-odds are interpreted as an increased likelihood of relationship formation and negative log-odds as a decreased likelihood of relationship formation. The red dotted line marks the "coefficient = 0" limit.

times of instability or resource scarcity after a catastrophic event.[22,53,58,59] A recent study in the same Cayo Santiago macaque population showed that weak connections were positively associated with survival.[39] Enhanced resilience during harsh times, like in the aftermath of a devastating hurricane, might be one route linking weak bonds to enhanced fitness.

In the degraded landscape produced by Hurricane Maria, it might be particularly important to seek out social support from a large pool of partners to access a rare yet diffuse resource like shade.[32] After Hurricane Maria, Cayo Santiago island was almost completely deforested (Figure 1A), which led to severe shade scarcity. In the Caribbean, foliage provides significant protection from high temperatures (Figure S8). As a consequence, an increased probability that monkeys would sit near others and engage in grooming might have resulted from individuals coalescing around this newly precious resource, which protects them from heat, and negotiating access to it by way of grooming. When trying to access a scarce and diffuse resource like shade, stronger bonds are not necessarily useful.[53] For example, monkeys might have turned to non-kin as partners after the hurricane to increase their number of access points to shade. Support from new partners and non-kin, which do not provide indirect fitness or rank-related benefits (given that new partners here were not higher ranking), might require reciprocity to be advantageous to both parties. This could explain why reciprocity partly structured relationship formation from the pre- to the post-hurricane epochs.

Even though we were unable to robustly quantify changes in aggression given the structure of our data, our findings indicate that monkeys became more tolerant of each other despite, or perhaps as a consequence of, decreased shade. It remains possible that increased affiliation reflected the need to secure social support in response to intensified competition over shade. Finally, investment in new social relationships could result from increased opportunities to interact with novel partners clustered in limited shade. Although monkeys that were more likely to be in proximity to other individuals after the hurricane were also more likely to be observed grooming, proximity to a specific individual did not predict the formation of a grooming relationship. This finding indicates a more active choice of grooming partner than the passive emergence of grooming in limited shade.

In the Anthropocene, living in climate-transformed landscapes can have myriad negative health consequences.[60] Devastating tropical storms like Hurricane Maria are predicted to increase in both frequency and intensity,[13,14] as well as become increasingly difficult to predict.[12] Going forward, studies of how animals adjust, socially or otherwise, to these massive transformations of their habitats will be important for addressing why some species, or individuals, are resilient and others more vulnerable. The rhesus macaque, which shows impressive proliferation in human-transformed landscapes,[61] provides important lessons for answering this question. In response to a major hurricane, the Cayo Santiago macaques not only became more tolerant of other monkeys but also formed new social connections—despite increased competition for scarce resources. Our findings support the hypothesis that social support is an important mechanism that gregarious primates can deploy to adapt to extreme environmental change.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.03.029.

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AUTHOR CONTRIBUTIONS

C.T., C.H.K., J.L., L.J.N.B., J.P.H., and M.L.P. conceptualized this study; C.T. and L.J.N.B. developed methodology specific to this study; C.T. and S.L. analyzed the data with input from L.J.N.B., J.L., H.M., N.S.-M., M.J.M. and M.L.P.; A.R.-L., C.H.K., A.B., M.M.W., and M.F. collected the data; C.T. and L.J.N.B. drafted the manuscript with input from all authors; J.P.H., M.M., N.S.-M. and M.L.P. reviewed and edited the manuscript; L.J.N.B. and M.L.P. supervised this work. All authors read and approved the manuscript.

DECLARATION OF INTEREST

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	IDENTIFIER	SOURCE
Deposited data		
Code and data	NA	https://github.com/camilletestard/Cayo-Maria
Software and algorithms		
R, RStudio	NA	RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

LEAD CONTACT

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Camille Testard (Camille.testard@pennmedicine.upenn.edu)

MATERIALS AVAILABILITY

This study did not generate new unique reagents.

DATA AND CODE AVAILABILITY

The dataset and code generated during this study are available at https://github.com/camilletestard/Cayo-Maria.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We studied a population of rhesus macaques living in a semi free-ranging colony on Cayo Santiago Island, Puerto Rico (18°09 N, 65°44 W). The colony 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. 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 two groups for which there was behavioral data before and after Hurricane Maria, groups KK and V, including 159 unique adult individuals (KK: n = 66, F = 44, M = 22; V: n = 93, F = 44, M = 49). These groups had home ranges on different parts of the island (Figure S1). Group V ranged alone on "small Cayo"; an area that was severed from the main part of island ("big Cayo") after the hurricane. In contrast, Group KK ranged on big Cayo with all other groups, mostly on the eastern part of the island which was the most de-vegetated after the hurricane. We used multiple available years of observational data (KK: 2015, 2017; V: 2015, 2016, 2017) to characterize social behaviors before the hurricane ("pre-hurricane").

