Reduced injury risk links sociality to survival in a group-living primate

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Abstract

Affiliative social relationships and high social status predict longer lifespans in many mammal species, including humans. Yet, the mechanisms by which these components of sociality influence survival are still largely unknown. Using 10 years of long-term data on the incidence of injuries in a free-ranging population of rhesus macaques (*Macaca mulatta*), we investigated two possible mechanisms that could underpin the relationship between sociality and survival: sociality (1) reduces injury risk; and/or (2) increases the probability of survival after an injury. Our results showed that injured animals had a near three-fold increase in the probability of dying, confirming that injuries can be fatal in this population. Crucially, we found that sociality may reduce an individual's injury risk, but had no effect on the probability of injured individuals dying. Individuals with more affiliative partners and higher social status experienced fewer injuries compared to less socially integrated or lower status animals, with the effect of social status varying with age. Females living in bigger groups were more likely to be injured than those in smaller groups, while in males, smaller groups were associated with higher chances of being injured. Our study contributes novel evidence that sociality does not provide fitness benefits via socially-mediated promotion of injury recovery, but instead can enhance fitness by reducing the risk of being fatally injured in the first place.

Uncovering the means by which sociality influences lifespan is of major interest to evolutionary biologists, social scientists and biomedical researchers [1, 2, 3]. Evidence from humans and other animals has provided increasing support for the benefits of affiliative social interactions on survival. The strength of social bonds [4, 5, 6, 7], the number of weak connections [8], the number of associates [9, 10, 11], the number of relatives in a group [12] and the number of indirect connections [11, 13] predict the lifespan of individuals; the general pattern being that those with more social partners are the ones that live longer. Similarly, socioeconomic status in humans and social status in other animals are also robust predictors of mortality risk [14, 15, 12, 5, 16, 17] with lower status individuals suffering a greater risk of death. But precisely how the social environment affects survival is less well understood.

One way for sociality to influence survival is by mitigating the costs of contest competition over resources. Dominance hierarchies, for instance, are believed to have evolved to reduce direct costs associated with competition for resources [18]. Nevertheless, social hierarchies still usually entail disparities in access to resources, with individuals higher in the hierarchy having priority access to food and mates at the expense of their subordinates [19], who may still need to compete for access. Affiliative partners can also help to reduce engagement in agonistic encounters by providing access to resources via cooperation and social tolerance [20]. For example, food sharing, cooperative feeding and co-feeding have been described in several mammals, including some species of bats [21], cetaceans [22, 23, 24], monkeys [25, 26] and apes [20]. Affiliative partners can also help to deter physical aggression from conspecifics by providing agonistic support. For instance, affiliative interactions predict the formation of coalitions in male and female African wild dogs (*Lycaon pictus*)[27], Camargue horses (*Equus caballus*) [28], macaques (*Macaca spp.*)[29, 30] and chimpanzees (*Pan troglodytes*) [31]. Agonistic support has also been widely documented in female-philopatric primate species where related females defend one another [32, 33, 34]. If social status or affiliative relationships reduce the chance of aggressive interactions, these components of sociality may directly enhance survival by allowing individuals to avoid costly outcomes, such as injuries.

In addition to mitigating the immediate costs of aggressive behaviors, sociality may also enhance survival through buffering mechanisms that influence an individual's health. Differences in access to resources according to social status, for instance, may determine the general body condition and health of individuals. Low social status has been related to higher disease risk [15], higher levels of inflammation [35, 36], reduced healing capacity [37] and overall impaired health in several mammal species, including humans [38, 39, 3]. Affiliative partners, on the other hand, can be valuable resources that can contribute to better health by providing access to food [40, 41] and reducing the burden of infections via hygienic behaviors (*i.e.*, grooming) [42, 43]. Better health status for high ranking or socially integrated individuals may translate into higher chances of survival in the face of adversity, for example, by improving the chances of healing following an injury.

Yet despite clear hypotheses for the potential mechanisms by which social status and affiliative relationships influence lifespan, there remains a lack of empirical evidence for these

mechanisms affecting survival. For example, several studies have shown associations between individual variation in sociality with markers of health and immunity [44, 45, 35, 36], yet the consequences of such differences in the face of naturally occurring challenges to health, and the downstream impact those differences might have on survival are unknown. Similarly, studies supporting a relationship between sociality and lifespan usually do not have the detailed physiological or health data required to test potential mechanisms connecting the two [1]. To fill this gap, we use a long-term data set containing both survival data and detailed information on injuries in a free-living population of rhesus macaques to test whether sociality mitigates the costs of competition (*i.e.*, injuries) and its consequence on survival.

We explore two injury-related mechanisms that can link sociality with survival. Specifically, we test whether social status and/or affiliative relationships: 1) influence the risk of being injured, and/or 2) alter an individual's survival trajectory after an injury (Fig. 1). We did so using 10-years of injury data collected *ad-libitum* together with demographic information from male and female rhesus macaques aged 4-29 years living on Cayo Santiago island, Puerto Rico. Rhesus macaques live in multi-male multi-female despotic societies, where access to resources is highly determined by an individual's position in the dominance hierarchy [46]. Previous studies have shown the benefits of affiliative partners and social status on the survival probability of monkeys in this population [12, 14, 8].Predators are absent from the island, ensuring injuries are mostly the result of physical aggression between conspecifics. Rhesus macaques are seasonal breeders with a mating season that can last from 3 to 6 months. During these periods both affiliative and agonistic interactions are usually heightened [47, 48] and, thus, important trade-offs between health, reproduction and survival may occur [49, 50].

Because our study hinged on the assumption that being injured was detrimental for survival in this population we first tested whether injuries inflicted by conspecifics increased the probability of death in these animals (Fig 1; red arrow). To test if sociality influences the risk of injury (mechanism 1), we asked whether social status and the number of affiliative partners were associated with an individual's injury risk (Fig 1; yellow arrow). Given the protective role of high social status and importance of affiliative partners in deterring aggression [20, 32, 18], we predicted that high status individuals and those with more affiliative partners would have a lower risk of injury. To test if sociality can alter the impact of injuries on survival (mechanism 2), we asked if social status and the number of affiliative partners affected the survival trajectories of injured individuals (Fig 1; green arrow). As both social status and social integration can determine differences in health status that may affect healing rates [39, 37, 51], we predicted that high status animals and those with more affiliative partners would have a lower hazard of death from an injury than low status individuals or those with fewer affiliative partners. Given extensive evidence suggesting that group size can be an important socio-ecological driver of the degree of competition and monopolization of resources [52, 53, 54], we also tested the effect of group size on injury risk and on survival after an injury. Our results demonstrate that sociality plays an important role in mediating the risk of injury, offering one of the few clear mechanistic links between

sociality and survival in a non-human mammal to date.

Results

Effect of injuries on survival

To quantify the extent to which injuries affect an individual's survival we used time-dependent mixed effects cox models [55, 56]. Animals that were injured were nearly three times more likely to die in the two months following the injury compared to animals that were not injured (Fig. 2A; Hazard (Hz) = 1.06 ± 0.17 (SEM), z = 6.58, $p < 0.01$, injuries (i) = 1041, deaths (d) = 443, N injured = 571, N uninjured = 1030), independent of their sex or the reproductive season when the injury occurred. Individuals that were severely injured (*e.g.* broken bones, exposed organs, multiple wounds or wounds in vital areas, see SI Materials and Methods for details) experienced even a higher hazard of death that was dependent on sex (Hz severity*sexM = 1.46 ± 0.72, z = 2.02, p = 0.04, i = 398, d = 107, N severely injured = 295). In males, severe injuries were associated with a higher chances of dying compared to non-severe injuries, while in females, severe and non-severe injuries had similar hazards of death (Fig. 2B).

