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ORIGINAL PAPER

Male coalitions and female behaviour affect male mating success independent of dominance rank and female receptive synchrony in wild Barbary macaques

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Abstract Dominant mammalian males should gain a reproductive advantage due to their greater fighting abilities. However, the extent to which they can monopolise access to females varies across species. In primates and recently other mammalian species, the Priority of Access (PoA) model is commonly used to measure the degree to which male rank and female receptive synchrony affect mating skew. Few studies have examined the factors which lead to deviations from the expectations of the model. Here, we investigate male mating skew in wild Barbary macaques (*Macaca sylvanus*). We examined four of the main factors which affect male mating success: the roles of male rank, female receptive synchrony, coalitionary activity and female behaviour. We found that male mating was skewed up the hierarchy, but there was a large deviation from the PoA model's expectations with high-ranked males not gaining as big a share as expected. Females frequently initiated sexual encounters, predominantly with mid-ranked males, increasing their mating success. Male coalitionary activity independently increased mating success. Frequent associations with females were costly to males as they were the targets of bridging coalitions, decreasing future mating opportunities for the targets. High-ranking males did not increase their mating success directly through bridging coalitions but acted to dilute the effects of female behaviour. By examining different factors affecting mating skew, we are able to show that alternative male and female mating strategies are effective in reducing the monopolisation potential of the dominant male.

Keywords Priority of Access model · Mating skew · Coalition · Female mate choice · Reproductive strategies · *Macaca sylvanus*

Introduction

Potential reproductive rates are usually higher among mammalian males compared to females, leading to male-biased operational sex ratios and consequently pronounced male–male competition for mating opportunities (Trivers 1972; Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjö 1996). Under these conditions, sexual selection favours traits that give males an advantage in physical contests such as body size, strength, weaponry and endurance (Plavcan and van Schaik 1997; Setchell 2003; Plavcan 2004; Emlen 2008). If males cannot exclude rivals from their group, reproductive competition and access to mating partners is often mediated via dominance rank among co-resident male rivals (Altmann 1962), with dominant males using their superior fighting abilities to defend access to receptive females (Shively and Smith 1985; Bercovitch 1988). How strongly male mating success is predicted by dominance rank, however, varies greatly, within and between species, particularly so among primates (Cowlishaw and Dunbar 1991; van Noordwijk and van Schaik 2004; Kutsukake and Nunn 2006).

The extent to which a dominant male can monopolise mating access to females within a group has been conceptualized in

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the Priority of Access model (hereafter the PoA model; Altmann 1962), which proposes that the ability of a dominant male to monopolize females depends on the degree of reproductive synchrony among females. The reasoning being that the dominant male can defend only one female at a time, hence if there are two females simultaneously receptive, the second-ranking male will also get his share of matings, and if there are three females receptive, the third-ranking male will also mate, and so on. The importance of reproductive synchrony as a predictor of alpha male mating or reproductive skew has been confirmed in comparative studies across primates (Kutsukake and Nunn 2006; Ostner et al. 2008b; Gogarten and Koenig 2013). The PoA model has often been applied in studies on primates (see Kutsukake and Nunn 2006) and more recently other mammalian species (Hirotani 1994; Say et al. 2001; Engh et al. 2002). For species exhibiting variable female receptivity, the PoA model may be favourable for tests of mating/reproductive skew compared to theoretical reproductive skew models as the former incorporates female receptive synchrony in the model, which is neglected by many reproductive skew models, but can be an important factor to consider in multi-male, multi-female groups (Port and Kappeler 2010). While most studies investigating the relationship between dominance rank and mating or reproductive success found a positive relationship (Cowlishaw and Dunbar 1991; Ellis 1995; Alberts et al. 2003; Majolo et al. 2012), it is also apparent that the strength of the relationship varies extensively across species of different genera, across species of the same genus or even within the same group over time (reviewed in Alberts 2012). So far, only a handful of studies directly tested the exact PoA expected distribution against the observed skew and investigated the factors driving the departure from the model (Alberts et al. 2003; Boesch et al. 2006; Hayakawa 2008; Wroblewski et al. 2009; Bissonnette et al. 2011; Dubuc et al. 2011).

A number of factors are thought to explain the deviation from the PoA model's expectations or more generally the variation in individual male mating success: energetic costs of mate-guarding, stability of the dominance hierarchy, invasions by non-resident males, male sexual coercion, male coalition formation and female mate choice (reviewed in Alberts 2012). Extended mate-guarding is energetically costly to males as it reduces foraging activity (Packer 1979; Alberts et al. 1996; Coltman et al. 1997; Mainguy and Côté 2008; Pelletier et al. 2009; Schubert et al. 2009) which may reduce mating success of high-ranking males (especially if coupled with large female group size and aseasonal reproduction, Alberts et al. 2003). Noë (1992) proposed a modified PoA model where only the highest ranking male baboons (*Papio* sp.) would benefit from extended mate guarding of females, and males below top should break up consorts using coalition formation to gain access to females (see below). Seasonal influxes of non-resident males have also been proposed as a way to break up the dominant male's monopoly; however, those invasions have mostly been observed in single male groups possibly because multi-male groups are usually able to repel intruders (Cords 2000; but see Borries 2000; reviewed by Alberts 2012). Instability in the male dominance hierarchy may also reduce the alpha male's ability to monopolise access to receptive females as challenges from rivals for the alpha position are likely to increase during periods of instability (Cowlishaw and Dunbar 1991).

