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

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Abstract

Members of social groups often form social relationships, which can 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 relationships exist between non-kin of the same sex. 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 and stability of non-kin bonds in a mix-related society, along with the extent to which kin availability predicts their formation. We found that in line with kin selection theory and previous work on this population, there was a clear kin bias in social bond partners. However, bonds with non-kin were nevertheless 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 that had fewer kin group mates were more likely to have 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.

Keywords: kinship, kin bias, relatedness, social bonds, social network, cooperation, non-kin bonds

Highlights

- Social bonds are important for fitness but research on non-kin bonds is scarce.
- Adult female rhesus macaques showed strong kin bias in social relationship strength.
- However, non-kin social bonds were more common, although less stable, than with kin.
- Females with fewer kin also had a greater proportion of social bonds with non-kin.
- Non-kin may serve important alternative functions in macaque society.

Introduction

Social relationships are associated with enhanced health, reproductive success, and longevity in humans and other social animals (Brent et al., 2017; McDonald, 2007; Silk et al., 2003; Snyder-Mackler et al., 2020). These findings, together with evidence that social tendencies have a genetic basis, suggest that social relationships evolved and serve an adaptive function (Brent et al., 2013; Fowler et al., 2009; Wice & Saltz, 2021). Yet, exactly why social relationships are linked to fitness benefits remains unclear (Brent et al., 2014; Ostner &

Schülke, 2018). A key step towards unravelling the ultimate function of social relationships is to understand who individuals have 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 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 existence 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; Schweinfurth & Taborsky, 2018). While social relationships between 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 relatives from non-kin (Tang-Martinez, 2001; Widdig, 2007), suggesting individuals sometimes actively choose non-kin group members as their social partners.

There are two main reasons why non-kin might be valuable social partners. First, individuals might prioritise 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 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 may engage in a ‘social bet-hedging’ strategy where relationships with non-kin act 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. This is, in part, because of a rarity in study systems with deep pedigrees that allow researchers to confidently assign individuals as distantly related or unrelated. Assessing the prevalence, strength and stability of non-kin social relationships, and how these factors are affected by kin availability, is a necessary first step to help us understand how and why relationships with non-kin 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. Multigenerational genetic pedigree data are available for this population, which allows reliable estimation of relatedness between almost all pairs of potential social partners. Macaques are female philopatric and live in large stable social groups consisting of multiple matrilines. We studied adult females as they are 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). Females differentiate maternal and paternal kin from non-kin in this population (Pfefferle et al., 2014; Widdig et al., 2001), and 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 between non-kin are compared to those between kin. We defined social bonds as the three strongest relationships a female has with other females in a given year, a definition that has been previously linked to survival outcomes in this population (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) more closely related adult females would be more likely to be socially bonded (i.e., to have them in their top three strongest relationships) than more distantly related ones, but that (1c) those social 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 females having non-kin social bonds. We predicted that (3) females with fewer kin available would have 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 semi-free-ranging and are provided with commercial feed daily and *ad libitum* access to water. As in the wild, the Cayo Santiago rhesus macaque females are philopatric and live in social groups that feature both related and unrelated females (Southwick et al., 1983).

Our dataset 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). Agonistic interactions were recorded both during focal samples and *ad libitum*. For each subject in each year, observers collected, on average, 5.33 hours (range: 0.75–10.83) of focal data and 95.75 proximity scans (range: 18–195) balanced across times of day and months of the year. 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 that were observed for less than two standard deviations below the mean focal observation time. In total, we had 347 adult female 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 was 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 (e.g., lactation). We were also able to identify genetic fathers for 337 of the 347 subjects. The parentage of the subjects could be traced back, on average, for 3.22 generations (range: 1–6 generations; see Figures A1, A2).

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, 2024). Relatedness coefficients between pairs of subjects ranged from 0 to 0.5625 (see Supplementary Materials Figures S1–S19 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 dyads with $r < 0.125$ as non-kin. We chose 0.125 as the threshold because female rhesus macaques on Cayo Santiago behave no differently towards distant relatives ($0.0005 < r < 0.125$) than towards true non-kin ($r < 0.0005$) (Kapsalis & Berman, 1996). This cutoff is also commonly used to delineate kin from non-kin in macaques (Chapais & Berman, 2004). Study subjects had on average 5.61 (range: 0–18) kin group mates and 50.23 (range: 14–71) non-kin group mates in a given year. Non-kin group mates always outnumbered kin group mates for any subject in any given year in this study.

