

RESEARCH ARTICLE

Sneaky Monkeys: An Audience Effect of Male Rhesus Macaques (*Macaca mulatta*) on Sexual BehaviorA.M. OVERDUIN-DE VRIES^{1,2*}, J.J.M. MASSEN², B.M. SPRUIJT², AND E.H.M. STERCK^{1,2}¹*Ethology Research, Animal Science Department, Biomedical Primate Research Center, Rijswijk, The Netherlands*²*Behavioral Biology, Utrecht University, The Netherlands*

Males and females have different sexual interests and subsequently may show conflicting sexual strategies. While dominant males try to monopolize females, promiscuity benefits females and subordinate males. One way to escape monopolization by dominant males is to copulate in their absence. We tested this inhibitory effect of males on the sexual behavior of their group members in captive group-living Rhesus macaques. Copulations between females and nonalpha males almost exclusively took place when the alpha male was out of sight. Furthermore, the inhibiting effect was not unique for the alpha male. An upcoming nonalpha male also inhibited copulations of its group members, and three other nonalpha males inhibited female copulation solicitations. Females adjusted their behavior to the presence of bystander males, as they initiated and accepted initiations more often in absence than in presence of bystander males. Although not significant, in males, a similar pattern was found. The observed reduction in mating behavior in presence of bystander males is in accordance with an “audience effect,” in which the behavior is modulated in relation to the presence or absence of third parties. This audience effect may serve as an important mechanism to reduce (aggressive) interruptions of subordinate male copulations. *Am. J. Primatol.* 74:217–228, 2012. © 2012 Wiley Periodicals, Inc.

Key words: audience effect; mating tactics; sexual behavior; primates; monopolization

INTRODUCTION

Primate males in species with multimale mating systems compete with each other and aim at preventing female promiscuity [Dixon & Anderson, 2002]. The most common male strategy is monopolization of females by higher ranking males. These high-ranking males concentrate their sexual behavior on receptive females by forming consorts [Alberts et al., 2006; Berard et al., 1994; de Ruiter & van Hooff, 1993] and mate guarding. In addition, dominant males can disrupt copulations and consorts of subordinate males by chasing the female away from the subordinate male [Chapais, 1983; Manson, 1996], indicating that dominant males can monopolize access to females. According to the Priority of Access model, this results in a correlation between male dominance rank and mating success [Altmann, 1962]. In many species, this correlation is found [for review, Cowlshaw & Dunbar, 1991; *Gorilla gorilla beringei*, Robbins, 1999; *Macaca fascicularis*, de Ruiter & van Hooff, 1993; *M. mulatta*, Massen et al. in press; *M. fuscata*, Garcia et al., 2009; *M. sylvanus*, Paul et al., 1993; *Mandrillus sphinx*, Wickings et al., 1993; *Pan troglodytes*, Boesch et al., 2006; Klinkova et al., 2005; *Papio anubis*, Alberts et al., 2006; Bulger, 1993]. However, especially when females ovulate in synchrony and receptive females

do not coordinate their movements [Ostner et al., 2008], males may fail to monopolize them for the full length of their fertile period, and the degree of monopolization can differ between species [reviewed in, van Noordwijk & van Schaik, 2004], populations [*M. fascicularis*, de Ruiter et al., 1992], subsequent years [*M. mulatta*, Berard, 1999; Berard et al., 1993; Smith, 1993], or may not even be found [*Cebus abella nigritus*, Alfaro, 2005; *M. mulatta*, McMillan, 1989; Dubuc et al., 2011]. This indicates that, especially in seasonal species where female synchrony is largest [Newton, 1988], not only male dominance may determine the distribution of male access to receptive females, but that subordinate males can also copulate and father a substantial part of the offspring [van Schaik et al., 2004]. One way for subordinate males to enhance their copulation opportunities is to minimize disruption of their copulations by copulating quickly and out of sight of high-ranking males.

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Female choice can overcome the effect of male dominance [Soltis et al., 1997]. In mammals, female choice often results in promiscuity [Dixon, 1998; van Noordwijk & van Schaik, 2000]. Although copulating with multiple males is costly for females when it results from male coercion [Smuts & Smuts, 1993], or when there is a high risk on sexual transmitted diseases [Nunn et al., 2000; Thrall et al., 2000], female promiscuity is often beneficial for females. A major ultimate benefit concerns protection against infanticide [mammals, Ebensperger, 1998; mice, Cicirello & Wolff, 1990; primates, Hrdy, 1979; Janson, 2000]. In primates, males that have copulated with a particular female refrain from attacking her subsequent offspring [Hausfater & Hrdy, 1984] and even actively defend it [Buchan et al., 2003]. In addition, promiscuity may benefit females by allowing cryptic female choice or sperm competition resulting in better quality offspring [Zeh & Zeh, 2003], avoiding sexual harassment, provisioning of goods and services by sexual partners, and drive the number of males that defend the group [reviewed in, Engelhardt, 2004; Wolff & Macdonald, 2004]. Promiscuity commonly represents a preferred female strategy, since females actively seek multiple copulation partners [Soltis, 2002], and in many species, females have evolved adaptations to improve their chances of being promiscuous [Birkhead, 2000]. For instance, a number of Old World monkeys and apes have exaggerated swellings in the anogenital region around the time of ovulation [Dixon, 1998]. The duration of sexual activity is longer in species with exaggerated swellings [Nunn, 1999], which increases the probability of copulating with more than one male. Besides, Catharine primate females have, compared to other mammals, extended sexually receptive periods that reduce male monopolization of females and facilitate female promiscuity [Engelhardt et al., 2004]. Female promiscuity can be indiscriminate [Nikitopoulos et al., 2005] or females may bias copulations toward particular males. This bias does not necessarily follow the male dominance hierarchy, since females may prefer novel over well-known males [*M. fuscata*, Inoue & Takenaka, 2008], or males that have a social bond with them [*M. mulatta*, Massen et al. in press; *Papio cynocephalus anubis*, Smuts, 1985] or young males [*M. mulatta*, Smith, 1994]. Since these males are often subordinate, females have developed tactics to escape from monopolization by higher ranking males, such as copulating out of sight of high-ranking males.

Sneaky copulations by a female and a subordinate male out of sight of the dominant male may result from high-level cognitive capacities, including visual perspective taking and tactical deception [Byrne & Whiten, 1990]. Alternatively, but not mutually exclusively, sneak copulations may result from an inhibiting effect that dominant individuals have on the sexual behavior of their group members.

One way of dominant males to hinder subordinate male mating success is to disrupt ongoing copulations, which has been reported in at least 13 different primate species [Dixon, 1998, p. 72, table 4.5]. Disruption can involve aggression such as chasing or attacking copulating individuals [*M. mulatta*, Chapais, 1983; Lindburg, 1971; Ruiz de Elvira & Herndon, 1986; *Pan troglodytes schweinfurthi*, Tutin, 1979]. Simple operant learning, combining sexual behavior in close proximity of disrupting individuals with punishment, may then result in a simple rule such as “freeze particular behavior when in close proximity of the dominant” [Amici et al., 2009].

