Which male and female characteristics influence the probability of extragroup paternities in rhesus macaques, *Macaca mulatta*?

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Extragroup paternity (EGP) is found across a wide range of species and may entail reproductive benefits, but may also entail costs to both sexes. While population and group parameters affecting the degree of EGPs are relatively well established, less is known about the individual characteristics that make males and females engage in alternative reproductive tactics such as EGP. Applying a combination of long-term demographic and genetic data from the rhesus macaque population of Cayo Santiago (Puerto Rico, U.S.A.), we investigate which male and female characteristics influence the probability of EGP to better understand the circumstances that shape the distribution and occurrence of EGP. Our results show that, against our expectations, higher-ranking females were more likely to produce EGP offspring than lower-ranking females. The probability of producing extragroup offspring was not significantly related to female or male age, male tenure or previous reproductive success. Furthermore, genetic relatedness between the parents did not affect the production of extragroup offspring, but extragroup offspring were more frequently produced early rather than late in a given mating season. Altogether, our analysis suggests that individual attributes and seasonal aspects create different opportunities and preferences for engaging in EGP as an alternative reproductive tactic. The observed patterns of EGP in rhesus macaques appear to be consistent with female mate choice for genetic benefits, which needs to be confirmed in future studies.

Extragroup paternity (EGP) or the production of offspring by parents from different reproductive units (groups or pairs) is found across a wide range of species of various taxa (e.g. red fox, *Vulpes vulpes*: Baker, Funk, Bruford, & Harris, 2004; Gunnison's prairie dog, *Cynomys gunnisoni*: Travis, Slobodchikoff, & Kefan, 1996; common mole-rat, *Cryptomys hottentotus*: Bishop, Jarvis, Spinks, Bennett, & O'Ryan, 2004; pilot whales, *Globicephala melas*: Amos, Barrett, & Dover, 1991; Verreaux's sifakas, *Propithecus verreauxi verreauxi*: Lawler, 2007). Species differences in rates of EGPs are relatively well described and relate to differences in opportunities and cost—benefit ratios of EGP associated with species and population parameters (meta-analysis on 26 mammalian species: Isvaran & Clutton-Brock, 2007; nonhuman primates: van Noordwijk & van Schaik, 2004).

Research on the selective pressures that may drive males and/or females to seek EGPs has been conducted mainly in birds and, to a lesser extent, in mammals. For males, the benefits of mating outside their reproductive unit are rather straightforward as they can gain additional reproductive success through EGP (Birkhead & Møller, 1993; Fietz et al., 2000; Gibbs et al., 1990; Lawler, 2007; Trivers, 1972; Weiß, Kulik, Ruiz-Lambides, & Widdig, 2016). Benefits of EGP are less evident for females but may include both direct and indirect benefits such as the acquisition of good or compatible genes (blue tits, *Parus caeruleus*: Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; alpine marmots, *Marmota marmota*: Cohas, Yoccoz, Silva, Goossens, & Allainé, 2006; humans, *Homo sapiens*: Thornhill & Gangestad, 1993), avoiding costs related to inbreeding (banded mongoose, *Mungos mungo*: Nichols, Cant, & Sanderson, 2015), enhanced resource acquisition (Greiling & Buss, 2000; Smuts, 1985), or reduced risk of infanticide (reviewed in Wolff & MacDonald, 2004). Moreover, increased mortality rates or decreased reproductive opportunities associated with dispersal (Alberts & Altmann, 1995) could be potentially abated when males or females seek out EGPs rather than dispersing into new groups to encounter other mating partners.

On the other hand, individuals engaging in EGPs can suffer costs such as an increased risk of sexually transmitted diseases (Kokko, Ranta, Ruxton, Lundberg, & Dudash, 2002; Westneat & Birch Rambo, 2000). Furthermore, individuals may receive increased levels of aggression and injuries outside their own group while seeking extragroup mating partners (Daly & Wilson, 1988; García-Navas, Ortego, Ferrer, & Sanz, 2013; McKibbin, Starratt, Shackelford, & Goetz, 2011; Nichols et al., 2015). EGPs can further present a cost, particularly for males, by reducing possibilities for within-group reproduction while pursuing mating partners elsewhere (Arct, Drobniak, & Cichoń, 2015; Lawler, 2007; Muniz et al., 2006; Widdig et al., 2017) or by increased predation pressure when moving between groups.