Calculating dominance ranks

To account for the effect social status may have on partner choice or relationship strength, 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 group mates 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 types of affiliative social interactions that are positively correlated (Pearson's r = 0.51) and widely used to quantify relationships in primates (Silk et al., 2013). The DSI between any dyad in a given year was calculated using two metrics: the proportion of time spent grooming, and the probability of being in proximity. We estimated the proportion of time spent grooming by dividing the duration of grooming between any two subjects by the combined focal sample time of both subjects. We estimated the probability of being in proximity by dividing the number of scans where any two subjects were observed in proximity by the total number of scans of both subjects. We then standardized each dyadic metric by dividing it by the relevant group mean for that year. We computed the DSI between any dyad in a given year by averaging their standardised estimated time spent grooming and time spent in proximity. 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 relatively stronger social relationships. Of the 27218 dyad-years (10994 unique dyads) in this study, 79% had a DSI of 0, reflecting no grooming or proximity were observed for that dyad. The highest DSI was 136.20.

We defined a subject's social bonds as her relationships with the 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 in this population (Ellis et al., 2019). Partners with a DSI < 1 were disqualified from inclusion as social bond partners even if they featured among the subject's top three in that year. A DSI of 1 represents the mean relationship strength in a social group, so we did not consider relationships with a DSI lower than 1 to be strong. It was therefore possible for a subject to have fewer than three social bonds (61 cases out of the 975 subject-years). Conversely, some subjects had more than three social bonds in a given year (35 cases out of 975 subject-years), as they had multiple bonds with the same DSI value. Most subjects had three social bonds in a given year based on our definition (879 cases out of 975 subject-years).

Statistical analyses

We conducted all statistical analyses using the R platform version 4.4.0 (R Core Team, 2024). We fitted generalised linear mixed models (GLMM) using the packages glmmTMB (Brooks et al., 2017; models 1a and 1b) and lme4 (Bates et al., 2014; all other models). We fitted all models using Maximum Likelihood estimation (ML), except for models 1a and 1b which we fitted using Restricted Maximum Likelihood estimation (REML) to better estimate the variance explained by the dyad random effect. We checked model assumptions in several ways. First, we confirmed model fit by plotting residuals against simulated residuals with the DHARMa package (Hartig, 2022). For multiple regressions, we checked multicollinearity using the VIF (variance inflation factor) function from the car package (Fox & Weisberg, 2018). For mixed-effects models, we checked normality of random intercepts with histograms. We also checked for zero-inflation in model 1a by comparing the observed number of zeros with expected zeros from simulations (n = 1000) using the simulateResiduals function and the testZeroInflation function in the DHARMa package and found that the response variable DSI was not zero-inflated (ratioObsSim = 1.07, two-sided p-value = 0.12). For models 1a and 1b (fitted using REML) we generated p-values for all fixed effects using a Wald test. For all other models (fitted using ML) we generated p-values using a Likelihood-ratio test. We chose $p < 0.05$ (two-tailed) as the threshold for hypothesis testing and reported parameter estimates with 95% confidence intervals (CI). We obtained predicted values from statistical models using the ggpredict function from the ggeffects package (Lüdecke, 2018).

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), females had stronger affiliative relationships with more closely related individuals in our study population (prediction 1a). To test this, we fitted a Tweedie 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 fitted a model using a Tweedie distribution because our response variable (DSI) was positive and continuous with many zeros (Gilchrist & Drinkwater, 2000). We included two female IDs, dyad ID, social group and year as random factors in this model.

Next, we investigated if degree of relatedness predicted the probability for a dyad to form a social bond (prediction 1b). To test this, we fitted a binomial GLMM (model 1b) where the response variable was whether a given adult female group mate was the subject's social bond partner (yes or no), and relatedness between the two individuals was the continuous predictor (n = 54436). We included subject and partner IDs, dyad ID, social group and year as random factors in this model.

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 with non-kin versus with kin. Rather than calculating the ratio of non-kin to kin social bonds for each subject-year, 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 (970 subject-years). We defined the response variable in the model as a two-column matrix composed of the number of non-kin bonds and the number of kin bonds. We had no fixed effects and included subject ID, social group and year as random factors. We extracted the intercept as the expected log-odds of a social bond being with non-kin.

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

Next, we investigated whether social bond stability was predicted 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 (n = 102 females) , we determined all partners with whom the subject had a social bond for at least one year and 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 (959 dyads) across all years of co-residence. We tested whether kinship affected bond stability using two measures: total number of years as social bond partners and variability of relationship strength (DSI) across years.