Such an inhibition of particular behavior by the mere presence of a bystander is called an audience effect. In some contexts, such as predator warning, audience effects prevent a signaler from giving costly signals without having an audience to receive the signal [Wich & Sterck, 2003]. In other contexts, such as greeting [Laporte & Zuberbühler, 2010], mother–infant interactions [Semple et al., 2009], and sexual behavior, audience effects reduce conflicts with potentially aggressive bystanders [Townsend & Zuberbühler, 2009]. Whether an audience effect on sexual behavior increases the reproductive success of subordinate males is dubious. On the one hand, an audience effect might lead to a higher rate of copulations by subordinate males in the absence of dominant disruptors and thus a higher incidence of successful copulations. On the other hand, the number of times a male can copulate per hour is limited, and thus, the total number of copulations by subordinate males may decrease by means of an audience effect. While, in a few primate species, the copulation frequency is correlated with reproductive success [reviewed in, de Ruiter & van Hooff, 1993], male mating success is also based on a number of other factors in a complicated interactive way; namely, consort behavior, the timing of copulation relative to ovulation, female partner preferences, the number of female partners, and troop composition [Takahata et al., 1999]. In conclusion, the most unequivocal benefit of an audience effect on sexual behavior is to reduce the amount of energy loss due to unsuccessful mating attempts in the presence of disruptors, and the amount of aggressive interactions between males and/or females [Townsend & Zuberbühler, 2009].

Since disruption is always accomplished by an animal higher in rank than at least one of the animals in the consorting pair [Ruiz de Elvira & Herndon, 1986], it is expected that higher ranking males inhibit copulations of lower ranking ones and not the other way around. Whereas disruption by males is common in Rhesus macaques, female Rhesus macaques rarely disrupt copulations [Dixon, 1998, p. 72, table 4.5]. Thus, it is expected that in this species, mainly males would have an audience effect on the sexual behavior of group members. During disruptions of copulations in Rhesus

macaques, females receive the brunt of aggression [Manson, 1996; Ruiz de Elvira & Herndon, 1986], which indicates that females would benefit from reducing interruptions. In contrast, for males no fitness loss is associated with the disruption of copulations [Berard et al., 1994]. Apparently, males buffer disrupted copulations by finding enough opportunities to copulate. Therefore, it is expected that female, but not male Rhesus macaques, pay attention to the presence of potentially disruptive bystanders.

Studies that report sneaky copulations in primates range from observations at a single field site [Kummer, 1968; Soltis et al., 2001] to a large compilation of such anecdotal observations [Byrne & Whiten, 1990], and some experimental data [Gygax, 1995; Ruiz de Elvira & Herndon, 1986]; unpublished experiment mentioned in Kummer et al. [1996]. Besides, audience effects, where the presence of particular individuals affects behavior of group members, have been found in primate sexual behavior. Female chimpanzees suppress their copulation calls when in proximity of high-ranking females [Townsend et al., 2008]. Similarly, female bonobos make their copulations calls less conspicuous when copulating with subordinate males [Clay et al., 2011]. However, there are still crucial questions that remain unanswered. First, the conducted studies address effects by a number of dominants, not differentiating between the effects of specific individuals (e.g. the alpha male). Second, studies [cf. Ruiz de Elvira & Herndon, 1986; Soltis et al., 2001] do not correct for time out of sight, and therefore cannot distinguish whether a decrease in time spent in sight of dominants or a decrease of sexual activity in view of dominants determines the observed decrease of copulations in view of dominants. Third, no studies investigated the separate contribution of males and females to initiate or accept sexual behavior depending on the bystanders present.

The present study assesses whether certain males, in a socially living Rhesus macaque group, inhibit sexual behavior of group members. Rhesus macaques live in multimale–multifemale groups, in which the alpha male fathers a large proportion of the offspring (19.4–30.0% [Widdig et al., 2004]). Nonetheless, Rhesus macaques are seasonal breeders and when multiple females are in estrus (some may be ovulating synchronously), high-ranking males cannot monopolize fertile females effectively [Altmann, 1962; Massen et al., in press]. We examine whether the presence of higher ranking males inhibits sexual behavior of lower ranking males. Additionally, we test whether males and/or females refrain from soliciting copulations depending on the bystanders present. These questions were studied with an observational set-up in a captive multimale–multifemale Rhesus macaque group.

METHODS

Subjects

Observations were conducted on one group of 29 socially housed Rhesus macaques in Rijswijk, the Netherlands. Seven adult females (>3.5 years [Smuts et al., 1987]) were included in this study (Table I). Six males of the group were sexually active during the observation period (Table I). Their ages ranged from 3 to 20 years. Rhesus macaque males are sexually mature from the age of 4.5 years [Smuts et al., 1987], but males can already fertilize females from at least the age of 3.4 years [calculated by subtracting the gestation length, 186 days [Wilson et al., 1988], from the lowest male age at

TABLE I. Females and Males That Were Study Subjects, Their Sexual Activity, Age, and Relative Dominance Rank in Period 1 and Period 2

Monkey	Sexually active (potential partners ^a)	Age at the start of the mating season (years)	Relative dominance rank period 1	Relative dominance rank period 2
Females				
Burly	Yes (4/3)	9	1	1
Monica	Yes (4/3)	4.5	2	2
(Edwina ^b)	Yes (4/3)	2.5	3	3
Missie	Yes (2/2)	7.4	4	8
(Tiny ^c)	Only period 1 (2/2)	21.2	5	4
Fladder	Only period 1 (2/2)	6.6	6	5
Vlam	Only period 1 (2/2)	8.5	7	6
(Curly ^{c,d})	No (5/-)	20.5	8	10
(Fat ^{c,d})	No (5/-)	30.2	9	9
Isis	Yes (5/5)	7.2	10	11
Dragon	Yes (5/5)	3.4	11	7
Males				
Gibbon ^e	Yes (8/-)	20.3	1	-
Hollo	Yes (6/3)	3.4	2	4
Lewinsky	Yes (4/4)	4.4	3	1
Bush	Yes (4/4)	4.4	4	2
Sand	Yes (4/4)	3.4	5	3
Adam	Only period 2 (6/3)	3.3	6	5

All females between brackets were excluded from the analysis; all males listed below were treated in the analysis both as bystander males and as males that were part of a copulating dyad.

^aNumber of potential partners during period 1/2 that were sexually active and nonkin (from another matriline).

^bToo young to reproduce.

^cMay be too old to reproduce.

^dDied during the second period.

^eDied before the second period.

infant birth, that is 3.8 years [Bercovitch et al., 2003]. The group consisted of three unrelated matriline, which created the opportunity for all the subjects to have multiple unrelated sexual partners (Table I). In addition, one copulation within a matriline was observed (Fig. 2: in one out of five sibling dyads (hollo and monica); zero out of five mother–son dyads). Observations were performed from October 19, 2007 until March 19, 2008. Rhesus macaques have a marked mating season and copulations were only observed from October 24, 2007 until February 22, 2008. During the observation period, a spontaneous rank reversal took place (on December 21, 2007), including a displacement of the alpha male. The alpha male showed signs of social defeat, that is he was completely passive and immobile for more than 1 day, behavior that occasionally follows the loss of rank in alpha individuals. If this state lasts for more than 1 day, individuals do not recover and are euthanized. Alpha 1 was the alpha male in period 1: from October 24, 2007 until December 20, 2007. Alpha 2 occupied the alpha position in period 2: from January 2, 2008 until February 22, 2008. Alpha 2 was already present during period 1 occupying dominance rank three. The data were analyzed separately for the two periods. The total observation time for both periods was, respectively, 71.3 and 133.5 hr.