METHOD DETAILS

Behavioral data collection

Prior to Hurricane Maria, behavioral data were collected using 10-min focal animal samples[62] on Teklogic Psion WorkAbout Pro © handheld computers, with Noldus Observer © software. The duration and partner identity of all positive (e.g., grooming) and negative (e.g., aggression, threats, submissions, and displacements) social interactions with adults were recorded. At the 0-, 5-, and 10-min marks of the focal follow, we collected instantaneous scan samples during which we recorded the state behavior of the subject (grooming, feeding, resting, and traveling) and the identity of all adults within two meters (i.e., in proximity). Importantly for this study, grooming, and proximity were mutually exclusive: grooming took precedence over proximity such that whenever two individuals were grooming they were not recorded as being in proximity as well. We balanced the collection of focal samples on individuals across time of day and across months to account for temporal variation in behaviors.

After Hurricane Maria (September 17, 2020), 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 state behavior of the subject, the identity of their adult social partner when relevant (i.e., if they were grooming) and 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 15mins 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. While aggressive interactions were recorded during scans after the hurricane they were only recorded during focal samples before the storm. Scan samples and focal samples can provide different estimates of brief behaviors like aggression that are not extended in time.[63] Given this limitation, we focused exclusively on affiliative behaviors in this study.

Our subjects were observed over a mean (SD) of 2.97 (0.75) years, always including 2018 (the post-hurricane year). We included on average 4.03 (1.61) h of focal follows and 88.33 (20.86) scan observations embedded within focal follows per individual per year pre-hurricane (see Data S1B for more details), and 448.74 (180.40) scans per individual post-hurricane (November 2017 - September 2018). Because of storms and Hurricane Maria, data collection stopped on August 31, 2017 and didn't resume until November 2nd, 2017.

Dominance ranks for individuals were determined separately for each group and year. Rank was also determined separately for males and females. For males, the direction and outcome of win-loss agonistic interactions recorded during focal animal samples or during *ad libitum* observations of a given year was used to determine rank for that year. For females, rank was determined using both outcomes of win-loss agonistic interactions and matriline rank. Female macaques inherit their rank from their mothers, and female ranks are linear and relatively stable over time.[41] In order to account for group size, dominance rank was defined by the percentage of same sex individuals outranked, and ranged between 0 to 100 (0 = lowest rank, outranks 0% of same sex individuals; 100 = highest rank, outranks 100%). We were interested in comparing top ranking macaques to mid- and low-ranking individuals, where the most important behavioral differences were likely to occur based on previous results.[64,65] Thus, we classified animals as either 'high' or 'low' ranking (with 'low' including both the medium and lowest ranking animals) based on the percentage outranked scale. Monkeys were classified as high ranking if they outranked > 80% of the monkeys of their group/sex and were classified as low ranking if they were outranked by $\leq$79% of monkeys of their group/sex.

Estimating uncertainty of pre-hurricane social networks

Our pre-hurricane social networks were built using an average of 88.33 (20.86) scan observations per individual per year, or 168.21 (41.22) observations per dyad (where either member of a dyad was observed). To ensure this amount of sampling was able to capture a useful representation of the underlying social structure, we evaluated the precision of our pre-hurricane social networks.[43] This method estimates the correlation between our measured interaction indices and the underlying interaction probabilities.[43] We first calculated the coefficient of variation (CV) of the observed probability of interacting, and then estimated the CV of the underlying interaction probabilities (*S*) via maximum likelihood, assuming the underlying associations follow a beta distribution. The ratio of *S* to the observed CV is an estimate of the portion of variance in interaction probability values that is accounted for by the variance in "true" interaction probabilities, rather than sampling variance, and therefore approximates the correlation between "true" and observed interaction indices. Correlations greater than 0.4 are considered to indicate useful representations of the underlying social structure.[43] In our pre-hurricane grooming networks, the average correlation across group-years was 0.781, with a min correlation of 0.72 and a max correlation of 0.86 (Data S1C).