First, we investigated whether females remained social bond partners with kin longer than with non-kin (prediction 2a). To test this, we fitted a binomial GLMM (model 2a) where the response variable was the number of years a partner was a social bond partner divided by the total number of years of co-residence, an approximation of bond duration accounting for the opportunity to form a bond. This ratio ranged from 0.125 (1 out of 8 years) to 1 (8 out of 8 years). We included kinship (non-kin or kin) as the predictor of interest in the model, and 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 found that the strength and stability of social bonds were correlated (Silk et al., 2010). We included subject ID and partner ID as random factors and included the dyad's total number of years of co-residence as weights in the model.

Next, we investigated whether the strength of a subject's relationship with non-kin bond partners varied more over time compared to those with kin bond partners (prediction 2b). We measured the degree of variability in relationship strength by calculating the coefficient of variation (CV: standard deviation/mean) in the DSI of a dyad across the years they were coresident. We then fitted a LMM (model 2b) with the CV as the response variable, 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 kin group mates had a higher probability of forming bonds with non-kin (prediction 3). The dataset included data from all six social groups, totalling 970 subject-years in which the subject had at least one bond. We ran a binomial GLMM (model 3), and we defined the response variable in the model as a two-column matrix composed of the number of non-kin bonds and the number of kin bonds. We included the subject's number of currently living kin adult female group mates as the predictor of interest. We also included the subject's age, dominance rank and group size as predictors to account for their potentially confounding effects: 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 a smaller proportion of kin available relative to non-kin (Blomquist et al., 2011; Brent et al., 2017). We included subject ID, social group and year as random factors in the model.

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 bias towards kin, both in the strength of social relationships (prediction 1a; model 1a: Tweedie GLMM, slope ± SE = 8.20 ± 0.24, CI = [7.74, 8.67], Wald test z value = 34.52, $P < 0.001$; Figure 1A) and in the propensity to be social bond partners (prediction 1b; model 1b: binomial GLMM, slope ± SE = 11.03 ± 0.42, CI = [10.20, 11.86], Wald test z value = 25.99, $P < 0.001$; Figure 1B). For example, the predicted average DSI for fully unrelated dyads ($r = 0$) was 0.86, while the predicted average DSI for closely related dyads with $r = 0.5$ was 36.62, or 43 times that of fully unrelated dyads (model 1a). Similarly, the probability for a fully unrelated female groupmate ($r = 0$) to feature in a subject's social bond partners was 3%, while the probability for a closely related group mate with $r = 0.5$ was 77%, or 26 times higher (model 1b). Despite such a prominent kin bias, subjects regularly had strong relationships with non-kin, as evidenced by our finding that social bonds with non-kin were more common than those with kin (prediction 1c; model 1c: binomial GLMM, intercept ± SE = 0.49 ± 0.17, CI = [0.14, 0.83]; Figure 1C). 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 a kin bias in the strength of social relationships and propensity to form bonds (models 1a and 1b) and our finding that females have more bonds with non-kin (model 1c) can be explained, at least in part, by the substantially larger numbers of available non-kin group mates (range: 14–71) compared to available kin group mates (range: 0–18). On average, subjects had 44.62 (range: 8–71) more non-kin than kin group mates.

