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Interactions Between Third Parties and Consortship Partners in Tonkean Macaques (*Macaca tonkeana*)

Arianna De Marco · Roberto Cozzolino · Francesco Dessì-Fulgheri · Bernard Thierry

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Abstract Sexual competition is potentially disruptive for the cohesion of social groups because stress and conflicts can extend to other group members. The displays and interactions of sexual partners are liable to influence the behavior of group-mates, which may need to observe them to anticipate possible consequences. We studied 2 captive groups of Tonkean macaques (*Macaca tonkeana*) to test whether group-mates pay more attention to consort partners, modify their activities and social interactions, and exhibit signs of stress during periods of sexual consortships. We found that group-mates approached the top-ranking male more frequently and were more frequently oriented toward the consort pair at the time of consortship than at other times. Group-mates spent less time sleeping, and devoted less time to manipulating the environment and more time to monitoring during consortship. This indicates that consortships may incur costs in individuals not involved in sexual competition. However, Tonkean macaques did not exhibit any signs of increased stress during consortship periods, as their rates of scratching and yawning did not differ between consortship and nonconsortship periods. This study shows that not only direct competitors but also other individuals monitor the behavior of sexual

A. De Marco (✉)
Parco Faunistico di Piano dell'Abatino, 02030 Poggio San Lorenzo, Italy
e-mail: ariannadem@yahoo.it

A. De Marco · B. Thierry
Département Ecologie, Physiologie et Ethologie, Centre National de la Recherche Scientifique, Strasbourg, France

A. De Marco · F. Dessì-Fulgheri
Dipartimento di Biologia Evoluzionistica Leo Pardi, Università degli Studi di Firenze, Florence, Italy

R. Cozzolino
Ethoikos, Radicondoli, Italy

B. Thierry
Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France

partners. It is likely that group-mates obtain information this way about ongoing action, and take decisions accordingly.

Keywords Macaca tonkeana · Polyadic interaction · Sexual consortship · Social tension · Stress

Introduction

In group-living animals, sexual competition is potentially disruptive for the cohesion of social groups. With their large body size and large canines, males can compete overtly for access to females (Plavcan 2004). Not only can they fight and wound each other or attack the female (Clutton-Brock and Parker 1995; Huffman 1987; Manson 1994), but conflicts can also extend to other group members, increasing social tension and inducing energy loss (Smuts and Smuts 1993; van Schaik *et al.* 2004). The majority of researchers have focused on the behavior of sexual partners and competitors, and little is known about their influence on group-mates. Recent studies have shown that the outburst of conflicts influences the behavior not only of opponents but also of uninvolved individuals; in hamadryas baboons (*Papio hamadryas hamadryas*) and Tonkean macaques (*Macaca tonkeana*), bystanders are more likely to affiliate with one another to cope with social tension after fights (De Marco *et al.* 2010; Judge and Mullen 2005). In several species, individuals use social grooming to reduce the tension generated when group members anticipate the competition induced by a forthcoming food distribution (*Macaca arctoides*: Mayagoitia *et al.* 1993; *Pan troglodytes*: Koyama and Dunbar 1996; *Cebus apella*: Polizzi di Sorrentino *et al.* 2010).

Given the cognitive abilities of monkeys, it is expected that bystanders acquire information by following the interactions occurring between sexual partners. Not only do monkeys know their own affiliative bonds and dominance relationships with others, but they are also aware of the social relationships linking their group-mates (Bergman *et al.* 2003; Bovet and Washburn 2003; Cheney and Seyfarth 1990; Dasser 1988). They can take relative ranks between their opponents and potential allies into account when recruiting support (Silk 1999). They also track the gaze of others and predict their behavior from subtle gestures and vocal cues (Bergman *et al.* 2006; Tomasello *et al.* 1998; Wood *et al.* 2007). In Tonkean macaques, for instance, individuals orient their food search using visual and olfactory cues conveyed by group-mates (Drapier *et al.* 1999 2002).

In several Old World monkeys, the swelling of the perineal skin conspicuously signals female sexual receptivity (Dixson 1998; Higham *et al.* 2008). Males react to changes in genital swelling and are more likely to mate when it is particularly large and brightly colored (Dixson 1998; Domb and Pagel 2001). Females can utter specific vocalizations during the reproductive period (Maestripieri and Roney 2005; Pradhan *et al.* 2006). The finding that males inspect and smell the perineal area of estrous females suggests that they exploit olfactory signals to monitor a female's reproductive condition (Hausfater 1975; Hdry and Whitten 1987). There are hints that olfactory cues indicate fertility in macaques (Cerda-Molina *et al.* 2006; Michael and Keverne 1968), but their importance in catarrhines remains questionable (Dixson 1998; Snowdon 2004).