Mechanism #1: Sociality affects the risk of injury

Effect of social status on injury risk

To test if high status animals were less likely to be injured or severely injured than low status ones, we compared their injury risk separately for males and females using logistic models. Given that observations of social interactions were only available for a subset of our subjects, we used proxies of social status previously used in female (matrilineal rank) [14, 12] and male rhesus macaques (group tenure length) [57, 58, 59] to maximize our statistical power. These proxies were significantly correlated with dominance ranks obtained from behavioral observations of win-loss interactions available for a subset of our subjects (see SI Materials and Methods for details). We found that social status in females had a strong effect on the likelihood of being injured, which was dependent on an individual's age (Odds rankLow*age = 0.3 ± 0.1, z = 3.02, $p < 0.01$, i = 448, N = 827). Low status females had a higher probability of being injured than high status females, and this probability increased with a female's age (Fig. 3A). Social status had no relationship with the risk of severe injuries in females (Odds = 0.13 ± 0.2, z = 0.65, p = 0.5, i = 135, N severely injured = 114). In males, social status also had a strong effect on the probability of being injured which was dependent on age (Odds status*age = 0.1 ± 0.03, z = 3.28, $p < 0.01$, i = 536, N = 748). In younger males, lower social status was associated with a higher incidence of injuries, while at older ages high status males had higher probability of being injured (Fig. 3B). The same pattern was observed when we focused our analysis on severe injuries (Fig. S2A, Odds status*age = 0.12 ± 0.04, z = 2.67, $p < 0.01$, i = 245, N severely injured = 168). Consistent with heightened male-male competition over females [48] and with male

harassment of females during the reproductive season [60], we also found that injury-risk increased for both males and females during the mating period compared to outside it, independent of their social status (injury: Odds females = 0.85 ± 0.28, z = 3.02, p < 0.01; Odds males = 1.2 ± 0.26, z = 4.6, p < 0.01; severe injury : Odds females = 1.04 ± 0.26, z = 4, p < 0.01; Odds males = 1.38 ± 0.25, z = 5.4, p < 0.01) .

Effect of affiliative partners on injury risk

To test whether animals with more affiliative partners were less likely to be injured or severely injured than those with fewer affiliative partners we used logistic models. To support robust statistical analyses, we relied on a proxy (*i.e.*, number of female relatives in the group) that has been previously shown to influence survival in this population [12]. Female rhesus macaques have a strong bias toward forming partnerships with their maternal kin [61] and this proxy has been positively correlated with network measures of social integration [62]. Males, on the other hand, are the dispersing sex and have few kin in their new groups, and so were excluded from this analysis. We found that the number of close relatives (relatedness coefficient (r) = 0.5, *i.e.*., mother-daughters and full siblings) in a female's group had a weak, but not significant, effect on her probability of being injured (Odds = -0.1 ± 0.05, z = -1.84, p = 0.06, i = 491, N = 851). However, the size of a female's extended family (r ≥ 0.125, *i.e.*, spanning three generations) was strongly associated with the likelihood of injury, with females experiencing a 13% reduction in the incidence of injuries for every one standard-deviation increase in their number of female relatives (Fig. 4A; Odds = -0.14 ± 0.06, z = -2.5, p = 0.01, i = 491, N = 851). The incidence of severe injuries was not affected by the number of close relatives(Odds = -0.06 ± 0.09, z = -0.6, p = 0.53, i = 147, N severely injured = 123) nor by the size of a female's extended family (Odds = -0.13 ± 0.09, z = -1.36, p = 0.18, i = 147, N severely injured = 123).

Mechanism #2: Sociality influences the survival of injured animals

Effect of social status on survival of injured animals

To assess whether social status or affiliative relationship buffer the detrimental effect of injuries on survival, we used time-dependent mixed effects cox models. We found no evidence of a buffering effect of social status on the survival of injured females (Hz injured*rankLow = -0.45 ± 0.46, z = -0.98, p = 0.33, i = 448, d = 103, N = 278) or injured males (Hz injured*tenure = 0.00009 ± 0.0002, z = 0.47, p = 0.64, i = 536, d = 97, N = 272). Similarly, no buffering effect of social status on survival was observed in severely injured females (Hz injured*rankLow = -0.51 ± 0.92, z = -0.55, p = 0.58, i = 135, d = 42, N severely injured = 114) or males (Hz injured*status = -0.0001 ± 0.0002, z = -0.67, p = 0.5, i = 245, d = 57, N severely injured = 168).

Effect of affiliative partners on survival of injured animals

We found no evidence for a relationship between survival after an injury and the number of close relatives a female had available at the time (Hz injured*nkin = -0.22 ± 0.28, z = -0.78 , p = 0.43, i = 491, d = 114, N = 294) or current size of her extended family (Hz injured*nkin = 0.03 ± 0.04, z = 0.59, p = 0.56, i = 491, d = 114, N = 294). Similarly, the number of affiliative partners did not influence the survival of severely injured females (Hz close kin = -0.82 ± 0.68, z = -1.21, p = 0.23; Hz extended family = 0.008 ± 0.09, z = -0.1, p = 0.92; i = 147, d = 45, N severely injured = 123).

Effect of group size on injury risk and survival post-injury

The socioecological model predicts that individuals living in bigger groups experience higher intra-group but lower intergroup competition than those living in smaller groups [54]. To test this prediction, we used logistic models to assess the risk of injury for females and males living in varying group sizes (n = 239 group sizes from 11 groups, range = 1 - 366, where one corresponds to extra group males or those living outside social groups). We found a strong sex-specific effect (Odds group size*sexM = -0.2 ± 0.07, z = -2.99, p < 0.01, i = 1041, N = 1601) whereby males living in bigger groups had a lower incidence of injuries while females living in larger groups had a higher risk of injury (Fig. 4B). This result holds even when extra-group males were not included. We observed the same pattern for severe injuries, but the effect was weak (Fig. S1B, Odds group size*sexM = -0.22 ± 0.11, z = -1.97, p = 0.05, i = 398, N severely injured = 295). In agreement with heightened intragroup competition over access to females [60, 63] and food to sustain high energetic demands [50], we found a greater incidence of any injury (Fig. S2C, Odds group size*season = 0.17 ± 0.08, z = 2.05, p = 0.04) and severe injuries (Fig. S2D, Odds group size*season = 0.31 ± 0.13, z = 2.4, p = 0.02) with increasing group size during the mating season.

Given that group size could also determine the potential of a group to monopolize resources over other groups [52] and, in that way, affect the health of its individual members, we additionally asked whether individuals living in bigger groups had higher chances of survival after an injury than those living in smaller groups. We did not find any evidence supporting this prediction, for all injuries (Hz injured*group size = -0.002 ± 0.002, z = -0.87, p = 0.38, i = 1041, d = 219, N = 571) or for severe ones (Hz injured*group size = -0.002 ± 0.03, p = 0.48, i = 398, d = 107, N = 295).

Post hoc mediation analysis

Mediation analyses can be used to test the significance of a mediator in the relationship between an independent and a dependent variable and to measure the effect size of that relationship [64]. Although useful, current mediation analysis approaches are unable to estimate effect sizes for data structured in a logistic manner, such as ours, nor are they able to cope with interaction terms in logistic regressions [65]. Given these limitations, we could not use mediation analysis to evaluate if the effect of social status or group size on

survival was mediated by injury risk because these results relied on an interaction with individual age and sex, respectively (Fig. 3, Fig. 4B), nor could we use it to estimate the effect size of any of our results. We did, however, use mediation analysis to assess if injury risk significantly mediated some of the effect of affiliative partners on survival (see SI Materials and Methods for details). Our mediation analysis confirmed a direct effect of affiliative partners on survival by showing that the size of a female's extended family significantly reduced her hazard of death (direct effect = -0.065 $\pm$ 0.02, z = -3.19, $p < 0.01$). It also confirmed that this relationship was significantly mediated by the risk of being injured (indirect effect z-score = -2.31, $p < 0.05$).