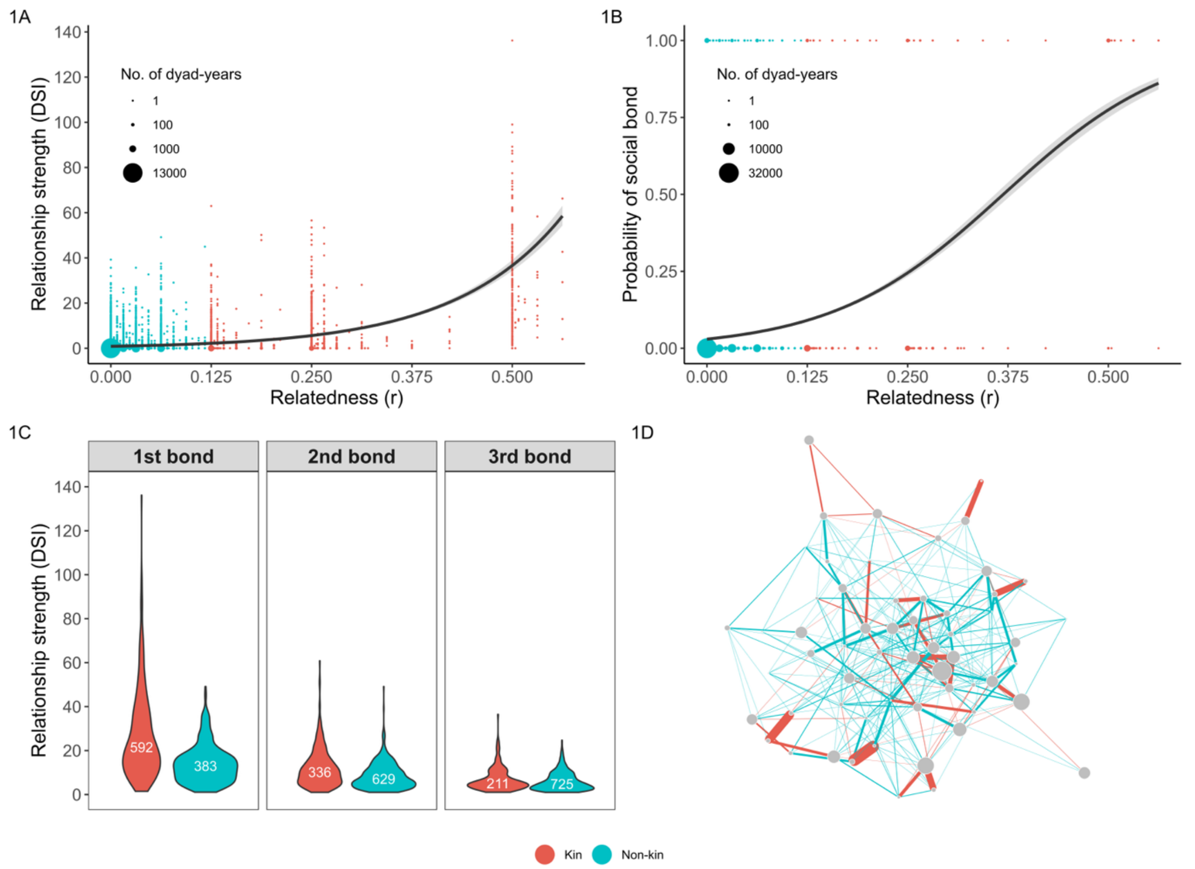

Figure 1. Kin bias in social relationships and prevalence of social bonds with kin (red) and non-kin (blue). (**A**) Correlation between relatedness (r) and relationship strength (DSI). The black line shows the predicted DSI based on relatedness from model 1a, with the grey bar showing 95% CI of the prediction. Points represent raw data from all dyad-years. (**B**) Correlation between relatedness (r) and the probability of being socially bonded. The black line and the grey bar show the predicted probability from model 1b with its 95% CI. Points represent raw data. (**C**) Violin plots showing the distribution of each subject's social bonds for a given year (three highest DSI values). The number displayed within each violin plot is the count of social bonds in that category. (**D**) Exemplar social network of group F in 2010. Each node in the network represents a subject, with the size of the node reflecting the subject's number of female kin groupmates, which is between 0 and 18 in F2010 (larger nodes indicate individuals who have more kin groupmates). The edges between nodes represent affiliative social relationships where DSI > 1, regardless of whether they were social bonds. Edge thickness reflects

relationship strength (DSI), with thicker edges reflecting stronger relationships. Social networks of the other 18 group-years can be found in the Supplementary Material (Figures S20–S38).

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 total number of years bonded and in relationship strength variability (Figure 2). Social bonds with non-kin were less likely to be maintained across years than those with kin (prediction 2a; model 2a: binomial GLMM, non-kin ± SE = -0.67 ± 0.088, CI = [-0.84, -0.49], $\chi^2(1) = 54.95$, $P < 0.001$; Figure 2A). Bonds with kin had a total duration of 2.63 years on average (range: 1–7 years), while social bonds with non-kin had a total duration of 1.22 years on average (range: 1–5 years). Notably, 83% of social bonds with non-kin didn't last for more than a year. Relationship strength with non-kin bond partners also varied more than with kin bond partners (prediction 2b; model 2b: LMM, non-kin ± SE = 0.57 ± 0.041, CI = [0.49, 0.65], $\chi^2(1) = 49.42$, $P < 0.001$; Figure 2B). For non-kin bond dyads, the predicted average coefficient of variation (CV) in DSI was 1.50, while for kin bond dyads, the predicted average CV was 0.93.

