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Assessing Variance in Male Reproductive Skew Based on Long-Term Data in Free-Ranging Rhesus Macaques

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ABSTRACT

The unequal share in male reproduction (male reproductive skew) has been reported across primate species. To explain the distribution of male reproduction within groups various skew models have been applied to primates, however the “dynamic tug-of-war” model first accounted for the specifics of primate sociality. This model assumes that an increase in the number of competing males, a high degree of female cycle synchrony and their interaction will result in a lower degree of male reproductive skew. Here, we first tested the predictors of this model in rhesus macaques (*Macaca mulatta*) using long-term demographic and genetic data (up to 9 groups over 22 seasons) of the Cayo Santiago population (Puerto Rico). We also tested an extended version including group size and sex ratio and their interaction with female cycle synchrony. Finally, we investigated which male attributes determine the probability to become a top sire (highest paternity share per group and season). Confirming studies, male rhesus macaques exhibited low to medium degrees of reproductive skew based on the multinomial index, *M*. Unlike predicted, reproductive skew was higher in groups with more males. The extended analysis suggested that reproductive skew increased with group size in more male-biased groups, but decreased with group size in female-biased groups indicating that the numbers of male and female group members matter. We detected no effect of female cycle synchrony on the variance of reproductive skew. Finally, only maternal rank predicted the probability to become a top sire as long as males resided in their natal group. Together, our results did not support predictions by the dynamic skew model in rhesus macaques, but strengthen studies suggesting that other factors in addition to male-male competition predict male reproductive output in rhesus macaques. Future skew studies should consider female choice and alternative male mating strategies.

1 | Introduction

Reproductive skew describes the unequal distribution of reproductive success in an animal society (Keller and Reeve 1994) and has been reported in a variety of taxa ranging

from insects, to primates (e.g., Garnier, Bruford, and Goossens 2001; Engh 2002; Haydock and Koenig 2002; Sumner et al. 2002; Cerchio et al. 2005; Rossiter et al. 2006; Wikberg et al. 2017). In a high skew society, one or a few individuals monopolize reproduction, whereas in a low skew society a

Abbreviations: CI, confidence interval; df, degrees of freedom; EGP, extra-group paternity; FCS, female cycle synchrony; GLMM, Generalized Linear Mixed Model; LRT, likelihood ratio test; M index, multinomial index; N, sample size; SD, standard deviation; SE, standard error; VIF, variance inflation factors.

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Summary

- Using long-term data of the rhesus macaque population on Cayo Santiago we show that reproductive skew increased with group size in male-biased groups, while the opposite was true for female-biased groups.
- We detected no effect of female cycle synchrony on the variance of reproductive skew. Natal males with high-ranking mothers were more likely to become top sires.
- Our results support did not support existing skew models, but strengthen previous studies stressing that, in addition to male dominance, female mate choice and alternative male mating strategies may be important drivers of male fitness.

more even distribution in reproductive output is observed (Cant and Johnstone 2000).

Many primate species live in multi-male, multi-female groups year-round. The extent to which males can monopolize reproduction is generally limited by their access to fertile females, resulting in intra-sexual competition (Trivers 1972; Clutton-Brock 1988; Andersson 1994; van Hooff 2000). Depending upon the degree of direct male-male competition, male reproductive skew among primate species can vary from (nearly) complete male monopolization (or high skew) (e.g., crested macaques, *Macaca nigra*: Engelhardt et al. 2017) to a medium skew (e.g., rhesus macaques, *Macaca mulatta*: Widdig et al. 2004) or low skew (no or nearly zero) (e.g., northern muriqui, *Brachyteles hypoxanthus*: Strier et al. 2011). The distribution of male reproduction has important implications for primate societies (Van Schaik and Kappeler 1997; Kappeler and van Schaik 2002), as it affects the genetic kin structure within and between social groups (Widdig 2013).

Several theoretical models of reproductive skew have been formulated to explain drivers of reproductive skew (reviewed in Clutton-Brock 1998; Nonacs and Hager 2011). However, many of these original skew models were not developed for primate societies and hence make assumptions that are not met in multi-male, multi-female primate groups (Gogarten and Koenig 2012). For example, so-called *transactional models* make various of explicit assumptions; specifically they assume that dominants have complete control over reproduction or group membership (cf. Vehrencamp 1983; Keller and Reeve 1994). Large group sizes, high degrees of male-male competition and the ability of many female primates to reject male mating attempts, however, limit male control over reproduction (Port and Kappeler 2010). In contrast, *compromise models* (or “limited control” model) have fewer limitations in their application to primates as they do not assume complete control of reproduction by certain individuals (Cant 1998; Reeve, Emlen, and Keller 1998). One type of compromise model, the tug-of-war model, predicts that with an increasing number of male competitors, the dominant’s share of reproduction will decline, i.e. reproductive skew will decrease (Port and Kappeler 2010), but ignores that males may successfully reproduce without engaging in open conflict (Port and Cant 2014). Nonetheless, evidence for the tug-of-war model was found in several primate species, for example, Verreaux’s sifakas, *Propithecus verreauxi*

(Kappeler and Schaffler 2008), long-tailed macaques, *Macaca fascicularis* (Engelhardt et al. 2006), rhesus macaques, *M. mulatta* (Widdig et al. 2004), and mountain gorillas, *Gorilla beringei* (Bradley et al. 2005).

The priority-of-access model (Altmann 1962) is a conceptual forerunner of compromise models, which has fewer underlying assumptions than traditional reproductive skew models and generally applies better to primate societies, in particular to aspects of male-male competition. Evidence for this type of model was reported in mandrills, *Mandrillus sphinx* (Charpentier et al. 2005; Setchell, Charpentier, and Wickings 2005), yellow baboons, *Papio cynocephalus* (Alberts, Watts, and Altmann 2003) and chimpanzees, *Pan troglodytes*; (Boesch et al. 2006; Bray, Pusey, and Gilby 2016). This model assumes that increasing female cycle synchrony (i.e., several females of a group are simultaneously receptive) reduces the dominant’s ability to monopolize reproduction, thereby decreasing reproductive skew (Altmann 1962; Port and Kappeler 2010). An analysis of 19 primate species found that reproductive skew declined with increasing female reproductive synchrony (as predicted by the priority-of-access model) and number of males in a group (as predicted by the tug-of-war model), although female synchrony explained more of the variation in paternity distributions than the number of competing males (Ostner, Nunn, and Schülke 2008). Hence, prior studies suggested that female cycle synchrony and the number of male competitors are the two key variables to predict the unequal distribution of reproductive success in male primates. Accordingly, reproductive skew is expected to decrease (i) with increasing female cycle synchrony as an alpha male cannot mate-guard several females at the same time, increasing mating opportunities for other males and (ii) with increasing number of males in the group as it is likely difficult for a dominant male to control reproductive attempts of other males (Boesch et al. 2006; Gogarten and Koenig 2012; Ostner, Nunn, and Schülke 2008; Port and Kappeler 2010).

