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Female social structure influences, and is influenced by, male introduction and integration success among captive rhesus macaques (*Macaca mulatta*)

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Abstract

Animal social structure is influenced by multiple socioecological factors. Of these, the links between changes to group demography through the arrival of new individuals and residents' social structure remain unclear. Across seven groups of captive rhesus macaques (*Macaca mulatta*), we examine how male introductions may be influenced by, and in-turn influence, aspects of female social structure. GLMMs revealed that males integrated more successfully into groups in which females showed more 'despotic' social structures, i.e., higher aggression rates, steeper dominance hierarchies, and greater rank-skew in allogrooming network connectedness. Yet during periods that followed males' social integration, females increased their social tolerance (decreased aggression and shallower hierarchies) and group cohesivity (less clustered allogrooming networks), but retained their tendencies to groom dominants. Our findings, independent of group size and matrilineal relatedness, help better understand how dispersal/immigration may influence social structure, and how assessing changes to social structure may inform macaque welfare and management.

Keywords

social structure; primate females; demographic changes; male social integration; dominance interactions; allogrooming networks; rhesus macaques; primate welfare and management

1. Introduction

Several group-living mammals show social organizations characterized by female philopatry and male dispersal (e.g., Asian elephants (*Elephas maximus*): Vidya & Sukumar, 2005; African lions (*Panthera leo*): Pusey & Packer, 1987; spotted hyenas (*Crocuta crocuta*): Frank, 1986; vampire bats (*Desmodus rotundus*): Wilkinson, 1985; Cercopithecine nonhuman primates: Kappeler & van Schaik, 2002). In particular, females form the core of

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the social group, while males tend to disperse upon reaching sexual maturity to maintain a strong gene pool and avoid inbreeding (Moore & Ali, 1984).

Among Cercopithecine nonhuman primates, assessing the bases for variation in female social structure is especially important because social interactions like competition and cooperation for resources are at the core of individual and group-level homeostasis and reproductive success (Sterck et al., 1997; Henzi & Barrett, 1999; Kappeler & van Schaik, 2002; Kappeler et al., 2015). For instance, in baboons (*Papio* spp.) and macaques (*Macaca* spp.), female-female agonistic interactions and affiliative exchanges such as social or (hereafter) allogrooming underlie the reinforcement of matrilineally inherited dominance rank positions (Chapais & Berman, 2004), and the establishment and maintenance of strong social bonds (Silk et al., 2003, 2010) and social network connections (Sueur et al., 2011a, b; Brent et al., 2013; Balasubramaniam et al., 2018). These aspects of female dominance hierarchies and social structure as indicated by the patterning and distribution of their allogrooming relationships have in turn been strongly linked to indicators of animal health (Balasubramaniam et al., 2016) and fitness (Silk et al., 2010; Brent et al., 2013).

Primate social structure may be influenced by their ecological or environmental exposure, and their evolutionary histories (Sterck et al., 1997; Kappeler & van Schaik, 2002). Within the macaque genus, aspects of female dominance and allogrooming social structure may be influenced by intrinsic characteristics such as inter-individual differences in genetic polymorphisms (Brent et al., 2013), animals' dyadic relatedness or kinship (Chapais & Berman, 2004; Schülke et al., 2013), and species' phylogenetic relatedness (Balasubramaniam et al., 2012a, b, 2018). At the same time, female social relationships may also be strongly influenced by environmental factors related to their social development and rearing history (Capitanio, 1984, 1985), seasonal differences in reproductive status (Xia et al., 2010), demographic factors like group size (Balasubramaniam et al., 2011, 2014), ecological variables like resource availability (Sterck et al., 1997; Balasubramaniam et al., 2011) and human food-provisioning (Ram et al., 2003; Balasubramaniam et al., 2011).

One critical gap in our understanding of variation in female social structure is the effects of sociodemographic events like male immigration into social groups (Barrett et al., 2012; Borgeaud et al., 2017; Baniel et al., 2018). Among captive groups of rhesus macaques (*Macaca mulatta*), here we take advantage of a male introduction process to determine whether between-group differences in aspects of female social structure may influence the likelihood of male introduction success. We also evaluate the potential impact of male immigration on female-female social structure. In nature, rhesus macaques live in multi-male-multi-female groups, in which females are philopatric, and males tend to disperse out of their natal group into new groups when they reach sexual maturity (Sade, 1972; Chapais & Berman, 2004; Thierry, 2007). The arrival of new males into groups can lead to intense male-male aggression in captive settings, and male-female aggression, physiological stress, and injuries in both natural and captive settings (Bernstein et al., 1977; Bercovitch, 1997; Georgiev et al., 2016; Marty et al., 2017; Rox et al., 2018, 2019). Therefore, the effective management of captive rhesus groups requires a careful monitoring of changes to both male-female and female-female social relationships following male introduction procedures (Rox et al., 2018, 2019). Additionally, studies of male introductions into captive macaque groups

have carefully monitored changes to animal behaviour and physiology through the processes of introduction (a husbandry process of male entry) and subsequent social integration (a natural process of the establishment of social position) (Rox et al., 2018, 2019). In doing so, such studies provide insights into the impact of male immigration and integration on the social interactions of wild primates (Rox et al., 2018, 2019).

In wild primates, male immigration and integration success may depend on group composition, with males possibly facing trade-offs between entering a group with many females providing increased mating opportunities, but with the potential cost of facing increased resistance from females (Cheney & Seyfarth, 1983; Rox et al., 2019). Considering these natural trade-offs, a study on captive rhesus macaques revealed that male introductions were more successful in groups with more females, and with fewer but larger matriline (Rox et al., 2019). Given the stressors associated with the immigration of new males, it stands to reason that the existing social dynamics among the females are likely to impact whether males are able to successfully enter the group. Moreover, male introductions have led to changes in female behaviour towards males, specifically heightened tolerance contingent on females' dominance rank, age and reproductive status (Rox et al., 2018). Conceivably, such changes to female behaviour, possibly also emerging as a response to a reduction in aggression and an increase in tolerance from the immigrating males themselves (e.g., olive baboons, *P. anubis*: Sapolsky & Share, 2004), can also lead to changes in female-female social behaviour.

Yet there is little information regarding how male entry into social groups influence, or is influenced by, female social structure. Limited studies to-date have yielded contrasting findings. In wild vervet monkeys (*Chlorocebus pygerythrus*), social network connectedness remained relatively consistent following male immigration, but the strength of network connectedness or centrality of some core individuals increased following immigration events (Borgeaud et al., 2017). Based on this finding, the authors speculated that resident females may show greater tendencies for social tolerance and social bond reinforcement following male immigration. On the other hand, in wild chacma baboons (*Papio ursinus*), the intensity of female-female competition increased following male immigration, suggesting that females competed among themselves for access to males and mating opportunities (Baniel et al., 2018).

Statistically controlling between-group differences in sociodemography and observational conditions (e.g., group size, sex-ratio, times of observation), here we add to published findings by examining whether female-female social interactions and their resulting social structure influences the likelihood of male introduction success, and conversely, the impact of male introductions on female social structure. To quantify female social structure, we focus on dominance interactions and the connectedness of allogrooming social networks, that form core aspects of primate social structure. In female macaques, the steepness of dominance hierarchies (Gammell et al., 2003; De Vries et al., 2006), and the extent of variation in social network connectedness or centralization (Sueur et al., 2011a, b), are commonly-used indicators of variation in social structure. Specifically, macaque groups characterized by steeper or more asymmetric dominance hierarchies, or by a greater concentration of social network connectedness among more dominant individuals, are said

to be more ‘despotic’ in their social structures. Conversely, more socially ‘tolerant’ groups show more shallow, symmetric dominance hierarchies and a more even distribution of social network connectedness across individuals irrespective of their rank (de Waal & Luttrell, 1989; Thierry et al., 2000; Sueur et al., 2011b; Balasubramaniam et al., 2012a, b, 2018). Moreover, social networks may also be used to determine the extent of cohesivity in animal social structure. For instance, the extent to which individuals form local clusters of partners with whom they preferentially interact within their network may also indicate a groups’ social cohesivity. In other words, high clustering coefficient may indicate lower group-wide connectedness and (thereby) group cohesivity (Flack et al., 2006; Beisner et al., 2011; Sueur et al., 2011a).