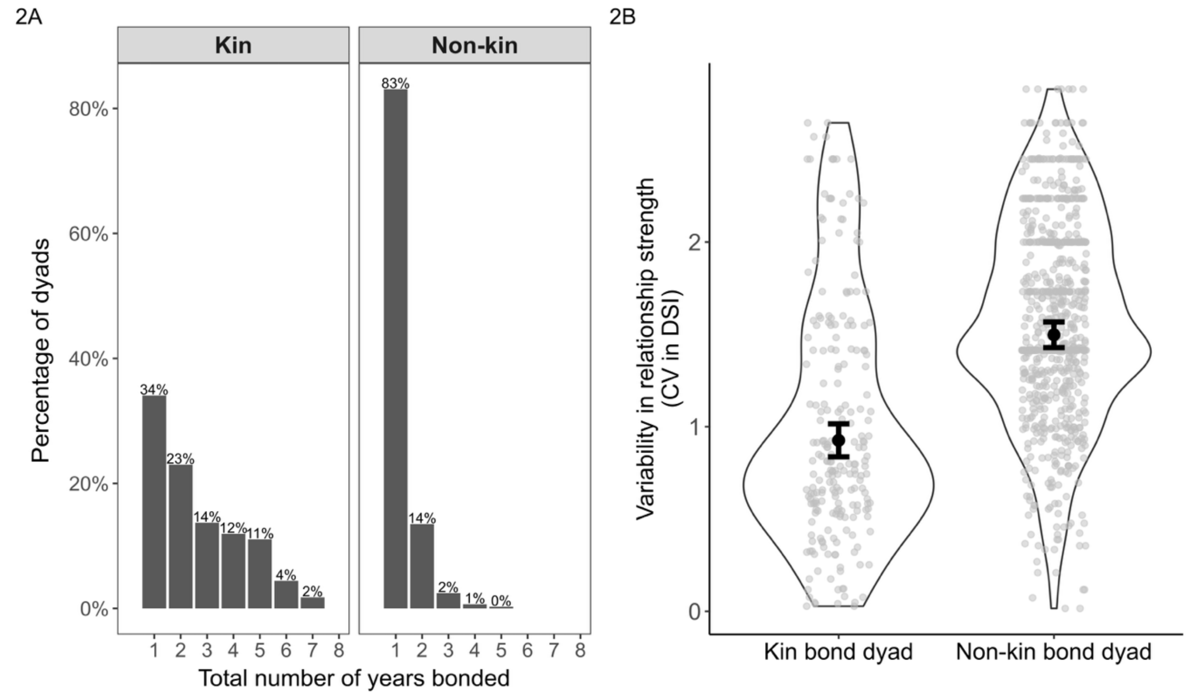

Figure 2. Stability of social bonds with kin and non-kin. (A) Percentage of kin and non-kin dyads broken down by the total number of years bonded. (B) Violin plots showing the density distributions of the variability in relationship strength (CV in DSI) across the years for kin bond partners and non-kin bond partners. The dot in the middle of each violin plot shows the predicted average CV based on model 2b, with the error bar showing the 95% CI. The grey points are raw data.

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 kin group mates (prediction 3; model 3: binomial GLMM, slope ± SE = -0.17 ± 0.016, CI = [-0.20, -0.14], $\chi^2(1) = 126.51$, $P < 0.001$; Figure 3). For example, a subject with five available kin was predicted to have, on average, 67% of her social bonds with non-kin, whereas for a subject with 10 available kin this was 46%. Nevertheless, many subjects with very large numbers of available kin (e.g., more than 10) still filled some of their three social bond slots with non-kin.