Males in multi-male groups can use aggressive strategies to attempt to increase their mating success with certain females, such as sexual coercion (Muller and Wrangham 2009). Males may use aggression to intimidate a female before her receptive period, "punish" her when she refuses to mate or after mating with other males (Muller et al. 2007, 2011). Alternatively, males can access receptive females through cooperation and combining their intrinsic fighting abilities via coalition formation (Noë and Sluijter 1990; Kuester and Paul 1992). By targeting a higher-ranking male and preventing him from mating, allies may effectively reallocate matings towards subordinate males ("levelling coalitions"; Pandit and van Schaik 2003). In the case that a non-dominant male receives a disproportionate share of mating success, one may expect that coalitions will target those males—regardless of their relative dominance rank. As well as a temporal loss of mating opportunities, prolonged coalition formation against a target can also lead to intimidation of the target (van Schaik et al. 2006; Berghänel et al. 2011b) and cause further negative consequences which may ultimately lead to reduced future reproductive success. Levelling coalitions can be of the "all-up" type (van Schaik et al. 2004a, also termed "conservative" by Chapais 1995), where two low-ranking males team up against a higher-ranking target, or "bridging" where a high- and a low-ranking male target an intermediate individual. Levelling coalitions have been observed in a range of primates, most predominantly in baboons and macaques (Smith et al. 2010), where they can have a pronounced effect on the mating distribution across males (reviewed in van Schaik et al. 2004a). Additionally, "all-down" coalitions (two higher-ranked males aggressing a lower-ranked target) are predicted to occur whenever all-up and bridging coalitions occur with a defensive function or to cause intimidation (van Schaik et al. 2004a).

Females can also influence the rank-based distribution of mating access, concentrating mating towards one male or mating promiscuously (Dixson 1998; Drea 2005). Female primates need to ensure that all males have a non-zero chance of paternity in order to reduce the risk of infanticide (van Schaik et al. 2004b). Assuming that higher-ranked males gain matings via their superior rank positions, females may thus preferentially mate with males at the lower end of the PoA expected mating distribution. Females can engage in certain strategies to attempt to achieve this by, for example, initiating more sexual encounters with particular males (Janson 1984), by mating conspicuously out of sight of other group members ("sneak copulations"; Berard et al. 1994; Alberts et al. 2006; Overduin-de Vries et al. 2013) or by selectively refusing copulations from certain males (Huffman 1987; reviewed by Dixson 1998; Drea 2005). Female primates may conceal ovulation or lengthen receptivity increasing receptive synchrony within groups which, in turn, reduces the ability of the alpha male to monopolise access and increases the opportunity for mate choice (reviewed by Kappeler 2012).

Here, we examined the factors determining male mating success in Barbary macaques (*Macaca sylvanus*), a species with a clear male dominance hierarchy and frequent male coalition formation (Kuester and Paul 1992; Berghänel et al. 2010, 2011a, b; Bissonnette et al. 2011). A previous study under free-ranging conditions at Affenberg Salem examined male mating success (Bissonnette et al. 2011) and found a poor fit of the observed mating skew to the PoA model. Low-ranked, post-prime males increased their mating success using coalitionary activity to target high-ranked males breaking up consortships in all-up levelling coalitions. Females initiated consortships with higher-ranked prime males to possibly counteract this coalitionary behaviour. In this provisioned group, male and female group size was largely inflated, and age structure was heavily biased towards old or very old males who formed coalitions against more recently immigrated young males (Berghänel et al. 2011a, b). In Gibraltar, free-ranging females actively solicited mating from high-ranking males during their most likely period of fertility (Brauch et al. 2008), highlighting the importance of female behaviour for male mating success in this species. In this study, we build on the work of Bissonnette et al. (2011) by studying wild Barbary macaques across three consecutive mating seasons living in a group with a more natural composition and age structure. In contrast to the previous study, we aimed at teasing apart the factors determining male mating success in a multivariate analysis simultaneously considering male coalitionary activity, female-initiated sexual behaviours as well as the effects of rank and synchrony.

The effect of female reproductive synchrony can vary between species depending on the information males can infer about female fertility and thus needs to be based on the species-specific fertility information available to males (Alberts et al. 2006; Wroblewski et al. 2009; Henzi et al. 2010). In the case of Barbary macaques, we have previously shown that males bias their mating behaviour towards periods of maximum sexual swellings, but do not differentiate between swellings during the conceptive phase, determined through hormonal assessment of the timing of ovulation, and those during gestation (Young et al. 2013). We thus include both cycle types in our estimate of female reproductive synchrony. We do not investigate the potential effects of male invasions because this should mainly play a role in one male group (see above) and because they were not observed during the study. Similarly, male sexual coercion occurred at very low levels during the study, and thus, we only reported the individuals involved in these behaviours. The energetic costs of mate guarding should not influence mating success in the species, as mate-guarding episodes in Barbary macaques are very limited in time (Kuester and Paul 1992; Heistermann et al. 2008; Bissonnette et al. 2011). It could be argued that with high levels of promiscuity and short consortships, the assumptions of the PoA model are not upheld in the species. However, male rank may still play a major role, despite a lack of extended consortships, in regulating access to receptive females with increasing female receptive synchrony reducing the alpha male's ability to monopolise mating access. When synchrony is low, subordinate males may shy away from mating opportunities due to intimidation or fear of aggression from higher-ranked males, and as more females become synchronously receptive, the opportunities of subordinates to mate will increase. Thus, even in species without extended mate-guarding periods, the rationale of the PoA model may still hold with high-ranking males losing control of mating access as more females become receptive.

We examined the role of four different factors in predicting male mating success in two steps. In the first step, we derived for each of the three mating seasons a mating distribution in relation to rank as predicted from the PoA model by considering both rank and the number of synchronously receptive females. We tested whether (1) observed and predicted mating distributions per season were significantly skewed, (2) mating success was correlated to rank, (3) the lowest rank that received any mating equalled the maximum number of synchronous females, and (4) we qualitatively assessed whether observed and expected mating distributions were similar. In the second step, we analysed daily male mating success and how it related to male rank position, female receptive synchrony and their interaction, as well as male coalitionary activity and the frequency of female-initiated sexual encounters. We expected males to manipulate the mating distribution via coalitions that prevented other males from access to females. If females were influencing males' mating success, we expected males with a greater frequency of sexual encounters initiated by females to have an increased mating success. We also expected those males who received the greatest frequency of sexual encounters initiated by females to become the most frequent targets of coalitionary aggression as other group males attempted to disrupt their mating opportunities.