As in other mammals, rates of EGP in primates likely reflect cost−benefit ratios as well as opportunities for EGP resulting from, for example, group structures, competitive regimes or kin structures. EGPs have been reported in pair-living primates (e.g. 7% in white-handed gibbons, *Hylobates lar*: Barelli et al., 2013; 44% in fat-tailed dwarf lemurs, *Cheirogaleus medius*: Fietz et al., 2000), as well as in several group-living species (e.g. 11% in toque macaques, *Macaca sinica*: Keane, Dittus, & Melnick, 1997; 16% in rhesus macaques: Ruiz-Lambides et al., 2017; 33% in Japanese macaques, *Macaca fuscata*: Soltis, Thomsen, & Takenaka, 2001; 42% in Verreaux sifakas: Lawler, 2007). Furthermore, rates of EGP may vary considerably between groups and years in the same species. In rhesus macaques, EGP rates between 0% and 65% were related to group characteristics such as sex ratio, group size, female synchrony and group instability (Ruiz-Lambides et al., 2017). This variation was suggested to reflect differences in male monopolization potential and female choice for novel males and, thus, variation in opportunity and presumed benefits of mating with diverse partners. Along the same lines, variation in rates of EGP in Verreaux sifakas was attributed to opportunities related to female choice, home range overlap and length of the mating season (Lawler, 2007). This reflected the general patterns observed in mammals that shorter mating seasons and limitations in male monopolization due to female synchrony were predictive of high EGP rates (reviewed in Isvaran & Clutton-Brock, 2007). However, while species and group differences are relatively well described, we currently lack studies on the characteristics of males and females that engage in EGPs, which is an integral part to understanding the circumstances that shape the distribution and occurrence of EGP.

The present study investigated individual characteristics of parents of within-group offspring and offspring sired by extragroup males in several groups of rhesus macaques. Rhesus macaques live in multimale, multifemale groups, with both males and females mating promiscuously. They are seasonal breeders with >72% of births within a 3-month period (Hernández-Pacheco et al., 2016a). Females are philopatric and form stable matrilineal hierarchies (Gouzoules & Gouzoules, 1987), whereby higher-ranking female macaques may be preferred consorts (Samuels, Silk, & Rodman, 1984; but see Hill, 1987). Furthermore, older females experience a higher degree of consortship than young females (Hill, 1987; Kaufmann, 1965), as young females tend to be less successful at rearing offspring (Altmann, 1980). Males typically disperse during adolescence (Sade, 1972) and obtain their rank in a new group by queuing (Dubuc, Muniz, Heistermann, Engelhardt, & Widdig, 2011). Male dominance rank is frequently correlated with mating success (Dubuc et al., 2011), and young males are less capable of monopolizing within-group females due to the queuing system (Dubuc, Muniz, Heistermann, Widdig, & Engelhardt, 2012). However, male monopolization potential is limited due to temporal and energetic costs of mate guarding as well as a limited ability to accurately assess a female's fertile period, which opens the opportunity for female mate choice (Dubuc et al., 2012; van Noordwijk & van Schaik, 2004). Females seem to prefer novel mates (Manson, 1995) and resist mating with males of long tenure or with related males (reviewed in Dubuc et al., 2011). Consequently, also male tenure, natal status and female mating preferences are likely to affect within-group mating opportunities. Altogether this suggests that individual attributes of males and females as well as the combination thereof provide ample variation in the benefits as well as opportunities for engaging in EGP, which makes the species an ideal system for investigating the circumstances that shape the distribution and occurrence of EGP.

For this study we use comprehensive genetic and demographic data from a semi-free-ranging population of rhesus macaques that inhabit the island of Cayo Santiago to investigate characteristics of the parents of within and extragroup offspring. Based upon the rhesus social system and behaviour outlined above, we expected lower-ranking and younger females to have greater opportunities and thus show higher levels of EGP than higher-ranking or older females. We expected young and short-tenure males to have fewer within-group mating opportunities and therefore engage more in EGP. We further expected adult males still residing in their natal group as well as males with low success in their own social group to benefit more from pursuing extragroup matings and thus show higher levels of EGP. As EGP should be particularly beneficial to increase outbreeding, we also expected parents engaging in EGP to show lower degrees of relatedness than parents belonging to the same social group. Finally, we expected male monopolization potential to be lower late in the mating season due to the accumulating costs of mate guarding and, consequently, a higher likelihood for offspring to result from EGP later in the season.

METHODS

Study Site and Studied Population

The study was conducted on the free-ranging population of rhesus macaques of the island of Cayo Santiago, Puerto Rico (18°09′N, 65°44′W), managed by the Caribbean Primate Research Center (CPRC). The monkeys are descendants of the 409 rhesus macaques captured in 12 districts of India and released on Cayo Santiago in 1938 (Rawlins & Kessler, 1986). Since its founding, no new animals have been added except through births, however, extensive genetic data suggest no risk of inbreeding depression (Widdig et al., 2017). Life history data have been continuously collected since 1956 by census takers on a near-daily basis. The resulting demographic database contains data on all live births, age, sex, maternal genealogy, migrations and deaths. All observed occurrences are noted immediately or within 2 days.