Housing Conditions and Experimental Cage

This study was performed making use of the normal housing conditions without hindering the animals' normal behavior. Some adjustments were necessary to visually separate the inside (72 m² and 2.85-m high) from the outside (260 m² and 3.1-m high) enclosure (Fig. 1). Two tunnels allowed the monkeys to walk freely between inside and outside enclosures, while visually separating both enclosures with nonsee-through flexible plastic flaps. The inside and outside enclosures were further visually separated by blinding the windows in between, using frosted window foil. The inside enclosure consisted of three compartments separated by concrete walls with openings through which the monkeys could walk freely. To monitor two inside compartments with two video cameras, the third inside compartment was locked during the observations. The monkeys were fed monkey chow, complemented by fresh fruit, vegetables, or bread on a daily basis. Water was provided ad libitum. The cages were provided with sawdust and permanent environmental enrichment consisting of fire hoses, tires, ladders, and a swimming pool. Extra enrichment containing food was provided at least every week [Vernes & Louwerse, 2010]. This research complied with protocols approved by the Animal Ethical Committee of the Biomedical Primate Research Center and with the legal requirements of the Netherlands. The research adhered to the American Society of Primatologists

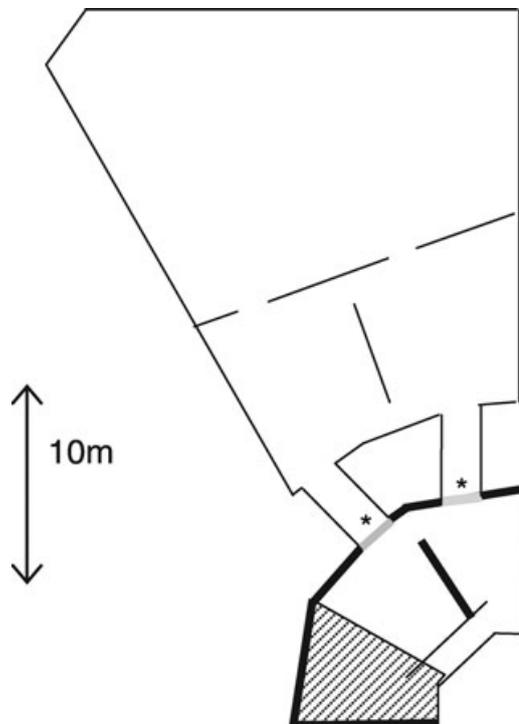


Fig. 1. Schematic layout of the cage. Inside enclosures were surrounded by a concrete wall, indicated by bold lines, the outside enclosure by wire mesh, indicated by thin lines. Openings in the wall are indicated with a (*), these permitted monkeys to walk through but not see through as they were covered by plastic flaps. The striped area was an inside compartment only available for the monkeys outside observation hours.

(ASP) Principles for the Ethical Treatment of Non Human Primates.

Data Collection

Observations in the outside enclosure were conducted by one observer using Noldus The Observer 5.0 while two cameras (Sony, DCR-SR72, Sony Corp., Tokyo, Japan) registered events in the inside enclosure. These videos were analyzed by the same observer using Noldus The Observer XT 7.0 (Noldus Information technology B.V., Wageningen, the Netherlands). Data were collected twice a day in observation slots of 2 hr, the first observation slot was between 9:15 and 12:23 hr and the second between 13:21 and 16:24 hr.

The presence of the focal animals in the inside or outside enclosure was recorded continuously during the outside observations. In addition, the presence of the alpha male in the inside enclosure was recorded during the analysis of the videos. During outside observations and video scoring, all occurrences of sexual (Table II) and dominance interactions were recorded with the main focus on sexual behavior.

The dominance hierarchy of the group was determined during each of the two observation periods, on the basis of submissive signals, that is teeth-baring

TABLE II. Sexual Behaviors of Rhesus Macaques [Based on Altmann, 1962; Manson, 1996]

Copulation solicitations and reactions	
Sexual presentation	Female presents the hindquarters in the direction of a male
Lift female	Male lifts a sitting female to standing position by pulling her upwards by her tail
Grasp waist	Male places his hand on the rump of the female
Ignore female solicitation	Male is not coming closer to nor trying to mount the female during the sexual presentation or within 10 sec after it stopped
Accept female solicitation	Male mounts the female during or within 10 sec after a sexual presentation
Ignore male solicitation	Female remains seated while the male grasps waist, or she walks away from the male for more than an arm length, or she presents sexually to the male, but sits down again or walks away when the male tries to grasp the legs of the female with his hind legs
Accept male solicitation	Female accepts that the male mounts her without one of the "ignore male solicitation" behaviors between the male solicitation and the mount
Copulation	
Mount	Male mounts the female by grasping her hind legs followed by one or more pelvic thrusts
Pelvic thrust	Movement of the hips of the male while mounted
Copulation	A series of more than one mount ^a . A copulation ends when the copulating dyad is more than an arm length away from each other for more than 5 min [Manson 1996]

^aA criterion of more than one mount is taken to define a copulation, because single mounts often occur in a nonsexual context. Mount series outside the breeding season are generally single mounts between heterosexual or homosexual dyads and are less often accompanied by thrusting [Hanby & Brown, 1974]. Single mounts inside the breeding season seldom end in ejaculation [Manson 1996] (in the current study no ejaculatory pause was observed during a single mount).

and unprovoked avoidance (to move away from a nonaggressive approaching animal). Teeth-baring is a good indicator of dominance rank [de Waal & Luttrell, 1985], since it is a unidirectional submissive display in Rhesus macaques and consistently reflects the relative status of adults independent of short-term contextual variation [Maestripieri & Wallen, 1997; van Hooff, 1962]. Because teeth-baring alone did not yield sufficient data, unprovoked avoidance behavior between two individuals was added. From the resulting matrix, the dominance hierarchy was

obtained [de Vries, 1998] using Matman 1.1 [de Vries et al., 1993], and in both periods, the dominance hierarchy was significantly linear (period 1: $h' = 0.40$, $P < 0.05$; period 2: $h' = 0.53$, $P < 0.001$) [de Vries, 1995].

Data Analyzes

The inhibiting effect of particular bystanders was studied on different aspects of sexual behavior. We concentrated on the effect of male and not on female bystanders, since copulation disruption by female Rhesus macaques is rarely reported [Dixon, 1998, p. 72, table 4.5] and less supported by theory [Niemeyer & Anderson, 1983]. First, the effect on copulations was determined. This was done for all possible bystander males, that is all males that were sexually active (Table I). We predicted high-ranking bystander males, but not low-ranking bystander males, to have an inhibiting effect on the copulations of their group members (see above). However, we included lower ranking males in the analysis as bystander males, to get a complete picture which individuals did and did not have such an effect, and to investigate whether the monkeys leave the entire group or are sensitive to a particular bystander male in the audience. Second, the effect of the bystander male on the rates of female or male copulation solicitations was determined. Females solicit copulations with "sexual presentations," while males solicit copulations both with "grasp waist" and "lift female" (Table II). Third, copulation solicitations often preceded copulations, but could be rejected by the partner (Table II). We tested whether females and males more often accepted copulation solicitations when a particular bystander male was out of sight than when he was in sight.