Sub-sampling procedure

In the year following the hurricane (2018), we were only able to collect instantaneous scan samples. As a result, we exclusively used scan samples to compare the social behavior of our study population before and after the hurricane (those collected after the hurricane as instantaneous scans, and those collected in the course of focal animal follows before the hurricane). There were therefore structural differences between our pre- and post-hurricane data that we needed to account for. Specifically: (1) scans were collected far more frequently post-hurricane, which increased the likelihood of picking up interactions compared to before the hurricane, and (2) our pre- and post-hurricane data were not collected equally across time of day (AM/PM) and time of year—though both of these factors may affect rates of affiliative behaviors, such as grooming. For example, monkeys were fed commercially purchased monkey chow exclusively in the morning, which may have a significant negative impact on their propensity to engage in affiliative interactions at that time. Additionally, rhesus macaques are seasonal breeders and there is seasonal variation in their social behavior.[66] Such biases in sampling effort can affect social network measures.[67] To cope with these structural issues, we thus developed a subsampling procedure (Figure S4) that equally balanced the number of observations pre- to post-hurricane, in addition to balancing across time of day and time of year, for all individuals. Using simulations, we show that this procedure limits the detection of individual or dyad-based differences in the probability of interaction pre-to-post hurricane when in fact there are none (see next section and Figure S5).

Furthermore, sampling effort and social dynamics may vary from one year to the next,[68] making it important to account for the variation across pre-hurricane years. Accordingly, we ran our sub-sampling procedure separately for each year pre-hurricane, creating a matched dataset pre-to-post hurricane for each group and pre-hurricane year considered. The latter point is important regarding our first analysis which used a generalized linear mixed model (GLMM) to model changes in probabilities of affiliative

behavior following the hurricane. While GLMMs can account for sampling biases,[69] we were not able to account for year-to-year variation by adding "year" as a random effect. This is because year and hurricane effects are confounded: practically all post-hurricane observations happened in one year (2018). For this reason, we also applied our sub-sampling procedure when running this GLMM allowing us to account for the effect of the pre-hurricane year used for comparison.

We provide a concrete example of our sub-sampling procedure here. When building a matched post-hurricane network for group V in 2016, we only considered individuals present in group V both in 2016 and in 2018 (after the hurricane). For each individual separately, we computed the number of observations in the morning versus afternoon, and across quarters of the year both pre and post-hurricane. For example, animal "00V" in 2016 had 27 scans in the morning and 30 in the afternoon. In 2018 (post-hurricane), she had 431 scans in the morning and 149 in the afternoon. We sub-sampled without replacement 27 observations in the morning and 30 in the afternoon from the post-hurricane data to match the 2016 (pre-hurricane) data. Similarly, data was matched across quarters of the year (henceforth quarter). So, before the subsampling procedure, 00V had 57 observations in 2016 compared to 580 post-hurricane, which were not sampled equally throughout the time of day and time of year pre- to post-hurricane. After the subsampling approach, 00V had 55 observations in 2016 and 55 in 2018, with the same number of observations in AM versus PM and across quarters pre-to-post hurricane. To build the V2016-pre/post dataset, we sub-sampled post-hurricane and/or pre-hurricane data to have them exactly match, for all individuals. Importantly, "year" in this sub-sampled dataset no longer indicated "data collection year" but rather "year of matched data." This coding of year allowed us to account for the pre-hurricane year we used as a baseline for comparison. The same sub-sampling procedure is used for all groups and pre-hurricane years. After one sub-sampling iteration, we sub-sampled our data to have matched pre- and post-hurricane datasets for V2015, V2016, V2017, KK2015 and KK2017. All analyses detailed below are *within*-individual or *within*-group comparisons and compared 5 pre-hurricane datasets to their matched post- hurricane counterparts. Overall, this procedure accounts for (1) differences in the amount of sampling between pre- and post-hurricane epochs—while interactions may be more likely to be picked up post-hurricane due to more frequent sampling, after sub-sampling they are not picked up often enough to drive the detection of a difference in interaction rates pre- to post-hurricane when in reality there is none (Figure S5); (2) differences in sampling effort throughout the day and across seasons; and (3) year-to-year pre-hurricane variation.

Our full dataset contained 97,415 scan sampled observations while the sub-sampled and matched dataset contained 37,950 scan sampled observations. Only observations that did not have a matched category pre- and post-hurricane were discarded. For example, 00V did not have any morning observations from October to December (Q4) in 2016; therefore, all morning Q4 data post-hurricane were discarded for that individual when building the matched post-hurricane dataset. Overall, our sub-sampling approach kept 89% of our full dataset (n = 86,666/97,415). To have all scans with an available match sub-sampled at least once, we needed to run at least 275 sub-sampling iterations (Figure S6). To make sure all our data were considered in our analyses we ran 500 sub-sampling iterations (each of the 5 matched datasets are generated 500 times).

Sub-sampling accounts for differences in sampling effort

Post-hurricane scans were collected far more frequently than pre-hurricane (see "Behavioral data collection" section). This can lead to the detection of interactions post-hurricane that existed pre-hurricane but were missed due to less frequent sampling. Using simulations, we show that subsampling is able to handle this mismatch between pre and post-hurricane datasets and limits the probability of false positives (Figure S5), i.e., the detection of differences in an individual's or a dyad's probability of interacting pre-to-post hurricane when in fact there are none. We describe our simulation step-by-step below.