We first examined whether the successful introduction of unrelated adult males into rhesus groups was influenced by between-group differences in female-female social structure. In wild primates, greater within-group social tolerance (or lower despotism) has been previously linked with a greater tendency among resident individuals to cooperate against perceived external threats, such as predators or conspecifics from other groups (Sterck et al., 1997). Thus, we expected that new, incoming males would face greater resistance in groups where more socially tolerant resident females cooperate against the perceived external threat posed by the male(s). In other words, we predicted that (P1) male integration success would be more likely in macaque groups characterized by greater, compared to lower, female-female despotism, or lower social tolerance. This would be characterized by (P1.1) greater overall frequencies of within-group agonistic interactions, and (P1.2) steeper dominance hierarchies and skew in their allogrooming social network connectedness towards dominant individuals, compared to females in groups that experienced unsuccessful introductions. Researchers have previously speculated that in primate social organizations characterized by female philopatry and male dispersal, resident individuals (females) may show increased tendencies for social tolerance, and greater cohesivity in their social networks, following male immigration and social integration (Borgeaud et al., 2017). Based on this, we predicted that (P2) successful male introductions should lead to a decrease in despotism, or an increase in social tolerance, among female rhesus macaques. This would be characterized by (P2.1) a decrease in frequencies of agonistic interactions, and (P2.2) a decrease in hierarchy steepness and skew in allogrooming social network connectedness towards dominants, in the post-introduction period compared to the pre-introduction period. In addition, we also predicted that (P2.3) allogrooming social networks would be more cohesive during the post-introduction period compared to the pre-introduction period.

2. Materials and methods

2.1. Study site, subjects and male introductions

The study was conducted at the Yerkes National Primate Research Center (YNPRC) Field Station in Lawrenceville, GA, USA. The rhesus macaque breeding colony at the YNPRC is primarily maintained in large, outdoor-housed breeding groups (18 to 170 animals), comprising multiple multigenerational matrilineal groups. Outdoor enclosures are between 0.06 and 0.38 acres in size, with attached indoor enclosures that are divided into two spaces: a smaller capture unit connected to a larger living space.

Subjects were 153 adult female rhesus macaques suitable for breeding (3–22 years old) across six different social groups (Table 1). We collected behavioural data on one of the groups during each of two male introductions in sequential years (Table 1). The independent treatment of these two events as separate ‘groups’ yielded an effective sample size of 167 females across seven groups (Table 1), on whom we collected ‘pre-introduction’ data prior to male introduction procedures and ‘post-introduction’ data following successful introductions. An additional eighth group was considered since this group met our definition of a successful introduction (given below), but those males were removed very soon after that point due to health problems. For that reason, there were insufficient post-introduction data to assess the group, and we have excluded them from this analysis.

Table 1 provides more details on the group sizes, number of breeding females (subjects), and sex-ratios, within each group. In nature, rhesus macaques typically live in multimale-multifemale groups with female-biased sex-ratios (Sade, 1972; Thierry, 2007). Single-male multi-female groups are uncommon in wild macaques (although not unheard of: Sinha et al., 2005). Thus, although three of our study groups had just a single breeding male and were thereby atypical of the social organizations of wild macaques, the generally large group sizes (33–84 individuals) and female-biased sex-ratios (2–30 females per male) of our groups were expected of semi free-ranging and wild macaque groups. We classified four groups as ‘small’ (33–44 individuals, including 14–18 adult female subjects) and three as ‘large’ (60–84 individuals, with 30–40 adult female subjects) (Table 1) (see more rationale for this classification in our data analysis explained below). All subjects were uniquely tattooed, and some were uniquely dye-marked.

Following completion of the pre-introduction behavioural observations, we began male introduction procedures for each of the seven groups, that lasted for 3–4 months (details in Bailey et al., 2020, 2021). At the beginning of each introduction period, resident breeding males were removed from all seven groups. This is common practice in naturalistic captive conditions to prevent intense male-male competition, a factor that may impact male integration success in the wild (Rox et al., 2018, 2019). Despite this difference, male introductions into captive multi-female groups may also be associated with similar, heightened levels of (male-female) competition, and may also frequently be unsuccessful (Rox et al., 2018, 2019). Moreover, the removal of breeding males prior to introduction procedures is also somewhat reflective of frequent male turn-over in wild macaque groups. For these reasons, we were convinced that male removals prior to introductions, consistently performed for all our study groups, would not impact our assessments of (changes to) female-female social structure, and may in fact lend itself to examining the clear effects of such turn-over and demographic changes on female social structure. Moreover, although we collected behavioural data during the introduction periods themselves, we refrained from analyzing that data in this study because the introduction periods (i) involved disproportionate numbers of male-female rather than female-female interactions which was the primary focus of this manuscript, and (ii) were shorter (and also varied across groups) in duration compared to the pre- and post-introduction periods.

Prior to introductions, the male groups were housed either in an introduction enclosure connected to the outdoor compound of the study group by shared chain-link fencing

(housing condition ‘enclosure’ as indicated in Table 1), or in run housing located elsewhere within the facility (housing condition ‘traditional’ as indicated in Table 1). The former was part of a relatively more recent introduction strategy that we adopted, which enabled physical or social contact with the females. In comparison, males in the ‘traditional’ run housing, rather than consistent contact with the females, were moved into part of the indoor enclosure that was attached to the compound containing the females during the day and were returned to the run housing each afternoon. Following behavioural cues such as reduced aggression and sexual interest, incoming adult males were allowed to explore the outdoor enclosures in the absence of females. The full contact portion of the introductions began when males were allowed to share the same enclosure spaces with the resident females. An introduction was deemed ‘successful’ when a sufficient number of males stayed in the group such that it had an adult male-to-adult female ratio of at least 1:10, which was maintained for at least 28 consecutive days, with males and females living in the same space. This was similar to the four-week time-frame proposed in previous studies (Brent et al., 1997; Rox et al., 2018, 2019). This step of ensuring successful male integration following an introduction (see Introduction for a clear distinction) was important because it represents the establishment of a social position within the group that follows female tolerance of incoming males (Rox et al., 2018, 2019) and, in a captive context, is necessary for creating a new social group. In other words, we deemed a male introduction procedure as being ‘successful’ only after the introduced males were socially integrated into the group (Rox et al., 2018, 2019; more details on our criteria may be found in Bailey et al., 2020, 2021). By these criteria, we deemed three out of seven attempted male introductions to be ‘successful’, two for a single group observed across two different years, and one for a second group (Table 1). We therefore observed the macaque groups that experienced a successful introduction for a further six months following the introduction period, to collect behavioural data during a post-introduction period (Table 1).

2.2. Ethical statement

The YNPRC facility and all its associated programs are AAALAC-accredited. All procedures involving animals were approved by the Emory University IACUC and were conducted in accordance with USDA Animal Welfare Regulations (9 CFR ss 3.129), ‘The guide for the care and use of laboratory animals’ (National Research Council, 2011), and institutional policies. All animals had unrestricted access to food and drinking water. They were provided with enrichment such as fresh produce, climbing and playing structures, foraging devices, and manipulanda.

2.3. Behavioural data collection

Two or three observers recorded behavioural observations simultaneously on one social group. During the pre-introduction periods, groups were observed for five to eight months, but for roughly the same amounts of time (Table 1). Each group was then observed for three months to monitor introduction success. Then observers collected data using the same technique for five to eight months of post-introduction on the three successful groups. A test of inter-rater reliability prior to the commencement of data collection revealed that all observers achieved a reliability score of 100% agreement in animal identification and 95% agreement on all behaviours. Data collection reliabilities were calculated using

Krippendorff's alpha and ranged between 0.85–1.00 across all observers (Krippendorff, 2011) for individual behaviours.

An event sampling method was used to collect data. This method caters well to contexts, such as captive housing, where all animals are equally observable within enclosed areas (Altmann, 1974; McCowan et al., 2008; Beisner et al., 2011, 2013). Specifically, we recorded data on female-female aggressive interactions and submissive signalling. Category of aggression (mild, moderate, severe) was recorded (see Bailey et al., 2020, 2021 for operational definitions) with the type of aggressive interaction (i.e., direct, intervention, redirect) and the number of participants. Submissive signalling behaviour that was recorded included silent bared-teeth displays, rump present, freeze/turn away, move away and run away. A scan sampling method (Altmann, 1974) was used to collect affiliative female-female allogrooming data, with a 20-minute inter-sample interval.