We calculated the rate of sexual behavior in the presence and absence of a particular bystander male for both periods separately. With "present," we mean in the same enclosure as the copulating couple. Recall from the cage description that the two enclosures were visually separated from each other. Since the monkeys were able to move around freely, their time spent with a particular bystander male differed from their time without this particular bystander male. A simple comparison between the number of sexual behaviors with and without a high-ranking bystander male could be biased by the fact that subordinate males spent less time close to higher ranking males. Therefore, we calculated, for both periods separately, the copulation rate for each female-male dyad across all time slots in which they were together in the same enclosure with the bystander male present $S(\text{pr})$, and similarly across all time slots that they were together in the same enclosure, but in absence of the bystander male $S(\text{ab})$. Subsequently, $S(\text{ab})$ was subtracted from $S(\text{pr})$ resulting in ΔS , which represents the size of the inhibiting effect by the

presence of the bystander male. To analyze the inhibition of alpha males, we combined the data for both periods by calculating a mean ΔS for each female-male dyad. This larger data set allowed us to carry out a general linear mixed model (GLMM) analysis with copulation rate as the dependent variable, presence of alpha male as fixed factor, and male and female identity as random factors. Subsequently, to disentangle the effect of both alpha males, we used a mean ΔS per female for each of the two periods separately and tested whether ΔS differed between the alpha present and absent condition using the paired *t*-test. A GLMM was not possible here because of the smaller data set with incomputable degrees of freedom. Females, and not males, were chosen as statistical units as we had more female than male subjects. The same procedure, using the *t*-test, was used for the effect of nonalpha males on copulation rates and for the effect of bystander males on female copulation solicitations and female acceptance of copulation solicitations. When studying the effect of bystander males on male copulation solicitation and male acceptance of copulation solicitations, males were used as statistical units. Since a few data sets significantly differed from a normal distribution (Shapiro-Wilk Normality Test, $\alpha \leq 0.05$, for small sample sizes of minimal $N = 3$) and transformation of the data did not change this, we used the nonparametric equivalent Wilcoxon signed-rank test for these data sets. We executed two-tailed tests with $\alpha \leq 0.05$. Additionally, we mention trends with $P < 0.10$. All statistical tests were performed using the software package "R" [Ihaka & Gentleman, 1996] version 2.7.1.

The analysis of the effect of the alpha males was based on more hours of observation than the analysis of the other males. For both alpha males, we simultaneously recorded events inside and outside and used both data sets for the analysis. The analysis of the other males was based only on the data set we collected in the outside enclosures and thus approximately half as many observation hours, since recognition of individual males during entrance and departure was difficult from the videos recorded in the inside enclosure. Hence, the chance of finding an effect for nonalpha males was smaller than for alpha males.

RESULTS

Distribution of Copulations in the Group

During the first period, 34 copulations (31 involving nonalpha males), 103 female solicitations (94 involving nonalpha males), and 62 male solicitations (56 involving nonalpha males) were observed. During period 2, 90 copulations (52 involving nonalpha males), 268 female solicitations (217 involving nonalpha males), and 152 male solicitations (101 involving nonalpha males) were observed. Copulation rates

were 0.88 and 0.67 copulations per observation hour in period 1 and 2, respectively. Alpha males showed aggressive interference of copulations in their view (alpha 1 interfered in 1 of 3 and alpha 2 in 4 of 8 copulations). Nonalpha males also interrupted copulations of their group members. In period 1, the second-ranking male interrupted two copulations, and in period 2, the third-ranking male once interrupted a copulation. Also, females interrupted copulations; the alpha-female and the second-ranking female both interrupted copulations once in period 1. In period 2, the first-, second-, and fourth-ranking females accomplished nine, three, and one interruptions of copulations, respectively. None of the other individuals interrupted copulations of group members. Aggression involved in interruptions was almost exclusively directed at an individual that was lower in rank than the aggressor, with one exception: the second-ranking female once directed her aggression toward the alpha male while he was copulating with the alpha female.

In general, males and females that copulated more than once during the mating season had more than one copulation partner (Fig. 2). This was evident for both period 1 and 2 with the exception of the lowest ranking male (he only copulated twice, both times with the same female). The mean number of receptive females per day was $2.30 \pm \text{SD } 1.49$ in period 1 and $2.12 \pm \text{SD } 1.24$ in period 2. There were seven instances (period 1 and 2, respectively, four and three instances) of females copulating with two males on the same day. Females often behave receptively toward more than one male per day by sexually presenting toward, on average, $1.3 \pm \text{SD } 0.50$ males (period 1 and 2, respectively, on average $1.28 \pm \text{SD } 0.50$ and $1.33 \pm \text{SD } 0.50$ males per day a female was sexually active). Alpha 1 was involved in 9% (3 of 34) of the copulations in period 1. Alpha 2 was involved in 42% (38 of 90) of the copulations in period 2. Hence, alpha 2 monopolized a higher proportion of the copulations than alpha 1 (exact binomial test: $P < 0.001$).

High-ranking males had a significantly higher number of copulations than low-ranking males in period 2, but not in period 1 (Spearman rank correlation: period 1, $r_s = -0.085$, $N = 6$, $P = 0.92$; period 2: $r_s = -1$, $N = 5$, $P < 0.05$). Female dominance rank was not related with the number of copulations (Spearman rank correlation: period 1: $r_s = -0.075$, $N = 7$, $P = 0.87$; period 2: $r_s = -0.16$, $N = 7$, $P = 0.73$).

The Effect of Bystander Males on Copulations

The presence of some bystander males may affect sexual behavior of group members. The key result is that females copulate less often with nonalpha males in the presence than in the absence of an alpha male (GLMM: $F = 21.56$, $df = 1$, $P < 0.01$). In the first period, 28 of 31 copulations with nonalpha males

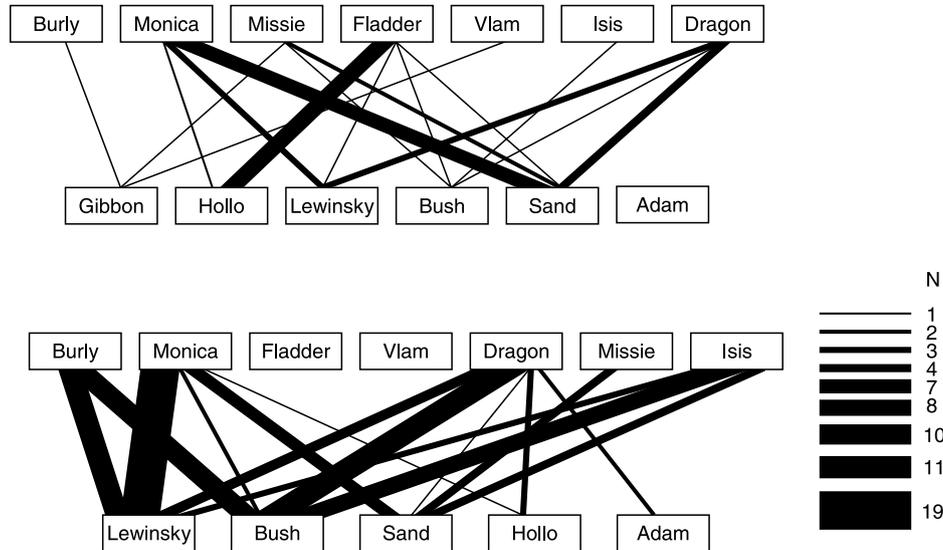


Fig. 2. Distribution of copulations in the group in period 1 (top) and period 2 (bottom). The weight of the line corresponds with the number of copulations (N) within a particular copulating dyad. Females are listed at the top row of each scheme, males at the bottom. The names of the males and females are sorted from high (left) to low (right) dominance rank.

