Social bonds between non-kin are common, but less stable, in a mixed-related society

Zhuli Cheng[a,b], André S. Pereira[a,c], Cayo Biobank Research Unit, Josué E. Negron-Del Valle[d], Daniel Phillips[d], Delphine De Moor[a*], Erin R. Siracusa[a*], Lauren J. N. Brent[a*]

[a] Centre for Research in Animal Behaviour, University of Exeter, Exeter, U.K.

[b] Evolutionary Genomics Unit, Okinawa Institute of Science and Technology, Japan

[c] Research Centre for Anthropology and Health, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

[d] Center for Evolution and Medicine, Arizona State University, Temple, AZ, U.S.A.

* Equal contribution

Corresponding author: delphinedemoor@gmail.com

Abstract

Members of social groups often form social relationships, which are known to carry important fitness benefits. Kin selection predicts that these relationships should be prevalent between kin, yet there is increasing evidence that, in societies that feature a mixture of related and unrelated individuals, social bonds are also formed with non-kin. Nevertheless, quantitative research on non-kin social relationships remains rare, hampering our understanding of their nature and adaptive value. Here, we combined long-term social and pedigree data from semi-free-ranging adult female rhesus macaques (*Macaca mulatta*) to quantify the prevalence, stability, and extent to which kin availability predicts the formation of non-kin bonds in a mix-related society. We found that in line with kin selection theory and previous work on this population, there was a clear kin bias in the formation of social bonds. However, bonds with non-kin were still more common than those with kin. We also found that bonds between non-kin were less stable: they were shorter in duration and varied more in strength across years in comparison to bonds with kin. Finally, we found that individuals who had fewer kin group mates were more likely to form social bonds with non-kin. Together this suggests that kin bonds might provide individuals with stable and predictable benefits, whereas non-kin bonds might be formed more opportunistically, to access specific or volatile resources and to compensate for a lack of kin. Future efforts to quantify and

characterise social bonds between non-kin in different societies will yield a better understanding of the proximate and ultimate causes of social bonds, including how they are formed and maintained and what functions they serve.

Introduction

Social relationships are associated with enhanced health, reproductive success, and longevity in humans and social animals (Brent et al., 2017; McDonald, 2007; Silk et al., 2003; Snyder-Mackler et al., 2020), and social tendencies are known to be under genetic control, suggesting that social relationships are an evolved trait that serves an adaptive function (Brent et al., 2013; Fowler et al., 2009; Wice & Saltz, 2021). Yet, exactly how social relationships link to fitness benefits remains unclear (Ostner & Schülke, 2018). A key step towards unravelling the ultimate function of social relationships is to understand who individuals form their relationships with.

Social relationships between related members of the same sex have long been believed to be more common and stronger than between non-kin in social mammals (Clutton-Brock, 2009; Smith, 2014). This is because cooperation between close relatives can lead to indirect fitness benefits in addition to direct fitness benefits, while cooperation with non-kin only provides direct fitness benefits (Hamilton, 1964). In line with this, kin biases in social relationships have been reported across the animal kingdom (reviewed in Smith, 2014). Yet, evidence for the formation of strong social relationships between non-kin is accumulating in a range of species (Carter et al., 2017; Dal Pesco et al., 2021; De Moor et al., 2020a; Gerber et al., 2020; Kerth et al., 2011; Langergraber et al., 2009; Sandel et al., 2020). While the formation of social relationships with non-kin could be attributed to an inability to discriminate kin from non-kin, there is convincing evidence that many social mammals can discriminate maternal and even paternal kin from non-kin (Tang-Martinez, 2001; Widdig, 2007), suggesting they actively choose non-kin as social partners.

There are two main reasons why non-kin might be valuable social partners. First, individuals might prioritise forming relationships with non-kin if the direct fitness benefits they provide outweigh the inclusive fitness benefits of kin partners (Clutton-Brock, 2009). For example, non-kin might be more competent partners (Chapais, 2006), better able to provide highly valuable commodities, such as coalitionary support (De Moor et al., 2020a; Schino, 2007), or knowledge of the environment (Haney & Fewell, 2018), compared to their close relatives. Second, relationships with non-kin might be formed to compensate for a current lack of close kin (Engh et al., 2006; Hill et al., 2011; Silk, 2006) or to preempt a future lack of kin (Carter et al., 2017). For example individuals can engage in a 'social bet-hedging' strategy where they form relationships with non-kin as a "safety network" of cooperation partners for when kin are not available (Carter et al., 2017). In contrast to the large body of research on kin biases in social relationships, quantitative analyses of social relationships between non-kin remain rare. Assessing the prevalence and stability of, and the effect of kin availability on non-kin social relationships might help us understand how and why these relationships are formed and maintained.