2.4. Calculations of behavioural and social network measures

From all aggression events, we calculated the total frequency of aggression given (in which the female initiated aggression) or received (in which she was the target of aggression) for each female in each group and period. From the submissive signalling data, we also calculated total frequencies of giving or receiving a submissive signal for each female in each group and period. From the dyadic submissive signalling data, for each individual in each group and period, we calculated each females' dominance rank using the Percolation-and-flow-Conductance or Perc method (the *Perc* R package: Fujii et al., 2015). From dyadic aggression events in which a clear winner emerged, we also calculated Normalized David's scores for each individual in each group and period. We used the dij dyadic dominance index that corrects for chance interactions (Gammell et al., 2003; de Vries et al., 2006). David's score is a cardinal measure of an individuals' relative success in dominance encounters that considers both its own wins-and-losses as well as the relative wins-and-losses of all the other individuals in the group with whom it has interacted.

From allogrooming interactions, we constructed social networks, and calculated measures of animals' network connectedness using the *Statnet* R package (Handcock et al., 2008). Our choices of network measures were carefully chosen based on our questions of interest, guided by the decision-trees provided in a recent review that aid animal behaviourists in choosing appropriate, hypotheses-driven social network measures based on their interests (Sosa et al., 2020). Specifically, we calculated values of allogrooming degree which is an indicator of an individuals' direct connections within its network (Newman, 2004), and eigenvector which is an indicator of an individuals' social connectedness that considers both its direct and its secondary grooming connections (Bonacich, 2007). In particular, eigenvector is a measure of an animal's central (versus peripheral) position in the group and its 'social capital' or 'support system', with higher values indicating greater centrality and social capital (Newman, 2004; Sueur et al., 2011a; Brent et al., 2013; Balasubramaniam et al., 2016). For the three groups that experienced a successful male introduction, we used the *Igraph* R package (Csardi & Nepusz, 2006) to calculate the local clustering coefficient (Newman, 2003) of each individual for both the pre- and the post-introduction periods. Clustering coefficient is an estimate of the extent to which individuals (or nodes) connected

to a specific individual are also connected to each other (i.e., of the tendency for an individual to form a cluster with others: Newman, 2003). Clustering coefficient therefore indicates the overall cohesivity or connectedness of a network, with many individuals of high clustering coefficient indicating a network that may be less cohesive than a network in which clustering coefficients are predominantly low, by way of being more prone to fragmentation if/once these animals are absent or removed (Newman, 2003; Flack et al., 2006; Sueur et al., 2011).

2.5. Data analysis

To determine whether each allogrooming social network was not impacted by observation time or sampling bias, we used a pre-network randomization test, or an edge swapping procedure (Farine, 2017; Farine & Carter, 2020). This approach preserves the total number of connections in the network, but randomly shuffles the edges to generate a set of random networks. We then compared the observed average connectedness, or mean strength, of macaques within their social network, to a distribution of mean strength scores calculated from the edge-swapped networks. In other words, this test determined whether for a given network size (number of nodes, which remain fixed in our captive macaque populations) and the total number of connections between them, the observed network strength measures were significantly greater than expected by chance, and thereby whether our sampling effort was adequate to generate statistically reliable network measures (Farine, 2017; Farine & Carter, 2020).

At the individual-level, we ran General Linear Mixed Models (GLMMs) to test our predictions, using the *Lme4* package in R (Bates et al., 2016). To determine whether male introduction success was more likely among groups in which females showed greater degrees of despotism (P1), we ran seven GLMMs. First, to determine whether rates of female-female aggression and submissive signalling were greater among groups that experienced successful compared to unsuccessful male introductions (P1.1), we ran four negative binomial GLMMs in which frequencies of aggression given and received and submissive signalling given and received were the outcome variables. As our primary predictor or main effect, we included 'male introduction success (successful versus unsuccessful)', i.e., the designation of females as belonging to groups that experienced either a successful or an unsuccessful introduction, as a primary predictor. Rather than set 'likelihood of introduction success' as a binary outcome, we chose to use behavioural measures of individual macaques as the outcomes, and 'introduction success' as a predictor. This is because using the former approach would make it impossible to account for between-group differences as random variables. As 'control' predictors, we included females' age, dominance rank, and average coefficient of relatedness (mean coefficient of genetic relatedness with all other females) as main effects since these attributes might potentially impact frequencies of agonistic interactions. We also controlled for potential between-group differences, and for differences across sampling year for the same group (III and IV: Table 1), by including a three-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1). We favoured this approach, as opposed to including group size as a continuous fixed effect, since this was an individual-level analysis that required controlling for, rather than quantitatively evaluating, group-level

effects, given the small sample size of just seven groups. Moreover, including group size as a continuous variable is essentially equivalent to accounting for the random effect for group ID, and including both would lead to model convergence issues. By categorizing group size into a smaller number of categories (from 6 unique groups to 2 categories), we had a clearer analytical distinction between the (random) effects being modeled by group size and the effects being modelled by group ID.

Second, to determine whether aspects of female-female dominance hierarchies and allogrooming network centrality skew towards dominants were greater for groups with successful versus failed male introductions (P1.2), we ran three Gaussian GLMMs. In the first model, the outcome was individuals' normalized David's scores, and the predictors were dominance rank, 'male introduction success', and an interaction between these variables to investigate differences in hierarchy steepness, i.e., the slopes of relationships between rank and David's scores (de Vries et al., 2006), between groups with successful versus failed male introductions. In the second model, the outcome was allogrooming degree. Predictors were dominance rank, 'male introduction success', and an interaction term between these variables to test for significant differences in allogrooming degree skew, i.e., the slopes of relationships between rank and grooming degree centrality (Sueur et al., 2011a, b) between groups with successful versus failed male introductions. In the third model, the outcome was allogrooming eigenvector, and we included the same predictors (dominance rank, 'male introduction success', and their interaction) to test for significant differences in allogrooming eigenvector skew (Sueur et al., 2011a, b), between groups with successful versus failed male introductions. For allogrooming degree and eigenvector, we used values that were rescaled into percentile scores that lay between 0 (lowest value) and 1 (highest value), in order to account for the potential effects of differences in group sizes on individuals' network connectedness (Balasubramaniam et al., 2018). In the models for allogrooming degree and eigenvector, we also included macaques' age and coefficient of relatedness as controls, to account for their potential effects on network measures. In all three models, we also included a three-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1), to control for between-group and between-period differences.

Given that individuals' degree and eigenvector measures are not independent (i.e., use many of the same network edges), we calculated p values for the degree and eigenvector models by comparing the observed model coefficient with a distribution of coefficients calculated following 1000 post-network 'node-swapping' randomizations of our data. We preferred this to pre-network randomizations because when group composition remains relatively unchanged and sampling effort is uniform across individuals (as was the case for our captive macaque groups), post-network permutations perform better while testing regression-based null hypotheses and are generally less susceptible to TypeI errors than pre-network randomizations (Farine, 2017; Farine & Carter, 2020; Weiss et al., 2020).

To test whether there was a decrease in despotism, or an increase in social tolerance, in female social structure during the post- compared to the pre-introduction period (P2), we ran seven more GLMMs. First, to determine whether rates of female-female agonistic interactions decreased during the post- compared to the pre-introduction period (P2.1), we

ran four negative binomial GLMMs similar to the models for P1.1, but only on the groups that experienced a successful male introduction. In these, we included ‘period of study (pre- versus post-introduction)’ in the place of ‘male introduction success’ as the primary predictor. As a random effect, we included a two-level nested effect of Group ID (level-2) and ‘year of observation’ (level-1), but group size was not included because the groups with successful male introductions were of similar sizes in both the pre- and post-introduction periods (Table 1).

To determine whether hierarchy steepness and the skew in social network connectedness towards dominants both decreased during the post- compared to the pre-introduction period (P2.2), we ran three GLMMs. In the first Gaussian GLMM, the outcome was normalized David’s scores, and the predictors ‘period of study (pre- versus post-introduction)’, dominance rank, and an interaction between these two terms. In the second GLMM in which we used a Poisson link function, the outcome was the count of allogrooming degree, and the predictors ‘period of study (pre- versus post-introduction)’, dominance rank, and an interaction between these two terms. In the third Gaussian model, the outcome was allogrooming eigenvector, and the predictors the same as in the models for David’s scores and grooming degree. In the degree and eigenvector models, we also included macaques’ average relatedness coefficient and age as ‘control’ predictor variables, to account for their potential effects on network connectedness (as in the models for P1.2). For degree and eigenvector, we used raw (rather than rescaled) scores of network measures since group sizes (the number of females) were the same across groups and periods in this analysis. In all three models, we included a two-level nested effect of Group ID (level-2) and ‘year of observation’ (level-1) as a random effect. Once again, we used a post-network randomization test or node-swapping procedure to calculate p values for the degree and eigenvector models.