Yet, results from previous studies were inconsistent with regard to variables influencing the degree of reproductive skew. Some primate studies supported an influence of both female cycle synchrony and number of males (Gogarten and Koenig 2012; Ostner, Nunn, and Schülke 2008; Port and Kappeler 2010), while others found evidence for only one factor (Kutsukake and Nunn 2006). Consequently, Port and Cant (2014) developed a dynamic tug-of-war model which explicitly accounts for these two factors and assumed an interplay between intragroup conflict (i.e., number of competing males) and its effectiveness for gaining reproductive success (i.e., female cycle synchrony). Hence this new skew model synthesizes the priority of access model with the tug-of-war model (Port, Schülke, and Ostner 2018). To date, this model has not been tested with empirical data.

To better understand variance in male reproductive skew it further is important to understand which male attributes predict the probability of males to have the highest paternity share (i.e., become the “top sire”). Male dominance affects reproductive success in many primate species (e.g., Engelhardt et al. 2006, 2017; Ostner, Nunn, and Schülke 2008), but also attributes such as male age, tenure or social skills have been found to determine

male reproductive success (e.g., Pereira and Weiss 1991; Bercovitch et al. 2003; Widdig et al. 2004; Schülke et al. 2010; Kulik et al. 2012; Arseneau et al. 2015). However, previous studies on male reproductive patterns have been limited to one or few groups and/or seasons, such that they were potentially affected by individual idiosyncrasies and exceptions. With long-term field studies accumulating genetic data over several years or decades, it is now possible to test available reproductive skew models and drivers of male reproductive success on large data sets of free-ranging primate populations.

Furthermore, most previous studies used the binomial index (B index) to calculate reproductive skew (Nonacs 2003), which has recently been shown to be sensitive to, for example, variation in group size, age structure, mean reproductive output and sample size, making comparisons between groups, year or even species less reliable (Ross et al. 2020; Mouginot et al. 2023). Therefore, Ross et al. (2020) have introduced the multinomial index (M index) which overcomes these limitations. The authors also re-analyzed published comparative data on reproductive skew and demonstrated that important empirical findings could not be replicated due to the biases in previous skew measures. These recent advances should be considered by primatologists interested in analyzing reproductive skew. Importantly, given the mathematical similarity between them, the M index can be calculated from the B index and vice versa, making the application of the M index straightforward (compare Ross et al. 2020).

Rhesus macaque reproduction has been studied intensively on the Cayo Santiago population over several decades, making them a prime system for studying male reproductive sharing. Based on Nonacs' B index (Nonacs 2003), previous studies suggested evidence for the limited control model and a medium degree of male reproductive skew in rhesus macaques across several groups and years (Widdig et al. 2004; Dubuc et al. 2011). Male reproduction in this population was also skewed across lifetime, with some males being extremely successful (up to 47 offspring), while 17.4% of males reaching adulthood never sired a single offspring in their life (Dubuc, Ruiz-Lambides, and Widdig 2014). The degree of male reproductive success was influenced by male age and dominance (Bercovitch et al. 2003; Dubuc et al. 2011; Widdig et al. 2004), although dominance does not predict paternity as strongly as in other primate species (Widdig et al. 2004; Dubuc et al. 2011), suggesting that not only dominance contributes to male fitness outcomes. Furthermore, female rhesus macaques can resist male mating attempts, prefer males with short tenure and actively solicit mating from preferred males, suggesting that female mate choice influences male reproductive output (Chapais 1983b; Manson 1992; Bercovitch 1997).

The present study aimed at assessing the intraspecific variance in male reproductive skew in rhesus macaques living on the island of Cayo Santiago (Puerto Rico) using extensive genetic and demographic data encompassing more than 3000 offspring (i.e., successful events of male reproduction) from up to 9 groups over 22 seasons. Based on Port and Cant (2014), our first analysis focused on the interplay between the number of males and female cycle synchrony. Specifically, we predicted that the degree of female cycle synchrony will affect the extent to which the number of males in the group influences reproductive skew. A high female

cycle synchrony is expected to spread male-male competition over a larger number of fertile females, which should therefore result in a lower degree of monopolization by a single male and lower reproductive skew. Under such a scenario, we expected the variation in the number of males in the group (i.e. number of potential competitors) to only have a weak influence on the degree of male reproductive skew. Contrary, if female cycle synchrony is low, the contribution of male-male competition over a given female will be high and the number of males is predicted to affect skew more strongly (Port and Cant 2014).

We also extended the original dynamic tug-of-war model by testing an additional prediction that is in accordance with the logic of the original tug-of-war model (and aspects of the priority of access model). Specifically, we replaced the number of males by an interaction between group size and sex ratio as a measure that reflects both the numbers of males *and* females in a group. The reasoning for doing so was our expectation that the relationship between the number of males and female cycle synchrony may additionally be modified by the actual number of females (and, hence, overall group size). In particular, we predicted that a high female cycle synchrony would reduce reproductive skew more in groups with many females than in groups with few females. In contrast, if female cycle synchrony is low, we did not expect the number of females to affect the degree of male reproductive skew, as the number of simultaneously receptive females should remain low and male monopolization potential high.

Our second goal was to test which male attributes are important for becoming the most successful (i.e., the top) sire within a group in a given season. Previous studies on rhesus macaques have shown that, although high-ranking and prime age males (9–11 years old) were more likely to produce a higher number of offspring (Bercovitch et al. 2003; Widdig et al. 2004) than other males. However, alpha males were never reported to be the top sires (Widdig et al. 2004; Dubuc et al. 2011). Consequently, we examined the possible influence of individual male characteristics on the probability to become a top sire in a given group and season. This analysis focused on the impact of male age, rank and whether he was still in his natal group when siring offspring. By asking which type of males are the *most* successful sires within a group and season (rather than how many offspring males produce) we take a slightly different perspective and complement previous studies on male reproductive success and reproductive skew.

2 | Methods

2.1 | Study Species and Study Population

Rhesus macaques live in promiscuous multi-male, multi-female groups and are seasonal breeders (Lindburg 1983; Seth and Seth 1986; Southwick et al. 1996). Females form kin groups with whom they are closely associated throughout their life, while males disperse from their birth group around puberty and may change groups several times in their life (Drickamer and Vessey 1973; Colvin 1986). Contrasting other primate species (e.g., Palombit 2003; Beehner et al. 2005; Marty et al. 2017), the

dominance hierarchies among male rhesus macaques seem more stable over time, with males reaching alpha status through succession (i.e., only through departure or death of higher-ranking males) (Bercovitch 1992; Berard 1999, but see Maestriperi and Higham 2010). Hence, adult tenure may be a good proxy of male social dominance (see adult tenure below).

The study is based on data originating from a population of rhesus macaques living on Cayo Santiago (hereafter: CS), a 15.2 ha island located 1 km off the coast of Puerto Rico (USA), managed by the Caribbean Primate Research Center (CPRC). The population was founded in 1938 with 409 animals captured in India and transferred to CS (Carpenter 1942a, 1942b). Since then, no animal has been added to the population except through natural births. According to previous analyses, 14.4% infants born do not survive their first year of life (Widdig et al. 2017) and the population endures natural disasters (hurricanes and disease outbreaks). Furthermore, a variable number of animals have been removed using different culling strategies across years to control the population size (see Hernández-Pacheco et al. 2013 for details). Genetic analyses based on STR markers found only low incidences of inbreeding in this population, suggesting inbreeding avoidance (Widdig et al. 2017). The animals are maintained under semi-natural conditions for behavioral and life history research. The monkeys are partly provisioned with commercial monkey chow while foraging on natural vegetation for about 50% of their feeding time (Marriott, Roemer, and Sultana 1989). Medical treatment is restricted to a tetanus vaccination administered at the age of 1 (Kessler, Berard, and Rawlins 1988; Kessler et al. 2015). Each individual is marked with a unique tattoo and ear notch (Kessler, Rawlins, and Kaufman 1986).