In this study we investigated social relationships between non-kin in semi-free-ranging rhesus macaques (*Macaca mulatta*) on the island of Cayo Santiago, Puerto Rico. Macaques are female philopatric and live in large stable social groups consisting of multiple matrilines. We studied adult females as they form the social core of macaque society and are known to establish differentiated dyadic relationships, the strength and stability of which have been shown to positively correlate with survival (Ellis et al., 2019). Multigenerational genetic pedigree data are available for this population, allowing us to reliably estimate relatedness between almost all pairs of potential social partners. Females have been shown to be able to differentiate maternal and paternal kin from non-kin in this population (Pfefferle et al., 2014; Widdig et al., 2001). Although female rhesus macaques bias their affiliative interactions toward kin, they are also known to affiliate with non-kin (Widdig et al., 2016).

To characterise social relationships between unrelated adult female rhesus macaques, we had three questions of interest. First, we asked how common social bonds with non-kin are. We defined social bonds as the three strongest relationships a female forms with other females (Ellis et al., 2019). We predicted that (1a) in line with previous research in this system, more closely related adult females would have stronger relationships than more distantly related ones. Therefore, we also predicted that (1b) adult females would be more likely to form social bonds with kin, but that (1c) those bonds would also feature some non-kin. Second, we asked whether social bonds with non-kin are as stable as those with kin. We predicted that (2a) females would remain social bond partners with kin longer than with non-kin. We also predicted that (2b) a female's relationship strength with kin social bond partners would be more stable than with non-kin social bond partners. Finally, we asked whether kin availability affects the probability of forming social bonds with non-kin. We predicted that (3) females with fewer kin available would form a higher proportion of their social bonds with non-kin.

Methods

Study population and observation methods

Our subjects were adult (≥ 6 yrs old) female rhesus macaques on Cayo Santiago, a 15.2-ha island off the coast of Puerto Rico. These animals are descendants of 409 macaques introduced in 1938 from Northern India (Altmann, 1962). The macaques on Cayo Santiago are free-ranging and are provided with commercial feed daily and ad libitum access to water. As in the wild, in the Cayo Santiago rhesus macaques females are philopatric and form social groups that feature both related and unrelated females (Southwick et al., 1983).

Our data set included six social groups in a total of 19 group-years (F: 2010-2017; HH: 2014 & 2016; KK: 2013 & 2015 & 2017; R: 2015-2016; S: 2011; V: 2015-2017). Each subject was observed using 10-min focal samples (or 5-min focal samples for group KK in 2017 and group HH in 2016). During the focal samples, trained observers continuously recorded the start and the end of grooming bouts given to or received by the subject, as well as the identities of her adult grooming partners (Altmann, 1974). The observers also collected proximity data by conducting scans at 5-min intervals during the focal sample and recording the adult partners that were within two metres of the subject (Brent et al., 2013). In addition to this we also collected agonistic interactions ad libitum. For each subject in each year, we collected on average 5.35 hours (range: 0.75 - 10.83) of focal data and 83.72 proximity scans (range: 12 - 164). A female that migrated between groups (n=1) and her daughters (n=2) were excluded from this study due to the potential peculiarity of their social behaviour. We also excluded adult females who had been observed for less than two standard deviations below the mean focal observation time. In total, we had 347 subjects, resulting in 975 subject-years. Each group-year had 51.32 adult females on average (range: 19-72).

Calculating relatedness

We constructed a pedigree of 7581 macaques of both sexes born between 1985 and 2016, using maternal and paternal identities inferred from genetic analyses provided by the Caribbean Primate Research Center (Widdig et al., 2016). Parentage identities were available for most of the study subjects. Specifically, genetic mothers were known for 340 of the 347 subjects. For the other seven subjects we inferred their mothers' identity based on behavioural observations. We were also able to identify genetic fathers for 337 of the 347 subjects. The family trees of the study females can be traced back, on average, for 3.22 generations (range: 1-6) (see Supplementary Materials).

Using the pedigree, we estimated pairwise coefficients of relatedness (r; (Wright, 1922) between all pairs of subjects using the kinship2 package (Sinnwell et al., 2014) in R (R Core Team, 2020). Relatedness coefficients between any pair of subjects ranged from 0 to 0.5625 (see Supplementary Materials for relatedness heatmaps of the 19 group-years). We defined dyads with $r \geq 0.125$ (including mother-daughter, sisters, half-sisters, grandmother-granddaughter, aunts and nieces, great-grandmothers and great-granddaughters, grandaunts and grandnieces, first cousins, half-aunts and half-nieces) as kin and with $r < 0.125$ as non-kin. We chose 0.125 as the threshold because female rhesus macaques on Cayo Santiago were found to behave no differently towards distant relatives ($0.0005 < r < 0.125$) than towards true non-kin (r=0) (Kapsalis & Berman, 1996). This cutoff is also a commonly used threshold to delineate kin from non-kin in macaques (Chapais & Berman, 2004). Based on this definition, the study subjects had on average 5.63 (range: 0-18) kin group mates in a given year and 52.10 (range: 14-71) non-kin groupmates. Notably, non-kin group mates always outnumbered kin group mates for any subject in any given year in this study.