Methods

Study site and subjects

The study was conducted on one wild, unprovisioned group of fully habituated Barbary macaques living in a deciduous cedar and oak forest in the Middle-Atlas Mountains of Morocco (33°24′9N–005°12′9W; Majolo et al. 2013). The study population breeds seasonally with a mating season from Sep. to Dec. and a corresponding birth season from Mar. to May. Data for this study were collected during three consecutive mating seasons (MS09, Oct.–Dec. 2009; MS10, Sep.–Dec. 2010; MS11, Sep.–Dec. 2011). The mating season was defined as the period of the first to the last observed ejaculatory copulation during either focal or ad libitum data collection. During the study period, the study group ("Green" group) consisted of seven to nine adult males and seven to eight adult females.

Behavioural data collection and construction of the hierarchy

Behavioural data were collected by CY and five field assistants (MS09 and MS10) and SH and one field assistant (MS11) from 0700 to 1900 hours. All data collectors were trained by CY, and inter-observer reliability was assessed repeatedly. All adult males in the group were subject to continuous focal animal observation of social and sexual behaviour (Altmann 1974), yielding a total of 902 focal hours during the three consecutive mating seasons (341 h MS09, 304 h MS10 and 257 h MS11). Data were collected using handheld HP iPAQ 114 series pocket PCs loaded with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, USA). With a randomised sequence, each male was subject of one 40-min focal sampling session per observation day.

Ejaculatory copulations were recorded and indicated by the occurrence of a distinct ejaculatory pause in pelvic thrusts (Kuester and Paul 1984) and/or the presence of fresh ejaculate around the female's genital area straight after the observed copulation had occurred. We did not include non-ejaculatory mounts in our analysis, as Barbary macaques are single-mount breeders. Moreover, previous studies (Heistermann et al. 2008) found no discernible pattern of non-ejaculatory mounts observed around the fertile phase compared to before and after this period, but males concentrated their ejaculatory copulation rate around the fertile phase. In our data, we found non-ejaculatory copulations to be evenly distributed across ranks and accounting for less than one third of all mounts observed. As ultimately only an ejaculatory copulation can lead to fertilisation, we only include ejaculatory copulations in our analysis. Male inspection of a female's anogenital region was also recorded (tactile, olfactory or visual), as well as females' refusal to mate with males and incidents where a male would actively break up and interfere in a male/female association ("Interference"). Consortship was defined as an exclusive male–female dyad in which individuals remained within 10 m of each other, as well as coordinated movements when walking and was restricted to the mating season (Paul 1989; Bissonnette et al. 2011). Previous studies on the species only included a consortship with a minimum duration of 5 min so as not to overestimate male–female associations due to other factors such as feeding in close proximity (Heistermann et al. 2008; Bissonnette et al. 2011). Using the same methods, our study yielded an average consortship duration of 17.6±11.1 min (mean ± SD).

The dominance hierarchy was based on a total of 620 male–male dyadic conflicts where a clear winner and loser of a conflict could be determined with no counter-aggression (MS09, 360; MS10, 73; MS11, 187). Following the methods of Young et al. (2013), a separate hierarchy was constructed for each mating season using corrected normalized David's scores (de Vries et al. 2006). The hierarchies were significantly linear with adjusted linearity indices (h') of 81.2 and a directional consistency index of 0.87 on average across the three seasons [assessed in MATMAN™ 1.1.4; Noldus Information Technology (2003) following de Vries et al. (2006)]. The proportion of known relationships was high (86.6 %), whereas the rate of counter-aggression (4.8 %), reversals (0 %) and two-way relationships (18.1 %) were low. Rank changes occurred between the alpha and the beta position, the third- and fourth-ranking males had stable ranks across the study period and one low-ranking male emigrated out of the group at the end of both the MS09 and MS10 mating seasons. Males were classified, firstly by their ordinal rank position each mating season, and as high, mid- and low-ranking using the following rationale: the Pandit/van Schaik coalition model (Pandit and van Schaik 2003) predicts that the targets of levelling coalitions will be the top-ranked or just below top, so males ranked first and second were classified as high ranking, leaving the remaining seven (MS09) and six (MS10/MS11) males to be classified as mid- and low-ranking. So males three to five were classified as mid-ranking, and males ranked sixth and below were classified as low-ranking.

Female attractivity

Anogenital swelling size was assessed visually using a three-point scale adapted from the methods of Aujard et al. (1998) and Heistermann et al. (1996). All data collectors were trained by CY, and swelling size was confirmed by at least two observers each day. For each swelling cycle, the maximum swelling period was calculated, as the 6-day window (day −2 to day −7) from detumescence. Using two of the three mating seasons, the probability of fertility was shown to be at its maximum and always above 0.5 during this 6-day window (Young et al. 2013). A day during the mating season which had one or more females at maximum swelling was termed an "attractive day", and a female was defined as in her "attractive period" on each day of her maximum swelling period.

Expected and observed mating success

Firstly, we calculated the expected mating success based on the PoA model (Altmann 1962). This is the proportion of ejaculatory copulations each male is expected to gain on a given day dependant on the number of females in their attractive period and the male's rank, e.g. if only one female was in her attractive period on a given day, the highest ranking male would be assigned all the copulations of that day (i.e. a proportion of 1) and all other males none. If two females were in their attractive period, the two highest ranking males would be assigned 0.5 each and all other males zero, etc. The total score for each rank and day was summed and divided by the total number of attractive days to give the expected proportion of copulations each rank position was expected to gain. The daily observed mating success equals the actual number of ejaculatory copulations each male gained on a given day divided by total number of ejaculatory copulations on that day for each attractive day. The observed mating success for each rank over the study period again was calculated by summing up the daily observed mating success for each rank and dividing it by the total number of the attractive days.