Research conducted in this study was approved by the CPRC and the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol number 4060105). The transfer of samples for paternity analyses was approved by Cites Export permission #05US101361/9, #06US112079/9, #07US133766/9, #08US163309/9, #09US200870/9, #09US230435/9, #11US28371A/9 and Cites Import permission #E-1426/05, #E-1082/06, #E-1207/07, #E-1215/08, #E01146/09, #E-00049/10, #E-00836/11). All methods were performed in accordance with the relevant guidelines and regulations and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. This article does not contain any studies with human participants performed by any of the authors.

2.2 | Demographic Data

Demographic data of the CS population, collected continuously since 1956, form a powerful basis for long-term studies. Specifically, sex, date of birth, date and cause of death, maternity, maternal genealogy and group changes (dispersal) are noted within 2 days of occurrence in a demographic database (Ruiz-Lambides et al. 2017). The mating season usually lasts ~6 months (May–October), followed by a corresponding birth season of ~6 months (November–April) (Widdig et al. 2004), whereby the onset of the seasons gradually shifted forwards over the decades due to an earlier onset of the spring raining season (Hoffman et al. 2008). Births occur 166.5 ± 7.4 days

(mean \pm SD) after conception according to the average gestation length (Silk et al. 1993), with an average interval of 3.5 days between births (Widdig et al. 2004). Males can freely migrate between groups and leave their natal group at 4.9 ± 1.3 years (mean \pm SD) (Weiß et al. 2016). When an individual disperses, daily census takers record its new group and check this assignment regularly for at least 2 months. If group membership remained constant, the first day seen in the new group is defined as the date of immigration for a given individual. Males were assigned to only one group on a given day. It was not possible to record demographic data blind when, for example, determining group residency (because our study involved animals in the field), however, census takers were blind to data on male reproduction (genetic paternity data).

2.3 | Genetic Data

2.3.1 | General Information

Since 1992, genetic paternity analysis have been conducted on the population, mainly using blood samples, with an increasing proportion of animals sampled across years (> 50% of the population since 1993, > 75% since 1995, and > 83% since 2000, except for years with major hurricanes). Generally, all animals on the island at least 1 year of age and not previously sampled for paternity analysis are targeted during the annual trapping season. With 14.4% infants not surviving until the age of 1 (Widdig et al. 2017), we missed a proportion of infants born in our current analysis (see below). Furthermore, because a small proportion of adult individuals (mainly males) could not be sampled, we could also not assign paternities to all sampled infants. As maternity derived from behavioral data was genetically confirmed for nearly all subjects in the genetic data base (> 98%, details in Widdig et al. 2017), we were confident to use the behavioral mother in cases when we lacked a genetic sample of the behavioral mother. At the time of the our study, animals were genotyped for up to 43 microsatellite markers (27.6 ± 1.6 ; mean \pm SD) (details in Widdig et al. 2017).

2.3.2 | Paternity Criteria

Paternity was determined using a combination of exclusion and likelihood analyses. For the exclusion method we applied different rules. First, paternity may have been assigned to a male having no mismatches with a given offspring across all common loci while all other males mismatched the offspring at two or more loci (strict rule). Second, paternity may have been assigned to a male having no mismatches with a given offspring across all common loci while one or more males mismatched the offspring at one locus only (relaxed rule). The minimum number of common loci for a paternity assignment to be valid was 12 for a given mother-sire-offspring trio or 15 loci for sire-offspring dyads. All cases of paternity established via the exclusion method were additionally supported at a 95% confidence level by maximum likelihood using Cervus 3.0 (Kalinowski, Taper, and Marshall 2007) (more details in Widdig et al. 2017).

Given than an average of 16% of offspring resulted from extra-group paternities (see Ruiz-Lambides et al. 2017, 2018 for

detailed studies), all mature males on the island were considered as potential sires if they fulfilled two conservative criteria: (i) males had to be alive at least 1 month before the conception of a given infant counting back 200 days from its date of birth, following a gestation length estimate of 166.5 ± 7.4 (Silk et al. 1993), and (ii) males had to be older than 1250 days of age on the birth date of the respective infant, based on the youngest age at male reproduction observed (Bercovitch et al. 2003).

2.4 | Data Sets

The demographic and genetic data included in the present study covered a range of up to 22 years (from 1993 until 2014) and up to 9 groups which were naturally formed (BB, CC, F, HH, KK, MM, R, S, and V). The number of adult males and females varied across groups and years (mean \pm SD, adult males = 36.12 ± 21.25 , adult females = 45.02 ± 29.97 , see Supplement 1, Table S2 for details) which is comparable to wild populations as they can vary between 10 and 125 individuals (Seth and Seth 1986; Southwick et al. 1996).

For the present study we focused on offspring born between 1993 and 2014 in the relevant groups ($N = 5075$ offspring identified from census records). To avoid a bias in the skew analysis when only a limited number of paternities were solved, we decided to include only groups and years with sufficient paternity data, that is, if (a) we were able to establish paternity for at least 75% of infants born in a given season and if (b) at least five offspring with known paternity were available (see Supplement 1, Table S1 for overview prior selection). This resulted in a selection of 102 group-year combinations (see Supplement 1, Table S2 for final selection). Within these groups and years, a total of 3794 offspring were born according to census records. We were not able to sample 539 of these offspring (14.21%), which were all babies (except two) who died before sampling at 1 year of age. Correspondingly, from 3255 offspring in our selection we had a corresponding sample. Of those we did not solve paternity for only 23 offspring (0.71%), as these cases did not fulfill our paternity assignment criteria (see above). For example, in some cases we were able to produce genotypes for less than 6 markers, in others, the best potential candidate had more than 1 mismatches indicating that the actual father was probably not sampled (see details in Widdig et al. 2017). In sum, from offspring with a sample available ($N = 3255$), we were able to assign paternity for 3232 offspring (99.29%).

In a second step, we explored male attributes to become a top sire or not. Top sires were group males with the highest proportion of offspring sired in a given group and year. This analysis was based on the same 102 group-year combinations, but additionally included all potential sires in the respective group and year. Hence, it incorporated 3684 reproductive events (i.e., group-year-sire combinations or data points) scoring for each of all 611 potential sires whether he was the top sire in his group of residency in the respective year or not. In several years and groups we found more than one top sire ($N_{KK2001} = 4$;

$N_{KK2005} = 4$; $N_{V2006} = 2$; $N_{F2008} = 2$; $N_{S2008} = 2$; $N_{R2009} = 2$; $N_{S2009} = 3$; $N_{F2010} = 2$; $N_{HH2011} = 2$; $N_{V2011} = 2$; $N_{KK2012} = 2$), hence more than one male was considered as top sire in our analysis. In 13 of the 102 group-year combinations, the top sire was an extra-group male (i.e., not resident to the respective group, see details on how we measured extra-group paternities below). Since our analyses focused the attributes of within-group males to become a top sires, and to be conservative, top sires being extra-group male were excluded from the data set and none of the within-group males was assigned the top sire status. In consequence, the second data set comprised 105 top sires.