Calculating dominance ranks

To enable us to account for the effect social status may have on social relationship formation, we computed yearly individual dominance ranks for each subject based on recorded win-losses in agonistic interactions. We defined rank as the percentage of adult female groupmates that were subordinate to the subject in the social group and year (Brent et al., 2013; Ellis et al., 2019).

Calculating the strength of social relationships

We used the Dyadic Composite Sociality Index (DSI; Silk et al., 2013) to quantify the strength of affiliative relationships between all pairs of subjects. The DSI is calculated by combining data on grooming and spatial proximity, two affiliative social interactions widely used to quantify relationships in primates (Silk et al., 2013). The DSI between any pair of subjects in a given year was calculated from two rates: grooming rate and proximity rate, with both rates standardised by the group mean (see Supplementary Materials for the correlation between grooming and proximity rates). More precisely, we calculated grooming rate by dividing the duration of grooming between the two subjects by the combined focal sample time on the two subjects. Similarly, we calculated proximity rate by dividing the number of scans with the two females in proximity by the total number of scans on the two females. We then standardised each behavioural rate by dividing the dyadic rate by the mean rate for that group-year. Finally, we obtained the DSI between any two subjects in a given year by averaging the standardised grooming and proximity rates. As such, the DSI represents the strength of affiliative relationship between two subjects relative to the average relationship strength between any two subjects from that group-year, with larger values indicating stronger social relationships. Of the 26785 dyad-years (10747 unique dyads) in this study, 80.30% had a DSI of 0, reflecting no grooming or proximity were observed for that dyad. The highest DSI was 129.65.

We defined a subject's social bond partners as the individuals with whom she had her three highest DSI values in a given year, a definition commonly used in non-human primates (Schülke et al., 2022; Silk et al., 2013), and a measure of social connection found to link to fitness to this population (Ellis et al., 2019). Partners with whom the subject had a relationship with a DSI < 1 (60 out of 965 subject-years) were disqualified from inclusion as one of a subject's social bond partners because a DSI of 1 represents the mean relationship strength in a social group and therefore should not be considered a strong relationship. It was therefore possible for a subject to have fewer than three social bonds. Conversely, some subjects had more than three social bond partners in a given year (34 out of 965 subject-years), as they had multiple partners with the same DSI value. Most subjects had three social bond partners in a given year based on our definition (871 out of 965 subject-years).

Statistical analyses

We conducted all statistical analyses using the R platform version 4.2.0 (R Core Team, 2020). We fitted linear mixed models (LMM) and generalised linear mixed models (GLMM) using the package lme4 (Bates et al., 2014). We checked model assumptions in the following ways: we confirmed model fit by plotting residuals against simulated residuals with the "DHARMa" package (Hartig, 2020); for multiple regressions, we checked multicollinearity using the "vif" (variance inflation factor) function from the "car" package (Fox and Weisberg, 2019); for mixed-effects models with continuous response variables, we checked normality of random factors with histograms; we checked for zero-inflation in the negative binomial model by comparing the observed number of zeros with expected zeros from simulations (n = 10000) using the "simulateResiduals" function and the "testZeroInflation" function in the "DHARMa" package (Hartig 2020), and found that the response variable DSI was not zero-inflated (ratioObsSim = 0.99, two sided p-value = 0.62). We evaluated the significance of the predictors in statistical models with likelihood ratio tests using the "drop1" function (test = "Chisq"). We chose $p < 0.05$ (two-tailed) as the threshold for hypothesis testing and reported parameter estimates with 95% confidence intervals (CI).

Question 1: How common are social bonds with non-kin?

First, we set out to confirm that, in line with previous studies (Bernstein et al., 1993; Widdig et al., 2016), affiliative relationships were biased towards kin in our study population (prediction 1a). To test this, we ran a negative binomial GLMM (model 1a) with pairwise DSI as the continuous response variable and pairwise relatedness as the continuous predictor for each dyad in each year (n = 27218). We chose a negative binomial model because the data were right skewed and overdispersed. Random factors included in this model were the two subjects IDs, dyad ID, social group and year.

Next, we investigated whether kin was more likely than non-kin to feature in a subject's social bond partners (prediction 1b). To test this, we ran a binomial GLMM (model 1b) for each subject with each of her partners in each year (n = 54436), with whether the partner was the subject’s social bond partner (yes or no) as the response, and kinship (non-kin or kin) as a categorical predictor. Random factors in this model were subject and partner IDs, dyad ID, social group and year.

Finally, to determine whether social bonds were prevalent between non-kin in this mixed-related society (prediction 1c), we quantified how many of a subject’s social bonds were formed with non-kin versus kin. Rather than calculating the ratio of non-kin to kin social bond partners for each subject, we accounted for repeated measures of the same subjects across multiple groups and years by fitting a binomial GLMM (model 1c). We included all subject-years in which the subject had at least one social bond (965 subject-years). The response variable in the model was the ratio of the number of non-kin social bond partners to the total number of social bond partners, and we used the total number of social bond partners as weights to account for the fact that not all females had three social bond partners. We had no fixed predictors and included subject ID, social group and year as random factors. We extracted the intercept as the expected log-odds of a social bond partner being non-kin.