Female behaviour

The influence of female mating behaviour on male mating success was investigated based on the number of female-initiated sexual encounters to males on attractive days (Hereafter "female invites"). A female invite was defined as an approach by a female towards a male within 1.5 m proximity followed by sexual behaviour (copulation, sexual inspection and/or consortship behaviour). For each attractive day, we then calculated the hourly rate of female invites from the number of focal hours each male was observed each day. This hourly rate was then divided by the number of receptive females each day to give a daily value of female invites per male per day. We also examined an additional female sexual behaviour, female's refusal to mate with males. We found this behaviour to be rare in our study group (39 observations during female attractive periods, only 3.2 % of all mounts observed) and therefore did not consider it in the analysis.

Coalitionary behaviour

A coalition was defined as a simultaneous aggression by two or more partners against a common target (Bercovitch 1988). Due to the rapid, often complex and subtle behaviours involved in coalitionary bouts, data were collected using hand-held Kodak Zx1 HD video cameras with the observer providing a full spoken commentary of the entire aggression as soon as an aggression began. Due to the open habitat and low density of ground vegetation as well as the conspicuous and noisy nature of coalitionary aggression, the vast majority of bouts were observed from the start. This was possible because many polyadic conflicts occurred during focal animal protocols and because the second observer was constantly seeking out situations that may cause polyadic conflicts to occur. Videos and spoken records together were analysed post hoc and either added to the focal protocol or ad libitum database. Behaviour was coded using the same protocol as during a focal follow. If the target was the last participant to show submission, he was deemed the loser of the coalition. Data shown here only include coalitions of multiple allies against one target. We classified coalitions into three categories: (1) "all-up", (2) "all-down" and (3) "bridging" (van Schaik et al. 2004a, 2006). Only coalitions that occurred in a sexual context were used for this analysis. Coalitions under a sexual context were defined as a coalition occurring during a focal follow where one of the coalition's participants also displayed male sexual behaviour (consortship or ejaculatory copulation) during the focal follow. The number of coalitions a male was an actor in each day was divided by the number of receptive females each day to give a daily value of the number of coalitions a male was an actor in. Coalitionary activity was not standardized for observation time as a male could join a coalition when not the focal subject and therefore could be an actor in a coalition at any time of day. Incidences of single males interfering in sexual encounters and breaking up a male/female dyad were rare (57 observations across the entire study period and 23 during female attractive periods) and therefore were also not considered in the analysis. The aggressor in the majority of these interactions (92 %) was one of the top three ranked males, although males ranked one to six were observed to interfere at least once. In total, 91 % of interferences were observed by a higher-ranked male against a lower-ranked male with a female. Individual interferences accounted for only 6.1 % of all aggressive interactions in a sexual context.

The cost of proximity to females

In order to examine whether time in proximity (within 1.5 m) of a female during her attractive period would increase a male's probability of becoming the target of a coalition, we calculated for each attractive day (see above), during focal follows, the time each male spent in proximity to the female during her attractive period. Additionally, for each male, we calculated the total focal time on each attractive day. We then calculated, for each attractive day and each male, (1) the number of coalitions each male received whilst in proximity to a female and (2) the number of coalitions each male received on attractive days not in proximity to a female during her attractive period. Hourly values for each male each day were calculated for (1) and (2), and we then averaged the daily values over the entire study period to give a mean hourly rate for each rank position and mating season.

Statistical analysis

A Spearman rank test was used to test for correlation of male rank and mean observed mating success for each rank position. The proportion of coalitions a male was a target of each mating season was related to the proportion of female-initiated sexual encounters each male received using a Pearson's correlation.

Two different indices were used to calculate the mating skew: firstly, the "lambda" index of mating skew (Kokko and Lindström 1997), which measures the overall skew regardless of the dominance rank. Lambda ranges from 0 (evenly distribution of mating) to 1 (completely skewed mating towards one male). Secondly, we used the binomial skew index (hereafter *B* index; Nonacs 2000, 2003); a positive *B* index indicates greater than expected skew, while more equally distributed mating is indicated by a negative value. A null hypothesis of random mating within the group can be tested against the observed skew using the *B* index ($B=0$). We tested both the observed and the expected PoA model's mating skew using the above methods. Both the lambda and *B* index were calculated using the Skew Calculator 2003 (set to 10,000 permutations) available online at https://www.eeb.ucla.edu/Faculty/Nonacs/PI.html.

A generalized linear mixed model (GLMM; Baayen 2008) was used to examine how male mating success was influenced by male rank, female receptive synchrony and the interaction of these two variables, coalitions in a sexual context and female behaviour. The dependant variable, male mating success, was measured on the basis of the number of observed ejaculatory copulations each male gained per day. We included total number of observed matings per day (log-transformed) as an offset variable in the model to control for variation in mating frequency due to the number of females available each day. Predictor variables were (1) a male's ordinal rank position each day, (2) the number of receptive females each day, (3) the daily rate of female invites received and (4) the daily number of coalitions as an ally in a sexual context. Male rank and female receptive synchrony were included as an interaction in the model to examine if the influence of male rank on mating success changed over the range of synchrony values. All predictor variables were *z*-transformed. Mating season and male identity were included as random factors.

We ran the GLMMs in R 2.14.0 (R Development Core Team 2012) using the function lmer of the R package lme4 (Bates et al. 2012). GLMMs were fitted with Poisson error structure and log-link function, and likelihood ratio tests were calculated using the R function anova. Significance of the individual fixed effects was determined based on the χ^2 and *p* values provided by lmer. Assumptions about the lack of overdispersion were respected for the analyses, and we checked whether collinearity was a potential problem by using variance inflation factors (VIF; Field 2005). VIFs were derived using the function vif of the R package car (Fox and Weisberg 2010) applied to a standard linear model excluding the random effects. VIFs which are not substantially greater than 1 and less than 10 indicate that covariation between predictors is not a problem (Bowerman and O'Connell 1990; Mayers 1990); in our analysis, the range was 1.00–1.06. Additionally, we examined the correlation between the predictor variables in the full model and found low correlations between all predictors, confirming the VIF analysis.