3 | Statistical Analysis

To assess the variation in male reproductive skew and predictors for becoming a top sire, we determined several variables per group and year, described in brief below and in detail in Supplement 2.

3.1 | Multinomial index

We used the multinomial index (M index) to calculate reproductive skew which was shown to be unaffected by many structural biases affecting other skew indices (Ross et al. 2020). The M index can take positive or negative values, whereby $M > 0$ implies that reproduction is positively skewed toward certain individuals (i.e., less equally distributed than expected by chance), $M = 0$ that reproduction is randomly distributed, and $M < 0$ that reproduction is shared more equally than expected by chance (Ross et al. 2020). We calculated M separately for each breeding year ($N = 22$) and group ($N = 9$) using the R package SkewCalc 1.0 (Ross and Hooper 2019).

3.2 | Female Cycle Synchrony

We have no detailed hormone data to assess female cycle synchrony (hereafter: FCS) for the entire study period and therefore estimated FCS per group and year based on records of live-births. For each birth we defined a 15 day conception window by subtracting the mean gestation length of 167 ± 7 days (Silk et al. 1993) from the birth day. We further determined the number of unique dates on which at least one female in a given group and season was in her conception window. The total length of a conception window (i.e., 15 days) was then divided by the total number of unique dates in a given group and season, resulting in an index for FCS between 0 and 1 (for more details and an illustrated example, see Supplement 2 and Figure S1 therein). In our data set, conceptions were neither fully synchronized nor unsynchronized, with a mean $FCS \pm SD$ of 0.14 ± 0.06 and a range from 0.07 to 0.6.

3.3 | Extra-Group Paternity

An extra-group paternity (EGP) rate was calculated for each group and year by dividing the number of offspring sired by a

male not present in the offspring's birth group during the 15 days of the estimated conception window through the total number of offspring in the respective group and year. In our data set, EGP rates varied between values of 0 and 1 with a mean \pm SD of 0.31 ± 0.27 . EGP rates were included in both the skew and top sire analysis.

3.4 | Adult Tenure and Maternal Rank as Proxy for Male Dominance Rank

We had no sufficient observational data to compute male rank for the entire study period and therefore used two proxies instead: (i) adult male group tenure and (ii) maternal rank. As longer tenure is highly predictive of higher male dominance (Drickamer and Vessey 1973; Vessey 1984; Vessey and Meikle 1987; Berard 1999) we counted the total number of days any adult male had resided in a respective group before the onset of a given mating season. The average male tenure in our samples was 616.8 ± 779.1 days (mean \pm SD).

As rhesus infants rank directly below their mothers (Datta 1988), maternal rank is a suitable proxy for male dominance rank before their natal dispersal (Kulik et al. 2015). We therefore computed maternal ranks (ranging from 0 to 1) for all males from ranks of their corresponding mother recorded during previous studies that were updated using an R-script written by L. Kulik. Average maternal rank for males was 0.58 ± 0.25 (mean \pm SD).

3.5 | Further Predictors

For each selected group and year we determined (i) the total group size (mean \pm SD 81 ± 49.5), (ii) the number of adult males (mean \pm SD 36 ± 21), (iii) the number of adult females (mean \pm SD 45 ± 30), (iv) the number of offspring born (mean \pm SD 37 ± 24.5) and the operational sex ratio (by dividing the number of females by the number of males, mean \pm SD 1.28 ± 0.39).

For the top sire analysis we additionally scored for each adult male (i) whether he was natal in a given group and year or not (hereafter: natal status), (ii) the proportional presence in a social group during a given mating season (hereafter: presence, mean \pm SD 0.75 ± 0.32) and male age in days (mean \pm SD 3151.3 ± 1956.7 days).

3.6 | Testing Variance in Reproductive Skew

We used General Linear Mixed Models (GLMM) (Baayen 2008) to test whether male reproductive skew was influenced (i) by the number of males, FCS or the combination thereof (as in the original Port and Cant model) in the given groups and years or (ii) by group size, sex ratio and/or FCS (our extension of the Port and Cant model). In both models, the M index (computed per group and season) served as the response variable and was sqrt-transformed to fit the assumptions of a Gaussian error structure.

3.6.1 | Testing the Original Port and Cant Model

In the first model, two predictors, number of males and FCS, and their interaction were incorporated as fixed effects test predictors as predicted by Port and Cant (2014). To control for a potential influence of EGPs, the proportion of EGP per group and season was included as another fixed effect. Furthermore, we controlled for an effect of group size. As group size was strongly correlated with the number of males, it could not be fitted directly and was instead incorporated indirectly by including the interaction between the number of males and the sex ratio (with low numbers of males and male-biased sex ratio representing the smallest, and high numbers of males and female-biased sex ratio the largest groups). To account for repeated measures of season and group ID, these terms were included as random intercepts. We initially included all possible random slopes to keep Type I error rates at the nominal level of 5%, but excluded random correlations, as their inclusion would have resulted in the number of random effects (154) exceeding the number of observations (102) (Schielzeth and Forstmeier 2009; Barr et al. 2013). As the model did not converge when including random slopes, we ran the model with the fixed effects and random intercepts described above, but without any random slopes, and subsequently included only the random slopes of predictors that were significant in the model without random slopes.

3.6.2 | Testing Our Extension of the Port and Cant Model

The second model was our extension of the original prediction by Port and Cant (2014). As outlined in the introduction, the model was motivated by our expectation that the relationship between the number of males and FCS may additionally be modified by the actual *number of females* (and, hence, overall group size). To address this prediction, the first model (comprising the number of males and FCS) therefore had to be expanded by an additional term that reflects the number of females, and by a three-way interaction that reflects the potential interplay between the three terms. However, the numbers of males and females were collinear and could not be fitted together. We therefore included these terms indirectly by fitting group size, sex ratio and their interaction instead. We thus addressed the predictions of the extended Port and Cant model with a three-way interaction between group size, sex ratio and FCS. Our model also included the three corresponding two-way interactions between group size, sex ratio, and female cycle synchrony as well as their main terms to achieve a valid model (Aiken and West 1991). All other variables were the same as in the first model but including only random slopes of significant predictors due to convergence issues.

All test and control predictors were checked with regard to their distribution and transformed if necessary. To ensure a symmetrical distribution, EGP, FCS and sex ratio were log-transformed. In addition, all continuous predictors were z-transformed to a mean of zero and a standard deviation of one to simplify the interpretation and facilitate model convergence (Schielzeth 2010).

Model fitting was done using the statistics software R (version 4.1.1; R Core Team 2021) and the function “lmer” of the package “lme4” (version 1.1.-27.1; Bates et al. 2015). To check whether the assumptions of normally distributed and homogeneous residuals were met, a visual inspection of a qq-plot and the fitted values against residuals was obtained. Both checks indicated no severe deviation from the assumptions. Model stability was assessed by excluding data points (i.e., a single group in a given year) one at a time from the data and comparing the model estimates derived for these data with those derived for the full data set. These checks did not reveal any influential groups or years. Variance inflation factors (VIF) were calculated using the function “vif” from the package “car” (Field 2005; Fox and Weisberg 2011) to detect potential collinearity issues between predictors. The results did not indicate any collinearity issues (all VIFs < 2.07).