Although the monkeys are provisioned with monkey chow (approximately 0.23 kg per monkey per day), they devote half of their foraging time on natural vegetation (Marriott, Roemer, & Sultana, 1989). There is no natural water source on the island; thus, automatic drinkers provide rain water ad libitum. Human intervention is limited to minimally invasive measurements during the annual 2-month trapping season. During this period, yearlings are tattooed to facilitate individual identification and are given tetanus primary immunizations, and 2-year-olds are given a tetanus booster. At the same time, physiological samples, including blood or tissue, are collected for paternity analysis. Due to the lack of predation, a proportion of animals has had to be removed to control population size (Hernandez-Pacheco et al., 2016b). During the nine birth cohorts (2004–2012) included in this study, the trend was to remove individuals younger than 3 years old (mean ± SD: 83 ± 33%), however, most individuals were sampled for parentage assignment prior to removal. At the onset of each

birth season (2004–2012), the population size averaged 913 ± 77 animals (mean ± SD, range 800–1016). Animals were distributed among six naturally formed groups with 57–284 individuals at any point in time, which is similar to values reported from the wild (Seth & Seth, 1986; Teas, Richie, Taylor, & Southwick, 1980). Other than by removal for population control, group sizes are regulated naturally by regular group fission events.

Parentage Assignment

Extensive efforts have been undertaken since 1992 to collect predominantly blood samples for parentage assignment, yielding genetic information for 4641 animals, genotyped on up to 43 STR markers (mean ± SD = 27.6 ± 1.6, described in Widdig et al., 2017). At the time of this study, the genetic database contained 3996 mother–offspring pairs for which maternity was initially identified by behavioural observations, then further genetically confirmed for 3946 (98.7%). All offspring with confirmed maternity were successively used in the paternity analyses. During our study period (birth cohorts 2004–2012), a total of 2079 live births were reported in the population. Of these infants, 14.62% died prior to being sampled, 1.97% were removed from the island together with their mother before being sampled, and we lacked genetic material for 0.05%, resulting in 1733 (83.36%) individuals being genotyped. Of these, we removed another 84 infants from the analysis because they were born into groups not present on the island for the entire study period due to group fissions or group removal. As a result, we considered a total of 1649 infants for this study.

We considered males as potential sires according to the following criteria: (1) males that were older than 1250 days of age (based on the earliest age of male reproduction: Bercovitch et al., 2003) and (2) present on the island when the offspring under consideration was conceived (i.e. at least 200 days before the day of birth of the respective infant, given a mean ± SD gestation length of 166.5 ± 7.4 days, according to Silk, Short, Roberts, & Kusnitz, 1993). Of the resulting 388 potential sires for all 1649 infants investigated, we were able to obtain a genetic sample from 376 (96.9%). We assigned paternity using different exclusion criteria as described in Ruiz-Lambides et al. (2017), and were able to additionally confirm paternity for all 1649 infants with likelihood analyses at the 95% level in Cervus 3.0 (Kalinowski, Taper, & Marshall, 2007).

Male Group Membership

To assign offspring to a within or an extragroup sire, we first determined group membership for each sire on each day. Group assignment was based on observations of the group that an individual was encountered in on a given day as recorded in the demographic database. A male was assigned as a member of a new social group when group residency remained constant for a minimum of 30 days after the first day the male was observed entering the new group. Males that were observed to prospect other social groups, to join bachelor groups or to be solitary for any period during the first 30 days remained under close observation until residency became stable for at least 60 days, at which point the day of immigration was defined as the first day the male was seen in the new group.

Identifying Extragroup Paternity

Following the strict criteria for group membership, we determined whether sires were residents or extragroup males at the time of offspring conception. We estimated time of conception (hereafter conception window) for each infant by backtracking 166.5 ± 7.4 days (mean ± SD) from its date of birth (gestation length provided by Silk et al., 1993), which resulted in a 15-day conception window obtained for each offspring. To avoid assigning an EGP to a possible migratory event, we scored EGPs conservatively by including in our definition of an EGP a total of 30 days prior to and 30 after the conception window (i.e. a total of 75 days). In summary, an EGP was identified if the offspring was sired by a male that was not resident in the offspring's social group during any of the 75 days. Accordingly, offspring sired by a male that resided in the offspring's group at any point during the 75 days was identified as a within-group offspring. As shown elsewhere, we identified a total of 264 (16%) extragroup paternities within the 1649 offspring included in the study (Ruiz-Lambides et al., 2017).

Ethical Note

Animals used in this study were part of the Cayo Santiago free-ranging population of rhesus macaques. All research procedures of this study were approved by the Caribbean Primate Research Center under the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico protocol number 4060105 and adhered to the standards set forth by applicable international, national and/or institutional guidelines for the care and use of animals.

Data Analysis

To analyse the individual characteristics of females and males (i.e. the mothers and fathers), and mother–father dyads that may affect the likelihood of an offspring being the product of within-group or extragroup paternity, we determined the following variables for each offspring.