TABLE III. Mean [and Range] of the Number of Copulations and Time Spent in Presence and Absence of Each Possible Bystander Male in Both Periods

Rank	No. of copulations per couple		Time spent (hours/couple)		
	Presence	Absence	Presence	Absence	
Period 1					
1	0.23 [0–1]	2.15 [1–7]	31.3 [27.3–35.2]	12.7 [7.1–19.7]	
2	0.53 [0–2]	0.93 [0–4]	5.0 [1.0–10.4]	3.3 [0.9–7.6]	
3	0.54 [0–4]	1.31 [0–5]	14.7 [11.9–17.2]	9.5 [7.3–15.8]	
4	0.92 [0–5]	1.17 [0–4]	6.7 [1.9–12.4]	3.7 [0.9–8.1]	
5	0.81 [0–3]	0.82 [0–4]	5.5 [2.2–9.7]	3.9 [0.6–7.9]	
6	0.69 [0–2]	1.23 [0–5]	3.9 [2.6–5.9]	3.2 [0.5–12.6]	
Period 2					
1	0.73 [0–2]	3.91 [1–9]	86.5 [80.2–99.1]	17.2 [13.7–19.9]	
2	0.40 [0–1]	2.60 [1–6]	4.1 [2.3–6.5]	5.0 [1.9–8.4]	
3	1.20 [0–5]	2.90 [1–9]	3.7 [2.4–6.4]	5.6 [2.3–9.2]	
4	1.08 [0–3]	3.00 [0–7]	3.2 [1.9–5.0]	6.1 [2.3–10.8]	
5	0.93 [0–6]	2.93 [0–9]	3.4 [1.4–5.6]	5.8 [0.6–10.0]	

Bystander males are represented by their dominance rank number; means and ranges are based on data per couple that copulated in the corresponding period.

occurred in absence of the alpha male. In the second period, 43 of 51 copulations occurred in absence of the alpha male. Per couple on average 0.23 and 0.73 copulations occurred in presence and 2.15 and 3.91 copulations in absence of alpha 1 and 2, respectively (Table III).

During period 1, five females copulated with non-alpha males (the first- and fifth-ranking female exclusively copulated with the alpha male). Females copulated with nonalpha males significantly more often in the absence of than in the presence of alpha 1 (paired *t*-test: $T = 4.9$, $df = 4$, $P < 0.01$, Fig. 3a). However, the alpha male was not the only male who inhibited copulations in period 1, since the presence

of the third-ranking male also inhibited copulations of group members (paired *t*-test: $T = 2.6$, $df = 6$, $P < 0.05$, Fig. 3b). Of the 28 copulations performed by other males than the third-ranking male, 17 were performed in his absence. Per dyad, on average, 0.54 copulations were performed in presence of the third-ranking male and 1.31 copulations in his absence (Table III). Two males that were higher in rank than the third-ranking male copulated more often in his absence than in his presence although both males spent more time together with a female in presence than in absence of the third-ranking male. The alpha male was observed to copulate two of three times in absence of the third-ranking male. The

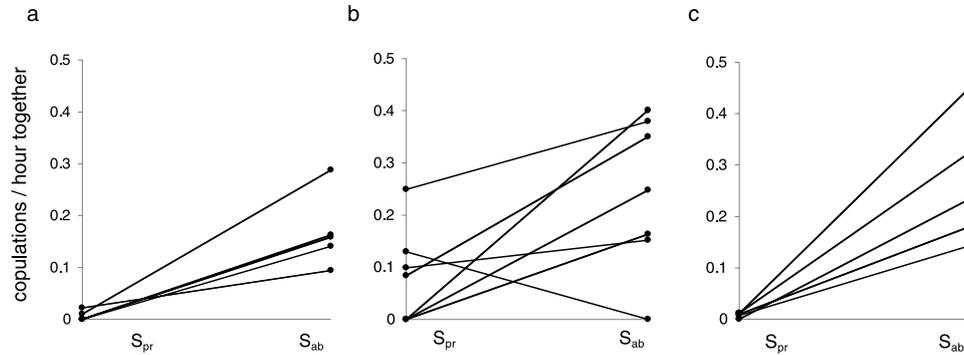


Fig. 3. The rate of copulations in situations with (S_{pr}) and without (S_{ab}) a particular bystander male's presence: (a) bystander male = alpha 1; (b) bystander male = third-ranking male in period 1; (c) bystander male = alpha 2. Each line in the figure represents a female; (a) $N = 5$, (b) $N = 7$, (c) $N = 5$.

second-ranking male copulated eight of ten times in absence of the third-ranking male. None of the other bystander males in period 1 had a significant effect on copulations of females with other males during either of the two periods (paired t -test: $P > 0.195$).

During period 2, five females copulated with non-alpha males (the third- and fourth-ranking females did not copulate). Also in this period, females started their copulations with nonalpha males significantly more often in the absence of than in presence of the alpha male (paired t -test: $T = 4.8$, $df = 4$, $P < 0.01$, Fig. 3c). None of the nonalpha bystander males in period 2 had a significant effect on copulations of females with other males during either of the two periods (paired t -test: $P > 0.109$).

The Effect of Bystander Males on Copulation Solicitations

In period 1, females sexually presented significantly more often to nonalpha males when alpha 1 was absent than when he was present (paired t -test: $T = 3.2$, $df = 5$, $P < 0.05$, Fig. 4a). However, in this period, the inhibition of female solicitation behavior was not exclusive to the alpha male, since three non-

alpha bystander males significantly inhibited female copulation solicitations toward other males. These inhibiting males were the second- (Paired t -test: $T = 2.8523$, $df = 5$, $P < 0.05$), the fourth- (Wilcoxon signed-ranks test: $Z = 21$, $N = 6$, $P < 0.05$), and sixth-ranking male (Wilcoxon signed-ranks test $Z = 26$, $N = 7$, $P < 0.05$). The third-ranking male had a trend of inhibiting female copulation solicitations (Paired t -test: $T = 2.5437$, $df = 5$, $P = 0.064$), and the fifth-ranking male had no significant effect (Paired t -test: $T = 1.10$, $df = 5$, $P = 0.322$).

Similarly in period 2, females solicited more often in the absence of than in the presence of alpha 2 (Wilcoxon signed-ranks test: $Z = 26$, $N = 7$, $P < 0.05$, Fig. 4a). Additionally, the fifth-ranking male had an inhibitory effect on the frequency of female solicitations in period 2 (Wilcoxon signed-ranks test: $Z = 21$, $N = 6$, $P < 0.05$). The remaining three males had no significant effect ($P > 0.136$).

Also for males, we determined whether they changed their behavior in the presence of a bystander male. In both periods nonalpha males tended to solicit copulations more often in presence than in absence of the alpha male (paired t -test: period 1: $T = 2.6$, $df = 3$, $P = 0.083$; period 2: $T = 2.7$, $df = 3$, $P = 0.074$) (Fig. 4b). None of the nonalpha bystander males had a significant effect on the copulation solicitations of other males in both periods ($P > 0.119$).

The Effect of Bystander Males on Acceptance of Copulation Solicitations

In period 1, six of seven females received copulation solicitations from nonalpha males. These females accepted solicitations from these males equally often in the absence of and in the presence of the alpha male (paired t -test: $T = -1.767$, $df = 5$, $P = 0.138$, Fig. 5a). Also, none of the other bystander males in period 1 had an effect on females accepting copulation solicitations from males ($P > 0.604$).