A likelihood ratio test (LRT) was used to assess the significance of the full model compared to the null model (lacking all test predictor variables) using the function “anova” with argument test set to “Chisq” (Dobson 2002; Forstmeier and Schielzeth 2011). The models were fitted using Maximum Likelihood rather than Restricted Maximum Likelihood, to allow for a LRT (Bolker et al. 2009). Individual predictors were further investigated only if the comparison between the full and the respective null model revealed significance ($p < 0.05$) or a trend ($p < 0.07$). Confidence intervals were computed with the function “confint.merMod” of the package “lme4” using 1000 parametric bootstraps. The data used (including predictor variables) for the skew analyses can be found in the Supplement 3.

3.7 | Testing Male Attributes to Become a Top Sire

To analyze the effects of individual male attributes on the probability to become a top sire or not, a logistic GLMM was performed with binomial error structure and “logit link” function (Baayen 2008). We included the male attributes age (in days), adult tenure (in days), maternal rank and natal status as fixed effects test predictors in this model. As high maternal rank was previously found to increase the probability of natal males to sire offspring (Weiß et al. 2016), we tested whether the probability to become a top sire depended on maternal rank conditional on natal status within a given group and year. Hence, we also included the interaction between maternal rank and natal status as fixed effects test predictor. The proportion of days each male spent in a group in the respective mating season (“presence”), the rates of EGP, FCS, the number of males in a given social group, the sex ratio as well as the interaction between sex ratio and number of males (reflecting group size) were included as fixed effects control predictors. Furthermore, season, group and male ID were incorporated as random intercepts together with male birth year to account for potential cohort effects. To keep Type I error rate at a nominal level of 5%, all possible random slopes as well as the correlations between random slopes and intercepts were initially included in the model (Schielzeth and Forstmeier 2009; Barr et al. 2013). As this model did not converge, we removed all random slopes and random correlations, and subsequently re-entered only random slopes of significant

test predictors. To facilitate model convergence, we also removed the random intercepts of season and group, which exhibited no measurable variance (i.e., were zero). In consequence, the model was finally fitted with the fixed effects predictors described above, random intercepts of male ID and male birth year as well as the random slope of natal status*maternal rank within male birth year.

The distributions of all test and control predictors were checked visually and transformed if necessary. To ensure a symmetrical distribution, age, EGP and FCS were log-transformed, while presence was square root-transformed. In addition, all predictors were z-transformed to a mean of zero and a standard deviation of one to be more easily interpretable and to facilitate model convergence (Schielzeth 2010).

The model was implemented in R (version 4.0.2; R Core Team 2020) using the function “glmer” of the package “lme4” (version 1.1-23) (Bates et al. 2015). The model was slightly underdispersed (dispersion parameter = 0.803), indicating that our p value estimates were likely conservative. Model stability and VIFs were obtained as in the first models and did not indicate any stability or collinearity issues (all VIFs < 1.91).

The significance of the full model as compared to the respective null model lacking the test predictors male age, adult tenure, maternal rank, natal status and the interaction between the latter two was tested as in the first models using a LRT (see above). p values for the individual predictors and interactions were obtained through a LRT using the function “drop1” only if the full-null model comparison was significant or a trend. Nonsignificant interactions were removed from the model to facilitate interpretation of lower-order terms. Confidence intervals were obtained using the function “bootMer” of the package “lme4” using 1000 parametric bootstraps including bootstrapping over the random effects (argument “use.u” set to TRUE). The data used (including predictor variables) for the top sire analyses can be found in the Supplement 4.

4 | Results

4.1 | Multinomial Skew Index

Across years and groups, the M index of reproductive skew varied from 0.1 (year 2005, group KK) to 6.59 (year 1996, group R), with an average annual skew of 1.85 ± 1.22 (mean \pm SD; Table 1).

4.2 | Variance in Reproductive Skew

In Model 1, which tested the two key variables number of males and FCS as well as their interaction, the test predictors had a significant effect on the degree of reproductive skew in a given group and year (LRT, $\chi^2 = 17.822$, $df = 4$, $p = 0.001$). In particular, reproductive skew significantly increased with the number of males in the group (Figure 1; Table 2). However, we detected no effect of female cycle synchrony on the variance in reproductive skew, neither in interaction with the number of males nor as a single term (Table 2).

TABLE 1 | Degree of skew over groups and years based on M index (Ross et al. 2020).

Group	N_{years}	M_{min}	M_{max}	Annual mean M
BB	5	0.272 (1998)	1.718 (2000)	0.970
CC	6	1.258 (2001)	2.565 (2000)	1.649
F	17	1.031 (1997)	2.719 (2005)	2.007
HH	11	0.239 (2006)	5.141 (2012)	2.132
KK	11	0.096 (2005)	1.463 (2012)	0.844
MM	2	1.264 (2013)	1.427 (2014)	1.345
R	20	1.229 (2007)	6.594 (1996)	2.749
S	18	0.365 (1997)	3.769 (1993)	1.488
V	12	0.461 (2006)	5.819 (2014)	1.903

Note: The table presents the groups, the number of years each group was considered in the analysis (N_{years}), the minimum and maximum M values observed (M_{min} or M_{max}) and the annual mean M index per group. The respective years in which the minimum or maximum M values occurred are shown in parentheses.

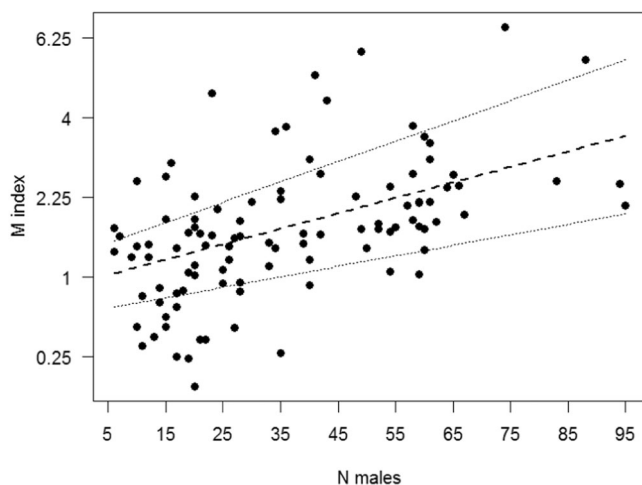


FIGURE 1 | Reproductive skew (M index) as a function of the number of males in a given group and year. Dashed lines depict the fitted model and dotted lines 95% confidence limits, conditional on the other predictors being at their average.

Also in the extended version of the model, which tested the effects of FCS, group size and sex ratio and their interactions, the test predictors significantly affected the degree of reproductive skew (LRT, $\chi^2 = 38.908$, $df = 7$, $p < 0.001$). This model indicated that reproductive skew was affected by the interplay between group size and sex ratio, whereby skew increased with group size in more male-biased groups while it decreased with group size in more female-biased groups. In other words, sex ratio had no apparent effect on reproductive skew in small groups while skew decreased with an increasing proportion of females in larger groups (Figure 2; Table 3). Similar to Model 1, we detected no effect of female cycle synchrony on the variance in reproductive skew neither in interaction with the other predictors nor as a single term (Table 3).