Rank of the mother
Females are positioned in a linear hierarchy, in which female offspring are ranked immediately below the mother, with the hierarchy remaining quite stable throughout their lifetime (Kulik, Amici, Langos, & Widdig, 2015a; Vessey, 1984). This allowed us to determine the rank of each mother at any point in time (as described in Kulik, Amici, Langos, & Widdig, 2015b) by updating female ranks obtained from long-term observations with any changes resulting from births and deaths and standardizing the resulting ranks per day from 0 (lowest) to 1 (highest).

Age of the mother/father
We obtained the age of the mother and father by calculating the difference between the mother's/father's date of birth and the offspring's estimated conception date (see above).

Previous reproductive success of the father
For each father, we determined his previous reproductive success from the genetic database, measured as the number of offspring he had sired in the previous season in the group he resided in at the time he sired the respective offspring under consideration. Hence, sires with an equivalent of 0 either did not produce offspring in the previous season, or they produced offspring in the previous season in another group than the current group. The reasoning behind this was that we expected males previously unsuccessful in their group of residence to be more likely to seek alternative reproductive strategies (e.g. EGPs) than successful sires.

Tenure of the father
Males, in contrast to females, disperse to new social groups (Sade, 1972) at adolescence and acquire their rank through a queuing system (Dubuc et al., 2011). Given that there was no

systematic data collection that allowed the assignment of rank for all sires included in this study, we used male tenure as a proxy for the father's rank (Berard, 1999; Vessey, 1984). We only considered tenure as an adult (i.e. older than 1250 days) in the respective group to account for sires that had not yet dispersed or had dispersed before adulthood. Hence, tenure resulted in a measure for each individual male in their respective group at the time of conception of the respective offspring.

Father's natal status

For each sire we determined whether he still resided in his natal group at time of the conception of the respective offspring or not (1 or 0, respectively).

Parental relatedness

Using the extensive genetic database (see above), we reconstructed pedigrees of each mother and father up to and including their grandparents' generation and calculated dyadic relatedness coefficients (r) based upon each parental dyad's pedigree relationship. In line with the low degrees of inbreeding recorded for the study population (Widdig et al., 2017), the vast majority ($N = 1544$) of parental dyads were unrelated up to and including the grandparent generation (93.75%), while 103 offspring did have related parents ($r = 0.0625$: $N = 66$; $r = 0.125$: $N = 26$; $r = 0.25$: $N = 10$; $r = 0.5$: $N = 1$).

Relative time of conception

To obtain a measure of whether an offspring was conceived early or late in the respective mating season, we calculated the number of days elapsed between an offspring's estimated conception date (see above) and the onset of the mating season. We divided this value by the length of the mating season (i.e. time span between first and last conception) in the respective year to obtain a relative measure that was comparable across years.

Group variables

We further determined four variables related to the characteristics of the social groups (see details in Ruiz-Lambides et al., 2017). In brief, we measured 'female synchrony' as the total number of days in a conception window (i.e. 15 days, see above) divided by the number of unique dates on which at least one female was in oestrus (i.e. in her conception window) to obtain the proportion of all unique dates that fit into a single 15-day conception window. 'Group instability' was measured as the sum of tenure loss due to resident males dying or leaving the group and tenure gain due to immigrant males entering the group between the end of the previous mating season and the end of the current mating season. Breeding group sex ratio and breeding group size exclusively considered adult individuals, whereby sex ratio was expressed as the number of adult females divided by the number of adult males.

Statistical Analyses

We used a generalized linear mixed model (GLMM, Baayen, 2008) to assess the impact of various predictor variables on the propensity to produce EGP offspring. The model used individual offspring as data points, with offspring resulting from within-group paternity versus extragroup paternity as the binomial response variable, fitted with log link function. As fixed effects test predictors, we included the rank of the offspring's mother, age of each offspring's mother and father, and the father's previous reproductive success. We expected a potential change in reproductive strategy in response to previous success to be more likely in older

males than in younger males, which is why we also fitted the interaction between previous reproductive success and father's age. Furthermore, we included the father's tenure as a proxy for rank, and whether or not he was still residing in his natal group. For the parent dyad, we fitted the parents' relatedness coefficient. Finally, we included the time of conception relative to the length of the mating season (i.e. relative time of conception).

As fixed effects control variables we included all group characteristics that were identified in a previous study to influence the number of EGPs per social group (Ruiz-Lambides et al., 2017), that is, breeding group sex ratio, group size and their interaction as well as female synchrony and group instability. Control variables were included to accurately estimate the test predictors but were not the focus of the study. We therefore only briefly describe and interpret results of the control predictors.