Discussion

Taken together, our results suggest that different components of the social environment can modulate the risk of suffering an injury and, therefore, the hazard of death. We found that high social status was associated with a lower injury risk for specific periods of males' and females' lives, and that a female's number of affiliative partners may help to prevent injuries. In contrast to previous research showing that individuals with higher social status had faster healing rates [37], we found that none of the measures of sociality analyzed affected the survival trajectories of injured animals.

To our knowledge, this is the first field study to quantify the consequences of injuries on the probability of death in a nonhuman primate. Other studies in wild populations of baboons (*Papio sp.*) and Afro-eurasian monkeys have established the social and demographic predictors of injury risk [66, 37, 67, 68, 69, 70], yet its consequences on survival have yet to be shown. We found sex-differences on the influence of severe injuries in survival that can reflect trade-offs between the energy allocated for reproduction versus immunity [4, 37].For instance, during the reproductive season the probability of being severely injured was substantially higher for both sexes. During this period, males may be particularly immunocompromised given the high amount of energy and resources required to sustain the effort associated with mating [49, 71], which can impair injury recovery. On the other hand, females usually have higher demand on their immune systems during lactation [4, 72], *i.e.*, outside the reproductive season. Therefore, females may cope better than males with severe injuries during the reproductive season at the expense of being more susceptible to the consequences of injury outside this period.

We found support for one of the hypothesized mechanisms linking sociality to survival, whereby sociality reduces an individual's risk of injury. High social status animals were injured less than those of lower status during specific periods of their life, and females with more affiliative partners (i.e., kin) were less likely to be injured than less integrated females and, thus, experienced lower hazard of death. Our results linking social status to reduced risk of injury are consistent with the skewed access to resources in systems with clear linear dominance hierarchies [19]. High status individuals may not need to engage in costly aggression for food or mates, in contrast to low status animals who must gain access through contests. Although we could not test for a mediation effect of injury risk

on the relationship between social status and survival, our results suggest that low status individuals experience greater hazard of death as a result of enhanced risk of injury. Our finding that social status did not influence the risk of injury in young females may be because at younger ages females' relative positions in the dominance hierarchy have yet to be fully established [73]. Further, we showed that older high status males were more likely to be injured than older low status males. This finding may reflect heightened aggressive challenges from lower status animals to those higher in the hierarchy as a consequence of a decline in the body condition with age [74] and, thus, the capacity of older high status males to maintain their dominance.

Previous studies in matrilineally-structured primate species, in which most of the affiliative relationships are with female relatives, have shown that females commonly engage in agonistic encounters to support and protect their kin [32, 33, 34], even when confronting higher status individuals [75]. In line with these studies, our results suggest that having more relatives available may provide a numerical advantage to deter physical aggression. Other mechanisms, such as social tolerance when accessing resources [20] could also explain fewer injuries in the presence of more affiliative partners. Interestingly, only the size of a female's extended family, not her number of close relatives, had a significant relationship with risk of injury. This suggests that the number of close relatives in a group (range in our study: 0-5) may not be enough to provide robust agonistic support or access to resources, compared to the size of a female's extended family (range in our study: 0 - 38).

We found no support for the second hypothesized mechanism that we explored to link sociality to survival; none of the measures of sociality analyzed influenced an individual's survival trajectory following injury. Despite a vast body of literature supporting differences in health and immunity between individuals of different social status [44, 35, 39], we found no evidence for an effect of social status on the survival trajectories of injured animals. These findings contrast with a previous study on wild baboons where high status males had faster healing rates than lower status males [37]. Although we did not quantify differences in healing times, our results suggest that the probability of recovering from an injury was not influenced by an animal's position in the dominance hierarchy. These differences might be explained in part by differences in features of the two study systems. Animals on Cayo Santiago are provisioned with food on a daily basis and access to the nutrients needed to support immune function might not be as skewed as they are in the wild [45].Notwithstanding, in both systems high social status has been associated with elevated levels of glucocorticoids and androgens [76, 77, 50], well known immune-suppressors, which suggest that in the Cayo Santiago population, unlike the baboons, the benefits of being of high status may not outweigh the costs in terms of injury recovery.

We also found, contrary to our predictions, that the benefits associated with affiliative partners, such as feeding tolerance [78, 79] and social hygienic behaviours [42, 43], seem not to have helped females to cope with the detrimental effect of injuries on their survival. It is possible that social hygienic behavior, such as removal of ectoparasites by grooming, have long-term health benefits but do nothing to enhance the short-term immune response required to heal damaged tissue [80].Additionally, grooming wounded areas may, in fact, be

detrimental for the healing process as it could lead to the removal of protective scabs [43]. This could be one reason why females with more affiliative partners, who are presumed to receive more grooming and to have more access to food via social tolerance, did not have improved survival trajectories after an injury. Previous research on this population has shown that the number of close relatives and the size of a female's extended family are associated with increased survival probability [12, 8]. The results of the current study suggest this relationship does not come about because of the reduced risk of death from injury. Further research is needed to elucidate to what extent other mechanisms involving health differences (e.g., disease susceptibility) play a role in the benefits of social partners in the survival of females in this population. Additionally, direct behavioral observations in a large sample of individuals with paired injury data will be required to explore refined ego-networks characteristics and to expand these results to affiliative relationships of males and unrelated females.

Finally, in support of predictions of the socioecological model [54], our results suggest that bigger groups reduce the costs associated with competition for male rhesus macaques, while in females, bigger groups were associated with greater injury risk. These findings imply that for males, which are the sex usually involved in intergroup encounters [81, 53], having more group mates may be advantageous possibly by reducing the *per capita* incidence of injuries via 'dilution effect' [82] or by the displacement of other smaller groups without engaging in physical agonistic interactions [83].The higher risk of injury in females living in bigger groups may be explained by increased intragroup competition, as females are the core of rhesus macaque social structure, which is strongly despotic [84]. In support of this, a study in the same population showed that females in larger groups engage more often in intragroup agonistic encounters than those living in smaller groups [52]. Heightened aggression among females living in bigger groups seems to contradict our previous results where females with more relatives in the group had lower chances of being injured. However, a female's extended family size did not have a strong correlation with the number of individuals in the group (Pearson's $r = 0.22$, $p < 0.01$), suggesting that our group size result may in fact reflect competition among non-relatives, including unrelated females and males (*e.g.*, sexual harassment). Contrary to our expectations, group size did not affect the survival of individuals that were injured. Trade-offs between the costs and benefits of group living may explain why no relationship was found, as medium group size has been suggested as the optimum in terms of energy expenditure for foraging and levels of intragroup competition in other primates [85].

In sum, our study provides evidence for a mechanism linking sociality to lifespan. Growing literature has supported a strong relationship between the social environment and survival in many mammal species [3], but the ultimate function of some components of sociality, such as social relationships, remain unclear [86]. Although sociality has been demonstrated to enhance health and immunity [44, 35, 45], here we showed that these benefits did not translate to an improved ability to cope with the risk of death from injuries. Instead, we found that sociality plays an important role in preventing individuals from suffering injuries that would likely lead to death. Given how rare injuries are in this population, we do not

expect that this is the only mechanism linking sociality to survival. Other mechanisms may include sociality-mediated differences in components of health related to disease susceptibility. In wild animal populations, social partners may also help with predator detection [87], predator mobbing [88], finding food sources [89], thermoregulation [90], among other possibilities. Nevertheless, here we provide rare empirical evidence for an ultimate function of social relationships, showing one mechanism by which high status and socially integrated individuals live longer. Demonstrating the relative importance of different mechanisms linking sociality and survival will be challenging but a crucial goal of future research. Our study provides insight into the essential role that long-term datasets that combine both demographic and health data will play in meeting this challenge.