To investigate the costs of proximity to females, we used a paired samples *t* test to compare the hourly rate males were coalitionary targets while in proximity versus not in proximity to a female during her attractive period. Where appropriate, we report mean values ± standard deviation (SD). All statistical analysis were carried out using R 2.14.0 software (R Development Core Team 2012). The level of significance was set at $\alpha<0.05$.

Results

Comparing expected and observed mating skew

We examined the observed mating skew and that expected by the PoA model for each mating season. Observed male mating skew was low across all three mating seasons indicated by a relatively low lambda (MS09=0.20, MS10=0.20 and MS11=0.37), but still significantly skewed (MS09: $B=0.02$, $p<0.01$; MS10: $B=0.02$, $p=0.02$; MS11: $B=0.07$, $p<0.01$), and therefore, mating did not occur at random. The lambda of expected male mating skew (MS09=0.58, MS10=0.69 and MS11=0.78) indicated greater skew than the observed mating skew, and mating was not expected to occur at random (MS09: $B=0.29$, $p<0.01$; MS10: $B=0.40$, $p<0.01$; MS11: $B=0.50$, $p<0.01$). We found strong negative correlations between male ordinal rank and observed mating success in all three mating seasons (Spearman correlation: MS09=$N=9$, $\rho=-0.84$, $p<0.01$; MS10=$N=8$, $\rho=-0.97$, $p<0.01$; MS11=$N=8$, $\rho=-0.97$, $p<0.01$), with higher-ranking males gaining a greater proportion of copulations than lower-ranking males. However, the observed mating skew was lower than the expected skew, i.e. the distribution was more even with the two top ranking males having lower than expected by the PoA model and the remaining males having higher than expected mating success (Fig. 1). All males were observed to gain matings (up to rank 9) which was much higher than the number of maximum number of synchronously receptive females (5).

Factors determining mating skew: rank, female synchrony, coalitions and female behaviour

Throughout all mating seasons, at least one female was in her attractive period on the majority of observation days, 80.7±6.7 % (mean ± SD; MS09=75.0 %, MS10=88.0 % and MS11=79.0 %), and on average, 1.8±0.5 (mean ± SD)

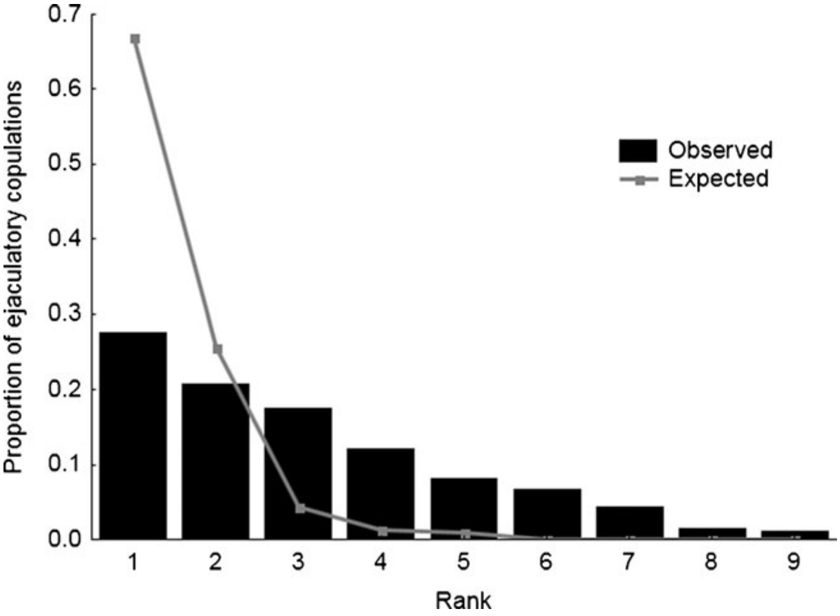

Fig. 1 Expected and observed mating success. During the three mating seasons, males occupied different rank positions, and mean values are calculated for each rank position. The mean mating success was significantly negatively correlated with ordinal rank position (Spearman correlation, $N=9$, $\rho=-1$, $p<0.01$)

females were in their attractive period on a given attractive day (MS09=2.3, MS10=1.9 and MS11=1.3). The maximum number of synchronously attractive females observed on a given day was 5 (MS09=5, MS10=4 and MS11=3).

We observed on average 1.7±0.6 coalitions per day during the mating seasons, and throughout the three mating seasons, 74.7±9.5 % of coalitions took place on attractive days. On attractive days, on average, 48.7±20.8 % of all coalitions occurred in a sexual context (see "Methods" section for definition); these were the coalitions we consider below. Coalitions which occurred in a sexual context ("levelling") were most frequently bridging (45.0 %), followed by all-down (34.5 %) and the least frequently all-up (20.5 %). Coalition formation was variable between the three mating seasons in terms of the main ranks of the allies and targets involved. Overall, the main allies in coalitions were high- and mid-ranked males. The three most frequent coalition allies in MS09 were the first (37.7 %)-, fifth (20.5 %)- and second (14.9 %)-ranked males. In MS10, it was the first (34.1 %), second (25.6 %) and third (18.9 %), and in MS11, it was the fourth (35.6 %)-, second (25.6 %)- and sixth (14.3 %)-ranked males. The main targets were high- and mid-ranked males. The three most frequent targets of coalitions in MS09 were the fourth (34.9 %)-, third (24.6 %)- and second (12.6 %)-ranked males. In MS10, it was the fourth (31.7 %), fifth (18.3 %) and third (15.9 %), and in MS11, it was the first (55.0 %)-, third (25.0 %)- and fourth (6.3 %)-ranked males.