Finally, we fitted as random effects the identity of an offspring's mother and father, birth group and birth season as well as the father's social group at the time of the offspring's conception. We also included random slopes of fixed effects that varied within the levels of a given random effect to obtain more reliable P values (Barr, Levy, Scheepers, & Tily, 2013). As fitting all possible random slopes led to convergence issues, we fitted only slopes that facilitated model convergence (i.e. the slopes of tenure of the father and group instability in mother's ID, relative time of conception within father's ID, age of the mother, age, tenure and previous reproductive success of the father and group instability within birth group, age and tenure of the father, relative time of conception, group instability and sex ratio within birth season, age of the mother, previous reproductive success of the father and relative time of conception within the father's social group). To ensure sufficient variation within all levels of the random effects and thus allow this procedure, we removed the only two offspring sired by males from one group (group CC) from the data set. As a result, we used 1647 data points (i.e. offspring) from 466 different mothers and 228 different fathers in the model.

To obtain comparable estimates and to facilitate model convergence, we z transformed all covariates to a mean of 0 and a standard deviation of 1. To achieve a more uniform distribution of skewed covariates, we also applied a square-root transformation to the age of the mother and father, tenure of the father, relative time of conception and group instability prior to z transformation. The model was fitted in R version 3.4.1 (R Core Team, 2017) using the package 'lme4' version 1.1–13 (Bates, Maechler, Bolker, & Walker, 2015) and the bobiqa optimizer for maximum likelihood estimates. We assessed model stability by removing one level of a random effect at a time, which indicated that the model estimates were affected by whether or not certain social groups (i.e. groups of residence) of the father (groups BB, V and X) were included in the model. Removal of fathers residing in these groups resulted in a stable model with comparable estimates for all test predictors, but remained unstable for one control predictor (group size), which accordingly should be interpreted with care. The subset model contained 1263 offspring from 315 different mothers and 161 different fathers and produced qualitatively similar results for all test predictors as the overall model on 1647 offspring. Due to the higher stability of the test predictor estimates in the subset model, we present the results of the subset model in the main text and provide the results of the overall model in the Appendix.

We calculated variance inflation factors (VIFs; Quinn & Keough, 2002) based on a standard linear model using the function 'vif' in the R package 'car' (Fox & Weisberg, 2011), which provided no indications of pronounced collinearity between predictors (largest VIF: 3.3). The model was underdispersed (dispersion parameter

0.282), indicating that our *P* value estimates were conservative. We determined the statistical significance of the full set of test predictors by comparing the fit of the full model with that of the null model lacking the test predictors, but comprising all other terms, with a likelihood ratio test (LRT, R function 'anova'; Dobson, 2002). We assessed the significance of the individual predictors with LRTs using the R function 'drop1'. To facilitate interpretation of main terms, the model was rerun without the nonsignificant interactions.

RESULTS

Overall, the full model significantly deviated from the null model (LRT: $\chi^2_{10} = 25.226$, $P = 0.005$), which indicates that the set of test predictors influenced the occurrence of EGPs. In contrast to our prediction, our results revealed that offspring sired by extragroup fathers were more likely conceived by higher-ranking females than by lower-ranking females (Table 1, Fig. 1), while we detected no influence of female age (Table 1).

Regarding attributes of fathers, our data suggested no significant effect of the father's age, his previous reproductive success (Table 1), or the interaction between the two (LRT of interaction: $\chi^2_1 = 1.798$, $P = 0.180$). Furthermore, neither male tenure nor whether males still resided in their natal groups at time of conception affected their propensity to sire EGP (Table 1).

Parents of EGP offspring were not more or less closely related than parents of within-group offspring (Table 1). Finally, in our study, rhesus macaques were less likely to produce EGP offspring the further the mating season progressed (Fig. 2).

Of the control predictors previously identified to influence frequencies of EGP per social group, neither sex ratio, female synchrony nor group instability affected the propensity of individual offspring to be the result of within-group or extragroup matings (Table 1). While our results suggest a positive effect of group size (Table 1), the model estimates fluctuated between positive and negative values for this predictor when certain groups were excluded and should be regarded with caution.

DISCUSSION

Our analysis covering several years and groups demonstrated that EGPs in rhesus macaques are affected by two main predictors,
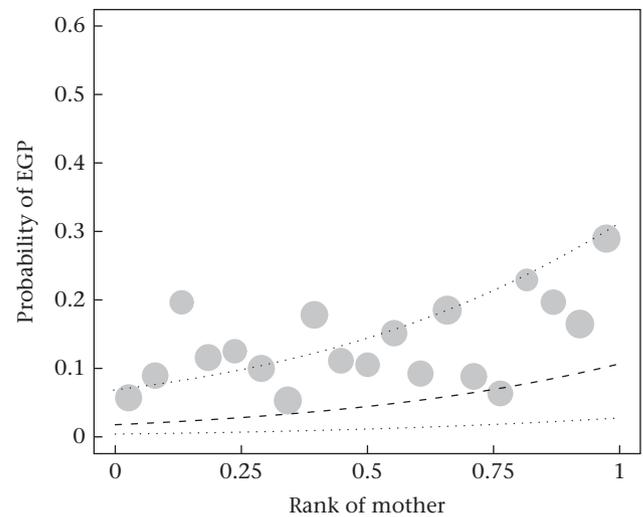
Figure 1. Probability of producing extragroup paternity (EGP) offspring as a function of the mother's rank (0 = low, 1 = high). Points show proportions of EGP offspring, with the rank of the mother grouped into 19 bins. The area of the points corresponds to the respective sample size (19–81 offspring per bin); the dashed line shows the fitted model conditional on the control predictors being at their average; the dotted lines show the confidence intervals of the model.