Finally, to test whether the cohesivity of allogrooming social networks increased following successful male introductions, we ran three Wilcoxon Z -tests to compare the mean allogrooming clustering coefficients across individuals in each of the three macaque groups that experienced a successful introduction was greater during the post-introduction period compared to in the pre-introduction period.

3. Results

For all groups and periods, pre-network randomization tests revealed that allogrooming social networks were not susceptible to sampling effort. Specifically, the mean connectedness or strength of macaques within their networks was significantly greater than a distribution of mean strengths calculated from permuted networks generated by randomly swapping the edges (Table A1 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895)).

3.1. Male introduction success and female social relationships

Analyses of the pre-introduction data revealed that groups with successful male introductions showed greater degrees of despotism (or lower levels of social tolerance) in female-female social relationships than groups with failed male introductions (support for P1).

First, in support of P1.1, we detected significantly higher frequencies of status signalling received (but not given), and a non-significant trend for higher frequencies of aggression given (but not received) among groups with successful male introductions than among those with failed introductions (Table 2; Figure 1; see Table A2 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895) for full model summary statistics). These effects were independent of the potential effects of females' age, relatedness coefficient, dominance rank, and indeed group- or period-specific differences.

Second, in support of P1.2, groups with successful male introductions showed steeper dominance hierarchies and a greater rank-related skew in allogrooming social network connectedness than groups with failed introductions. For hierarchy steepness, our GLMM revealed a significant interaction between dominance rank and 'introduction success' on David's score (Table 3A), the exploration of which revealed that hierarchy steepness was greater for groups with successful introductions than groups with failed introductions (Table 3; Figure A1 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895)). For rank-related skew in network connectedness, our GLMMs showed a significant interactive effect of dominance rank and 'introduction success' on both allogrooming degree (Table 3) and eigenvector (Table 3). Exploring these interactions indicated that the rank-related skew in degree and eigenvector were both greater for groups with successful introductions than for groups with failed introductions (Table 3; Figure 2a, b).

3.2. Changes to female–female social structure following successful male introductions

Across three macaque groups with 'successful' male introductions, we found that male introductions led to a decrease in some aspects of despotism, or an increase in some aspects of social tolerance, in female social structure (partial support for P2).

First, in support of P2.1, frequencies of female-female aggression given and received, but not status signalling given and received, were both significantly lower during the post- compared to the pre-introduction period (Table 4; Figure 3; for full model summary statistics, see Table A3 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895)). Frequencies of status signalling given and received also decreased during the post-introduction period, but not significantly so (Table 4; Figure 3; Table A3 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895)).

Second, in partial support of P2.2, there was a significant decrease in female hierarchy steepness, but not in the extent of rank-related skew in allogrooming social network connectedness, among the macaque groups during the post-introduction period compared to the pre-introduction period. The first GLMM showed a significant interactive effect of between rank and 'period' on David's scores (Table 5), which indicated that hierarchy steepness was shallower during the post-introduction period compared to in the pre-introduction period; Table 5). For rank-related skew in allogrooming network connectedness, our GLMMs showed that the neither allogrooming degree (Table 5) nor eigenvector (Table 5) showed a significant interactive effect of dominance rank and 'period of observation'. In other words, contrary to our predictions, the rank-related skew in allogrooming degree and eigenvector did not show a significant decrease during the post-introduction period compared to in the pre-introduction period (Table 5).

Finally, changes to the overall connectedness and structure of female allogrooming networks indicated an increase in group cohesivity during the post- compared to the pre-introduction periods. In two out of three cases following a successful male introduction, we found a significant decrease in the mean local clustering coefficients of macaques, which indicated an increase in network connectedness and thereby cohesivity during the post-introduction period compared to the pre-introduction period (Table 6; Figure A2 at [10.6084/m9.figshare.14846895](https://doi.org/10.6084/m9.figshare.14846895)).

4. Discussion

In this study, we address a gap in our understanding of animal sociality and group living by evaluating how changes to a group's sociodemographic environment pertaining to the entry and integration of new individuals (or the introduction of males) are linked to variation in aspects of social structure among resident individuals (females). Across seven groups of captive rhesus macaques, we found that the female social structure both strongly influenced, and was in turn influenced by, male introductions and successful integration into the group. Below we discuss our findings in terms of their implications for our current understanding of the adaptive basis of social structure and for the management of captively housed nonhuman primates.

We found that the introduction and integration of new males was more successful for rhesus macaque groups in which females showed more despotic than tolerant social structures. That is, male introductions were more successful in groups where females were showing higher rates of giving aggression and receiving submissive status signalling, steeper dominance hierarchies, and greater rank-related skew in the centrality of female allogrooming networks prior to male introductions. One reason for why males integrated more successfully into groups in which females showed more despotic social structures may be that it is a by-product of larger numbers of females and matriline sizes, which are often characteristic of greater within-group female-female competition and despotism (Sterck et al., 1997; Sueur et al., 2011; Balasubramaniam et al., 2014). Indeed, larger group size and matriline size have been previously linked to successful male integration among captive rhesus macaques (Rox et al., 2018, 2019). However, this was unlikely to be the case here because we controlled for both group size (as a categorical variable, given our sample size of seven groups) and average degrees of relatedness linked to matriline size in our analyses. In other words, our results suggest that successful male introductions may be related to the patterning and distribution of females' social interactions independent of demographic characteristics like kinship, female age, and group sizes. Specifically, male integration is likely easier when intense female-female intra-group competition takes precedence over females' tendencies to challenge a new incoming male.

Other likely explanations for the links between female despotism and male integration success may be related to greater skew in the concentration of social capital or ties of support within their affiliative networks among females in more despotic groups. Specifically, a greater concentration of social capital among dominants, as indicated by a stronger correlation between dominance rank and allogrooming degree and particularly eigenvector centrality (Balasubramaniam et al., 2016; Brent et al., 2013). as we found here,

might mean that dominant females in despotic social groups may be more readily available, attractive social partners for incoming males seeking social support that would facilitate their integration (social competition hypothesis: Kawai, 1960; Seyfarth, 1977, but see Rox et al., 2018). Indeed, analyses of male-female interactions suggest that novel adult males preferentially interacted with more socially central adult females (Beisner et al., 2019). On the other hand, such a skew in the concentration of social capital might also mean that less socially well-connected subordinates may be more prone to forming strong affiliative ties of social support and potential mating opportunities with incoming males and thereby facilitate their social integration. Evidence (or lack thereof) for either of these processes awaits more comprehensive assessments (on-going, but beyond the scope of this study) of the factors that influenced novel males' interactions with resident females during the male introduction phases.

Our temporal comparisons of post- versus pre-introduction periods for the three groups that experienced a successful male introduction revealed a significant reduction in female-female aggression and hierarchy steepness and in two out of three cases, a significant decrease in the extent to which females' allogrooming social networks were clustered. Together, these findings, consistent with a previous, longitudinal study of wild vervet monkeys that revealed similar associations between female social networks following male immigrations (Borgeaud et al., 2017), suggest that male entry and successful integration resulted in a shift from despotism towards greater levels of female-female social tolerance, and increased group cohesivity through forming new network connections. These findings are consistent with previous work on captive rhesus macaques that revealed that male introductions led to lower aggression and heightened affiliation within groups (Beisner & McCowan, 2013; Rox et al., 2018, 2019; Bailey et al., 2020, 2021). Our network approach expands on these studies to reveal that changes to individual behaviour extend to influencing higher-order changes to group social structure that are indicative of increased social tolerance (through a reduction in aggression and hierarchy steepness) and cohesivity following male entry and integration.

One reason for the increase in social tolerance and group cohesivity following successful male introductions may be related to stress-coping. There is strong evidence that arrival of new individuals into primate social groups is associated with heightened stress, both in the wild (Alberts et al., 1992; Bergman et al., 2005; Marty et al., 2017) and in captivity (Bernstein et al., 1977; Rox et al., 2018). To cope with stress, females may reduce aggression that can lead to heightened stress, and increase the diversity of their allogrooming network connectedness (as would be captured by a decrease in clustering) because increasing partner diversity may buffer individuals from social or environmental stress (Sapolsky, 2005; Young et al., 2014; Snyder-Mackler et al., 2020). A second, non-independent explanation may be that females increase and extend their allogrooming effort to other females that form strong associations with the incoming male, in exchange for potentially gaining greater access to mating opportunities.