Question 2: Are social bonds with non-kin as stable as those with kin?

Next, we investigated whether social bond stability was affected by kinship. For this question we only used data from group F for which we had 8 consecutive years of data. For each subject from group F, we determined all partners with whom the subject had a social bond for at least one year and with whom she co-resided for at least two years. We then extracted data on the strength of the relationship (DSI) between the subject and each of these partners (n = 970 dyads) across all years of co-residence. We tested whether kinship affected bond stability using two measures: bond duration and variability of the dyad's DSI values across the years.

First, we investigated whether bonds with non-kin would last for fewer years than bonds with kin (prediction 2a). For each partner, we defined their bond duration with the subject as the number of years they featured among the subject's top three partners, divided by the dyad's total number of co-residing years. This proportion ranged from 0.13 (1 out of 8 years) to 1 (8 out of 8 years). We then fitted a binomial GLMM (model 2a) with bond duration as the response variable and kinship (non-kin or kin) as a categorical predictor. We also included the dyad's maximum annual DSI as a continuous predictor to account for any potential effect of bond strength on bond duration, since previous research on female chacma baboons found that the strength and persistence of social bonds were correlated (Silk et al., 2010). We included subject ID and partner ID as random factors.

Next, we investigated whether a subject's relationship strength with non-kin bond partners varied more over time than with kin bond partners (prediction 2b). We measured the degree of variability in relationship strength as the coefficient of variation (CV) of the DSI of a dyad across the years they were groupmates, calculated as the ratio of the standard deviation to the mean. We then fitted a LMM (model

2b) with the coefficient of variation (CV) of a dyad's DSI as the response and kinship (non-kin or kin) as the predictor and subject ID and partner ID as random factors.

Question 3: Does kin availability affect the probability of forming social bonds with non-kin?

Finally, we tested whether subjects with fewer adult female kin group mates had a higher probability of forming bonds with non-kin (prediction 3). For these analyses we used data from all six social groups. The dataset included 965 subject-years in which the subject had at least one bond. To test this, we ran a binomial GLMM (model 3) on the ratio of number of non-kin social bond partners to the total number of social bond partners, and used the total number of social bond partners as weights to account for the fact that not all females had three social bond partners, and subject ID, social group and year as random factors. We included the subject's number of kin group mates as the predictor of interest in the model. We also included the subject's age, dominance rank and the group size as predictors to account for potential confounds. The probability of forming bonds with kin is known to increase with age in female rhesus macaques (Siracusa et al., 2022), while both low-ranking individuals and those living in larger groups are likely to have relatively fewer kin available.

Ethical Note

Collection of field data and use of the Cayo Santiago long-term database were approved by the Institutional Animal Care and Use Committee of the University of Puerto Rico (protocol no. A6850108) and by the Ethics Committee for the School of Psychology, University of Exeter.

Results

Question 1: How common are social bonds with non-kin?

As expected, we found a strong kin bias, both in the strength of affiliative social relationships (prediction 1a; model 1a: $\beta = 9.31$, SE = 0.27, 95% CI [8.77, 9.85], $p < 0.001$) and in the propensity to form social bonds with kin (prediction 1b; model 1b: $\beta = -2.09$, SE = 0.15, 95% CI [-2.38, -1.80], p <

0.001) (Table 1; Figure 1). For example, the predicted average DSI for fully unrelated dyads (r =0) was 0.15, while the predicted average DSI for the most closely related dyads (r = 0.5) was 16, or 105.09 times that of fully unrelated dyads (model 1a). Similarly, the probability for kin to feature in a subject's social bond partners was 8.08 times the probability for non-kin. Despite such prominent kin bias, subjects regularly formed strong relationships with non-kin, as evidenced by the fact that social bonds with non-kin were actually more common than those with kin (question 1c; model 1c: intercept = 0.49, SE = 0.17, 95% CI [0.14, 0.83]). On average, 62% of a subject's social bond partners were predicted to be non-kin and 38% were predicted to be kin. This inconsistency between preferring to form relationships with kin but having more bonds with non-kin can be explained by the substantially larger numbers of available non-kin (range: 16 - 71) compared to available kin (range: 0 - 13) (Fig 1).