the mother's rank and the timing of reproduction relative to the onset of the mating season. We found no effect of other individual or dyadic characteristics of the parents.

Mothers of extragroup offspring being higher-ranking than mothers of within-group offspring was against our predictions. We had expected high-ranking females to be preferred mating partners and, therefore, to be less capable of pursuing mates outside of their group due to male aggression and coercion (Barrett, Shimizu, Bardi, Asaba, & Mori, 2002; Slater, Schaffner, & Aureli, 2008). However, our results may be partly explained by the higher amount of kin support that high-ranking females receive when defending themselves against male harassment (reviewed in Markham, Lonsdorf, Pusey, & Murray, 2015; Smuts & Smuts, 1993). Males may not attempt to force mating with these females, which may result in greater opportunities for higher-ranking females to pursue EGPs. Another possible explanation could be that rhesus males often

Table 1
Results of the GLMM examining the effects of parental attributes on the probability of producing extragroup offspring

	Estimate	SE	CI (2.5%)	CI (97.5%)	χ^2	*P*
Test predictors						
Intercept[a]	−3.147	0.729	−5.918	−1.636	—	—
Rank of mother	0.550	0.138	0.277	1.028	13.931	**<0.001**
Age of mother	−0.314	0.450	−1.347	0.597	0.460	0.498
Age of father	−0.107	0.212	−0.613	0.366	0.206	0.650
Reproductive success of father	−0.360	0.414	−1.249	0.429	0.678	0.410
Tenure of father	0.847	0.527	−0.195	2.391	2.063	0.151
Father natal	0.238	0.528	−0.960	1.422	0.138	0.711
Parental relatedness (*r*)	0.084	0.111	−0.243	0.330	0.442	0.506
Relative time of conception	−0.680	0.261	−1.378	−0.166	4.325	**0.038**
Control predictors						
Group size	−1.382	0.441	−3.107	−0.476	6.583	**0.010**
Sex ratio	0.091	0.251	−0.479	0.727	0.103	0.748
Female synchrony	−0.418	0.262	−1.126	0.129	1.919	0.166
Group instability	−0.443	0.421	−1.373	0.375	1.032	0.310

Identity of an offspring's mother, identity of father, birth group and birth season, as well as the father's social group were included as random effects with a random slopes structure as described in the main text. Values in bold indicate significant outcomes. The nonsignificant interactions for reproductive success∗male age and for group size∗sex ratio were removed from the model. All continuous predictors were *z* transformed to a mean of 0 and a standard deviation of 1; mean ± SD of the original variables were 0.497 ± 0.289 (rank of mother), 3423 ± 1625 days (age of mother), 3225 ± 1080 days (age of father), 1547 ± 1035 days (tenure of father) and 101.1 ± 35.2 days (relative time of conception).

[a] LRT results not shown for intercept as these have a very limited interpretation.
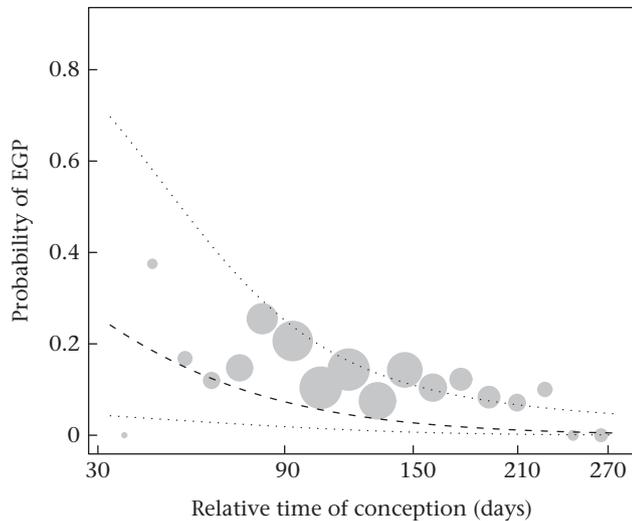
Figure 2. Probability of producing extragroup paternity (EGP) offspring as a function of conception day relative to mating season. Points show proportions of EGP offspring, with the conception day grouped into 18 bins. The area of the points corresponds to the respective sample size (2–206 offspring per bin); the dashed line shows the fitted model conditional on the control predictors being at their average; the dotted lines show the confidence intervals of the model.