Unlike rates of aggression that showed a significant decrease, rates of giving and receiving status signalling did not show a significant decrease following successful male introductions. This may be because females require, and therefore resort to using, status signalling in non-aggressive contexts to maintain or reinforce the certainty of their ranks (Vandeleest et

al., 2016), that may be particularly important to maintain dominance status following the reduction in aggressive interactions after male introductions. Furthermore, unlike dominance steepness, we found that the extent of skew in allogrooming social network connectedness towards high-ranking females did not decrease significantly following successful male introductions. In other words, females largely seemed to retain their tendencies to groom dominants, i.e., groom up the dominance hierarchy (Seyfarth, 1977), following the arrival and integration of new males. This suggests that, despite an overall increase in female-female social tolerance and group cohesivity following male introductions, allogrooming may still be vital for subordinate females to gain rank-related benefits from dominants, e.g., access to support, mating opportunities, tolerance while feeding (Seyfarth, 1977; Henzi & Barrett, 1999; Barrett et al., 2002; Schino & Aureli, 2008), in the post-introduction periods. Confirmation of this explanation awaits future research.

We conducted longitudinal assessments of post-introduction behaviours only for the three groups that experienced a successful male introduction. In other words, the lack of a longitudinal ‘control’ group in our study means that we are unable to comment on whether the groups that did not experience successful male introductions also showed increases in female-female social tolerance following unsuccessful male introductions. While we therefore advertise a degree of caution in interpreting our findings, we nevertheless remain convinced that they are valid given our effective within-group comparison wherein each group that was observed longitudinally effectively served as its own control. Another consideration is the impact of cross-group differences in the housing of introduced males on our findings. While it is conceivable that these differences may have impacted males’ familiarity with females, and thereby interactions between introduced males and resident females during the introduction phase, we had no reason to expect the introduction process itself to affect post-introduction female-female behaviour. We will investigate both these potential limitations in future research.

From an evolutionary or adaptive perspective, our findings may provide insights into how demographic processes like immigration events may be influenced by, and (more so) themselves influence, social behaviour among group-living species. Our implementation of social network analysis is especially significant in this regard. During the past 15 years, network approaches have been heavily implemented to quantitatively assess inter-individual and comparative inter-group variation in animal social structure (reviewed in McCowan et al., 2008; Wey et al., 2008; Sueur et al., 2011a; Farine & Whitehead, 2015). Yet the majority of these studies have focused on the influence of socioecological and demographic factors on “static” networks constructed for data cumulated for animal groups over a specific time-frame, with fewer studies focusing on the temporal dynamics of adaptive changes to social networks (reviewed in Borgeaud et al., 2017). Our study addressed this gap, by evaluating how the sociodemographic changes associated with potential arrival and integration of new males may lead to changes to social network structure, when other confounding factors were controlled (e.g., group size, animal attributes and relatedness) or absent (e.g., predation, intergroup encounters). Specifically, the finding that animals retained their previous social network ties with dominant individuals, while adding new connections that led to greater group cohesivity without compromising on their relationships with dominants, suggest that rhesus macaques (and indeed other nonhuman primates like vervet monkeys: Borgeaud et

al., 2017) may retain their pre-existing, core relationships while adaptively responding to sociodemographic changes. Whether such retention is specific to animal taxa with advanced cognitive abilities (Dunbar, 1992) awaits more longitudinal or temporal evaluations of social network changes versus degrees of concordance (as in the study on vervet monkeys: Borgeaud et al., 2017), as well as cross-species comparative studies of changes to network dynamics being indicative of social complexity (as suggested by Borgeaud et al., 2017).

Our findings are of considerable practical value to colony managers. We add to a growing body of literature that reveals a number of potential benefits from successful introductions of males (1) moderating aggression and/or wounding through behaviours like conflict policing (Beisner et al., 2012; Bailey et al., 2020, 2021; Crast et al., data not shown; our results here), (2) increasing female reproductive success and infant births that are critical for biomedical research (Crast et al., data not shown) and (3) greater social tolerance and group cohesion (Flack et al., 2006; Rox et al., 2019; our results here).

The current work also offers strategies to colony managers to increase the welfare of captive rhesus macaque breeding groups when conducting multi-male introductions. Colony managers could assess female-female social structure prior to deciding which males to introduce and the timing of such introductions. For example, if a group of resident females is showing lower degrees of despotism, our findings suggest that introduced males are less likely to be successful. To compensate for the reduced odds of success in such scenarios, colony managers might need to select males with traits associated with better chances of successful introduction, such as prime age males with more social experience, or with a proven track record of being able to resist female aggression (Bailey et al., 2020, 2021). Finally, since heightened aggression has often been associated with social instability among captive rhesus macaques, it is conceivable that our finding that male integration success was more likely in groups showing greater despotism (aggression) may be interpreted as counter-intuitive to the assumption that social group stability is a pre-requisite for male introduction success (Beisner et al., 2011, 2012; Rox et al., 2018). However, our results showed that aggression, though greater in frequency, was largely unidirectional as is typical among rhesus macaques (Thierry, 2007), and was also strongly correlated to submissive status signalling that is indicative of increased (rather than decreased) social stability (Beisner et al., 2012). In other words, heightened aggression and despotism in these groups, rather than being indicative of social (in)stability, may be more indicative of being a characteristic feature of their despotic social structure. In this light, we suggest that colony managers use such behavioural and social network indicators (as we have done) to better distinguish between 'social structure' and 'social stability'. Such distinctions are critical in light of how previous research on other captive rhesus macaque populations have revealed how social network connectedness, depending on broader contexts that are indicative of social stability (or lack thereof), may positively versus negatively impact macaques' health (Beisner et al., 2011; Balasubramaniam et al., 2016; Vandeleeest et al., 2016).

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Appendix

Appendix

Table A1.

Results of pre-network randomization tests that compared the observed mean strength of macaques within their grooming networks, with a distribution of mean values calculated from 1000 permuted networks generated by randomly swapping the edges of the original networks.

Group ID	Number of nodes (females)	Mean strength (pre-introduction)	Mean strength (post-introduction)
I	40	27.78 ^{**}	
II	30	34.92 ^{**}	
III ^a	14	27.43 ^{**}	21.57 ^{**}
IV ^a	14	26.43 ^{**}	27.43 ^{**}
V	14	29.23 ^{**}	24.92 ^{**}
VI	18	21.88 ^{**}	
VII	37	36.97 ^{**}	

^aThe same group observed in sequential years.

^{**} $p < 0.01$.

Table A2.

Negative binomial GLMMs examining the relationship between male introduction success and the behavioral outcomes of individuals': aggression given, aggression received, submissive status given and submissive status received.

Predictor	β	SE	z	Pr(> z)
Outcome: Aggression given				
(Intercept)	2.81	0.08	37.13	<0.01 ^{**}
Introduction (unsuccessful vs successful)	-0.27	0.16	-1.65	0.09 ^(*)
Age	-0.05	0.11	-0.45	0.65
Dominance rank (Percentile)	1.23	0.11	10.93	<0.01 ^{**}
Relatedness coefficient	0.02	0.12	0.19	0.85
Outcome: Aggression received				
(Intercept)	2.80	0.10	28.43	<0.01 ^{**}
Introduction (unsuccessful vs successful)	-0.31	0.21	-1.49	0.14
Age	-0.68	0.09	-7.82	<0.01 ^{**}
Dominance rank (Percentile)	-1.08	0.08	-12.72	<0.01 ^{**}
Relatedness coefficient	0.02	0.09	0.28	0.78
Outcome: Status given				
(Intercept)	3.57	0.12	28.62	<0.01 ^{**}
Introduction (unsuccessful vs successful)	-0.39	0.24	-1.61	0.11
Age	-0.35	0.09	-4.05	<0.01 ^{**}

Predictor	β	SE	z	Pr(> z)
Dominance rank (Percentile)	-1.14	0.09	-12.47	<0.01**
Relatedness coefficient	-0.04	0.09	-0.45	0.66
Outcome: Status received				
(Intercept)	3.28	0.13	24.99	<0.01**
Introduction (unsuccessful vs successful)	-0.54	0.26	-2.07	0.04*
Age	0.21	0.12	1.68	0.09(*)
Dominance rank (Percentile)	2.14	0.13	16.59	<0.01**
Relatedness coefficient	-0.35	0.14	-2.57	0.01*

In each model, we included a 3-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1).

* $p < 0.05$;

** $p < 0.01$;

(*) $0.05 < p < 0.10$.

Table A3.

Negative binomial GLMMs examining the relationship between period of study and the behavioral outcomes of individuals': aggression given, aggression received, submissive status given and submissive status received, for groups that experienced a successful male introduction.