First, we simulated two datasets with 500 scan observations each. These simulated observations represented pre- and post-hurricane observations for one individual. Each observation can take two possible values: 1 if the individual was observed interacting (i.e., grooming) and 0 if not. Our goal was to quantify false positive rates with and without sub-sampling, such that we set the individual's probability of grooming (henceforth "p(grooming)") to be the same in pre- versus post-event simulated datasets (i.e., no true difference in p(grooming)). To model the sparser sampling pre-hurricane in our actual dataset, we only considered a fixed subset of the simulated pre-event data available for comparing pre- and post-event p(grooming). We chose a range of 20-150 observations, in 10 observation increments, which approximates the range of observations per individual we have in our actual dataset. To model the mismatch in amounts of data available between pre- and post-hurricane in our actual dataset, all simulated 500 observations were available to estimate post-event p(grooming), which is approximately the amount of data available per individual in our post-hurricane sample. To match the sparser pre-event data, we sub-sampled through the 500 post-event observations using the same amount of data as pre-event (ranging in 10 observation increments from 20-150, analogous to the sub-sampling used in the manuscript). After sub-sampling, we computed p(grooming), i.e., number of grooming events (or 1's)/total number of observations, for both pre and post-event data, and subtracted the pre value to the post value to obtain the difference in p(grooming). After 1000 iterations of the sub-sampling procedure, we ended up with a distribution of differences in p(grooming). If the 95%CI of the p(grooming) difference did not contain 0, we considered the difference significant (as in our manuscript). We re-ran steps 2 and 3 1000 times to compare 1000 different subsets of the simulated pre-event data of different sizes (n observations = 20, 30, 50...150). We then computed the probability of a false positive (# differences detected/ # iterations) given a sparse pre-event sample of each fixed size. Finally, we also varied the value of p(grooming) from 0.01 to 0.3 ([0.01, 0.05, 0.1, 0.15, 0.20, 0.3]), and ran steps 3-5 for each value of p(grooming).

This simulation showed that our sub-sampling procedure deals properly with differences in sampling effort between the pre- and post-hurricane epochs and prevents unacceptable false positive rates. False positives occurred < 5% of the time regardless of the

sample size and p(grooming) simulated (Figure S5A). By contrast, if we had failed to use this sub-sampling approach but only bootstrapped the pre- and the post-event datasets, then our p(false positives) would have been much higher (Figure S5B).

Overall, the estimated precision of our pre-hurricane networks[43] and sub-sampling simulations show respectively that: 1. pre-hurricane networks correlate highly with the true underlying social structure ($r > 0.7$, min = 0.71, max = 0,86, Data S1C); 2. we controlled analytically for the mismatch in the amount of data pre- versus post-hurricane (Figure S5). Both make it unlikely to detect changes in relationships or social structure due to missed relationships pre-hurricane. However, to ensure that our results were not driven by individuals with lower numbers of scan samples (< 1.5 SD away from the mean, i.e., < 60 scans), we also re-ran our analyses for questions 2-5 (analyses described below) excluding these individuals (n = 23) and found no qualitative difference in our results.

Testing independence of observations post-hurricane

The statistical analyses we used throughout our study assume independence of observations: within one scan sample, observing an individual grooming or in proximity should not impact the probability of observing another individual in the same states. To test whether our sub-sampled group-wide instantaneous scans post-hurricane suffered from a lack of independence, we ran a simulation to compare the *observed* distribution of the probability of grooming events across scans after sub-sampling (henceforth "p(groom)") to a *theoretical* distribution assuming independence of observations. We computed both distributions as follows: for each observed scan sampling session, we computed the p(groom) (#grooming events in scan 'A'/ all scan 'A' observations). Then, we generated a matched simulated scan sample with the same number of observations but where the outcome of each observation (groom or no-groom) was assigned randomly with a specified probability (i.e., a weighted coin) using the base r function 'sample'. This specified probability matches the observed mean p(groom) across all scan samples, such that the mean theoretical p(groom) in simulated scans matches the observed mean (0.03). Finally, we ran a Chi-square Goodness of fit test using chisq.test in R to test the difference between distributions. The distributions were statistically indistinguishable (chi-square Goodness of fit test, $p > 0.2$, Figure S7), indicating that our observations can be considered independent for analytical purposes. We ran the same analysis for proximity data as well (which is less sparse, mean p(proximity) = 0.18) and found the same result.