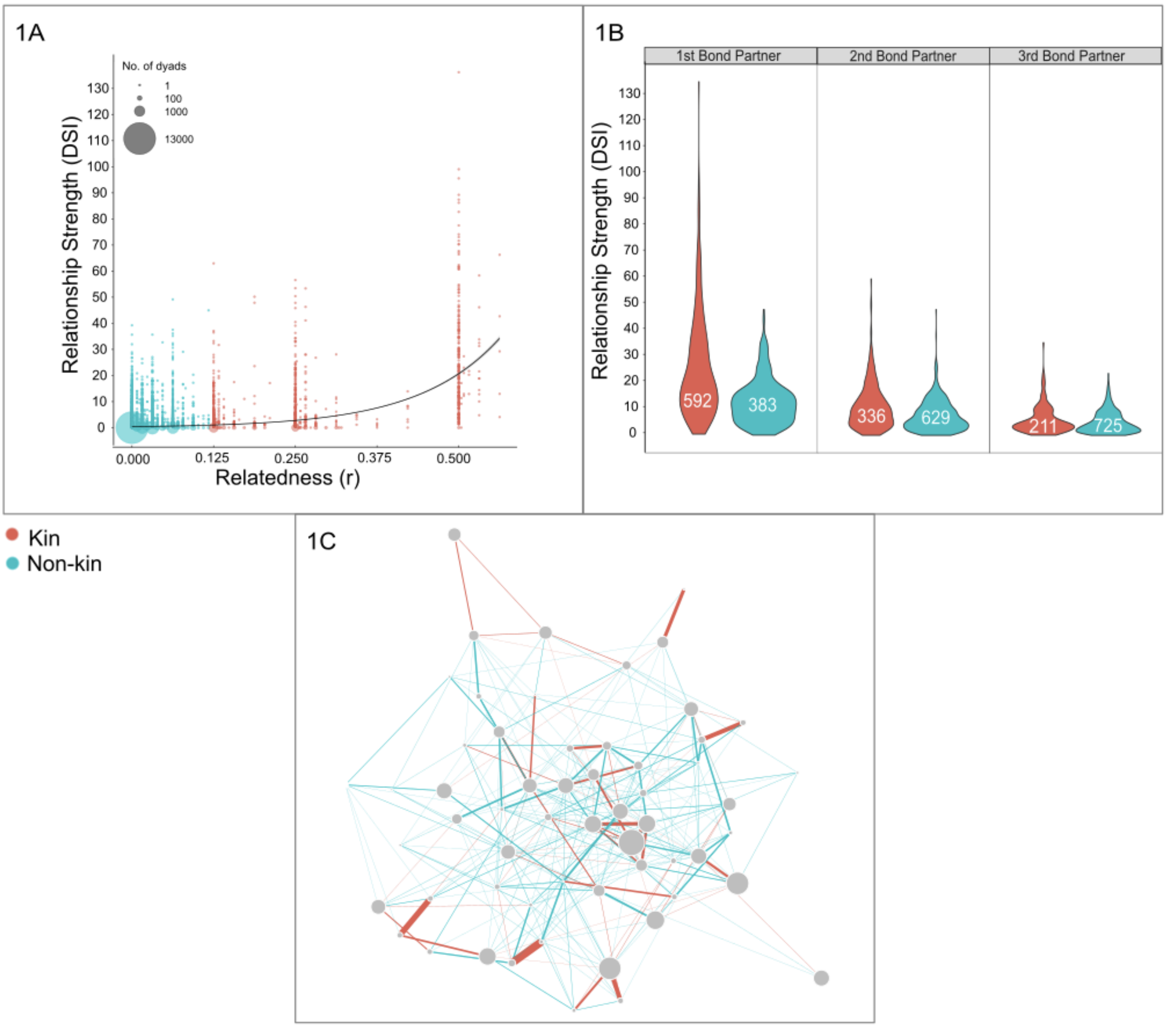

Figure 1: Kin bias in social relationships and prevalence of social bonds with kin (red) and non-kin (blue). (A) The relationship between relatedness (r) and relationship strength (DSI) from model 1a. The shaded grey bar shows the 95% confidence interval around the predicted values (black line). Points represent raw data from all dyads. (B) Violin plots showing the distribution of each subject's top three social bond partners (highest DSI values). The number displayed within each violin plot is the count of social bonds in that category. (C) Social network of group F in 2010. Each node in the network represents a subject, with the size of the node proportional to a subject's number of available kin groupmates. The edges between nodes represent affiliative social relationships, regardless of whether they are a subject's social bond partner. Edge thickness is proportional to relationship strength (DSI). Only edges with a DSI greater than 1 are plotted. Social networks of the other 18 group-years can be found in Supplementary Materials.

Question 2: Are social bonds with non-kin as stable as those with kin?

We found that social bonds with non-kin were significantly less stable than those with kin, both in terms of bond duration and variability in the strength of bonds (Table 1; Figure 2). Social bonds with non-kin were less likely to be maintained over time (prediction 2a; model 2a: $\beta = -0.67$, SE = 0.09, 95% CI [-0.84, -0.49], $p < 0.001$). On average, social bonds with kin lasted for 2.63 years, whereas those with non-kin only lasted for 1.22 years. Notably, 83% of social bonds with non-kin lasted only one year while only 34% of social bonds with kin lasted one year. Social bonds with non-kin also varied more in strength than bonds with kin (prediction 2b; model 2b: $\beta = 0.57$, SE = 0.04, 95% CI [0.49, 0.65], $p < 0.001$). For social bonds with non-kin, the predicted average coefficient of variation (CV) in DSI was 1.50, while for social bonds with kin the predicted average CV was 0.93.