In period 2, all seven females received copulation solicitations by nonalpha males. Females tended to

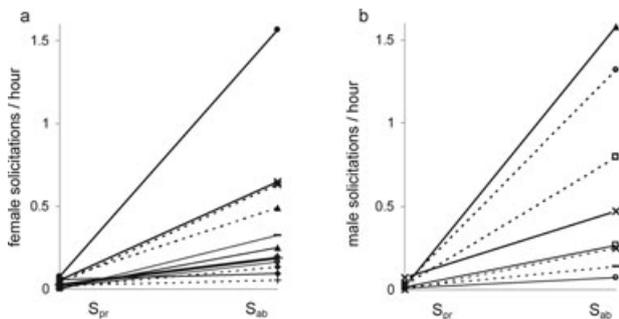


Fig. 4. The rate of copulation solicitations by females (a) and subordinate males (b) in situations with (S_{pr}) and without (S_{ab}) the alpha male present. Solid lines represent period 1, while dotted lines represent period 2. Similar symbols are used for the same individual in both periods.

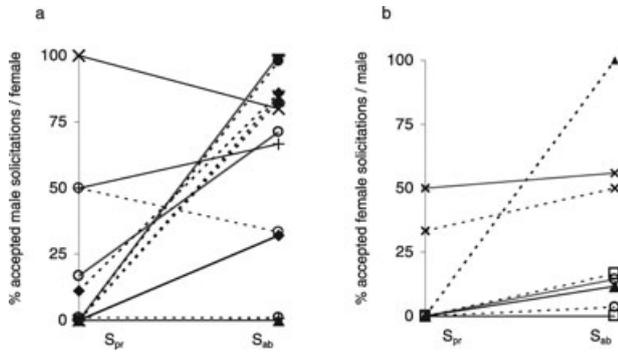


Fig. 5. The proportion of copulation solicitations accepted by females (a) and males (b) in situations with (S_{pr}) and without (S_{ab}) the alpha male present. Solid lines represent period 1, while dotted lines represent period 2. Similar symbols are used for the same individual in both periods.

accept solicitations more often in the absence of than in the presence of the alpha male (paired t test: $T = 2.6$, $df = 6$, $P = 0.073$, Fig. 5a). None of the other males in period 2 had an effect on females accepting copulation solicitations from other males ($P > 0.578$).

Also for males, we determined whether they adjusted their acceptance of female copulation solicitations to the presence of bystander males. Males tended to accept copulation solicitations from females more often in absence than in presence of alpha 1 (paired t -test: $T = 2.5$, $df = 3$, $P = 0.088$) and alpha 2 had no significant influence on the acceptance of copulation solicitations by males (Wilcoxon signed-ranks test: $Z = 10$, $N = 4$, $P = 0.125$) (Fig. 5b). None of the nonalpha males had a significant inhibiting effect on male acceptance of female copulation solicitations in both periods ($P > 0.200$).

DISCUSSION

We investigated the mating pattern of female and male Rhesus macaques, a primate species with a promiscuous mating pattern. Our results show that females and nonalpha males copulate at higher rates and show sexual solicitations and tend to accept these solicitations more often in the absence than in the presence of the alpha male. These audience effects may not be limited to the alpha males, but were also found in some nonalpha males.

Since females gain potential benefits from promiscuity and nonalpha males also aim to copulate, but the alpha male monopolizes females, females and nonalpha males may avoid copulating in presence of the alpha male. Such an inhibition of sexual behavior by the mere presence of an individual can be categorized as an audience effect. In primates, audience effects have been shown in different contexts such as greeting [Laporte & Zuberbühler, 2010], predator warning [Wich & Sterck, 2003], mother–infant interactions [Semple et al., 2009], and in sexual contexts [Townsend & Zuberbühler, 2009].

Adding to the literature on audience effects in sexual contexts, our results show that indeed female Rhesus macaques copulate with nonalpha males more often when the alpha male is temporarily absent. This is in line with our prediction and agrees with previous findings [Kummer et al., 1996; Ruiz de Elvira & Herndon, 1986]. Since we, in contrast to Ruiz de Elvira and Herndon [1986], corrected the number of copulations in the presence and absence of the alpha male for the actual time each dyad spent in these conditions, our analysis precludes that effects such as subordinates avoiding or being chased away by dominant individuals were responsible for the results, but shows that the rate of copulations was affected. However, whether the audience effect represents a shift of sexual behavior resulting in a higher rate of sexual behavior by females and subordinate males in the absence of the alpha-male, or represents a reduction of sexual behavior because sexual behavior by females and subordinate males is reduced in presence of the alpha male, remains unclear.

Our data suggest that the audience effect is not unique for the alpha male, since also nonalpha males had an inhibiting effect on the rate of sexual behavior of their group members. In period 1, the third-ranking male had a significant inhibiting effect on copulations of group members. On the one hand, this result is tentative, as this male later became the alpha male, and thus his ascending trajectory may have caused his audience effect. On the other hand, three other nonalpha males that were not rising alpha males also inhibited female solicitations to males. Although the inhibiting males were not necessarily the highest ranking males, which is not in line with our prediction, at least it is clear that some nonalpha males inhibit sexual behavior of females. Copulating out of view of nonalpha males may prevent interruption of copulations by males other than the alpha male [Berard et al., 1994; Chapais, 1983; Manson, 1996; Ruiz de Elvira & Herndon, 1986; this study]. What's more, the third-ranking male also inhibited copulations of even higher ranking males, including the alpha male. Although this seems counterintuitive, because alpha males often consort females and chase away other males [Alberts et al., 2006; Berard et al., 1994; de Ruiter et al., 1994], also the sexual behavior of the alpha male can be interrupted by other males [Ruiz de Elvira & Herndon, 1986]. Despite alpha male consorts, Rhesus macaque alpha males are in some groups not the most frequent copulating males (this study) or not even responsible for most of successful copulations [Duvall et al., 1976]. Therefore, it may be as important for an alpha male as for other males to reduce interruptions of copulations. Nevertheless, since alpha males are able to consort females during their fertile phase, it may be less relevant for them if they have a few copulations disrupted. Notwithstanding, even for alpha males, preventing disruptions reduces energy

loss due to unsuccessful copulations and aggression-based injuries. Thus, future research should consider a possible audience effect of nonalpha males on all other individuals in the group, including an effect on higher ranking males.

In contrast with previous research, which rarely reports copulation disruption by female Rhesus macaques [Dixon, 1998, p. 72, tabel 4.5], our study revealed that females were responsible for more disruptions of copulations than males. This contrast may be due to the dominance position of our alpha female, which was higher than the alpha male in period 2. However, this does not explain why two other females displayed a considerable amount of disruptions. Therefore, it would be worthwhile to study an audience effect of females on Rhesus macaque sexual behavior.

Male and Female Coordinated Responses to the Audience

Potentially, both subordinate males and females involved in a copulation may benefit from hiding the copulation. However, when copulations of subordinate Rhesus macaque males with females are disrupted, it is mostly the female that experiences the brunt of the aggression [Manson, 1996; Ruiz de Elvira & Herndon, 1986]. Therefore, mainly females are expected to benefit from hiding their copulations with subordinate males. In contrast, male Rhesus macaques that are disrupted during copulations do not have reduced fitness compared to undisrupted males [Berard et al., 1994]. Thus based on the literature, it is predicted that females, but not males, adjust their behavior to the presence of an audience. Indeed, when ignoring the trends, females, but not males, more often solicit and accept solicitations to copulate in the absence than in the presence of bystander males. However, when trends are considered meaningful, males were found to solicit and accept more solicitations in absence than in presence of the alpha male in both periods. Therefore, the absence of a significant audience effect on male sexual behavior may be due to our low number of males, and consequently the low statistical power, rather than the absence of an effect. This suggests a benefit of hiding sexual behavior for both partners involved in a copulation. Alternatively, females may benefit, while males have an indirect benefit when females are more willing to copulate in occluded conditions, and this may result in a male sensitivity to the audience.