Ecological changes and mortality after Hurricane Maria

We quantified changes to vegetation cover and temperature as a result of Hurricane Maria. We measured vegetation cover from two years before to two years after Hurricane Maria using satellite images from Sentinel-hub EO-Browser. We used images from Landsat 8, a satellite operated by the US Geological Survey that has a 16-day repeat cycle (i.e., visiting Cayo Santiago every approximately 16 days). Images from Landsat 8 can be viewed in many formats, including "Normalized Difference Vegetation Index" (NDVI) image format. NDVI is the most widely used remote sensing index for assessing vegetation cover.[70] NDVI is measured using the near-infrared radiation from photosynthetic pigments to assess the photosynthetic activity of vegetation.[70] For Landsat 8, NDVI is automatically calculated by the database with the following band combination ((Band 5 – Band 4) / (Band 5 + Band 4)) which isolates bands that reflect photosynthetic activity.

We created a geojson shapefile of coordinates outlining the entirety of Cayo Santiago, including both the large and small islands, which allowed us to specifically search for images in which there was no cloud cover over the island. We compiled NDVI scores (0 representing no vegetation and 1 representing full vegetation cover) from satellite images with 0% cloud cover over Cayo Santiago from September 21, 2015 to November 29, 2019 (approximately 2 years pre- and 2 years post- Maria). In total, we used 89 images, 42 from before Hurricane Maria (09/21/2015–09/10/2017) and 47 from after (09/26/2017–11/29/2019). Following Hurricane Maria, vegetation on the island decreased by 63% (t test, $p = 3.7 \times 10^{-25}$).

To evaluate the death toll following the hurricane (Figure 1B), we used the CPRC long-term demographic data to compute the monthly number of adult deaths per 100 adult monkeys from 1998 to 2018. We only included adults because the exact date of death of infants and juveniles had an estimated error margin of up to 8 months due to the difficulty in individually recognizing and tracking young animals who had not yet received their unique ID tattoos (in addition to adults being the focus of this study). We also compared the death rate following hurricane Maria to previous studies of population changes following disasters (Data S1A). Death rates in those previous studies included individuals of all ages, such that we also included all individuals to compute the death rate reported in Data S1A – note that this is a conservative estimate (i.e., on the high end) since some of these deaths could have happened before the hurricane or outside of our study period. Study periods in previous studies ranged from 1 day to 1 year following disasters, such that we chose six months as the death rate analysis period (i.e., death rate = number of individuals who died between October 2017 and March 2018 / Number of individuals alive in September 2017).

QUANTIFICATION AND STATISTICAL ANALYSIS

Note that we exclusively used scan data when comparing pre- and post-hurricane probability of affiliation and social networks, since post-hurricane data did not include focal follows. Focal data was only used when estimating individuals' pre-storm strength of connection to monkeys who later died after the hurricane in analysis 2, and gregariousness pre-hurricane in analyses 2 and 4, because focal samples are most appropriate when examining individual-level characteristics and patterns of behavior.[71] Furthermore, our analyses relied on the assumption that scan observations were independent of one another, an assumption we validated using simulations (details in the section "Testing independence of observation post-hurricane," Figure S5).

Probability of affiliative interactions increased after the hurricane

The first goal of our study was to evaluate the influence of Hurricane Maria on probabilities of social interaction. We focused on two measures of sociality: the probability of being scanned in a state-of-proximity (henceforth the proximity) and the probability of being scanned in a state-of-grooming (henceforth the grooming). We used a generalized linear mixed model from R package lme4 (GLMMs),[72] to assess the significance of the hurricane on probability of proximity and grooming. Our dependent variables were binary (e.g., an individual can be scanned in a grooming state = 1; or not = 0), so we used a binomial family model with a logit link function. We controlled for time of day (AM/PM), time of year (quarters), the interaction between time of year and hurricane status, and demographic variables age, sex, and rank by including them as fixed effects. Individual ID and year were included as random effects. We checked the multicollinearity of independent variables using "check_collinearity" from R package "performance"[73]—all our independent variables had a low variance inflation factor (< 1). We sub-sampled our data 500 times, ran a binomial model for each subsampling iteration, and reported the mean estimates and 95% confidence interval for all our regressors.

Monkeys that were socially isolated before the hurricane showed the greatest increase in affiliation after it

We evaluated whether individuals' gregariousness pre-hurricane and their relationship to partners who died in the six months following the hurricane predicted changes in their probability of grooming (henceforth p(grooming)) and being in proximity to others (henceforth p(proximity)) from the pre- to the post-hurricane period. Gregariousness in the grooming model was based on grooming data while gregariousness in the proximity model was based on proximity data. For the change in p(grooming) model, we also tested whether p(grooming) changes could be explained by changes in p(proximity), by including change in p(proximity) as a predictor.