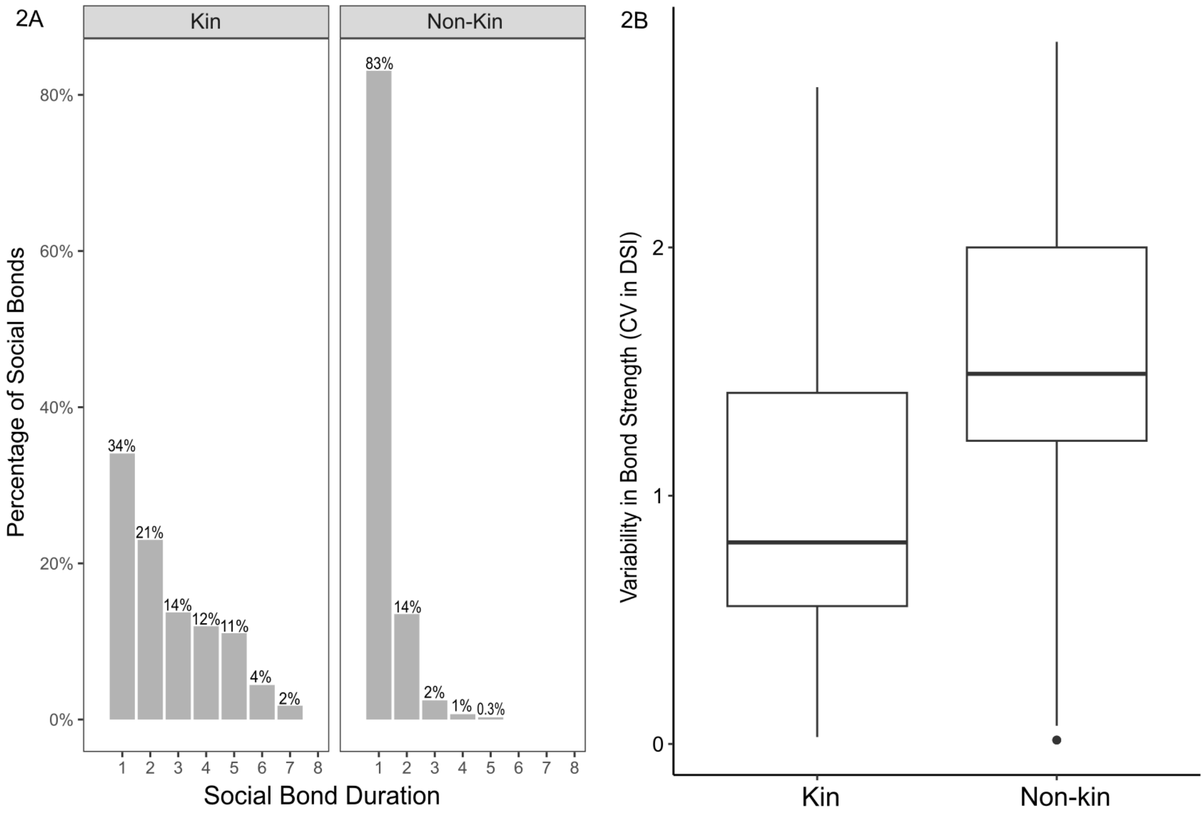

Figure 2. Stability of social bonds with kin and non-kin. (A) Percentage of social bonds with kin and non-kin broken down by bond duration in years. (b) Boxplots showing the variability in bond strength (CV in DSI) across the years for kin bond partners and non-kin bond partners. Centre lines show the medians; box limits indicate the 25th and 75th percentiles. Whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles if not exceeding the limits of the data points. Data beyond the end of the whiskers are plotted individually.

Question 3: Does kin availability affect the probability of forming social bonds with non-kin?

We found that subjects had significantly more social bonds with non-kin when they had fewer adult female kin groupmates (prediction 3; model 3; $\beta = -0.17$, SE = 0.02, 95% CI [-0.20, -0.14], $p < 0.001$; Table 1; Figure 3). For example, a female with one kin available was predicted to have on average 78% of her social bonds with non-kin, whereas a female with 10 kin available this was 43%. Nevertheless, many females with a large number of available kin, sometimes more than 10, still formed some of their social bonds with non-kin.