Materials and Methods

Subjects

A full description of materials and methods is provided in the Supplementary Information. Briefly, we studied free-ranging rhesus macaques from the Cayo Santiago population, in Puerto Rico. We focused on all males and females (4 years of age or older) that were alive between the years 2010 and 2020, a period for which records on injuries exist. For all individuals, birth dates, removal dates [91] and death dates were known within a few days from the field site demographic records (see Fig. S1 for details on sample sizes).

Observation of injuries

Injuries were collected *ad libitum* by staff members during the daily monitoring of social groups for demographic purposes. Observers updated the records every time they encountered the injured animal during their daily census routine with an average update time for an injured individual across the 10 years of 42.17 days. Here, we include injuries such as bites, scratches, cuts and abrasions along with other clearly observable injuries such as fractures and exposed organs. Additionally, we classified these injuries based on their degree of severity, where severe injuries were those involving broken bones, exposed organs, multiple wounds and any wound in vital areas, including head, neck, abdomen or genitalia (n = 398). All other injuries were considered non-severe (n = 643).

Measures of sociality

Given that observations of social interactions were only available for a subset of our subjects, we used established proxies of sociality to maximize our statistical power (n injuries = 292 vs 1041). As proxy of social status, we used group tenure in males [57, 58, 59] and matrilineal rank in females [14, 12]. To quantify affiliative relationships, we focused only on females, who don't disperse and whose relationships are matrilineally-structured and biased [92]. As proxy for affiliative partners, we used the number of female relatives in a group [12] based on two relatedness thresholds (r = 0.5 and r $\geq$ 0.125). To determine group size, we sum

all females and males ($\geq$ 4 years old) that were in an individual's social group based on demographic records.

Statistical approach

For all of the statistical analyses we defined a two-month time window (hereafter, bimonthly interval) as the period from which the injury status could transition from injured to not injured based on the average update time for an injured animal (i.e., average time between two consecutive records) and the computed average healing time (see SI for details). Thus, all variables were evaluated on a bimonthly basis (i.e., each row in the dataset represents a two-month interval). For each of the questions we ran two models, one that included injury status based on all injuries (model 1) and other that included injury status for severe injuries only (model 2).

Effect of injuries on survival

To establish the effect of injuries on survival we used time-dependent cox proportional hazard (cox ph) models. The predictor of interest was the injury status (*i.e.*, all injuries or severe injuries) along with other relevant variables that may influence survival probability, such as reproductive season (*i.e.*, mating vs no-mating) and sex. Age was accounted for implicitly in the models. Additionally, we included random effects for individual ID and bimonthly interval. We tested for interaction effects among our predictors and only retained them if statistically significant to avoid issues of overfitting.

Mechanism #1: Sociality affects the risk of injury

To assess the effect of social status, number of affiliative partners and group size on the risk of injuries, we used logistic models where the response variable was the bimonthly injury status. We used sex-separated models for the effect of social status, females only for the effect of affiliative partners, and models with both sexes for the effect of group size. We included age and reproductive season as predictors, and also included sex as a predictor in the group size model (see SI for details). We included random effects for individual ID and bimonthly interval. We tested for interactions among our predictors and retained them if significant.

Mechanism #2: Sociality influences the survival of injured animals

To examine the effect of sociality (social status, number of affiliative partners, and group size) on the survival of injured animals we used time-dependent cox ph models. The predictor of interest was specified by an interaction term between the bimonthly injury status and the sociality measure. We included sex (for group size model only) and reproductive season as fixed effects in the model, along with random effects for individual ID and bimonthly interval. Additionally, for models including social status and number of affiliative partners we included group size to control for its potential effect on the number of relatives available

and survival [2]. Given that the main predictor was an interaction term, we did not attempt to fit other interactions.

Post hoc mediation analysis

To further confirm our findings that sociality significantly influences survival by reducing risk of injury we ran a mediation analysis. This method is not suitable for cox survival models or models including interaction terms, thus we ran models as logistic regressions and only tested the mediation effect of injury risk on the relationship between affiliative partners and survival. We could not assess mediation of injury risk in the relationship of social status and group size with survival, because both models included interaction terms. We followed the method proposed by Iacobucci [93] to test mediation using logistic regressions (see SI Materials and Methods for details).

Ethics

This research complied with protocols approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol no. A6850108) and by the University of Exeter School of Psychology's Ethics Committee. The Caribbean Primate Research Center (CPRC) Animal Care and Use Program is evaluated and approved by the IACUC.

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References

[1] J. Ostner and O. Schülke, "Linking Sociality to Fitness in Primates: A Call for Mechanisms," *Advances in the Study of Behavior*, vol. 50, pp. 127–175, 2018.

[2] J. B. Silk, "The adaptive value of sociality in mammalian groups," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 362, no. 1480, pp. 539–559, 2007.

[3] N. Snyder-Mackler, J. R. Burger, L. Gaydosh, D. W. Belsky, G. A. Noppert, F. A. Campos, A. Bartolomucci, Y. C. Yang, A. E. Aiello, A. O'Rand, K. M. Harris, C. A. Shively, S. C. Alberts, and J. Tung, "Social determinants of health and survival in humans and other animals," *Science*, vol. 368, no. 6493, p. eaax9553, 2020.

[4] E. A. Archie, J. Tung, M. Clark, J. Altmann, and S. C. Alberts, "Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons," *Proceedings of the Royal Society B: Biological Sciences*, vol. 281, no. 1793, 2014.

[5] J. B. Silk, J. C. Beehner, T. J. Bergman, C. Crockford, A. L. Engh, L. R. Moscovice, R. M. Wittig, R. M. Seyfarth, and D. L. Cheney, "Strong and consistent social bonds enhance the longevity of female baboons," *Current Biology*, vol. 20, pp. 1359–1361, 2010.

[6] F. A. Campos, F. Villavicencio, E. A. Archie, F. Colchero, and S. C. Alberts, "Social bonds, social status and survival in wild baboons: A tale of two sexes: Social effects on survival in baboons," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 375, no. 1811, 2020.

[7] J. Holt-Lunstad, T. B. Smith, and J. B. Layton, "Social Relationships and Mortality Risk: A Meta-analytic Review," *PLoS Medicine*, vol. 7, no. 7, p. e1000316, 2010.

[8] S. Ellis, N. Snyder-Mackler, A. Ruiz-Lambides, M. L. Platt, and L. J. N. Brent, "Deconstructing sociality: the types of social connections that predict longevity in a group-living primate," *Proceedings of the Royal Society B: Biological Sciences*, vol. 286, p. 20191991, dec 2019.

[9] S. Ellis, D. W. Franks, S. Nattrass, M. A. Cant, M. N. Weiss, D. Giles, K. C. Balcomb, and D. P. Croft, "Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance," *Proceedings of the Royal Society B: Biological Sciences*, vol. 284, no. 1865, p. 20171313, 2017.

[10] C. M. Nuñez, J. S. Adelman, and D. I. Rubenstein, "Sociality increases juvenile survival after a catastrophic event in the feral horse (Equus caballus)," *Behavioral Ecology*, vol. 26, no. 1, pp. 138–147, 2015.

[11] M. A. Stanton and J. Mann, "Early Social Networks Predict Survival in Wild Bottlenose Dolphins," *PLoS ONE*, vol. 7, no. 10, pp. 1–6, 2012.