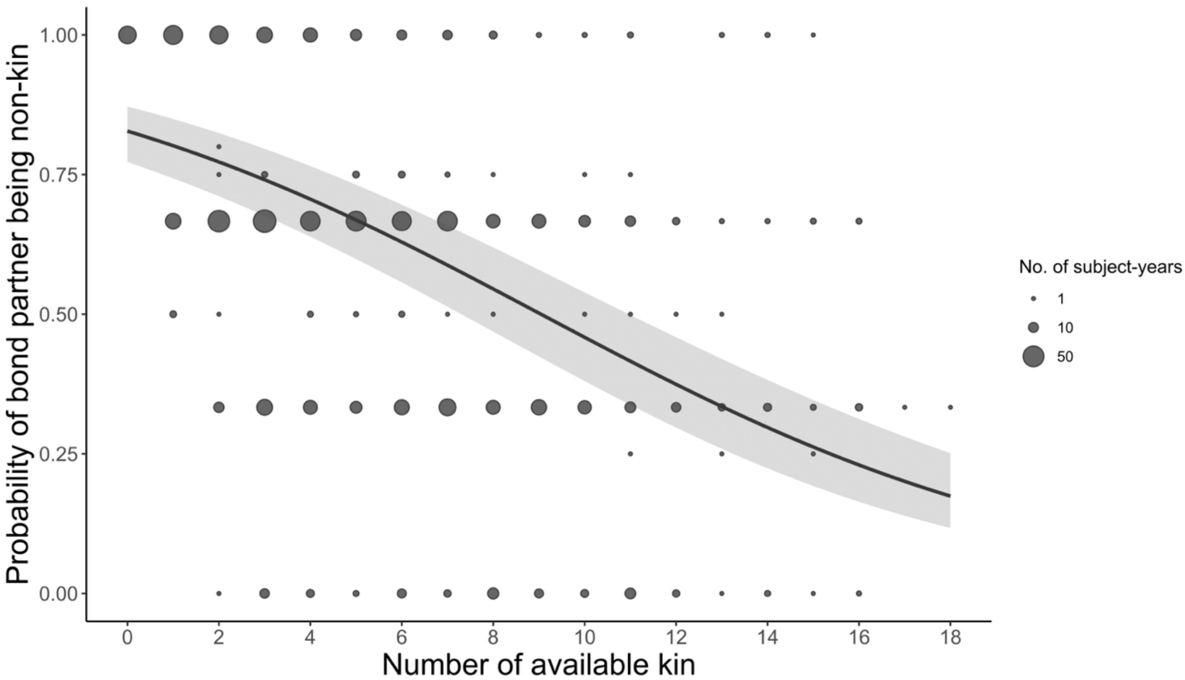

Figure 3. The influence of kin availability on the probability of social bonds between non-kin. The grey line shows the predicted correlation between kin availability and the probability of a social bond partner being non-kin, based on model 3. The shaded grey bar shows the 95% CI around the predicted values. Points represent proportions based on raw data.

Discussion

In this study, we set out to characterise the non-kin bonds of adult female rhesus macaques by describing their prevalence, strength and 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 have social bonds with non-kin.

Our finding that female rhesus macaques 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 and other mammals (Archie et al., 2006; De Moor et al., 2020b; Grebe et al., 2022; Möller, 2012; Ren et al., 2018; Rossiter et al., 2002; Silk, 2006; Smith, 2014; Smith et al., 2010). 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; 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. Even if females have a higher propensity to form strong bonds with non-kin, the sheer number of non-kin available could result in females having more non-kin bonds than kin bonds. For example, in our dataset females have many more partners with $r = 0$ (37 partners on average) than partners with $r = 0.5$ (0.48 partners on average). As a result, even though dyads with $r = 0$ only have 3% chance of having a social bond, while dyads with $r = 0.5$ have a 77% chance, there are more social bonds between partners with $r = 0$ ($37*0.03 = 1.10$ bonds) than with partners with $r = 0.5$ ($0.48*0.77 = 0.37$ bonds). This explanation might be especially true in our study population, which lives on an island free of predators and is food supplemented. As a result of these unique conditions, females live in particularly large groups, which might lead to greater relative availability of non-kin than in the wild.

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 could serve an adaptive function that is not filled (or is less well filled) by kin bonds (Carter et al., 2017; De Moor et al., 2020a). This has been suggested to occur because non-kin may be more competent at certain social tasks or more compatible partners (Chapais, 2006), and they may provide access to resources or commodities that kin cannot (Smith et al., 2022).

One possible explanation for the prevalence of non-kin social bonds that is supported by our findings is that females might be taking advantage of the greater availability of non-kin to act as a "safety net" for times 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. This result is in line with findings in blue monkeys, where the probability of females having strong social bonds with non-kin is higher in years in which they have less close kin available (Richardson & Cords, 2025). "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 risky (Carter et al., 2017). In our system, groups are mostly composed of non-kin dyads and females can sometimes find themselves with a limited number of available close kin (Widdig et al., 2016). It might, therefore, pay for individuals to invest in strong non-kin relationships to establish a social network from which they can draw when kin are limited.