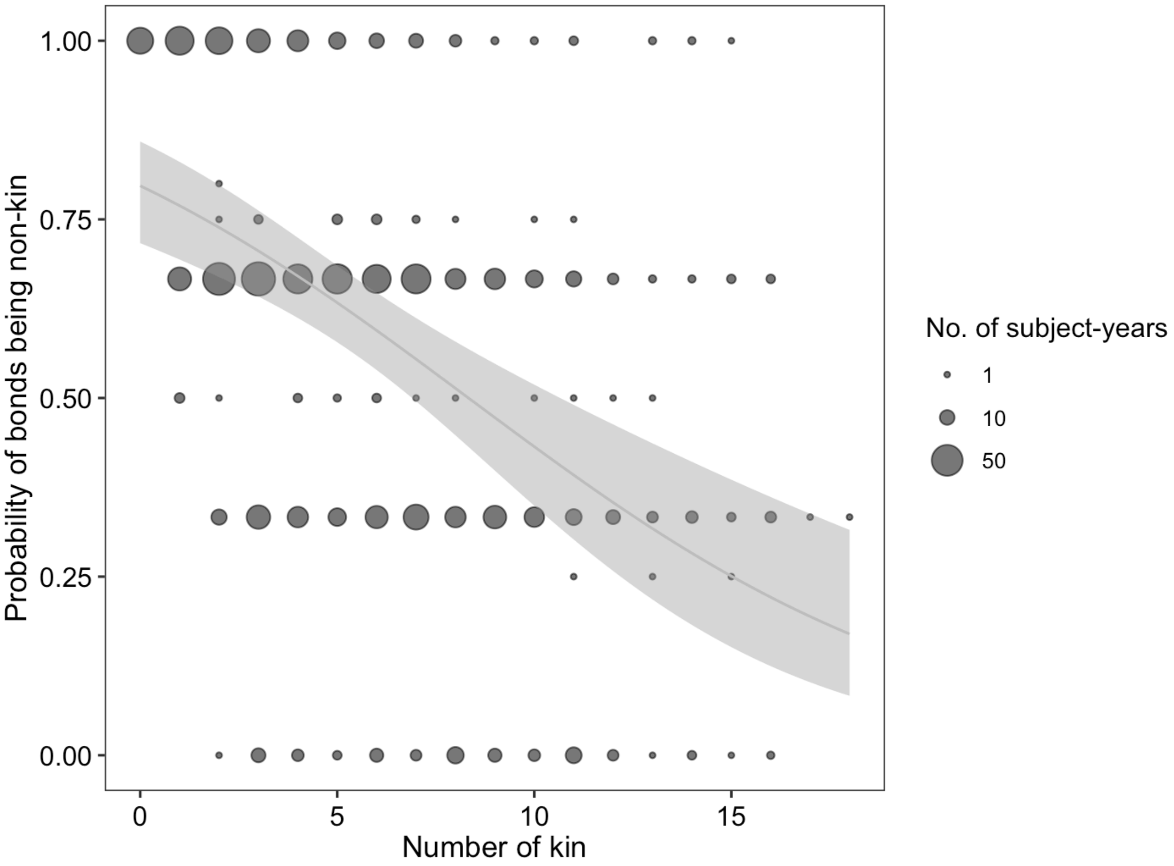

Figure 3. The influence of kin availability on the probability of forming social bonds with non-kin. The grey line shows the predicted relationship between kin availability and the probability of social bonds being formed with non-kin, based on model 3. The shaded grey bars show the 95% confidence intervals around the predicted values. Points represent raw proportions.

Discussion

In this study, we set out to characterise the non-kin bonds of adult female rhesus macaques by describing their prevalence, stability and the effect of kin availability on their formation. We found that, despite a pronounced kin bias in the strength of affiliative social relationships, social bonds with non-kin occurred and were even more common than those with kin. However, non-kin bonds were less stable than kin bonds: bonds with non-kin varied substantially more in strength than bonds with kin and typically did not last for more than one year. We also found that, when females had fewer kin partners available, they were more likely to form social bonds with non-kin.

Our finding that female rhesus macaques did indeed bias their affiliative relationships toward kin is in line with past research on this system (reviewed in Widdig et al., 2016) as well as many other studies on primates (Silk, 2006) and other mammals (Smith, 2014). Given that cooperation between close relatives can provide both direct and indirect fitness benefits while cooperation with non-kin only provides direct benefits (Hamilton, 1964), such biases are not surprising. However, despite marked preferences for kin partners, evidence that social relationships are not exclusively restricted to relatives has been mounting (Carter et al., 2017; Christakis & Fowler, 2014; Dal Pesco et al., 2021; De Moor et al., 2020a, 2020b; Gerber et al., 2020; Möller, 2012; Smith et al., 2003). Our results support these findings and demonstrate that non-kin bonds are actually more prevalent than those with kin in this system.

This greater number of non-kin bonds could be explained by the fact that there are simply substantially more non-kin in a female's social group than there are kin. For example, let's say a female's probability of bonding with any given non-kin partner is only 0.2, compared to a probability of 0.8 to bond with kin. If she has 50 non-kin and 5 kin individuals available in the group, the number of non-kin bonds she is likely to form is 10 (0.2*50), whereas the number of kin bonds she is likely to form is 4 (0.8*5). That is, the sheer number of non-kin available could result in females having more non-kin bonds even given a higher probability to bond with non-kin.