Audience effects on sexual behavior are expected when alpha males cannot well monopolize females and females have the option to mate promiscuously (see Introduction). Therefore, audience effects will co-occur with indicators of female promiscuity such as seasonal breeding, which complicates monopolization for the alpha male [Emlen & Oring, 1977],

exaggerated swellings, which increase the duration of sexual activity [Nunn, 1999], and extended female receptive periods, which obscure female fertility [Heistermann et al., 2001]. Moreover, for an audience effect, a clear dominance hierarchy and disruptions of copulations may be required. Indeed, Rhesus macaques have all these characteristics (promiscuity [Small, 1990], a clear dominance hierarchy [Miller & Murphy, 1956], and disruptions of copulations [Manson, 1996; Ruiz de Elvira & Herndon, 1986]) and exhibit audience effects (this study). Similarly, chimpanzees also largely fit these characteristics (promiscuity [Hasegawa & Hiraiwa-Hasegawa, 1990], clear female dominance hierarchy [Wittig & Boesch, 2003], and disruption of copulations [Tutin, 1979]) and show audience effects [Townsend & Zuberbühler, 2009]. However, whether audience effects depend on one or on a particular combination of features remains to be studied.

In conclusion, several audience effects on sexual behavior of Rhesus macaques were found. First, the rate of sexual behavior of female and subordinate male Rhesus macaques is higher in the absence of than in the presence of the alpha male. Second, also the presence of some nonalpha bystander males reduced the rate of sexual behavior. Third, one nonalpha bystander male had an audience effect on higher ranking males's sexual behavior including the alpha male. Furthermore, females altered their sexual behavior in response to an audience effect, while for males it is less certain. This indicates that females, but possibly not males, benefit from hiding their copulations. Altogether, monopolization by the alpha male may be opposed by a relatively high rate of sexual behavior from females with subordinate males in his absence, but also by a relatively low rate of sexual behavior by females with the alpha male in the presence of some nonalpha males.

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REFERENCES

- Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim Behav* 72:1177–1196.
- Alfaro JW. 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). *Am J Primatol* 67:313–328.

- Altmann SA. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Ann N Y Acad Sci* 102:338–435.
- Amici F, Call J, Aureli F. 2009. Variation in withholding of information in three monkey species. *Proc R Soc B Biol Sci* 276:3311–3318.
- Berard J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates* 40:159–175.
- Berard JD, Nürnberg P, Epplen JT, Schmidtke J. 1993. Male rank, reproductive-behavior, and reproductive success in free-ranging rhesus macaques. *Primates* 34:481–489.
- Berard JD, Nürnberg P, Epplen JT, Schmidtke J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* 129:177–201.
- Bercovitch FB, Widdig A, Trefilov A, Kessler MJ, Berard JD, Schmidtke J, Nürnberg P, Krawczak M. 2003. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften* 90:309–312.
- Birkhead T. 2000. Promiscuity: an evolutionary history of sperm competition and sexual conflict. London: Faber & Faber. 272 p.
- Boesch C, Kohou G, Néné H, Vigilant L. 2006. Male competition and paternity in wild chimpanzees of the Tai forest. *Am J Phys Anthropol* 130:103–115.
- Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. *Nature* 425:179–181.
- Bulger JB. 1993. Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 127:67–103.
- Byrne RW, Whiten A. 1990. Tactical deception in primates: the 1990 database. *Primate Report* 27:1–101.
- Chapais B. 1983. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. *Behav Ecol Sociobiol* 12:215–228.
- Cicirello DM, Wolff JO. 1990. The effects of mating on infanticide and pup discrimination in white-footed mice. *Behav Ecol Sociobiol* 26:275–279.
- Clay Z, Pika S, Gruber T, Zuberbühler K. 2011. Female bonobos use copulation calls as social signals. *Biol Lett* 7:513–516.
- Cowlshaw G, Dunbar RIM. 1991. Dominance rank and mating success in male primates. *Anim Behav* 41:1045–1056.
- de Ruiter JR, Scheffrahn W, Trommelen GJJM, Uiterlinden AG, Martin RD, van Hooff JARAM. 1992. Male social rank and reproductive success in wild long-tailed macaques. In: Martin RD, Dixon AF, Wickings EJ, editors. *Paternity in primates: genetic tests and theories*. Basel, Switzerland: Karger. p 175–191.
- de Ruiter JR, van Hooff JARAM. 1993. Male dominance rank and reproductive success in primate groups. *Primates* 34:513–523.
- de Ruiter JR, van Hooff JARAM, Scheffrahn W. 1994. Social and genetic-aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* 129:203–224.
- de Vries H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim Behav* 50:1375–1389.
- de Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim Behav* 55:827–843.
- de Vries H, Netto WJ, Hanegraaf PLH. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* 125:157–175.
- de Waal FBM, Luttrell LM. 1985. The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *Am J Primatol* 9:73–85.
- Dixon AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings. Oxford: Oxford University Press. 546 p.
- Dixon AF, Anderson MJ. 2002. Sexual selection, seminal coagulation and copulatory plug formation in primates. *Folia Primatol* 73:63–69.
- Dubuc C, Muniz L, Heistermann M, Engelhardt A, Widdig A. 2011. Testing the priority-of-access model in a seasonally breeding primate species. *Behav Ecol Sociobiol* 65:1615–1627.
- Duvall SW, Bernstein IS, Gordon TP. 1976. Paternity and status in a rhesus monkey group. *J Reprod Fertil* 47:25–31.
- Ebensperger LA. 1998. Strategies and counterstrategies to infanticide in mammals. *Biol Rev* 73:321–346.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215–223.
- Engelhardt A. 2004. The significance of male and female reproductive strategies for male reproductive success in wild longtailed macaques (*Macaca fascicularis*). Göttingen, Germany: Cuvillier verlag. 109 p.
- Engelhardt A, Pfeifer JB, Heistermann M, Niemitz C, Van Hooff JARAM, Hodges JK. 2004. Assessment of female reproductive status by male longtailed macaques, *Macaca fascicularis*, under natural conditions. *Anim Behav* 67:915–924.
- Garcia C, Shimizu K, Huffman M. 2009. Relationship between sexual interactions and the timing of the fertile phase in captive female Japanese macaques (*Macaca fuscata*). *Am J Primatol* 71:868–879.
- Gygax L. 1995. Hiding behaviour of long-tailed macaques (*Macaca fascicularis*): I. Theoretical background and data on mating. *Ethology* 101:10–24.
- Hanby JP, Brown CE. 1974. The development of sociosexual behaviours in Japanese Macaques *Macaca fuscata*. *Behaviour* 49:152–195.
- Hasegawa T, Hiraiwa-Hasegawa MI. 1990. Sperm competition and mating behavior. In: Nishida T, editor. *The chimpanzees of the Mahale mountains*. Tokyo: University of Tokyo press. p 115–132.
- Hausfater G, Hrdy SB. 1984. Infanticide: comparative and evolutionary perspectives. New York: Aldine. 598 p.
- Heistermann M, Ziegler T, van Schaik CP, Launhardt K, Winkler P, Hodges JK. 2001. Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proc R Soc Lond B Biol Sci* 268:2445–2451.
- Hrdy SB. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13–40.
- Ihaka R, Gentleman R. 1996. R: a language for data analysis and graphics. *J Comput Graph Stat* 5:299–314.
- Inoue E, Takenaka O. 2008. The effect of male tenure and female mate choice on paternity in free-ranging Japanese macaques. *Am J Primatol* 70:62–68.
- Janson CH. 2000. Primate socio-ecology: the end of a golden age. *Evol Anthropol* 9:73–86.
- Klinkova E, Hodges JK, Fuhrmann K, de Jong T, Heistermann M. 2005. Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *Int J Primatol* 26:357–384.
- Kummer H. 1968. Social organization of Hamadryas baboons: a field study. Chicago, IL: University of Chicago Press. 189 p.
- Kummer H, Anzenberger G, Hemelrijk CK. 1996. Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *J Comp Psychol* 110:97–102.
- Laporte MNC, Zuberbühler K. 2010. Vocal greeting behaviour in wild chimpanzee females. *Anim Behav* 80:467–473.
- Lindburg DG. 1971. The rhesus monkey in north India: an ecological and behavioural study. In: Rosenblum LA, editor. *Primate behaviour: developments in field and laboratory research*. New York: Academic Press. p 1–106.
- Maestriperi D, Wallen K. 1997. Affiliative and submissive communication in rhesus macaques. *Primates* 38:127–138.