Females initiated 43.8±8.6 % (mean ± SD) of all sexual encounters on attractive days. The ranks of males which females initiated sexual encounters with varied between mating seasons. The three most frequent recipients of female-initiated sexual encounters were, in MS09, the third (21.0 %)-, fifth (18.5 %)- and fourth (17.3 %)-ranked males. In the MS10, it was the third (32.4 %), fourth (17.6 %) and fifth (14.7 %), and in the MS11, it was the first (38.5 %)-, third (19.2 %)-, and fourth (11.5 %)-ranked males. We found a positive relationship for all three mating seasons between the proportion of female-initiated sexual encounters each male received with the proportion of coalitions a male was a target of with a trend for MS10 (Pearson's correlation: $r=0.61$, $df=7$, $p=0.08$) and strong significant effect for MS09 (Pearson's correlation: $r=0.77$, $df=7$, $p=0.01$) and MS11 (Pearson's correlation: $r=0.93$, $df=7$, $p\leq0.01$).

We ran a GLMM to investigate the influence of the four predictor variables and the interaction of male rank and female receptive synchrony on male mating success. Male ordinal rank explained the greatest amount of variance in the data and had a negative influence indicating that the higher males ranked, the higher was their mating success on a given day (Table 1). The number of synchronous females per day positively influenced male mating success, and it did so after controlling the response by the total number of copulations by all males and females observed that day as an offset term. This indicates that as female receptive synchrony increased, many males' mating success also increased. The interaction between male rank and female receptive synchrony was not significant, but the relationship with the response was positive, which suggests that the effect of rank tends to decrease with increasing synchrony. Both of the main effects were significant, thus not rank alone, but also synchrony had an independent effect on male mating success.

A large proportion of variance in male mating success was explained by female behaviour, i.e. the number of times a male was approached by a female in a sexual context which

Table 1 GLMM Poisson regression results for the relationship between observed mating success (controlling for number of matings per day) and male ordinal rank, the number of synchronously receptive female, the interaction of male rank and female receptive synchrony, female-initiated sexual encounters and a male being an ally in a coalition (N=701)

Independent variable	GLMM estimate	SE	Z	**p** ($>\|Z\|$)
Intercept	−1.360	0.092	−14.771	<0.01
Female-initiated sexual encounters	0.243	0.080	6.412	<0.01
Male rank	−0.412	0.038	−5.150	<0.01
Number of synchronous females	0.368	0.054	6.770	<0.01
Ally in a coalition	0.111	0.041	2.693	0.01
Interaction of rank and synchrony	0.063	0.049	1.287	0.20

may be interpreted as female preference (Fig. 2). Another and an independent part of the residual variance was explained by male coalitionary activity, i.e. the more often a male was an ally in a coalition against another male in a sexual context, the higher his mating success was (Fig. 3).

The cost of proximity to females

Across all males in the group, we found that the rate of coalitionary attacks received was increased when the male was in proximity of a female in her attractive period (mean=0.82/h) compared to when no such female was close (mean=0.01/h; paired t test: t=3.53, df=8, p<0.01).

Discussion

Our results show that mating in Barbary macaques was skewed up the hierarchy with the highest-ranking males gaining the greatest mating success across consecutive mating seasons. The observed mating skew by rank was very low though and much lower than predicted by the PoA model. The assumptions of the PoA model are based on rhesus macaque (*Macaca mulatta*) biology (Altmann 1962). Thus, the large difference between observed and predicted mating distribution may not be surprising in a species without extended male mate-guarding regulating access to females. We found, however, a crucial aspect of the model to be relevant in Barbary macaques, i.e. female reproductive synchrony significantly affected male mating success.

The PoA model has been tested in various primate (see Kutsukake and Nunn 2006) and other mammalian species (Hirotani 1994; Say et al. 2001; Engh et al. 2002). Support for the PoA model, however, is mixed. It has been shown to be a good predictor of mating success in many species (Bulger 1993; Weingrill et al. 2000, 2003; Soltis et al. 2001; Alberts et al. 2003; Takahashi 2004; Setchell et al. 2005; Boesch et al. 2006; Wroblewski et al. 2009), but not so in other studies (Say et al. 2001; Engh et al. 2002; Widdig et al. 2004; Hayakawa 2008; Newton-Fisher et al. 2010; Bissonnette et al. 2011; Dubuc et al. 2011; this study). This mixed support may be due to varying measures of female receptivity (Alberts et al. 2006; Wroblewski et al. 2009; Henzi et al. 2010), as the information males can infer about female reproductive state varies greatly between taxa. Alternatively, the strict assumptions of the model may not be met in species where extended periods of mate-guarding may be less pronounced, for example, hyenas, *Crocuta crocuta* (Engh et al. 2002), domestic cats, *Felis catus* L. (Say et al. 2001), and Barbary macaques (Bissonnette et al. 2011; this study) leading to a poor fit. However, rhesus macaque mating and reproductive skew also showed a poor fit (Widdig et al. 2004; Dubuc et al. 2011), although they are the species the model was originally designed for, and thus should meet the model's assumptions. We argue that even without extended male mate guarding of receptive females, high-ranking males can use their status to increase their access to females and that female receptive synchrony will

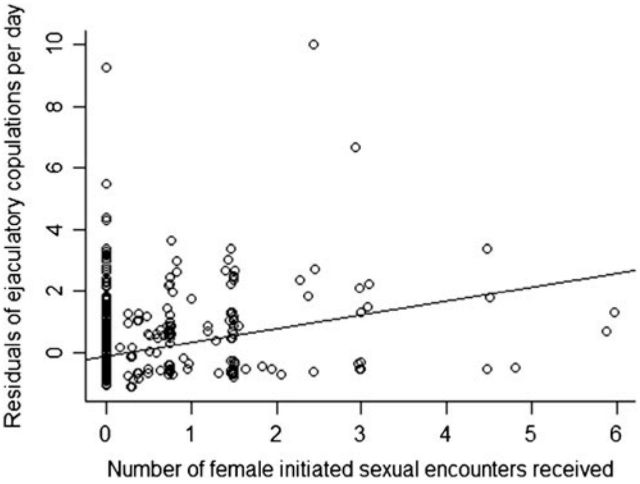

Fig. 2 Relationship between the observed mating success and the number of female-initiated sexual encounters per hour a male received per hour (controlling for number of receptive females, see "Methods" section). The y-axis represents the residuals of male ejaculatory copulation rate (controlling for number of matings per day) obtained from a GLMM including male rank, female receptive synchrony and number of coalitions as an actor as fixed factors, and male identity and mating season as random factors