Predictor	β	SE	z	Pr(> z)
Outcome: Aggression given				
(Intercept)	1.37	0.26	5.18	<0.01**
Period (post- vs pre-introduction)	-0.82	0.17	4.92	<0.01**
Age	-0.03	0.02	-1.61	0.11
Dominance rank (Percentile)	2.30	0.31	7.52	<0.01**
Relatedness coefficient	-0.13	0.44	-0.29	0.77
Outcome: Aggression received				
(Intercept)	4.11	0.22	18.93	<0.01**
Period (post- vs pre-introduction)	-0.79	0.13	6.16	<0.01**
Age	-0.10	0.02	-6.35	<0.01**
Dominance rank (Percentile)	-1.81	0.23	-7.83	<0.01**
Relatedness coefficient	-0.09	0.34	-0.28	0.78
Outcome: Status given				
(Intercept)	5.00	0.32	15.86	<0.01**
Period (post- vs pre-introduction)	-0.49	0.35	1.40	0.16
Age	-0.07	0.01	-4.49	<0.01**
Dominance rank (Percentile)	-1.93	0.21	-9.13	<0.01**
Relatedness coefficient	-0.09	0.31	-0.29	0.77
Outcome: Status received				
(Intercept)	1.87	0.31	5.99	<0.01**
Period (post- vs pre-introduction)	-0.61	0.36	1.71	0.09(*)
Age	-0.03	0.02	-1.96	0.05*

Predictor	β	SE	z	Pr(> z)
Dominance rank (Percentile)	3.47	0.24	14.45	<0.01 **
Relatedness coefficient	-1.15	0.37	-3.16	<0.01 **

In each model, we included a 3-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1).

* $p < 0.05$;

** $p < 0.01$;

(*) $0.05 < p < 0.10$.

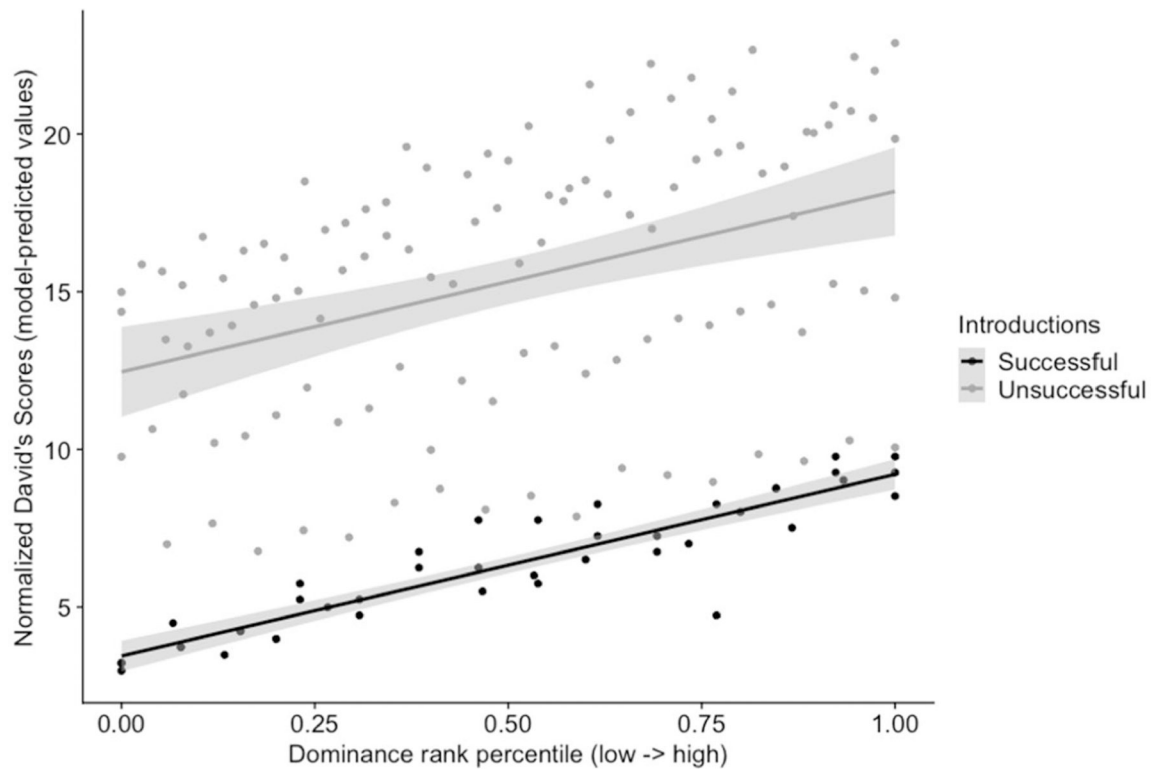


Figure A1.

Relationship between dominance rank and Normalized David's Scores that indicate significant differences in the slopes, i.e., in hierarchy steepness, for groups that experienced successful (black) versus unsuccessful (grey) male introductions.

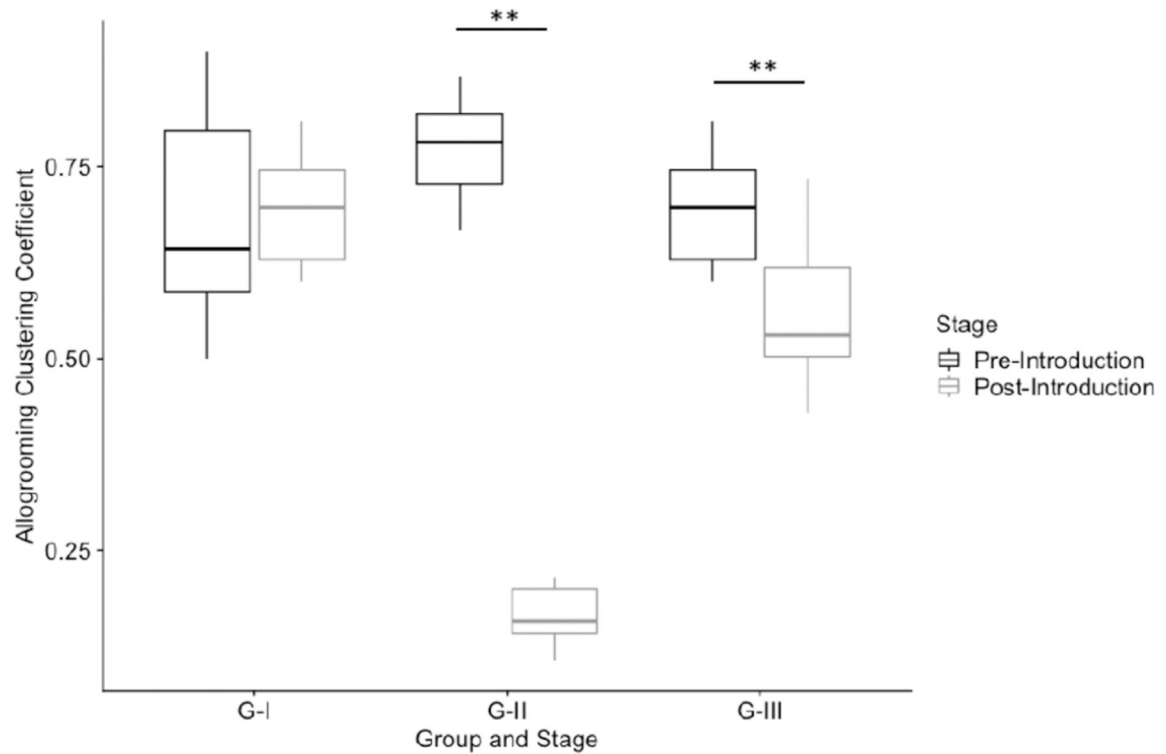


Figure A2.

Box and whisker plots showing the mean grooming clustering coefficients by period, for each of three groups that experienced successful male introductions.