4.3 | Top Sire

Overall, the set of test predictors had a clear influence on the probability to be a top sire or not (LRT: $\chi^2 = 26.192$, $df = 5$, $p < 0.001$). In particular, the interaction between a male's natal

status and his mother's rank had an impact on his probability to be a top sire (Table 4; Figure 3). More specifically, the higher the maternal rank of a male was, the higher was his probability to become a top sire, but this was primarily the case for males still residing in their natal group (Table 4; Figure 3). Age and adult tenure of males in a given year did not affect the probability to become a top sire (Table 4).

5 | Discussion

Using one of the most comprehensive data sets available for free-ranging nonhuman primates, this study investigated factors contributing to intraspecific variation in reproductive skew and becoming the top sire in a strictly seasonal species, the rhesus macaques. Our analyses suggest that male reproductive skew increased with the number of group males, which is contrary to the prediction arising from the dynamic skew model by Port and Cant (2014). Our extended analysis additionally revealed that the degree of reproductive skew was not so much affected by the number of males per se, but by the interplay between sex ratio and group size and thus, by the number of males and females. Furthermore, we detected no effect of female cycle synchrony on male reproductive skew in either of our analyses, further contrasting the model predictions by Port and Cant (2014). Finally, maternal rank seemed to be a major factor determining the probability to become a top sire in our study population, but only for males still living in their birth group, while male tenure (as proxy for male dominance irrespective of maternal rank) did not influence the probability to become a top sire.

5.1 | Variance in Reproductive Skew

Previous reports about the role of FCS on reproductive skew were inconsistent both on an inter-specific and on an intra-specific level. For instance, a comparative analysis of reproductive skew on 19 primate species (including rhesus macaques) showed that female reproductive synchrony explained the variation in paternity distributions well (Ostner, Nunn, and Schülke 2008), while another analysis on mating skew across 31 primate species (again including rhesus

TABLE 2 | Results of the GLMM (Model 1: original Port and Cant model) testing the two-way interaction between FCS and number of males on the variance of male reproductive skew.

Term	Estimate	SE	Lower CI	Upper CI	χ^2	<i>p</i>
Intercept	1.313	0.059	1.142	1.429	^a	^a
FCS	-0.001	0.041	-0.117	0.105	0.001	0.977
n males	0.206	0.075	0.050	0.331	6.698	0.010
FCS:n males	-0.005	0.043	-0.094	0.082	0.014	0.906
EGP	-0.059	0.041	-0.138	0.033	1.941	0.164
Sex ratio	-0.092	0.058	-0.207	-0.053	2.062	0.151
n males:sex ratio	-0.085	0.041	-0.146	-0.017	2.817	0.093

Note: The table shows the fixed effects test and control predictors with their estimated coefficients (estimate), standard errors (SE) and 95% confidence intervals (lower CI, upper CI) as well as χ^2 and *p* values of LRTs conducted on the final model (i.e., excluding nonsignificant interactions and including random slopes of significant predictors). Values for the dropped interactions FCS:n males and n males:sex ratio (in gray) were taken from a model before their exclusion. "n males" indicates number of males. Bold values indicate statistically significant effects.

^aNot presented because of having a very limited interpretation.

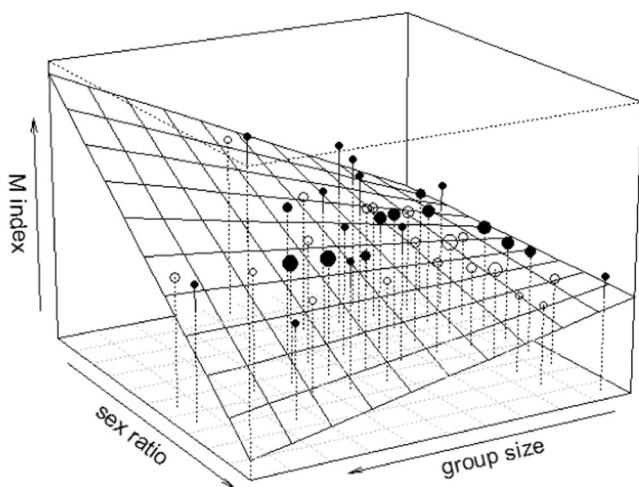


FIGURE 2 | Reproductive skew (M index) as a function of group size and sex ratio. Group size ranges from 17 to 228 (mean 81.1) and sex ratio from 0.53 (male-biased) to 3.17 (female-biased). The plane depicts the fitted model conditional on the other predictors being at their average, circles in black show data points above and unfilled circles data points below the model plane. The area of the circles corresponds to the respective sample size per grid cell (range 1–7).

macaques) could not find an association between FCS and male mating skew (Kutsukake and Nunn 2006). At an intraspecific level, FCS was found to affect male reproductive skew in chimpanzees (Boesch et al. 2006) and mandrills (Setchell, Charpentier, and Wickings 2005), but not in capuchin monkeys (*Cebus capucinus imitator*) (Wikberg et al. 2017). One likely reason for these differences may be different methodological approaches used for computing FCS. For instance, due to a lack of corresponding hormonal data, Ostner, Nunn, and Schülke (2008) used reproductive seasonality (i.e., duration of birth season) as proxy for reproductive synchrony, assuming that females will overlap more when breeding seasons are shorter, while Kutsukake and Nunn (2006) additionally used duration of estrus as well as three measures of estrus overlap. In our present study we used birth dates to approximate FCS, as we also lack hormonal data over the entire range of our study period. Future studies on male reproductive skew should ideally include hormonal data to assess FCS.

Differences between species might further be related to how well males can assess which females are fertile or not based on external cues of fertility such as anogenital swellings. In various species of catarrhine primates, the maximal swelling size is typically associated with the most fertile period, although this relationship is weak in some species (Street, Cross, and Brown 2016). Rhesus macaque females lack such swellings, but their facial coloration changes across their cycle (Dubuc et al. 2009) and may represent a possible signal for males to detect the fertile phase. However, high-ranking males tended to prolong mate-guarding into the luteal phase with null probability of fertilization (Dubuc et al. 2012), suggesting that male rhesus macaques may not have precise information about female ovulation. This lack of information opens the opportunities for alternative male mating strategies as well as female mate choice (Dubuc et al. 2012), as also suggested in Assamese macaques, *M. assamensis* (Fürtbauer et al. 2011a, 2011b). If males are unable to precisely detect female cycle stage, it does not seem surprising that FCS does not have an effect on male reproductive skew. Accordingly, male ability to detect female cycle stages might be an important factor explaining differences in the relationship between FCS and male reproductive skew across primate species.

Most studies examining inter- and intraspecific variation of reproductive skew in primates found strong evidence that the number of males in a group predicts the degree of male reproductive skew. Typically, an increasing number of male competitors decreased the degree of mating or reproductive skew (e.g., Boesch et al. 2006; Ostner, Nunn, and Schülke 2008; Bray, Pusey, and Gilby 2016). This was explained by a lower ability of dominant males to monopolize reproduction when the number of competitors is high. In contrast, our study found that an increasing numbers of group males increased the degree of male reproductive skew. At first glance, our results are in line with previous studies in our study population showing that an increasing number of group males leads to an increase in male reproductive skew (tabs. 1 and 2 in Widdig et al. 2004). Importantly, our results of the extended model put the effect of the number of males, as tested in the first model, into perspective: skew was affected by the interplay between group size and sex ratio, and thus, in fact, by the number of males and the number

TABLE 3 | Results of the GLMM (Model 2: our extension of the Port and Cant model) testing the three-way interaction between FCS, sex ratio and group size on the variance of male reproductive skew.