- Manson JH. 1996. Male dominance and mount series duration in Cayo Santiago rhesus macaques. *Anim Behav* 51:1219–1231.
- Massen JJM, Overduin - de Vries AM, de Vos-Rouweler AJM, Spruijt BM, Doxiadis GGM, Sterck EHM. In press. Male mating tactics in captive rhesus macaques, *Macaca mulatta*: the influence of dominance, markets and relationship quality. *Int J Primatol*. DOI: 10.1007/s10764-011-9552-5
- McMillan CA. 1989. Male age, dominance, and mating success among rhesus macaques. *Am J Phys Anthropol* 80:83–89.
- Miller RE, Murphy JV. 1956. Social interactions of rhesus monkeys: 1. Food-getting dominance as a dependent variable. *J Soc Psychol* 44:249–255.
- Newton PN. 1988. The variable social organization of hanuman langurs (*Presbytis entellus*), infanticide, and the monopolization of females. *Int J Primatol* 9:59–77.
- Niemeyer CL, Anderson JR. 1983. Primate harassment of matings. *Ethol Sociobiol* 4:205–220.
- Nikitopoulos E, Heistermann M, De Vries H, van Hooff JARAM, Sterck EHM. 2005. A pair choice test to identify female mating pattern relative to ovulation in longtailed macaques, *Macaca fascicularis*. *Anim Behav* 70:1283–1296.
- Nunn CL. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim Behav* 58:229–246.
- Nunn CL, Gittleman JL, Antonovics J. 2000. Promiscuity and the primate immune system. *Science* 290:1168–1170.
- Ostner J, Nunn CL, Schülke O. 2008. Female reproductive synchrony predicts skewed paternity across primates. *Behav Ecol* 19:1150–1158.
- Paul A, Kuester J, Timme A, Arnemann J. 1993. The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates* 34:491–502.
- Robbins MM. 1999. Male mating patterns in wild multimale mountain gorilla groups. *Anim Behav* 57:1013–1020.
- Ruiz de Elvira M, Herndon JG. 1986. Disruption of sexual behaviour by high ranking rhesus monkeys (*Macaca mulatta*). *Behaviour* 96:227–239.
- Semple S, Gerald MS, Suggs DN. 2009. Bystanders affect the outcome of mother-infant interactions in rhesus macaques. *Proc R Soc B Biol Sci* 276:2257–2262.
- Small MF. 1990. Consortships and conceptions in captive rhesus macaques (*Macaca mulatta*). *Primates* 31:339–350.
- Smith DG. 1993. A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* 34:471–480.
- Smith DG. 1994. Male dominance and reproductive success in a captive group of rhesus macaques (*Macaca mulatta*). *Behaviour* 129:225–242.
- Smuts BB. 1985. Sex and friendship in baboons. New York: Aldine de Gruyter. 303 p.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT. 1987. Primate societies. London: The University of Chicago Press. 578 p.
- Smuts BB, Smuts RW. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Study Behav* 22:1–63.
- Soltis J. 2002. Do primate females gain nonprocreative benefits by mating with multiple males? Theoretical and empirical considerations. *Evol Anthropol* 11:187–197.
- Soltis J, Mitsunaga F, Shimizu K, Nozaki M, Yanagihara Y, Domingo-Roura X, Takenaka O. 1997. Sexual selection in Japanese macaques II: female mate choice and male-male competition. *Anim Behav* 54:737–746.
- Soltis J, Thomsen R, Takenaka O. 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Anim Behav* 62:485–494.
- Takahata Y, Huffman MA, Suzuki S, Koyama N, Yamagiwa J. 1999. Why dominants do not consistently attain high mating and reproductive success: a review of longitudinal Japanese macaque studies. *Primates* 40:143–158.
- Thrall PH, Antonovics J, Dobson AP. 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. *Proc R Soc Lond B Biol Sci* 267:1555–1563.
- Townsend SW, Deschner T, Zuberbühler K. 2008. Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS ONE* 3:1–7.
- Townsend SW, Zuberbühler K. 2009. Audience effects in chimpanzee copulation calls. *Commun Integr Biol* 2:282–284.
- Tutin CEG. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav Ecol Sociobiol* 6:29–38.
- van Hooff ARAM. 1962. Facial expressions in primates. *Symp Zool Soc Lond* 8:97–125.
- van Noordwijk MA, van Schaik CP. 2000. Reproductive patterns in eutherian mammals: adaptations against infanticide? In: van Schaik CP, Janson CH, editors. *Infanticide by males and its implications*. Cambridge: Cambridge University Press. p 322–360.
- van Noordwijk MA, van Schaik CP. 2004. Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Kappeler PM, van Schaik CP, editors. *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press. p 208–229.
- van Schaik CP, Pandit SA, Vogel ER. 2004. A model for within-group coalitional aggression among males. *Behav Ecol Sociobiol* 57:101–109.
- Vernes MK, Louwse AL. 2010. BPRC's enrichment manual for macaques & marmosets. Rijswijk, the Netherlands: Biomedical Primate Research Centre. 80 p.
- Wich SA, Sterck EHM. 2003. Possible audience effect in Thomas Langurs (primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *Am J Primatol* 60:155–159.
- Wickings EJ, Bossi T, Dixon AF. 1993. Reproductive success in the mandrill, *Mandrillus sphinx*: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. *J Zool* 231:563–574.
- Widdig A, Bercovitch FB, Streich WJ, Saueremann U, Nürnberg P, Krawczak M. 2004. A longitudinal analysis of reproductive skew in male rhesus macaques. *Proc R Soc Lond B Biol Sci* 271:819–826.
- Wilson ME, Walker ML, Pope NS, Gordon TP. 1988. Prolonged lactation infertility in adolescent rhesus monkeys. *Biol Reprod* 38:163–174.
- Wittig RM, Boesch C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *Int J Primatol* 24:847–867.
- Wolff JO, Macdonald DW. 2004. Promiscuous females protect their offspring. *Trends Ecol Evol* 19:127–134.
- Zeh JA, Zeh DW. 2003. Toward a new sexual selection paradigm: polyandry, conflict and incompatibility. *Ethology* 109:929–950.