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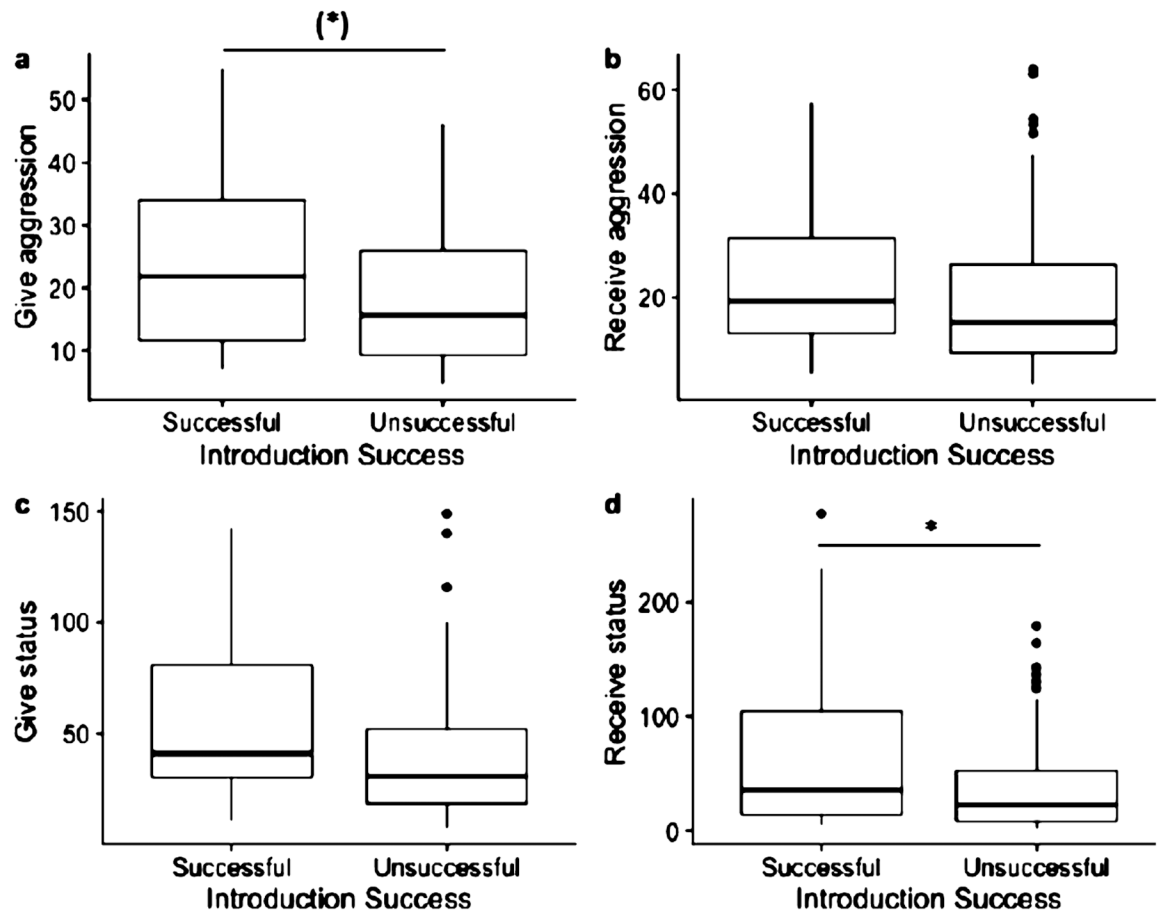


Figure 1. Rates of aggression and status signalling in groups with successful versus unsuccessful male introductions. * $p < 0.05$; (*) $0.05 < p < 0.10$.

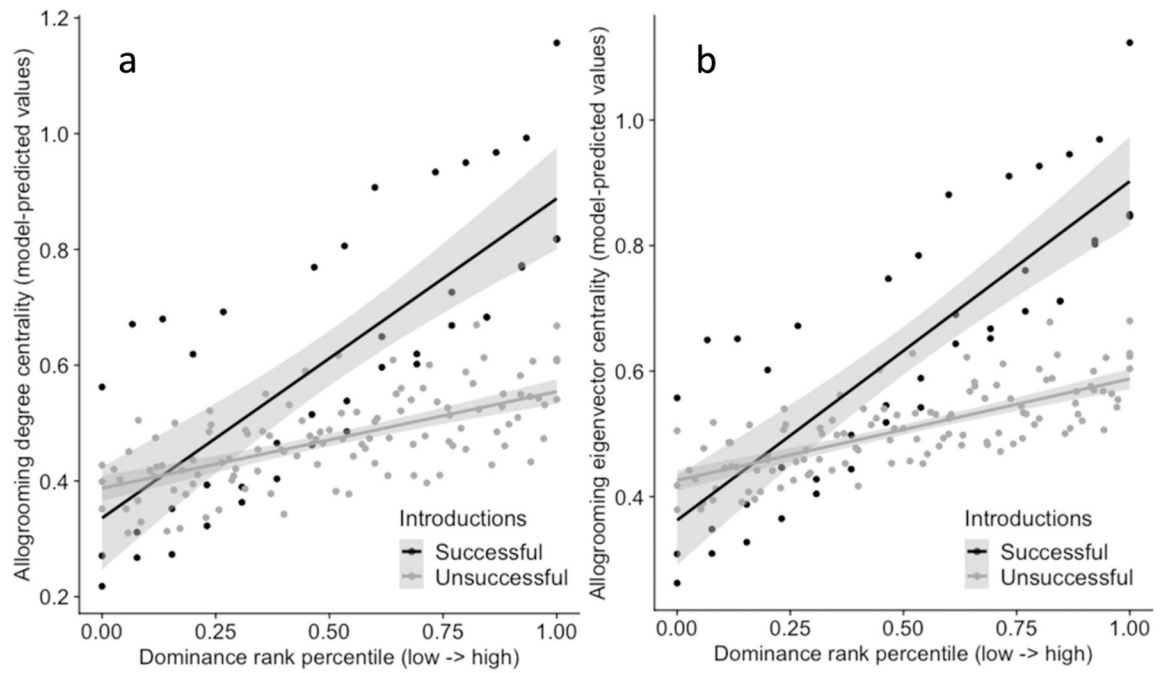


Figure 2. Relationship between dominance rank and allogrooming (a) degree and (b) eigenvector centrality for groups that experienced successful versus unsuccessful male introductions.

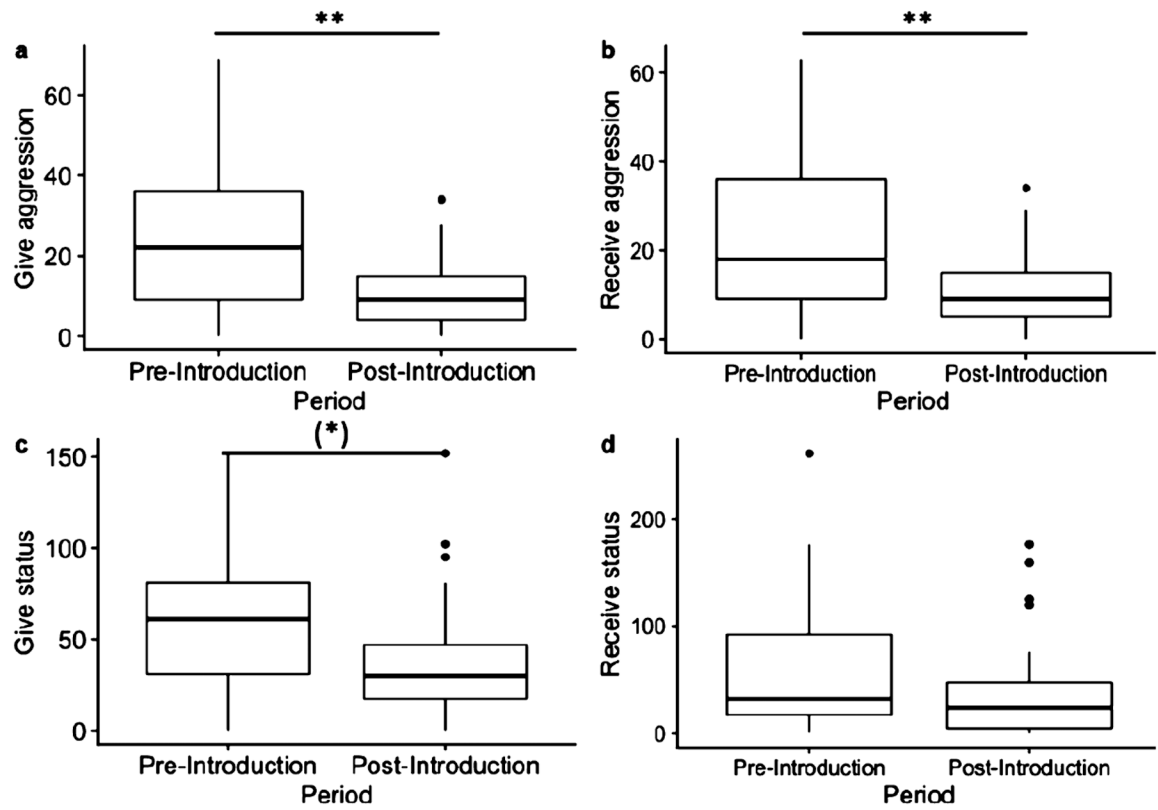


Figure 3.