Term	Estimate	SE	Lower CI	Upper CI	χ^2	<i>p</i>
Intercept	1.308	0.053	1.169	1.459	a	a
FCS	-0.012	0.041	-0.107	0.130	0.081	0.776
Group size	0.204	0.060	0.070	0.361	a	a
Sex ratio	-0.199	0.050	-0.375	-0.154	a	a
FCS:group size	-0.023	0.042	-0.090	0.116	0.277	0.599
FCS:sex ratio	-0.026	0.048	-0.254	0.050	0.290	0.590
Group size:sex ratio	-0.155	0.050	-0.382	-0.099	5.905	0.015
FCS:group size:sex ratio	-0.082	0.062	-0.205	0.045	1.630	0.202
EGP	-0.051	0.040	-0.130	0.038	1.488	0.222

Note: The table shows the fixed effects test and control predictors with their estimated coefficients (estimate), standard errors (SE) and 95% confidence intervals (lower CI, upper CI) as well as χ^2 and *p* values of LRTs conducted on the final model (i.e., excluding nonsignificant interactions and including random slopes of significant predictors). Values for the dropped interactions FCS:group size:sex ratio, FCS:group size and FCS:sex ratio (in gray) were taken from a model before their exclusion. Bold values indicate statistically significant effects.

^aNot presented because of having a very limited interpretation.

TABLE 4 | Results of the GLMM (Model 3) testing the effects of male attributes on the probability to be a top sire or not.

Term	Estimate	SE	Lower CI	Upper CI	χ^2	<i>p</i>
Intercept	-4.227	0.265	-5.327	-3.886	a	a
Male age	-0.056	0.149	-0.370	0.232	0.139	0.709
Tenure	0.106	0.137	-0.158	0.398	0.594	0.441
Natal status	-1.032	0.492	-2.396	-0.240	b	b
Maternal rank	0.202	0.141	-0.098	0.522	b	b
natal status:mat. rank	1.275	0.397	0.618	2.278	13.154	< 0.001
Presence	0.676	0.167	0.409	1.120	21.557	< 0.001
EGP	-0.004	0.111	-0.235	0.231	0.001	0.973
FCS	0.165	0.112	-0.087	0.387	2.051	0.152
n males	-0.526	0.162	-0.910	-0.224	11.158	0.001
Sex ratio	-0.017	0.106	-0.247	0.180	0.026	0.871
n males:sex ratio	0.019	0.102			0.036	0.849

Note: The table shows the fixed effects test and control predictors with their estimated coefficients (estimate), standard errors (SE) and 95% confidence intervals (lower CI, upper CI) as well as χ^2 values and *p* values of LRTs conducted after dropping the nonsignificant interaction n males:sex ratio (in gray) from the model. "mat. rank" indicates maternal rank. Bold values indicate statistically significant effects.

^aNot presented because of having a very limited interpretation.

^bValues not shown because there is no meaningful interpretation of terms part of an interaction.

of females. In groups with more males than females, male reproductive skew increased with group size, while it decreased with group size in groups containing more females than males. Interpreted from a different perspective, sex ratio did not affect male skew in small groups while skew decreased with an increasing proportion of females in larger groups. In other words, male reproductive skew is affected by the number of males in the group, but the patterns are actually more complex than previously suggested and depend on both, the absolute and relative numbers of males *and* females in the group. Notable, the proportion of EGP was relatively high (about 30%) in our data set. Based on the results of previous studies on EGP in our study population (Ruiz-Lambides et al. 2017, 2018), we therefore included the rate of EGP as control predictor in both skew models. However, EGP rates shown no effect on the magnitude of male reproductive skew.

Overall, the intraspecific variance of male reproductive skew in rhesus macaques cannot be explained by the predictions of the dynamic tug-of-war model or an extended version thereof. Comparative studies should explore whether the dynamic skew model is better supported in primate species in which male dominance strictly determines male reproduction, and also consider how male ability to detect female cycle stage, female mate choice and alternative male mating strategies contribute to the variance in male reproductive skew.

5.2 | Male Reproductive Success (Top Sire)

Maternal rank and natal status had a combined impact on the probability to become a top sire in a given group and year. The probability of a male to be a top sire increased with higher

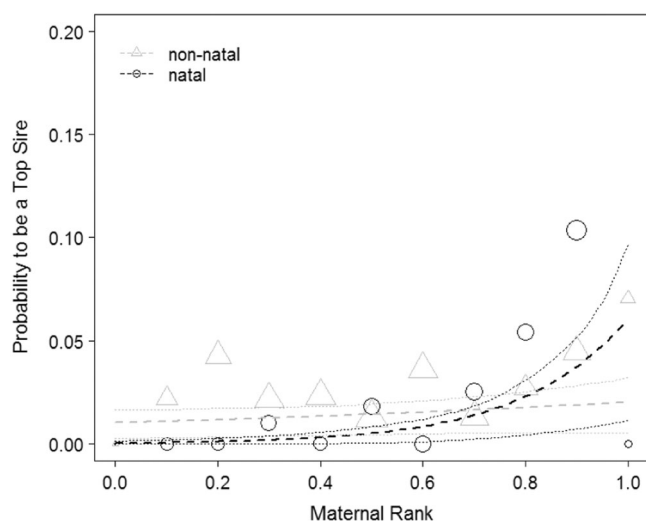


FIGURE 3 | Probability to become a top sire as a function of maternal rank (from 0 = low to 1 = high), conditional on whether a male was natal in a group he sired offspring in or not. Circles and triangles show proportions of males being a top sire with maternal rank values binned into 10 sections (black circles for natal males, gray triangles for non-natal males). The area of the circles/triangles corresponds to the respective sample size (natal males: 0 to 475 males per bin, non-natal males: 1 to 473). Lines depict the fitted model (dashed black for natal males, dashed gray for non-natal males) and 95% confidence limits (dotted black for natal males, dotted gray for non-natal males) conditional on the other predictors being at their average.

maternal rank, but only if the respective male was still natal in the group he sired offspring in. As in many other primate species, rhesus macaque infants rank directly below their mothers (Datta 1988). High-ranking mothers may thus positively affect infant growth (yellow baboons: Altmann and Altmann 2005; chimpanzees: Samuni et al. 2020) or sexual maturation of their sons (rhesus macaques: Bercovitch 1993; Dixson and Nevison 1997; yellow baboons: Altmann and Altmann 1995a, 1995b), attainment of adult dominance rank (yellow baboons: Altmann and Altmann 1995a) or reduce their sons' stress levels (yellow baboons: Onyango et al. 2008). Primate mothers may even affect their adult offspring fitness. For example, the presence of bonobo mothers increased the mating success of low- and medium-ranking males relative to the highest-ranking male (Surbeck, Mundry, and Hohmann 2011), and males with their mothers in their group enjoyed higher paternity success (Surbeck et al. 2019). Furthermore, sons of high-ranking female rhesus macaques tended to have a greater reproductive output in their natal group than sons of low-ranking females (Smith and Smith 1988; Bercovitch, Widdig, and Nürnberg 2000), a pattern that was also found in Barbary macaques, *M. sylvanus* (Paul and Kuester 1996). Recent research including several primate species has emphasized that maternal condition and survival is highly critical for offspring fitness even with inter-generational effects (Zippel et al. 2021).