[12] L. J. N. Brent, A. Ruiz-Lambides, and M. L. Platt, "Family network size and survival across the lifespan of female macaques," *Proceedings of the Royal Society B: Biological Sciences*, vol. 284, no. 1854, p. 20170515, 2017.

[13] E. Vander Wal, F. M. van Beest, and R. K. Brook, "Density-Dependent Effects on Group Size Are Sex-Specific in a Gregarious Ungulate," *PLoS ONE*, vol. 8, no. 1, p. e53777, 2013.

[14] G. E. Blomquist, D. S. Sade, and J. D. Berard, "Rank-Related Fitness Differences and Their Demographic Pathways in Semi-Free-Ranging Rhesus Macaques (Macaca mulatta)," *International Journal of Primatology*, vol. 32, no. 1, pp. 193–208, 2011.

[15] S. Stringhini, C. Carmeli, M. Jokela, M. Avendaño, P. Muennig, F. Guida, F. Ricceri, A. D'Errico, H. Barros, M. Bochud, M. Chadeau-Hyam, F. Clavel-Chapelon, G. Costa, C. Delpierre, S. Fraga, M. Goldberg, G. G. Giles, V. Krogh, M. Kelly-Irving, R. Layte, A. M. Lasserre, M. G. Marmot, M. Preisig, M. J. Shipley, P. Vollenweider, M. Zins, I. Kawachi, A. Steptoe, J. P. Mackenbach, P. Vineis, M. Kivimäki, H. Alenius, M. Avendano, H. Barros, M. Bochud, C. Carmeli, L. Carra, R. Castagné, M. Chadeau-Hyam, F. Clavel-Chapelon, G. Costa, E. Courtin, C. Delpierre, A. D'Errico, P.-A. Dugué, P. Elliott, S. Fraga, V. Gares, G. Giles, M. Goldberg, D. Greco, A. Hodge, M. K. Irving, P. Karisola, M. Kivimäki, V. Krogh, T. Lang, R. Layte, B. Lepage, J. Mackenbach, M. Marmot, C. McCrory, R. Milne, P. Muennig, W. Nusselder, S. Panico, D. Petrovic, S. Polidoro, M. Preisig, O. Raitakari, A. I. Ribeiro, A. I. Ribeiro, F. Ricceri, O. Robinson, J. R. Valverde, C. Sacerdote, R. Satolli, G. Severi, M. J. Shipley, S. Stringhini, R. Tumino, P. Vineis, P. Vollenweider, and M. Zins, "Socioeconomic status and the 25 × 25 risk factors as determinants of premature mortality: a multicohort study and meta-analysis of 1·7 million men and women," *The Lancet*, vol. 389, no. 10075, pp. 1229–1237, 2017.

[16] D. L. Cram, P. Monaghan, R. Gillespie, B. Dantzer, C. Duncan, H. Spence-Jones, and T. Clutton-Brock, "Rank-Related Contrasts in Longevity Arise from Extra-Group Excursions Not Delayed Senescence in a Cooperative Mammal," *Current Biology*, vol. 28, no. 18, pp. 2934–2939.e4, 2018.

[17] D. Von Holst, H. Hutzelmeyer, P. Kaetzke, M. Khaschei, and R. Schönheiter, "Social rank, stress, fitness, and life expectancy in wild rabbits," *Naturwissenschaften*, vol. 86, no. 8, pp. 388–393, 1999.

[18] K. E. Holekamp and E. D. Strauss, "Aggression and dominance: an interdisciplinary overview," *Current Opinion in Behavioral Sciences*, vol. 12, pp. 44–51, 2016.

[19] T. H. Clutton-Brock and E. Huchard, "Social competition and selection in males and females," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 368, no. 1631, p. 20130074, 2013.

[20] L. Samuni, A. Preis, A. Mielke, T. Deschner, R. M. Wittig, and C. Crockford, "Social bonds facilitate cooperative resource sharing in wild chimpanzees," *Proceedings of the Royal Society B: Biological Sciences*, vol. 285, no. 1888, p. 20181643, 2018.

[21] G. S. Wilkinson, "Reciprocal food sharing in the vampire bat," *Nature*, vol. 308, no. 5955, pp. 181–184, 1984.

[22] A. R. Hoelzel, "Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy," *Behavioral Ecology and Sociobiology*, vol. 29, pp. 197–204, oct 1991.

[23] T. Simila and F. Ugarte, "Surface and underwater observations of cooperatively feeding killer whales in northern Norway," *Canadian Journal of Zoology*, vol. 71, no. 8, pp. 1494–1499, 1993.

[24] K. A. Rossbach, "Cooperative feeding among bottlenose dolphins (Tursiops truncatus) near Grand Bahama Island , Bahamas," *Aquatic Mammals*, vol. 25, pp. 163–167, 1999.

[25] C. Dubuc, K. D. Hughes, J. Cascio, and L. R. Santos, "Social tolerance in a despotic primate: Co-feeding between consortship partners in rhesus macaques," *American Journal of Physical Anthropology*, vol. 148, no. 1, pp. 73–80, 2012.

[26] F. B. M. de Waal, K. Leimgruber, and A. R. Greenberg, "Giving is self-rewarding for monkeys," *Proceedings of the National Academy of Sciences*, vol. 105, no. 36, pp. 13685–13689, 2008.

[27] M. S. De Villiers, P. R. Richardson, and A. S. Van Jaarsveld, "Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus)," *Journal of Zoology*, vol. 260, no. 4, pp. 377–389, 2003.

[28] C. Feh, "Alliances and reproductive success in Camargue stallions," *Animal Behaviour*, vol. 57, no. 3, pp. 705–713, 1999.

[29] O. Schülke, J. Bhagavatula, L. Vigilant, and J. Ostner, "Social bonds enhance reproductive success in male macaques," *Current Biology*, vol. 20, no. 24, pp. 2207–2210, 2010.

[30] C. Young, B. Majolo, O. Schülke, and J. Ostner, "Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques," *Animal Behaviour*, vol. 95, pp. 23–32, 2014.

[31] J. T. Feldblum, C. Krupenye, J. Bray, A. E. Pusey, and I. C. Gilby, "Social bonds provide multiple pathways to reproductive success in wild male chimpanzees," *iScience*, vol. 24, no. 8, p. 102864, 2021.

[32] J. B. Silk, S. C. Alberts, and J. Altmann, "Patterns of coalition formation by adult female baboons in Amboseli, Kenya," *Animal Behaviour*, vol. 67, no. 3, pp. 573–582, 2004.

[33] J. B. Silk, "Altruism Among Female Macaca Radiata: Explanations and Analysis of Patterns of Grooming and Coalition Formation," *Behaviour*, vol. 79, pp. 162–188, 1982.

[34] B. Chapais, C. Gauthier, J. Prud'Homme, and P. Vasey, "Relatedness threshold for nepotism in Japanese macaques," *Animal Behaviour*, vol. 53, no. 5, pp. 1089–1101, 1997.

[35] N. Snyder-Mackler, J. Sanz, J. N. Kohn, J. F. Brinkworth, S. Morrow, A. O. Shaver, J.-C. Grenier, R. Pique-Regi, Z. P. Johnson, M. E. Wilson, L. B. Barreiro, and J. Tung, "Social status alters immune regulation and response to infection in macaques," *Science*, vol. 354, no. 6315, pp. 1041–1045, 2016.

[36] J. Tung, L. B. Barreiro, Z. P. Johnson, K. D. Hansen, V. Michopoulos, D. Toufexis, K. Michelini, M. E. Wilson, and Y. Gilad, "Social environment is associated with gene regulatory variation in the rhesus macaque immune system," *Proceedings of the National Academy of Sciences*, vol. 109, no. 17, pp. 6490–6495, 2012.