consort females outside of the fertile period, while consorts cover only about half of the conception period (Dubuc et al., 2012). This suggests that males are unable to precisely determine conception, allowing females greater freedom to choose partners outside of their group. In this case, the prevalence of EGP in high-ranking females would be indicative of a greater preference, rather than different opportunities, for extragroup mating in high-ranking females than in low-ranking females. Along the same lines, the lack of a female age effect in our analysis would imply that young and old females had similar opportunities and preferences for EGP. A comparison of these patterns with other species is difficult because the relationship between individual characteristics and EGP appears to have been investigated mainly for males (see below). Dominant females have been reported to engage in EGP in cooperatively breeding meerkats, *Suricata suricatta* (Leclaire, Nielsen, Sharp, & Clutton-Brock, 2013), but rates of EGP were not compared between dominant and subordinate females.

In many avian species, older males are more successful at gaining extragroup offspring (Cleasby & Nakagawa, 2012), although this is not always the case (Mulder, Dunn, Cockburn, Lazenby-Cohen, & Howell, 1994). Also in the present study we did not to detect a significant relationship between EGP and male age as well as a male's previous reproductive success in his current group of residency or his natal status. The latter is noteworthy as a previous study on factors influencing natal dispersal found that more than two-thirds of the natal males that started reproducing before dispersal were observed to engage in EGPs (Weiß et al., 2016), suggesting that it might be a means for natal males to find unrelated females willing to mate with them. Similarly, EGP was more common in a population of Australian magpies, *Gymnorhina tibicen*, with low rates of juvenile dispersal than in a population with high dispersal rates (Durrant & Hughes, 2005). While neither of these two studies specifically compared rates of EGP between natal and dispersed individuals, natal female banded mongooses, *M. mungo*, indeed conceived more extragroup offspring than dispersing ones (Nichols, Cant, Hoffman, & Sanderson, 2014). In the present study, results suggest that engaging in EGPs is similarly beneficial in natal

and non-natal males, although we cannot exclude that incentives, such as inbreeding avoidance or reduced within-group mating opportunities, may differ.

Other male attributes previously associated with EGP include dominance rank, whereby subordinates were reported to more frequently sire extragroup young, for instance, in meerkats (Young, Spong, & Clutton-Brock, 2007). Similarly, we had predicted more EGPs in short-tenured (and, hence, typically subordinate) rhesus males because they are often (but not always) less successful in reproducing inside their social group (Berard, 1999). Our results, however, suggest no significant effect of tenure on EGP in rhesus males. Furthermore, the positive direction of the relationship between tenure and EGP more closely resembles the patterns described in various group-living bird species such as superb fairywrens, *Malurus cyaneus* (Dunn & Cockburn, 1999), and Seychelles warblers, *Acrocephalus sechellensis* (Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001), which has been attributed to females choosing high-quality and/or compatible extragroup mates (Dunn & Cockburn, 1999; Richardson, Komdeur, Burke, & Schantz, 2005). Also, rhesus females were repeatedly suggested to prefer novel mates to increase the genetic diversity of their offspring and avoid inbreeding (Berard, 1999; Bercovitch, 1997). Such a preference is supported by a previous study in the same population, which suggested that females in stable groups pursue more EGPs than females in groups with a larger flux of males to avoid males with whom they have shared long co-residency (Ruiz-Lambides et al., 2017). To further elucidate whether novelty and/or dominance rank affect the occurrence of EGPs in rhesus macaques, future studies should combine genetic and demographic data with behavioural observations of mating behaviour and male dominance relationships.

Inbreeding avoidance is being considered as one of the reasons for engaging in EGP (Pusey & Wolf, 1996). If individuals pursued EGP to optimize outbreeding we would expect lower relatedness among parents of extragroup offspring than of within-group offspring, which was not the case in the present study. This is likely owing to the low incidence of breeding among relatives in the study population, which indicates that inbreeding avoidance mechanisms effectively operate (Widdig et al., 2017). Furthermore, although rhesus groups contain close relatives, the average relatedness within groups is low in macaques (de Ruiter & Geffen, 1998) and the benefits of EGP have been suggested to be higher in groups with high within-group relatedness such as cooperatively breeding mammals (Nichols et al., 2015). For instance, in banded mongooses, extragroup mates were less related to the mother than withingroup mates, resulting in extragroup offspring being more heterozygous and more likely to survive (Nichols et al., 2015). Females further adjusted extragroup mating to the risk of inbreeding by engaging more in EGP in more related groups (Nichols et al., 2015). Similar to banded mongooses, dominant female meerkats engaged more in EGP the more genetically similar their social mate was, yet this did not result in extrapair mates being more distantly related to the females than their social mates (Leclaire et al., 2013).