A delay in natal dispersal has been reported by several studies of wild populations (Altmann and Altmann 1995b; Jack, Sheller, and Fedigan 2012; Marty et al. 2017). Such a time lag may help males to maximize body mass and fighting abilities, with natal males also becoming reproductive

active (Altmann and Altmann 1995b). In our sample, 25.8% offspring were sired by natal males. The age of these males ranged from 4 to 24 years, whereby 774 (81.3%) of these natal males were younger than 9 years (prime age). A longer presence in the natal group may also improve the opportunity for males to start their reproduction in a well-known social environment, in which natal males can benefit from already established social bonds apart from dominance rank. Indeed, the probability to reproduce increased with natal dispersal age in rhesus macaques, such that late dispersers were more likely to start reproducing in their natal group (Weiß et al. 2016).

As male rhesus macaques mature, they leave the system of social inheritance of maternal rank (at the latest once they left their natal group) and mainly queue for dominance, i.e. they enter the group at the bottom of the hierarchy (Bercovitch 1992; Berard 1999) contrasting other primate species, in which males fiercely fight over dominance (e.g. Marty et al. 2016, 2017). However, previous studies suggested that maternal rank could affect a males' reproductive success even after natal dispersal (Barbary macaques: Paul, Kuester, and Arnemann 1992). Nevertheless, the results of our present study suggest that rhesus males benefit from high maternal rank only while still in the natal group.

Our present analysis also revealed that neither adult male tenure, as an established proxy for male dominance in our study species, nor male age influenced within-group reproductive performance of male rhesus macaques. Although several studies described a positive relationship between rank and fitness in male rhesus macaques (Carpenter 1942a, 1942b; Chapais, 1983a, 1983b; Hill 1987; Kaufmann 1967; Lindburg 1983; Manson 1992; Widdig et al. 2004), others did not find such a relationship (Berard et al. 1993; Loy 1970; McMillan 1989). Conclusively, the results of previous studies lead to the suggestions that the effect of rank on reproductive success in male rhesus macaques is variable and likely to be influenced by several other factors, such as alternative male mating strategies and female mate choice (Bercovitch 1992; Bercovitch and Nürnberg 1997; Berard 1999; Altmann, Watts, and Altmann 2003; Widdig et al. 2004; Inoue-Murayama, Kawamura, and Weiss 2011; Dubuc et al. 2011). Indeed, rhesus females were shown to be able to resist mating with former partners and actively solicit low-ranking, novel males more than high-ranking ones with long tenure (Manson 1992, 1997; Bercovitch 1997; Chapais 2011). Hence, female mate choice for novel partners may partly counteract competitive advantages of higher-ranking and older, more experienced males, resulting in the lack of an association between tenure, or age, with the probability to become top sire.

The idea of female mate choice mediating the distribution of paternities is also supported by data on EGP in the study population. We did not consider sires of EGP and their attributes in our top sire analysis, as we were primarily interested in the attributes of group sires including their tenure. However, our previous studies on EGP on the Cayo Santiago population showed that the probability of producing extra-group offspring was enhanced for higher-ranking than for

lower-ranking females, while it was not related to female and male age, male tenure or previous reproductive success (Ruiz-Lambides et al. 2018). In addition, we found a tendency for EGPs to increase as the proportion of females increased in larger groups, but no such effect in smaller groups. Thus EGPs were influenced by a similar complex interplay between group size and group composition as reproductive skew. Furthermore, as group instability and female reproductive synchrony decreased, the number of EGPs tended to increase. Overall this supported the hypothesis that the group structure affects the occurrence of EGPs, which might be mediated by male mating opportunities, male monopolization potential, and/or female choice (Ruiz-Lambides et al. 2017).

Our results need to be interpreted with some limitations in mind. Based on the demographic records, 5072 offspring were born during our study period, but we could not use all born offspring for our analyses due to incomplete genetic data. In consequence, we decided to only compute M indices for groups and years with a minimum number and percentage of solved paternities to avoid biased skew estimates, which reduced the number of data points for the skew models by 25.5% from a total of 137 theoretically possible group-year combinations to 102, with skew measures based on 3232 offspring with solved paternities out of 3794 born in these groups and years. This decision presumably led to a slight reduction in statistical power, but given the nonetheless extensive data set we preferred this option over an imprecise computation of the key variable. Notably, the majority of offspring that needed to be dropped from the analyses comprised infants which died in their first year of life and thus before being sampled for paternity analysis. However, we consider it unlikely that unsampled infants systematically affected the proportion of actual versus potential sires (and thus, skew indices), but to fully exclude this possibility we would need to know if the number of sires systematically differs between surviving and non-surviving infants. While there has been an extended effort in recent years to sample also dead infants, this task is extremely difficult as mothers carry the dead corpus for several days (e.g. Sugiyama et al. 2009), and bodies can rarely be found before they degrade in the tropical climate. Furthermore, we could not solve all paternities, but with only 0.71% of offspring not assigned to a father this seems unlikely to have a noticeable impact on our results. In turn, this indicates that if we had a DNA sample of the infant, we most likely could assign paternity. Another aspect to consider is that male group membership cannot always be assigned accurately for a given day, as migration and fission events are dynamic processes that may take weeks or even months. Given our conservative definition of group membership (i.e., the first day seen in the new group was assigned as immigration date if subsequently confirmed for > 2 consecutive months), males still changing back and forth between their old and new group would appear to be extra-group sires if siring offspring in their old group, and within-group sires if siring offspring in their new group. Accordingly, some within-groups sires may have been assigned as extra-group males due to methodological decisions on how to define group membership. Finally, and typically for longitudinal studies, we lacked hormonal data to assess female cycle synchrony as well as male dominance data so that we could only approximate these measures. Ideally, future study should also

include hormonal and dominance data, but this is problematic in long-term studies as continuous data collection over decades is challenging and typically depends on collective efforts across numerous projects.

6 | Conclusions

While our results partly support an influence of predictors previously suggested to affect male reproductive skew, they also pinpoint that the relationships between the number of male competitors and reproductive skew are complex and modulated by other parameters. Overall, results are in line with other studies suggesting that other factors than male dominance are main determinants of male reproductive output in rhesus macaques. In particular, female mate choice and alternative male mating strategies need to be considered when investigating intra- and interspecific variation in male reproductive success.

Author Contributions

Anja Widdig: conceptualization (equal), data curation (equal), formal analysis (supporting), funding acquisition (lead), project administration (lead), resources (lead), supervision (equal), writing—original draft (equal), writing—review and editing (equal). **Lisa Engel:** conceptualization (equal), data curation (equal), formal analysis (equal), visualization (supporting), writing—original draft (equal), writing—review and editing (equal). **Angelina Ruiz-Lambides:** data curation (equal), funding acquisition (supporting), resources (supporting), writing—review and editing (equal). **Constance Dubuc:** conceptualization (supporting), writing—review and editing (equal). **Brigitte M. Weiß:** conceptualization (equal), data curation (equal), formal analysis (equal), project administration (supporting), supervision (equal), visualization (lead), writing—original draft (supporting), writing—review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data tables used in our analysis are available in the Supporting Information Material.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.