[37] E. A. Archie, J. Altmann, and S. C. Alberts, "Social status predicts wound healing in wild baboons," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 109, no. 23, pp. 9017–9022, 2012.

[38] R. M. Sapolsky, "Social Status and Health in Humans and Other Animals," *Annual Review of Anthropology*, vol. 33, no. 1, pp. 393–418, 2004.

[39] R. M. Sapolsky, "The Influence of Social Hierarchy on Primate Health," *Science*, vol. 308, no. 5722, pp. 648–652, 2005.

[40] A. V. Jaeggi and M. Gurven, "Natural cooperators: Food sharing in humans and other primates," *Evolutionary Anthropology*, vol. 22, no. 4, pp. 186–195, 2013.

[41] J. R. Stevens and I. C. Gilby, "A conceptual framework for nonkin food sharing: Timing and currency of benefits," *Animal Behaviour*, vol. 67, no. 4, pp. 603–614, 2004.

[42] M. Y. Akinyi, J. Tung, M. Jeneby, N. B. Patel, J. Altmann, and S. C. Alberts, "Role of grooming in reducing tick load in wild baboons (Papio cynocephalus)," *Animal Behaviour*, vol. 85, no. 3, pp. 559–568, 2013.

[43] A. Pérez Pérez and J. J. Veà, "Allogrooming behavior inCercocebus torquatus: The case for the hygienic functional hypothesis," *Primates*, vol. 41, pp. 199–207, apr 2000.

[44] J. A. Anderson, A. J. Lea, T. N. Voyles, M. Y. Akinyi, R. Nyakundi, L. Ochola, M. Omondi, F. Nyundo, Y. Zhang, F. A. Campos, S. C. Alberts, E. A. Archie, and J. Tung, "Distinct gene regulatory signatures of dominance rank and social bond strength in wild baboons," *bioRxiv*, p. 2021.05.31.446340, 2021.

[45] M. A. Pavez-Fox, J. E. Negron-Del Valle, I. J. Thompson, C. S. Walker, S. E. Bauman, O. Gonzalez, N. Compo, A. Ruiz-Lambides, M. I. Martinez, M. L. Platt, M. J. Montague, J. P. Higham, N. Snyder-Mackler, and L. J. Brent, "Sociality predicts individual variation in the immunity of free-ranging rhesus macaques," *Physiology & Behavior*, vol. 241, no. November, p. 113560, 2021.

[46] B. Thierry, "Social epigenesis," in *Macaque Societies* (B. Thierry, M. Singh, and W. Kaumanns, eds.), pp. 267–290, Cambridge: Cambridge University Press, 2004.

[47] L. J. N. Brent, A. MacLarnon, M. L. Platt, and S. Semple, "Seasonal changes in the structure of rhesus macaque social networks," *Behavioral Ecology and Sociobiology*, vol. 67, no. 3, pp. 349–359, 2013.

[48] J. H. Manson, "Male aggression: a cost of female choice in rhesus macaque," 1994.

[49] J. P. Higham, M. Heistermann, and D. Maestripieri, "The energetics of male-male endurance rivalry in free-ranging rhesus macaques, Macaca mulatta," *Animal Behaviour*, vol. 81, no. 5, pp. 1001–1007, 2011.

[50] J. P. Higham and D. Maestripieri, "The Costs of Reproductive Success in Male Rhesus Macaques (Macaca mulatta) on Cayo Santiago," *International Journal of Primatology*, vol. 35, no. 3-4, pp. 661–676, 2014.

[51] R. M. Wittig, C. Crockford, A. Weltring, K. E. Langergraber, T. Deschner, and K. Zuberbühler, "Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations," *Nature Communications*, vol. 7, no. 1, p. 13361, 2016.

[52] K. N. Balasubramaniam, E. S. Dunayer, L. J. Gilhooly, K. A. Rosenfield, and C. M. Berman, "Group size, contest competition, and social structure in Cayo Santiago rhesus macaques," *Behaviour*, vol. 151, pp. 1759–1798, 2014.

[53] B. Majolo, A. deBortoli Vizioli, L. Martínez-Íñigo, and J. Lehmann, "Effect of Group Size and Individual Characteristics on Intergroup Encounters in Primates," *International Journal of Primatology*, vol. 41, no. 2, pp. 325–341, 2020.

[54] C. Van Schaik, "Why Are Diurnal Primates Living in Groups?," *Behaviour*, vol. 87, no. 1-2, pp. 120–144, 1983.

[55] T. Therneau, "Using Time Dependent Covariates and Time Dependent Coefficients in the Cox Model," *R package Survival Vignettes*, pp. 1–8, 2012.

[56] T. Therneau, "coxme: Mixed Effects Cox Models. R package version 2.2-16.," *Cran*, 2020.

[57] J. H. Manson, "Do female rhesus macaques choose novel males?," *American Journal of Primatology*, vol. 37, no. 4, pp. 285–296, 1995.

[58] C. Dubuc, S. Winters, W. L. Allen, L. J. N. Brent, J. Cascio, D. Maestripieri, A. V. Ruiz-Lambides, A. Widdig, and J. P. Higham, "Sexually selected skin colour is heritable and related to fecundity in a non-human primate," *Proceedings of the Royal Society B: Biological Sciences*, vol. 281, no. 1794, p. 20141602, 2014.

[59] C. M. Kimock, C. Dubuc, L. J. N. Brent, and J. P. Higham, "Male morphological traits are heritable but do not predict reproductive success in a sexually-dimorphic primate," *Scientific Reports*, vol. 9, no. 1, p. 19794, 2019.

[60] F. B. Bercovitch, "Reproductive strategies of rhesus macaques," *Primates*, vol. 38, no. 3, pp. 247–263, 1997.

[61] A. Widdig, P. Nurnberg, M. Krawczak, W. J. Streich, and F. B. Bercovitch, "Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques," *Proceedings of the National Academy of Sciences*, vol. 98, no. 24, pp. 13769–13773, 2001.

[62] L. J. N. Brent, S. R. Heilbronner, J. E. Horvath, J. Gonzalez-Martinez, A. Ruiz-Lambides, A. G. Robinson, J. H. P. Skene, and M. L. Platt, "Genetic origins of social networks in rhesus macaques," *Scientific Reports*, vol. 3, p. 1042, dec 2013.

[63] J. Kuester and A. Paul, "Female-Female Competition and Male Mate Choice in Barbary Macaques (Macaca Sylvanus)," *Behaviour*, vol. 133, pp. 763–790, 1996.

[64] T. J. VanderWeele, "Mediation Analysis: A Practitioner's Guide," *Annual Review of Public Health*, vol. 37, pp. 17–32, 2016.

[65] J. J. Rijnhart, J. W. Twisk, I. Eekhout, and M. W. Heymans, "Comparison of logistic-regression based methods for simple mediation analysis with a dichotomous outcome variable," *BMC Medical Research Methodology*, vol. 19, no. 1, pp. 1–10, 2019.

[66] M. E. Arlet, J. R. Carey, and F. Molleman, "Species, age and sex differences in type and frequencies of injuries and impairments among four arboreal primate species in Kibale National Park, Uganda," *Primates*, vol. 50, no. 1, pp. 65–73, 2009.

[67] E. A. Archie, J. Altmann, and S. C. Alberts, "Costs of reproduction in a long-lived female primate: Injury risk and wound healing," *Behavioral Ecology and Sociobiology*, vol. 68, no. 7, pp. 1183–1193, 2014.

[68] H. A. MacCormick, D. R. MacNulty, A. L. Bosacker, C. Lehman, A. Bailey, D. Anthony Collins, and C. Packer, "Male and female aggression: lessons from sex, rank, age, and injury in olive baboons," *Behavioral Ecology*, vol. 23, pp. 684–691, may 2012.