To compute individual grooming and proximity probabilities pre- and post-hurricane, we used the sub-sampling approach described above to match scans for groups KK and V, pre- and post-hurricane, for each year pre-hurricane separately. After each sub-sampling iteration, we computed p(grooming) (= number of grooming events/total number of scans) and p(proximity) (= number of proximity events/total number of scans) for all individuals pre- and post-hurricane separately. Changes in probabilities of affiliative interactions were calculated by subtracting the pre value to the post value, such that a positive change indicated an increase in probability pre-to-post hurricane.

To evaluate an individual's level of gregariousness pre-hurricane, we computed individuals' grooming index and proximity index, separately for each year pre-hurricane using focal samples and scan samples respectively. *Grooming index* is a standardized measure of the amount of time spent grooming per individual, computed as follows: we summed the amount of time (seconds) a subject was observed grooming (or being groomed) for the entire year, divided this sum by the number of hours they were followed that year (to control for observational time), and further standardized this ratio by dividing by the mean for that group and year (to control for group differences in average sociality, which may be influenced by group size and other factors). This grooming index is robust to differences in observational time and represents how gregarious an individual is *relative to* other members of their group.[38] Importantly, the latter gregariousness predictor was computed using focal data (available pre-hurricane only) and is distinct from p(grooming) pre-hurricane used to compute the dependent variable in our model. *Proximity index* was calculated by summing the number of times a subject was observed in proximity to another monkey for the entire year, and standardized the same way as the grooming index. This proximity index, like the grooming index, is robust to differences in observational time and group average sociality. Finally, using focal data we quantified the *strength of relationship to monkeys who died* in the six months following the hurricane by summing the time spent grooming one another before the hurricane (separately for each year pre-hurricane), divided by the average number of hours followed for the two monkeys, and further standardized by the mean strength of grooming bond for that group and year.

Although our dependent variables were bounded between −1 and 1, their distributions approximated a normal distribution (Figure S2). We used linear mixed models from R package lme4 (LMMs)[72] to assess the significance of pre-hurricane level of gregariousness and relationship to deceased monkeys in predicting change in grooming and proximity probabilities in two separate models. In both models we controlled for demographic variables age, sex, and rank included as fixed effects. Individual ID and year were included as random effects. For change in grooming probability model, we also included pre-to-post hurricane change in probability of being in proximity as a predictor (fixed effect). Multiple model assumptions were visually checked using "check_model" from the R package "performance"[73] (normality of residuals, normality of random effects, heteroscedasticity, homogeneity of variance and multicollinearity). After confirming that assumptions were met on several sub-sampling iterations, we sub-sampled our data 500 times, ran a predictive model for each subsampled data, and reported the mean estimate and 95% confidence interval (CI) of our fixed-effect coefficients.

In our models, the pre-hurricane values of p(grooming) or p(proximity) (henceforth "p(affiliation)") and measures of social integration pre-hurricane are related (they both rely on grooming and proximity behavior pre-disaster). Thus, the negative relationship observed between individuals' level of social integration pre-hurricane and their change in probability of affiliation pre-to-post hurricane (Figure 3B in the main text) may be partly due to regression toward the mean (RTM,[74]). This raises the question of whether there are differential effects between individuals with initially low and high social integration values beyond what is expected from the RTM effect. One reasonable prediction of a differential effect is a change in the variance of the population.[75,76] If the null hypothesis that variances at the two time points are equal is rejected, then this is a good indication that our differential effect is above what is expected from RTM.[75] We ran a Pitman t test on the pre- and post- p(groom) and p(proximity) values on 500 subsampling iterations and found statistically different variance on each iteration (95% CI t-value = [6.28 11.96], df = 272, $p < 0.0001$). We conclude that the differential effect observed (the negative relationship between change in p(affiliation) and baseline social integration) is larger than the effect expected by RTM alone.

Monkeys increased the quantity but not intensity of their social relationships after the hurricane

To compare both the number and the intensity of social relationships before and after the hurricane, we used the sub-sampling approach described above to generate subsampled social networks using R package 'igraph'[77] (500 iterations for each group and year). Edge weights were computed by counting from scan samples the number of grooming events between two individuals and dividing this count by the average number of times each member of the dyad was scanned.

To evaluate whether individuals had a greater number of unique partners after the disaster compared to before, we asked whether grooming networks were denser. Network density is the proportion of unique pairwise connections observed over all possible pairwise connections.[42] We computed non-weighted network density for all sub-sampled networks by using the 'edge_density' function in igraph. At each subsampling iteration, we calculated the difference between matched pre- and post-hurricane grooming network densities, for each group and year pre-hurricane separately (i.e., 5 differences were computed since there are 5 group-year combinations, pre- and post). We report the mean pre-/post-hurricane difference in network density and 95% CI. We considered a change in network density as statistically significant if the 95% CI of pre-/post-hurricane difference did not include 0. Note that this bootstrapping-based analytical approach does not allow for the inclusion of group membership or year as a covariate, and for that reason we analyzed data separately by group and year (Table S3).