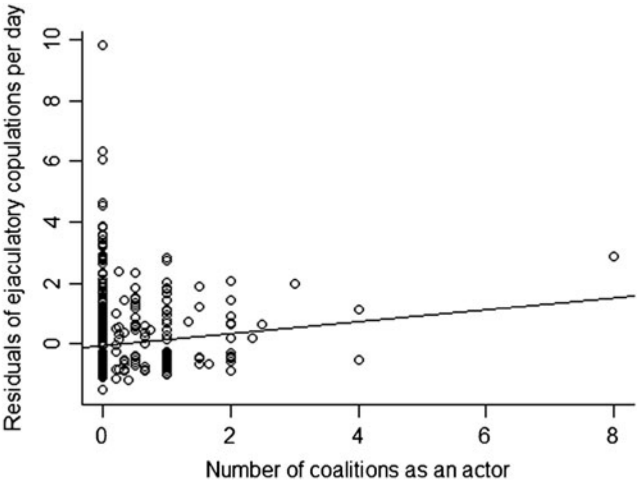

Fig. 3 Relationship between the observed mating success and the number of coalitions a male was an actor in (controlling for number of receptive females, see "Methods" section). The *y*-axis represents the residuals of male ejaculatory copulation rate (controlling for number of matings per day) obtained from a GLMM including male rank, female receptive synchrony and number of female-initiated sexual encounters a male received as fixed factors, and male identity and mating season as random factors. We re-ran the GLMM model without the outlier, and the results of the GLMM did not change

affect the efficiency of this strategy. Therefore, both male rank and female receptive synchrony can still play a large role in influencing male mating success even in species with an absence of extended mate-guarding periods.

By first examining the roles of male rank and female synchrony, we set the stage for exploring additional factors influencing male mating success, using multivariate analysis. We found a large amount of the residual variance in male mating success to be explained by female behaviour and male coalitionary activity. Females were found to initiate sexual interactions primarily with mid-ranking males, which may explain why mid-ranking males accumulated larger numbers of matings than one may expect in a small group where a mean of only 1.7 and rarely more than three females were mating in synchrony. We investigated whether the inability of high-ranking males to monopolize access to these females may result from levelling coalitions breaking up consortships and reallocating matings to lower-ranking males as previously described for semi-free ranging Barbary macaques (Bissonnette et al. 2011). In support of this idea, the risk of being target of an aggressive coalitionary attack increased with the time a male spent with attractive females. But male coalitionary behaviour did not target the top-/just below top-ranking male as the Pandit/van Schaik coalition model (Pandit and van Schaik 2003) predicted and as found in the previous study (Bissonnette et al. 2011). In our study group, which was smaller and lacked the large number of old and very old males of the previous study, coalitions were mainly bridging between high- and lower-ranking males against mid-ranking targets. Upon closer inspection, the discrepancy between studies only concerns the ranks of allies and targets but not the context of the coalitionary attacks. The targets of both studies were those males that received most attention from the females in the group which were the top-ranking males in the previous and the mid-ranking males in our study. Thus, coalitions in our study may have functioned mainly to counterbalance against the effect of female behaviour, and the participation of low-ranking males in these coalitions may explain their non-zero share of matings.

As mentioned in the "Introduction" section, male mating skew can be influenced not only by female mate choice and male coalition formation but also by several other factors, including energetic costs of mate guarding, number of competitors in a group, stability of the dominance hierarchy, male sexual coercion and invasions by non-resident males (reviewed in Alberts 2012). These factors vary in the degree to which they affect mating success in different species, for example, in some species, there is less potential for female mate choice or an absence of male coalition formation [e.g. in mandrills (*Mandrillus sphinx*; Setchell et al. 2005) or chacma baboons (*Papio hamadryas ursinus*; Weingrill et al. 2003)]. In species with extended mate-guarding periods, the energetic costs of mate guarding may significantly reduce mating skew (Packer 1979; Rasmussen 1985; Alberts et al. 1996; Coltman et al. 1997; Mainguy and Côté 2008; Pelletier et al. 2009; Schubert et al. 2009). In our study, there was little evidence of male sexual coercion, male–female associations being broken up by individual males, and invasions from non-resident males. Thus, these factors are not considered to have affected male mating skew.

Demographic and individual male characteristics may additionally influence male mating skew in primate groups. In our study, one male left the group during two mating seasons for 1 month creating possible instability of the hierarchy, which may have affected the alpha male's ability to monopolise access to females (Cowlishaw and Dunbar 1991). High-ranking males may prefer multiparous over nulliparous females (Newton-Fisher et al. 2010) or concentrate mating to conception swellings (Wroblewski et al. 2009), but in our study, all females were multiparous, and high-ranking males mate equally often during conception and non-conception swellings (Young et al. 2013). Males far apart in age are expected to have larger power differentials, and therefore, males living in groups with a wider age range may engage in alternative strategies, such as coalition formation, to compensate for reduced fighting ability, whereas males closer in age are more likely to compete one-on-one (Alberts et al. 2003). Age differences in wild populations are likely to be smaller than in free-ranging conditions; however, mating skew was similar in the study on semi-free-ranging Barbary macaques exhibiting a wide age range (Bissonnette et al. 2011), suggesting that age span alone may not play a prominent role in influencing male mating skew.