[69] C. Drews, "Contexts and Patterns of Injuries in Free-Ranging Male Baboons (Papio Cynocephalus)," *Behaviour*, vol. 133, pp. 443–474, 1996.

[70] J. A. Feder, A. Lu, A. Koenig, and C. Borries, "The costs of competition: injury patterns in 2 Asian colobine monkeys," *Behavioral Ecology*, vol. 30, no. 5, pp. 1242–1253, 2019.

[71] R. M. Petersen, M. Heistermann, and J. P. Higham, "Social and sexual behaviors predict immune system activation, but not adrenocortical activation, in male rhesus macaques," *Behavioral Ecology and Sociobiology*, vol. 75, no. 12, 2021.

[72] M. L. East, E. Otto, J. Helms, D. Thierer, J. Cable, and H. Hofer, "Does lactation lead to resource allocation trade-offs in the spotted hyaena?," *Behavioral Ecology and Sociobiology*, vol. 69, no. 5, pp. 805–814, 2015.

[73] L. Kulik, F. Amici, D. Langos, and A. Widdig, "Sex Differences in the Development of Aggressive Behavior in Rhesus Macaques (Macaca mulatta)," *International Journal of Primatology*, vol. 36, no. 4, pp. 764–789, 2015.

[74] J. Altmann, L. Gesquiere, J. Galbany, P. O. Onyango, and S. C. Alberts, "Life history context of reproductive aging in a wild primate model," vol. 1204, pp. 127–138, 2010.

[75] I. S. Bernstein and C. L. Ehardt, "Age-sex differences in the expression of agonistic behavior in rhesus monkey (Macaca mulatta) groups.," *Journal of comparative psychology (Washington, D.C. : 1983)*, vol. 99, pp. 115–132, 1985.

[76] S. A. Cavigelli and M. J. Caruso, "Sex, social status and physiological stress in primates: the importance of social and glucocorticoid dynamics," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 370, no. 1669, p. 20140103, 2015.

[77] L. R. Gesquiere, N. H. Learn, M. C. M. Simao, P. O. Onyango, S. C. Alberts, and J. Altmann, "Life at the Top: Rank and Stress in Wild Male Baboons," *Science*, vol. 333, no. 6040, pp. 357–360, 2011.

[78] C. Fichtel, A. V. Schnoell, and P. M. Kappeler, "Measuring social tolerance: An experimental approach in two lemurid primates," *Ethology*, vol. 124, pp. 65–73, jan 2018.

[79] F. E. de Oliveira Terceiro, M. d. F. Arruda, C. P. van Schaik, A. Araújo, and J. M. Burkart, "Higher social tolerance in wild versus captive common marmosets: the role of interdependence," *Scientific Reports*, vol. 11, no. 1, p. 825, 2021.

[80] S. Guo and L. DiPietro, "Factors Affecting Wound Healing," *Journal of Dental Research*, vol. 89, pp. 219–229, mar 2010.

[81] D. L. Cheney and R. M. Seyfarth, "The influence of intergroup competition on the survival and reproduction of female vervet monkeys," *Behavioral Ecology and Sociobiology*, vol. 21, pp. 375–386, 1987.

[82] R. W. Wrangham, "Evolution of coalitionary killing.," *American journal of physical anthropology*, vol. Suppl 29, pp. 1–30, 1999.

[83] A. C. Markham, S. C. Alberts, and J. Altmann, "Intergroup conflict: Ecological predictors of winning and consequences of defeat in a wild primate population," *Animal Behaviour*, vol. 84, no. 2, pp. 399–403, 2012.

[84] B. Thierry, "Covariation of conflict management patterns across macaque species," in *Natural Conflict Resolution* (F. Aureli and F. de Waal, eds.), pp. 106–128, Berkeley, California: University of California Press, 2000.

[85] A. C. Markham, L. R. Gesquiere, S. C. Alberts, and J. Altmann, "Optimal group size in a highly social mammal," *Proceedings of the National Academy of Sciences*, vol. 112, no. 48, pp. 14882–14887, 2015.

[86] L. J. Brent, S. W. Chang, J.-F. Gariépy, and M. L. Platt, "The neuroethology of friendship," *Annals of the New York Academy of Sciences*, vol. 1316, pp. 1–17, may 2014.

[87] J. Micheletta, B. M. Waller, M. R. Panggur, C. Neumann, J. Duboscq, M. Agil, and A. Engelhardt, "Social bonds affect anti-predator behaviour in a tolerant species of macaque, Macaca nigra," vol. 279, no. 1744, pp. 4042–4050, 2012.

[88] J. M. Kern and A. N. Radford, "Social-bond strength influences vocally mediated recruitment to mobbing," *Biology letters*, vol. 12, no. 11, 2016.

[89] D. Páez-Rosas, L. Vaca, R. Pepolas, R. Wollocombe, T. De Roy, and G. Rivas-Torres, "Hunting and cooperative foraging behavior of Galapagos sea lion: An attack to large pelagics," *Marine Mammal Science*, vol. 36, no. 1, pp. 386–391, 2020.

[90] L. A. Campbell, P. J. Tkaczynski, J. Lehmann, M. Mouna, and B. Majolo, "Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles," *Scientific Reports*, vol. 8, no. 1, pp. 1–8, 2018.

[91] R. Hernandez-Pacheco, D. L. Delgado, R. G. Rawlins, M. J. Kessler, A. V. Ruiz-Lambides, E. Maldonado, and A. M. Sabat, "Managing the Cayo Santiago rhesus macaque population: The role of density," *American Journal of Primatology*, vol. 78, no. 1, pp. 167–181, 2016.

[92] D. Chikazawa, T. P. Gordon, C. A. Bean, and I. S. Bernstein, "Mother-daughter dominance reversals in rhesus monkeys (Macaca mulatta)," *Primates*, vol. 20, no. 2, pp. 301–305, 1979.

[93] D. Iacobucci, "Mediation analysis and categorical variables: The final frontier," *Journal of Consumer Psychology*, vol. 22, no. 4, pp. 582–594, 2012.

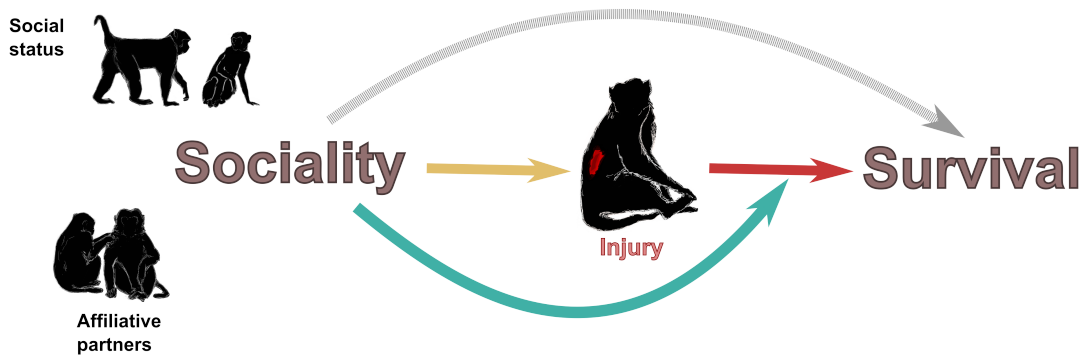

Figure 1: Injury-related mechanisms by which components of sociality (social status, affiliative partners) can influence survival. A direct effect of sociality on survival (gray arrow) has been well established in mammals [4, 5, 7, 10, 11], including studies in the Cayo Santiago population [12, 8]. We explore mechanisms related to injury by which the relationship between sociality and survival might come about. According to the first mechanism, sociality influences the risk of injury (**yellow arrow**) and, therefore, survival (**red arrow**). According to the second mechanism (**green arrow**), sociality affects the survival trajectories of injured individuals.