Next, we tested whether individuals had stronger relationships after the hurricane compared to before. Strength of relationships was measured as the weight assigned to edges in the grooming networks. Importantly, weights *were not standardized* within group and year. Standardizing would occlude any change in relationship strength in the post-hurricane year. Furthermore, we specifically tested the effect of the hurricane on *non-zero* weights. We asked whether dyadic relationships, *when there were any*, were stronger post-hurricane. Importantly, pairs compared were not necessarily the same before and after the hurricane. Individuals only needed to interact in one of the two time points to be considered in this analysis (e.g., A groomed B before the storm but not after). Before using a linear mixed model to assess the effect of the hurricane on relationship strength (categorical predictor 0 = pre-hurricane, 1 = post-hurricane), we log-transformed relationship strength indices (i.e., weights) to meet assumptions of normality and constant variance. We controlled for the demographic characteristics of the subject who gave grooming to its partner (age, sex, and rank) by including them as fixed effects. Individual ID, partner ID and year were included as random effects. After visually confirming that assumptions (normality of residuals, normality of random effects, heteroscedasticity, homogeneity of variance and multicollinearity) were met on several sub-sampling iterations using check_model from R package "performance"[73], we sub-sampled our data 500 times, ran a linear mixed model for each subsampled dataset and report the mean estimate and 95% CI of our regression coefficients.

We also wanted to assess whether individuals strengthen their relationships to *familiar* partners in particular—that is partners that interacted at least once in the three years prior to the hurricane *and* afterward. We used the exact same approach as described above, but this time only including dyads which interacted at least once *both* before and after the hurricane.

Individuals interacted with different types of partners following the hurricane

To evaluate whether allocation of grooming between different partner types, or partner preference, changed following the hurricane, we measured the proportion of total group-level grooming occurring among different partner types, and compared these group-level proportions pre-to-post hurricane. Our analysis aimed at answering the following question: out of all grooming interactions within a given group and a given year pre-hurricane, what proportion occurred between, for example, kin versus between non-kin and did this group-level allocation of grooming efforts change following the hurricane? This analysis was done at the group level rather than individual level because of our lack of statistical power to assess inter-individual differences in partner preference changes following the hurricane.

Animals were defined according to their sex, rank, gregariousness level, and kinship to all potential partners. All subjects fell into one category of each aforementioned attribute. For example, A is "less gregarious," "high ranking," "female" and is related to partner B (they are considered kin). Animal B on the other hand is "more gregarious," "low ranking" and a "male." Therefore, the dyad "A groom B" was categorized as "kin," "less gregarious®more gregarious," "high→low" and "female→male." Note that grooming dyads were directional, such that "B groom A" fell under a different category from "A groom B." For any one network, we assessed partner preference by measuring the proportion of overall grooming that occurred between dyads of different types. *For example*, pre-hurricane 50% of all grooming might have occurred between females, while only 10% might have occurred between males. This allocation of grooming effort may change after the hurricane such that 40% of all grooming interactions might occur between females and 20% might occur between males. This would indicate a shift in partner preferences, where males interacted proportionately more among each other and females less so (note that these numbers are simply used as an example and do not reflect a real result).

To calculate relatedness (or kinship) between social partners, we used information on maternal assignment taken by the Caribbean Primate Research Center (CPRC) dating back to the sites' inception in 1938. Paternity assignment was based on 29 microsatellite markers for most animals born after 1985. Every subject in our sample had a known maternity; 97% had known paternity. We used the kinship2 package in R to calculate the pairwise kin coefficients for all individuals within the sample.[78] To be considered "related," a dyad had to have a relatedness coefficient of at least 0.125 (i.e., sharing at least 12.5% of their genetic material or having at least a common grand-parent[79]). Sex was based on the CPRC census data. For social rank, we used categorical rank (low versus high) as described in the "behavioral data collection" section. To calculate gregariousness, we used focal animal sample data collected before the hurricane to compute a standardized measure of time spent grooming, or *grooming index* per individual, as follows: we summed the amount of time (secs) a subject was observed grooming (or being groomed) for the entire year, divided this sum

by the number of h they were followed that year, and further standardized the ratio by dividing by the mean for that group and year. Thus, this grooming index is robust to differences in observational time and group size; and represents how gregarious an individual is *relative to* other members of their group. Individuals were categorized as "more gregarious" if their grooming index was in the top 20th percentile of their group, and "less gregarious" if otherwise–the same threshold that was used for separating low from high ranking individuals in this and previous studies.[64]