An additional factor considered to influence male mating success is the costs of extended mate guarding. Barbary macaque males, however, may not suffer energetic costs of extended mate guarding as consortship duration is very short, but short-term associations with females may still be costly. Males who associated with females, in our study, were frequent targets of coalitionary aggression. Increased aggression leads to greater risk of injury (Paul and Kuester 1988; Kuester and Paul 1992), increased energy expenditure during the contest (Muller and Wrangham 2004) and increased physiological stress (Wallner et al. 1999; Ostner et al. 2008a), as well as a reduction in future mating opportunities (Bercovitch 1988; Bissonnette et al. 2011). Thus, males may incur costs unrelated to extended mate guarding but with similar detrimental outcomes to a male's mating success.

Female mating behaviour can play a major role affecting male mating skew by influencing monopolisability of females in their attractive period. Female mating behaviour can either increase (Janson 1984; Boinski 1987; Brauch et al. 2008) or decrease (Strier 1996; Widdig et al. 2004) male mating skew depending on whether females select one or many mating partners. Japanese macaque (*Macaca fuscata*) females show preferences for mating with lower-ranked males suggesting that even in these highly despotic macaques, female behaviour can play a role (Soltis et al. 1997). In some species, female refusal to mate with certain males may indicate female preferences for certain partners (Huffman 1987), but refusal rate in our study was too low to add important information to our results. Female mating behaviour in our study did seem to affect male mating success with females showing preference towards the alpha male, as well as mid-ranking males (third and fourth rank). By doing so, this would reduce the mating share distributed towards the top-ranked males whilst simultaneously increasing the share of the mid-ranked males. Possible explanations as to why females select these mid-ranked males may be due to the prospective remaining tenure length of the alpha male, with females investing in males moving up the hierarchy as those will be the best protector for their future offspring (Alberts et al. 2003; van Noordwijk and van Schaik 2004; Clarke et al. 2009).

Females may also engage in frequent sexual encounters with immigrant males (Berghänel et al. 2010; Bissonnette et al. 2011; but see rhesus macaques, Manson 1995), who may soon rise in rank and also increase genetic diversity. In our study group, the position of the mid-ranked males did not increase over the 3-year study period, suggesting that neither novelty nor future rank increase would explain their attractiveness to females. Alternatively, females may have been merely attempting to reduce future risks of infanticide by increasing paternity confusion across the highest ranked males (van Schaik et al. 2000; van Noordwijk and van Schaik 2004), or selecting males for other factors such as MHC compatibility and quality (Setchell and Huchard 2012), inbreeding avoidance (Zeh and Zeh 2001) or post-copulatory sperm competition (Dixson 1998).

In addition to female behaviour, a male's coalitionary activity was found to have a pronounced independent influence on male mating success in our study. The Pandit/van Schaik model (Pandit and van Schaik 2003) predicts that coalitions in a levelling context should be all-up coalitions against top or males just below top rank or be bridging coalitions formed between kin. These all-up levelling coalitions have been observed in baboons (Packer 1979; Bercovitch 1988; Noë and Sluijter 1990, 1995) and semi-free-ranging Barbary macaques (Bissonnette et al. 2011). In our study, high- and lower-ranking males teamed up to form bridging coalitions against mid-ranking males. van Schaik et al. (2004a, 2006) predicted that bridging coalitions should only be profitable for the higher-ranked partner if the allies are kin [with males dispersing from their natal groups (Kuester and Paul 1999; Modolo et al. 2008) the chances of co-resident males being kin are reduced]. The rationale being that males compete for a non-shareable resource, and the dominant male should have the greatest fighting abilities and be able to monopolise access to females without cooperation of other individuals (van Schaik et al. 2004a, 2006). However, if the alpha male cannot completely control mating access, for example, due to female behaviour as in this study, and as such, matings are being concentrated towards other group members, bridging coalitions may be a viable option. By forming bridging coalitions with lower-ranked males, the high-ranked male may not necessarily increase his mating success directly but will disrupt future mating opportunities of the mid-ranked males and prevent individual females to concentrate mating in a particular mid-ranking rival. Coalitionary activity has been shown to result in a consortship changeover in approximately half of the coalitions observed in studies in baboons and macaques (Bercovitch 1988; Noë 1992; Bissonnette et al. 2011) with one ally gaining a mating opportunity with the contested female directly after the coalitionary bout and not necessarily the highest ranked ally. However, coalitions can also be utilized to intimidate other group members (Berghänel et al. 2011b) as the dyadic dominance relationship between the target and each of the allies can be affected by the joint aggression. In future dyadic contests between the target and one of the allies over access to a receptive female, the ally's chance of success is increased due to their increased external power (Berghänel et al. 2011b). Therefore, by forming coalitions, a male can limit the mating success of other group members, which indirectly increases their own mating success.

Overall, we found, even in a species without extended male mate guarding, that both male hierarchal position and female receptive synchrony are important predictors of male mating success. We suggest that both factors should be considered in future studies looking to examine mating/reproductive skew (Port and Kappeler 2010), not only in primates but mammalian multi-male, multi-female groups with variable female receptive synchrony. Importantly, the information available to males about female reproductive state (the extent of this information varies widely among taxa) needs to be available for an assessment of the predicted PoA distribution. In addition to male rank and female receptive synchrony, several other factors can influence male mating success in mammalian species, and recent advances in multivariate statistics allow the influence of these factors to be considered independently. In Barbary macaques, we found that although male mating success is skewed up the hierarchy, it is poorly predicted by expectations of the PoA model. Both male coalitionary aggression and female behaviour acted to limit the alpha males' capacity to monopolise access to females in our study. Together with other results (Schülke et al. 2010), this suggests that cooperation increases male reproductive success in male dispersal species. The PoA model may provide a good framework with which to investigate male mating success in species with variable female receptive synchrony, even in the absence of extended male mate-guarding periods. A multi-level approach to examine male mating/reproductive success, firstly looking at a species fit to the PoA model and then the additional factors which independently affect mating skew, may advance our understanding of the relationship between male dominance rank and mating/reproductive success in different taxa and, in turn, male and female reproductive strategies overall.

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Ethical standards This study complies with Moroccan, German and British regulations regarding the ethical treatment of research subjects.

Conflicts of interest The authors declare that they have no conflict of interest.

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