However, while it is possible that the prevalence of non-kin among an individual's social bond partners can purely be reduced to a numbers game, our results demonstrating that females' bonds with non-kin are less stable and are prevalent even when many kin are available indicate that other factors might be at play. Recent findings have lent credence to the idea that non-kin bonds might actively be selected for and could serve an adaptive function (Carter et al., 2017; De Moor et al., 2020a). This has been suggested to occur because there are unique features of non-kin or roles that non-kin can fulfil which kin cannot: non-kin are typically more numerous (Krause & Ruxton, 2002), they may also be more competent at certain social tasks or more compatible partners (Chapais, 2006), and they may provide access to resources or commodities kin cannot (Smith et al., 2022).

One possibility supported by our findings is that females might be taking advantage of the greater availability of non-kin to form a “safety net” for when close kin are limited or unavailable. This is illustrated by the fact that females are more likely to have non-kin bond partners when they have fewer kin available. ‘Social bet-hedging’ theory posits that investment in cooperative partnerships with non-kin may be beneficial where reliance on a smaller kin network alone may be too risky (Carter et al., 2017). In our system, groups are mostly composed of non-kin dyads and, as a result, females might find themselves with a limited number of available close kin (Widdig et al., 2016). Therefore, it might pay off for females to invest in strong non-kin relationships as this provides a network of ‘backup partners’ which females can draw from and replace their social bond partners when kin are limited.

In addition, it appears that females do not form bonds with non-kin exclusively as a means to compensate for the lack of available close kin. Our results suggest that females form bonds with non-kin even when they have three or more kin available in the group. For instance, 96% of our study females who had five available kin still had at least one non-kin social bond partner, and in fact 16% of females with five available kin actually formed all of their bonds with non-kin. This suggests that females may be actively choosing to bond with some non-kin over kin, strongly suggesting that non-kin bonds may serve a different function in macaque society.

In support of this idea, females in this study also formed less stable bonds with non-kin, suggesting that bonds with non-kin might be more opportunistic and might serve a different purpose than those with kin. This finding is in agreement with a study in yellow baboons (Papio cynocephalus), which showed that the most enduring bonds tend to be formed by close kin, while those between non-kin, or more distant kin, tend to be more ephemeral (Silk et al., 2006). Forming enduring, strong, and stable relationships might be important for providing females with predictable benefits that are likely to be important in highly competitive environments, such as in despotic societies, where kin support each other to attain and maintain dominance status (Strauss & Holekamp, 2019). It makes sense that such stable partnerships would be formed with kin where inclusive fitness benefits make investment in long-term social relationships, and the cost of high-risk support more feasible. Meanwhile, the formation of shorter, less stable relationships with non-kin might be used for short-term gain - including accessing more “volatile” commodities, which are environmentally or seasonally dependent, such as access to infants (Barrett & Henzi, 2002), or access to limiting resources such as shade (Testard et al., 2024). Bonds with non-kin partners might also provide access to commodities that females cannot get from their relationships with kin. For example, females from low-ranking matrilines might benefit from forming bonds with high-ranking non-kin for food access or agnostic support (Tiddi et al., 2012). In addition, non-kin may be more competent partners than non-kin, leading individuals to form stronger relationships with non-kin, sometimes even at the expense of kin (De Moor et al., 2020a).

While it might initially seem less beneficial to invest in partners who only provide direct fitness benefits, non-kin partners might provide access to cooperative benefits that kin cannot, such that the direct benefits of cooperation with non-kin alone outweigh the inclusive fitness benefits of cooperation with kin. It remains to be seen whether females’ apparent investment in non-kin in this system improves fitness outcomes, especially in the absence of kin, but this would be an interesting direction for future research.

Conclusion

Overall, our findings suggest that we need to rethink the current narrative that bonds among non-kin are either an unimportant aspect of the social environment for most individuals or an anomaly that can be overlooked. Our results illustrate that social bonds among non-kin are actually more prevalent than bonds with kin in female rhesus macaques, and provide some evidence to suggest that this prevalence of non-kin bonds is not just a consequence of the greater availability of non-kin. Instead, non-kin appear to be actively sought out as partners because they serve a different function or act as an opportunistic safety net. Given that non-kin are an important part of the social environment in many species (Pereira et al., 2023), future research should seek to build on our results and explore the prevalence of social bonds with non-kin across different societies, including how these bonds are formed and maintained and what functions they serve. Future research should seek to build on our results and explore the prevalence of social bonds with non-kin across different societies, including how these bonds are formed and maintained and what functions they serve. Doing so will help to unveil the adaptive function of affiliative relationships and the relative importance of direct and indirect benefits in shaping the evolution of social behaviour.

Acknowledgements

We thank the Caribbean Primate Research Center (CPRC) for access to the field station and pedigree data. The CPRC is supported by the National Institutes of Health. An Animal and Biological Material Resource Center Grant [P40OD012217] was awarded to the University of Puerto Rico from the Office of Research Infrastructure Programs, National Institutes of Health (ORIP). Behavioural data used in this study are a component of the Cayo Biobank Research Unit consortium. We are also very grateful to the members of the Brent laboratory and the Centre for Research in Animal Behaviour for comments and suggestions that increased the quality of this work. This work was supported by a European Research Council Consolidator grant (FriendOrigins - 864461) to L.J.N.B.

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