In addition, it appears that females do not have bonds with non-kin exclusively as a means to compensate for the lack of available close kin. Our results suggest that females have bonds with non-kin even when they have enough kin available to fully occupy their three top relationship strength slots. 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 filled all of their bond slots with non-kin. This suggests that females may be actively choosing to bond with some non-kin over kin, and that non-kin bonds may serve a different function than kin-bonds in macaque societies.

In further support of this idea, non-kin bonds were less stable in this study. This finding is in agreement with a study in yellow baboons (*Papio cynocephalus*), which showed that the most enduring bonds tend to be between close kin, while those between non-kin, or more distant kin, tend to be more ephemeral (Silk et al., 2006). Stable strong relationships might provide individuals with predictable benefits that may be important in highly competitive environments, where partners support each other to attain and maintain dominance status (Strauss & Holekamp, 2019). It makes sense that such stable partnerships would be between kin where inclusive fitness benefits make investment in long-term social relationships, and the cost of high-risk support, more feasible (Fisktjønmo et al., 2021; Montgomery et al., 2023). Meanwhile, less stable relationships 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 limited resources such as shade (Testard et al., 2024) or mates (Teunissen et al., 2018). Bonds with non-kin partners might also provide access to commodities that females cannot get from their relationships with kin. For example, low-ranking individuals might bond with high-ranking non-kin to gain food access or agnostic support (Tiddi et al., 2012). In addition, non-kin may be more competent (i.e., better at certain social tasks) partners than kin, leading individuals to build stronger relationships with non-kin, sometimes even at the expense of kin (De Moor et al., 2020a; Schweinfurth & Taborsky, 2018).

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 enhances fitness, but this would be a valuable direction for future research.

Conclusion

Overall, our findings suggest that strong social relationships between non-kin are an important aspect of the social environment and not an anomaly that can be overlooked. Social bonds between non-kin were more prevalent than bonds with kin in female rhesus macaques, and we provide some evidence to suggest that this prevalence may be explained by other factors beyond just the greater availability of non-kin. Instead, non-kin may be actively sought out as partners because they serve a different function or act as an opportunistic safety net. This is emphasized by the fact that females had bonds with non-kin even when they had plenty of kin available. While our results may be influenced to some extent by the large group sizes in the Cayo Santiago population—leading to a higher relative availability of non-kin for females compared to the wild—many species naturally live in social groups that include at least some unrelated individuals of the same sex (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. Doing so will clarify the broader relevance of our findings as well as 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.

Data Availability

The data and R code used for the analyses are available at the following link: https://github.com/zhuli-cheng/msc-non-kin-macaque-friends.

Inclusion and Diversity Statement

Our study includes scientists based in the country where the study was conducted and is composed of a mixed gender team.

Declaration of Conflicts of Interest

None.