Rates of aggression and status signalling during the post- compared to the pre-introduction periods, for groups that experienced successful male introductions. ** $p < 0.01$; (*) $0.05 < p < 0.10$.

Table 1.

The study groups, male introduction success, and data collection periods.

Group demographic characteristics				Observation details		Introduction details	
ID	Size	Breeding females (Subjects)	Sex-ratio (♀:♂)	Period	Hours	Number of males successfully introduced	Male housing condition
Pre-introduction period							
I	84	40	20	March 2017–August 2017	154	0	Traditional
II	64	30	30	March 2017–September 2017	169	0	Traditional
III*	33	14	2	March 2017–September 2017	165	3	Traditional
IV*	33	14	4.67	March 2018–August 2018	166	4	Enclosure
V	41	14	14	March 2018–August 2018	159	3	Enclosure
VI	44	18	18	March 2018–September 2018	168	0	Enclosure
VII	60	37	18.5	March 2019–September 2019	168	0	Traditional
Post-introduction period							
III	33	14	4.67	January 2018–June 2018	163		
IV	33	14	3.5	February 2019–September 2019	168		
V	41	14	4.67	February 2019–September 2019	166		

* The same group observed in sequential years.

Table 2.

Results of four negative binomial GLMMs examining the relationship between male introduction success and individuals': aggression given, aggression received, submissive status given and submissive status received, across seven rhesus macaque groups ($N = 156$).

Outcome	Predictors				
	Intercept	Age	Dominance rank	Relatedness coefficient	Introduction (successful vs unsuccessful)
Aggression given	2.02 ^{**}	-0.01	2.03 ^{**}	0.08	0.27 ^(*)
Aggression received	4.60 ^{**}	-0.07	-1.78 ^{**}	0.09	0.31
Status given	5.19 ^{**}	-0.04	-1.88 ^{**}	-0.15	0.39
Status received	1.94 ^{**}	0.02	3.54 ^{**}	-1.33 [*]	0.54 [*]

Values in cells indicate β coefficients (effect sizes) for predictor variables (listed in the first row) for each of the four models. In each model, we included a 3-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1).

* $p < 0.05$;

** $p < 0.01$;

^(*) $0.05 < p < 0.10$.

Table 3.

GLMMs examining the effects of an interaction between females' dominance rank and male introduction success on the outcome of their normalized David's scores (i.e., hierarchy steepness), allogrooming social network degree (i.e., degree rank-related skew), and allogrooming social network eigenvector (i.e., eigenvector rank-related skew).

	β	SE	t	$P_{r(> t)}$	P_{perm}
Outcome: Normalized David's scores					
(Intercept)	13.82	5.14	2.69	0.17	
Introductions (Unsuccessful vs Successful)	1.72	3.80	0.45	0.68	
Rank (Successful introductions)	-0.50	0.03	-17.07	<0.01**	
Rank (Unsuccessful introductions)	-0.22	0.01	-28.98	<0.01**	
Introductions: Rank	0.28	0.03	9.32	<0.01**	
Outcome: Allogrooming degree					
(Intercept)	0.31	0.12	2.53	0.03*	
Introductions (Unsuccessful vs Successful)	0.00	0.14	0.03	0.98	
Rank (Successful introductions)	0.53	0.12	4.43	<0.01**	<0.01**
Rank (Unsuccessful introductions)	0.16	0.07	2.18	0.03*	0.04*
Age	0.01	0.00	2.03	0.04*	
Relatedness coefficient	0.04	0.17	0.22	0.83	
Introductions: Rank	-0.37	0.14	-2.59	0.01*	0.01*
Outcome: Allogrooming eigenvector					
(Intercept)	0.33	0.11	3.03	0.01*	
Introductions (Unsuccessful vs Successful)	0.02	0.12	0.18	0.86	
Rank (Successful introductions)	0.51	0.12	4.30	<0.01**	<0.01**
Rank (Unsuccessful introductions)	0.16	0.07	2.11	0.04*	0.04*
Age	0.01	0.00	1.80	0.07(*)	
Relatedness coefficient	0.07	0.16	0.43	0.67	
Introductions: Rank	-0.36	0.14	-2.52	0.01*	0.01

In each model, we included a 3-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1). For models on degree and eigenvector, p_{perm} represents p values calculated based on comparing observed model coefficients with coefficients generated based on network measures calculated from 1000 permuted networks generated from post-network 'node-swapping' randomizations.

* $p < 0.05$;

** $p < 0.01$;

(*) $0.05 < p < 0.10$.

Table 4.

Results of four negative binomial GLMMs examining the differences in individuals': aggression given, aggression received, submissive status given and submissive status received, during the post-introduction compared to the pre-introduction period, across macaque groups that experienced a successful male introduction.

Outcome	Predictors				
	Intercept	Age	Dominance rank	Relatedness coefficient	Stage (post- vs pre-introduction)
Aggression given	1.37 ^{**}	-0.03	2.29 ^{**}	-0.13	-0.82 ^{**}
Aggression received	4.11 ^{**}	-0.10	-1.81 ^{**}	-0.09	-0.79 ^{**}
Status given	4.99 ^{**}	-0.06	-1.93 ^{**}	-0.09	-0.49
Status received	1.86 ^{**}	-0.03	3.46 ^{**}	-1.15 ^{**}	-0.61 ^(*)

Values in cells indicate β coefficients (effect sizes) for predictor variables (listed in the first row) for each of the four models. In each model, we included a 2-level nested random effect of categorical 'group ID' (level-2), and 'year of observation' (level-1).

* $p < 0.05$;

** $p < 0.01$;

^(*) $0.05 < p < 0.10$.

Table 5.

GLMMs examining the effects of an interaction between females' dominance rank and period of study on the outcome of their normalized David's scores (i.e., hierarchy steepness), allogrooming social network degree (i.e., rank-related skew in degree) and allogrooming network eigenvector (i.e., rank-related skew in eigenvector), for macaque groups that experienced a successful male introduction.

	β	SE	t	$P_{r(> t)}$	P_{perm}
Outcome: Normalized David's scores					
(Intercept)	8.56	0.36	23.53	<0.01**	
Period (post- vs pre-introduction)	-1.35	0.51	2.62	0.11	
Rank (Post-introduction)	-0.32	0.01	-26.89	<0.01**	
Rank (Pre-introduction)	-0.50	0.01	-42.58	<0.01**	
Introductions: Rank	-0.19	0.02	-11.10	<0.01**	
Outcome: Allogrooming degree					
(Intercept)	0.45	0.16	2.72	0.04*	
Period (post- vs pre-introduction)	0.04	0.21	0.17	0.87	
Rank (Post-introduction)	0.31	0.14	2.23	0.03*	0.04*
Rank (Pre-introduction)	0.57	0.14	4.04	<0.01**	<0.01**
Age	0.00	0.01	0.00	1.00	
Relatedness coefficient	-0.11	0.17	-0.65	0.52	
Introductions: Rank	0.25	0.19	1.30	0.20	
Outcome: Allogrooming eigenvector					
(Intercept)	0.24	0.02	11.17	<0.01**	
Period (post- vs pre-introduction)	0.03	0.02	1.51	0.14	
Rank (Post-introduction)	0.05	0.03	1.84	0.07(*)	0.05*
Rank (Pre-introduction)	0.11	0.03	4.19	<0.01**	<0.01**
Age	0.00	0.00	0.28	0.78	
Relatedness coefficient	-0.01	0.03	-0.31	0.76	
Introductions: Rank	0.06	0.04	1.69	0.10	

In each model, we included a 3-level nested random effect of categorical 'group size' (level-3), 'group ID' (level-2), and 'year of observation' (level-1). For models on allogrooming degree and eigenvector, p_{perm} represents p values calculated based on comparing observed model coefficients with coefficients generated based on network measures calculated from 1000 permuted networks generated from post-network 'node-swapping' randomizations.

* $p < 0.05$;

** $p < 0.01$;

(*) $0.05 < p < 0.10$.

Table 6.

Comparisons of allogrooming local clustering coefficients during the post-introduction versus pre-introduction periods for each of the three groups with successful male introductions.

Group	Wilcoxon Z test (clustering coefficient for post- versus pre-introduction)
G-III	$N = 14, W = 84, p = 0.53$
G-IV	$N = 13, W = 169^{**}$
G-V	$N = 14, W = 173.5^{**}$

**
 $p < 0.01$.

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