We used our sub-sampling approach to generate grooming networks (500 iterations) for groups KK and V, matched pre- and post-hurricane, for each year pre-hurricane. Thus, at each iteration 10 grooming networks were computed (there are 5 group-year combinations, pre- and post). It is important to note here once more that grooming networks were exactly matched pre- to post-hurricane: they contained the same individuals and the same number of observations per individual before and after the hurricane. To compute edge weights, we counted the number of grooming events between two individuals (or nodes) and divided this count by the average number of times each member of the dyad was scanned. Those weights were then further standardized by dividing by the mean edge weight for that group and year. Thus, edge weights were robust to differences in observational time and group size as well. At each subsampling iteration, the proportions of edge weight attributed to each dyadic category (i.e., sum of weights for dyad category X/ sum of all weights) were computed for all the networks generated (n = 10). In other words, at each iteration we computed 10 proportions per dyadic category (5 pre-hurricane, 5 post-hurricane). Finally, we calculated the difference in grooming proportions between matched pre- and post-hurricane networks, for each partner-type category. We report the mean pre-to-post hurricane difference in proportions per dyadic category and the 95% CI. We consider a change in partner preference for a partner-type category as significant if the 95% CI did not include 0. Note that this bootstrapping-based analytical approach does not allow the inclusion of group membership as a covariate, and for that reason we report our results separately by group (Table S5). Moreover, only pre-to-post hurricane differences consistent across pre-hurricane years used for comparison will be significant. Our pre-/post-hurricane comparisons are within-subject, such that our results are limited to the individuals and pre-hurricane years for which we had matched post-hurricane data (i.e., years 2015-2017).

Reciprocity and closure of triads drive the formation of network edges from pre- to post-hurricane networks

To evaluate which mechanisms may explain relationship formation before and after the hurricane we used Temporal Exponential Random Graph Models (TERGMs).[46] We generated balanced, sub-sampled, grooming, and proximity networks, separated by group, year, and hurricane status (as described previously). Grooming networks were used as the response variable in our TERGMs. Proximity networks were computed to include probability of being in proximity between a dyad as an edge covariate in our model. In other words, we asked whether proximity networks predicted the observed grooming networks. Proximity network edge weights were computed by counting the number of proximity events between two individuals (or nodes), divided by the average number of times each member of the dyad was scanned, standardized by the mean weight for that group and year.

At each sub-sampling iteration, we created a "dynamic network structure" using the networkDynamic R package,[80] which combined unweighted pre- and post-hurricane social networks. Thus, this dynamic network structure had two time-steps (pre and post). TERGM models take this dynamic network as input. It also requires the specification of two models: formation and dissolution. The formation model captures relationship formation dynamics while the dissolution captures dissolution dynamics. These two models are specified separately. For the formation model, we included network density (using "edges"), reciprocity (using "mutual"), and proximity as edge covariate (using "edgecov"). For modeling triad closure, model degeneracy[81] (a common problem in fitting ERGMs in which the algorithms converge to an empty or full network) did not allow us to use the simple triad census, which counts each triad type as a term in the models. As an alternative, we chose the term 'gwesp' to test for the prevalence of triads in our networks. In the ERGM models, gwesp is a geometrically weighted term, which was found to be effective at overcoming the degeneracy problems[82] and models the number of edges that serve as a common base for distinct triangles.[83] Network density was included as a predictor because it drives the propensity for triad closure and reciprocity, and therefore needs to be controlled for. For the dissolution model, we only included network density and proximity—as including reciprocity and closure of triads lead to degeneracy of the model (i.e., parameter estimation rarely or never converged). We used the Markov chain Monte Carlo maximum likelihood estimation procedure[46] for fitting TERGMs to the networks using stergm function from R package "ergm"[84]. This method creates networks from an initial guess of parameter estimates and updates these estimates iteratively to find parameters that replicate the observed network. The model goodness of fit and MCMC simulations were assessed visually for several sub-sampling iterations using "gof" and "mcmc.diagnostics" functions respectively.[84]

TERGMs are not equipped to evaluate networks from multiple groups simultaneously.[46] Thus we had to run our models separately for each group and year pre-hurricane used for comparison. We sub-sampled our data 500 times, ran five TERGM for each subsample (as we have 5 group and year combinations) and report the mean estimate and 95% confidence interval of our regressor coefficients for the formation model - which was the focus of this analysis. Positive parameters in the formation model indicate a higher likelihood than chance that a relationship will form from the first to the second time step. Note that this analysis takes non-weighted networks as its inputs, and is the only analysis in this study that directly compares a specific dyad's relationship pre- versus post-hurricane. Therefore, it is most susceptible to missed interactions or incomplete networks, and should be interpreted with caution.