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Appendix

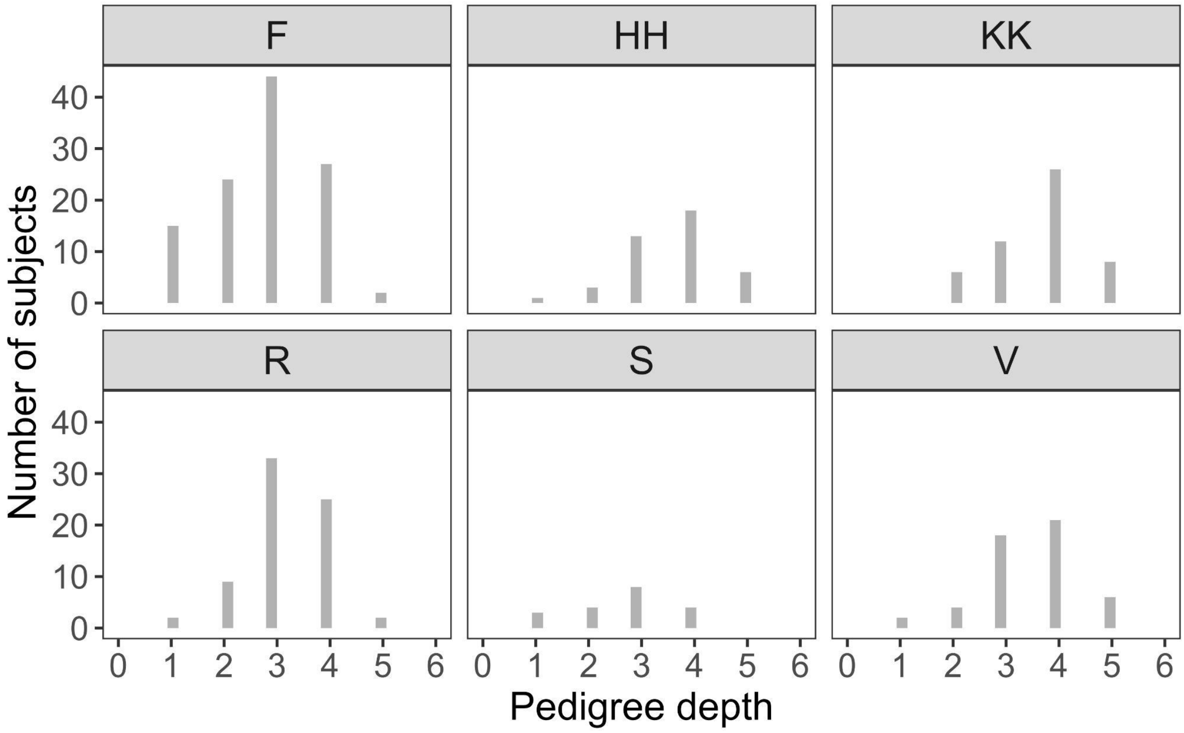

Figure A1. Distribution of pedigree depth for the 347 subjects from the six social groups.

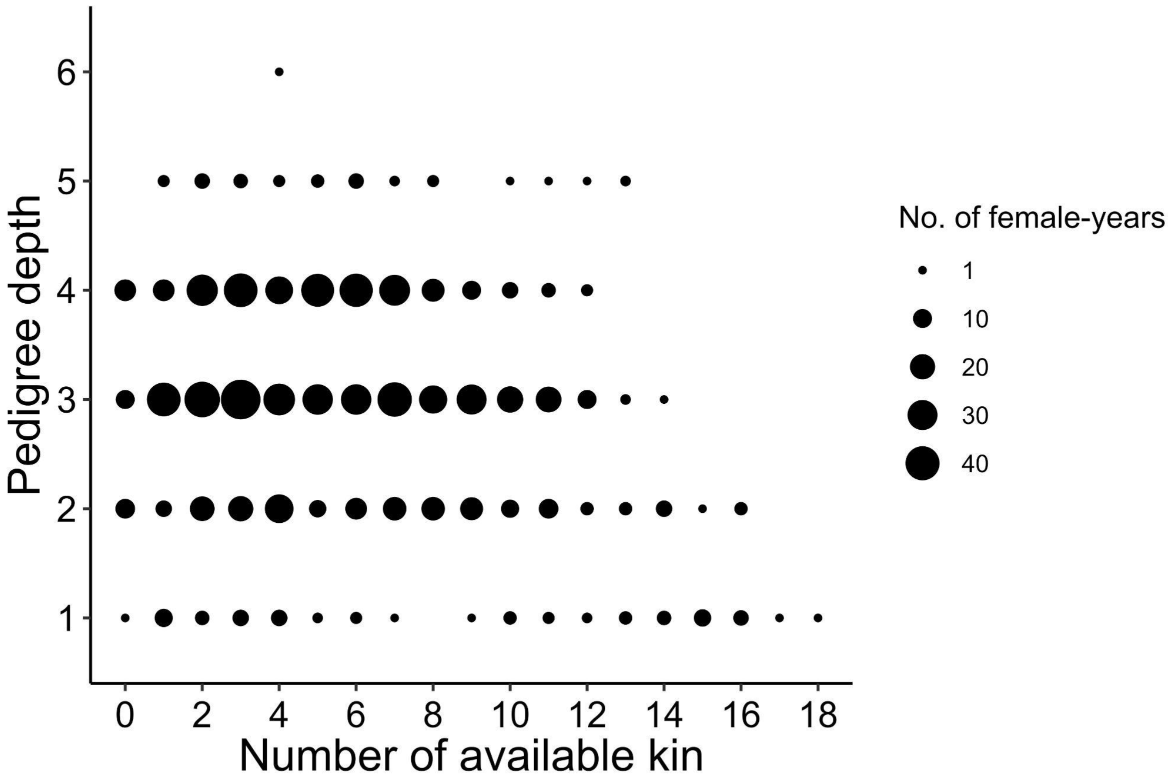

Figure A2. Number of available kin as a function of pedigree depth. Although some of the subjects have few available kin, this was not caused by a lack of information on their pedigree.

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