In our study the relative time of conception within a given mating season was related to the likelihood of producing extragroup young, which was more frequent earlier in the season. Contrary to our prediction, this suggests that the timing of EGPs is not related to males becoming increasingly incapable of mate guarding fertile females over the course of an energetically costly breeding season (10% reduction in body weight in the study population, Bercovitch & Nürnberg, 1997). In a socially monogamous passerine, the wheatear, *Oenanthe oenanthe*, males pursued EGPs mainly at the beginning of the breeding season when their own

partner was not yet fertile and invested in mate guarding primarily later in the season (Currie, Burke, Whitney, & Thompson, 1998). We cannot assess whether this could also explain the observed pattern in group-living species such as rhesus macaques, as we lack comprehensive behavioural data on mate guarding over our long study period and are not aware of other studies that have addressed the relative timing of EGP in group-living species. Our results speak against the possibility that females seek out extragroup males later in the season if within-group mating did not result in a pregnancy or the pregnancy failed in its early stages. Rather, the early prevalence of EGPs in rhesus macaques may be related to dispersal patterns, as male group changes are biased towards the mating season (Lindburg, 1969) and males may accordingly roam in preparation for group changes particularly at the beginning of the mating season.

Finally, we incorporated into our analysis predictors previously reported to affect variation in the number of EGP across groups and seasons in the studied population (Ruiz-Lambides et al., 2017). EGP was more likely to occur in smaller groups, in which unfamiliar males are scarce, which supports the idea that EGPs may result from a female preference for novel mating partners (Berard, 1999; Bercovitch, 1997). While a certain instability in model estimates requires the result of group size to be treated with care, group size was also found to matter in an earlier study on group parameters affecting EGP (Ruiz-Lambides et al., 2017). In that study the effect of group size was dependent on the sex ratio, and the number of EGPs was further affected by group instability and female synchrony. We could not confirm the latter results in the present study, but response variables differed in the two studies and decisions of single individuals engaging in EGP may be based on different criteria than the patterns responsible for group means. Both studies, however, suggest, that the occurrence of EGPs is at least partly related to the opportunities and preferences of females to engage in EGP.

One of the challenges in our study was to define what is an EGP offspring. As we wanted to avoid attributing offspring conceived during a potential migratory event as EGP, we chose a conservative definition, which may have led to an underestimation of EGPs. As a result, overall rates of EGP were relatively low, but still well within the range of EGPs observed in other mammals, including primates (see Introduction). In combination with the complexity of the data set, our results can be considered as conservative, suggesting that the detected effects are rather robust (as also evidenced by replicating these findings in the less stable model), but effects with relatively large, albeit nonsignificant estimates, such as tenure, may warrant further investigation.

In conclusion, our data suggest that greater opportunities and/ or a stronger preference resulted in high-ranking females engaging in more EGPs, and that most EGP offspring were conceived at the beginning of the breeding season. As such, similar to birds (Kempenaers et al., 1992; Suter, Keiser, Feignoux, & Meyer, 2007) and other mammals (Cohas et al., 2006; Nichols et al., 2015), EGP in rhesus macaques could be affected by females choice of mates that increase the genetic diversity and quality of their offspring. Whether this is indeed the case should be investigated in future studies that assess the benefits of EGP by comparing genetic diversity as well as fitness of within-group and extragroup offspring.

Acknowledgments

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Appendix

Table A1
Results of the GLMM examining the effects of parental attributes on the likelihood of producing extragroup offspring

	Estimate	SE	χ^2	*P*
Test predictors				
Intercept[a]	−2.832	1.379	−	−
Rank of mother	0.336	0.105	8.958	**0.003**
Age of mother	−0.263	0.222	1.261	0.262
Age of father	−0.059	0.154	0.130	0.718
Reproductive success of father	−0.337	0.339	0.907	0.341
Tenure of father	0.571	0.388	1.829	0.176
Father natal	0.633	0.419	1.839	0.175
Parental relatedness (*r*)	0.087	0.087	0.919	0.338
Relative time of conception	−0.553	0.230	3.920	**0.048**
Control predictors				
Group size	−1.196	0.635	2.775	*0.096*
Sex ratio	0.233	0.185	1.205	0.272
Female synchrony	−0.535	0.219	3.655	*0.056*
Group instability	−0.265	0.365	0.504	0.478

The model was computed like the main model but is based on 1647 offspring. Identity of an offspring's mother, identity of father, birth group and birth season, as well as the father's social group were included as random effects with a random slopes structure as described in the main text. Values in bold indicate significant outcomes; values in italics denote trends. The nonsignificant interactions for reproductive success ∗ male age and for group size ∗ sex ratio were removed from the model. All continuous predictors were *z* transformed to a mean of 0 and a standard deviation of 1.

[a] LRT results not show for intercept as these have a very limited interpretation.