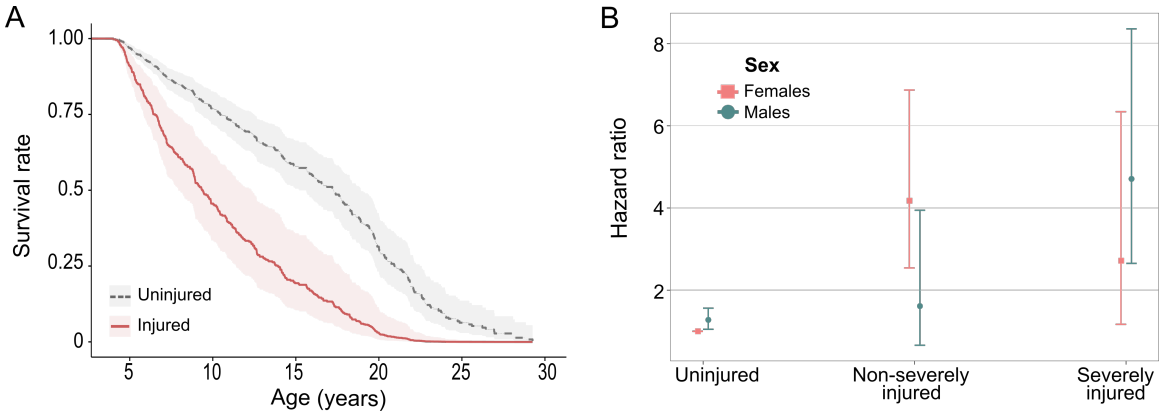

Figure 2: Effect of injuries on survival. **A)** Survival curves adjusted for covariates for injured and uninjured individuals. Injured individuals (red solid line, n = 571, 294 females, 277 males) had near a 3-fold increase in the probability of dying compared to uninjured animals (gray dashed line, n = 1030, 557 females, 473 males)(Hz = 1.06 ± 0.17, z = 6.58, p < 0.01, injuries (i) = 1041, deaths (d) = 443). Curves represent males during the mating season, but those for females were similar. Shaded areas represent standard errors. **B)** Hazard ratios of death for females and males as a function of the severity of injuries. Severe injuries increased the hazard of death relative to non-severe injuries in males (green circles, n uninjured = 473, n non-severely injured = 189, n severely injured = 251), but not in females (Pink squares, n uninjured = 557, n non-severely injured = 232, n severely injured = 147) (Hz severity*sexM = 1.46 ± 0.72, z = 2.02, p = 0.04, i = 398, d = 107).

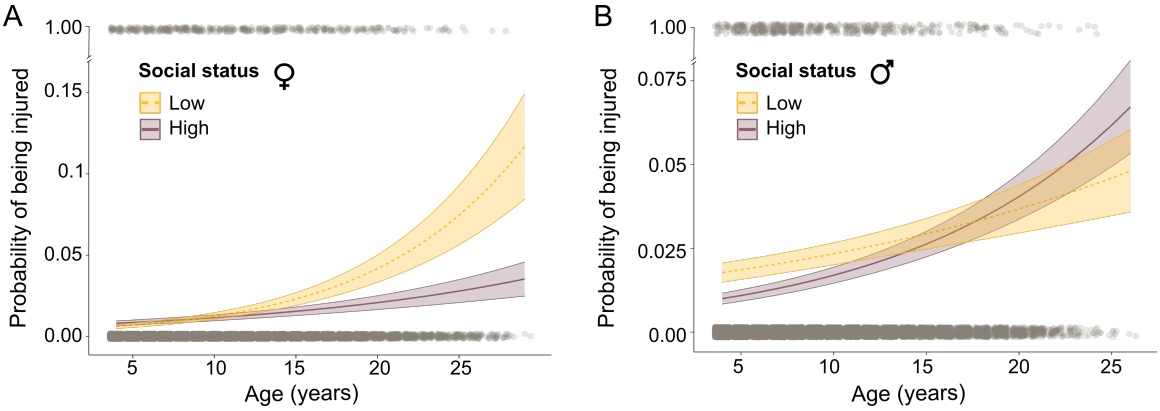

Figure 3: Predicted injury risk in relation to social status. **A)** Injury risk for females as a function of social status and age. Low status females (yellow dashed line, $n = 420$, 237 injuries) had higher chances of being injured than high status females (purple solid line, $n = 407$, 211 injuries), with increasing probabilities for older females (Odds rankLow*age = 0.3 ± 0.1, z = 3.02, p < 0.01). **B)** Injury risk for males as a function of social status and age. For visualization, social status was categorized by selecting the 20th (273 days of tenure) and 80th (2029 days of tenure) percentiles depicting low status (yellow dashed line) and high status (purple solid line), respectively ($n = 748$, 536 injuries). Younger males from low status had higher injury risk than high status young males, yet the opposite occurred at later ages (Odds tenure*age = 0.1 ± 0.03, z = 3.28, p < 0.01). In both plots, shaded areas represent standard errors and gray dots the raw data used in the models (top: injured, bottom: uninjured).

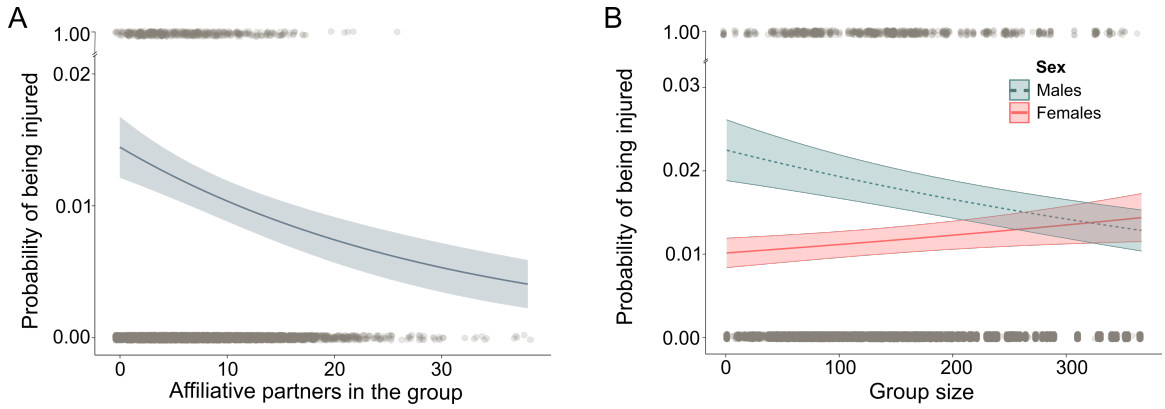

Figure 4: Predicted injury risk as a function of affiliative partners and group size. **A)** Injury risk for females as a function of the number of affiliative partners in a group. X-axis represents the number of female relatives (extended family, r $\geq$ 0.125) present in a female's group (n = 851, injuries (i) = 491). Females with more relatives had lower chances of suffering from an injury compared to females with fewer relatives (Odds = -0.14 $\pm$ 0.06, z = -2.5, p = 0.01, i = 491). **B)** Injury risk as a function of group size and sex. Females (pink solid line, n = 851, 491 injuries) living in bigger groups had higher probability of being injured than females living in smaller groups, while in males (green dashed line, n = 750, 550 injuries) bigger groups had a lower chance of being injured compared to males in smaller groups (Odds group size*sexM = -0.2 $\pm$ 0.07, z = -2.99, p $<$ 0.01, i = 1041). In both plots, shaded areas represent standard errors and gray dots the raw data used in the models (top: injured, bottom: uninjured).