Whether sexual displays are reliable indicators of female fitness (Pagel 1994) or intracycle signals of the distribution of ovulation (Nunn 1999), it is certain that they convey information to competing males about the fertility of a potential mate (Deschner *et al.* 2003; Emery and Whitten 2003; Higham *et al.* 2008). The information provided by sexual displays is available not only to dominant males but also to other group members, albeit probably in different ways according to the distance between individuals (Higham *et al.* 2009). Signaling interactions represent an additional source of information about relative features that can be used by conspecifics to direct their behavior (McGregor 2005). In chacma baboons (*Papio hamadryas ursinus*), higher-ranking males monopolize mating by remaining close to sexually receptive females. Using playback experiments, Crockford *et al.* (2007) have demonstrated that lower-ranking males specifically react when informed that dominant males and estrous females are temporarily apart, indicating that they can track changes in the status of consortship and quickly identify mating opportunities. In Barbary macaques (*Macaca sylvanus*), males respond more strongly to playbacks of copulatory calls uttered by females during ejaculatory copulations than after those recorded during nonejaculatory copulations, meaning that they eavesdrop on mating outcome (Pfefferle *et al.* 2008).

Tonkean macaques originate from the island of Sulawesi, Indonesia, and form multimale, multifemale groups. Females show clear behavioral, morphological, and endocrine changes throughout the ovarian cycle (Aujard *et al.* 1998; Thierry *et al.* 1996). Around the ovulatory period they display brightly colored and voluminous genital swelling, and emit a specific estrus call (Masataka and Thierry 1993; Thierry *et al.* 1996). Reproduction occurs all year round. There is usually only one periovulatory female available at any one time, and the top-ranking male is able to monopolize sexual access to her over several days in a sexual consortship (Thierry 2010).

We investigated changes in the behaviors of group-mates at the time of sexual consortship in 2 groups of Tonkean macaques. Because periods of sexual competition correspond to heightened levels of conflicts between males (Thierry, *unpubl. data*), group-mates may need to follow the interactions occurring around sexual partners to anticipate better their potential consequences even if this imposes a load on their activity budget. On the other side, the top-ranking male has to maintain his monopoly over the estrous female by keeping other individuals at a distance. We predicted that during consortship 1) group-mates should pay more attention to sexual partners and possibly approach them; 2) the top-ranking male should prevent the approaches of group members, increasing his rate of conflicts with other males; 3) group-mates should spend more time monitoring at the expense of other activities; and 4) group-mates should exhibit signs of stress in relation to the context of sexual competition.

Methods

Subjects

We studied 2 captive groups of Tonkean macaques. The first group was housed in an enclosure *ca*. 120 m^2 and 4 m high at the Strasbourg Orangerie Zoo, France. This

group was founded 20 yr before our study, and at the time of study consisted of 20 individuals, including 4 adult males, 4 adult females, 3 subadult males, 2 subadult females, 2 juvenile males, 3 juvenile females, and 2 infants. The second group was maintained in an enclosure *ca.* 1000 m^2 and 5 m high at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy. This group was founded 4 yr before our study and consisted of 10 individuals, including 3 adult males, 2 adult females, 1 subadult male, 1 subadult female, 1 juvenile male, 1 juvenile female, and 1 infant at the time of our study. Three births were recorded during the study: Two infants were born in the Strasbourg group and 1 in the Rieti group. We defined subadults as individuals 4 and 5 yr of age and juveniles as individuals 1–3 yr old. Enclosures were furnished with perches, slides, wooden structures, ropes, and platforms. Monkeys were fed with commercial monkey diet pellets on daily basis. They received fresh fruit and vegetables outside observation hours. Water was available *ad libitum*.

Observational Methods

A. De Marco collected data between 09:00 h and 14:00 h from May to November 2006 in the Strasbourg group, and from January to July 2007 in the Rieti group. Sexual consortship involves male mate guarding of an estrous female and is defined as the continuous following of a swollen female by an adult male (Aujard *et al.* 1998; Nunn 1999). In this study, only the top-ranking male was able to consort with estrous females. Focal group-mates were individuals ≥4 yr old other than the consort pair (Fig. 1). A. De Marco collected data related to the consortship periods of 2

Fig. 1 Group-mates oriented toward consorting partners.

different females in each group; for each female she recorded data during 10 consortship days and as many control days, i.e., no swollen female present in the group, totaling 80 d of record.

A. De Marco used instantaneous group scan sampling (Altmann 1974) at 30-min intervals over 5 h/d to record the activities of group-mates (feeding, manipulating the environment; sleeping, i.e., resting with eyes closed; monitoring, i.e., looking around while resting), and whether consort partners were sitting in contact with one another. She also recorded whether the focal subject's face was oriented toward each consort partner, i.e., the individual's axis is within an angular sector of 90°, the bisector being the line between group-mate's face and partner's body, and whether the consort male was located in a guarding position between the group-mate and the swollen female, i.e., the individual's axis is within an angular sector of 90°, the bisector being the line between group-mate's face and female's body, to prevent other individuals from approaching her.

A. De Marco used focal sampling (Altmann 1974) to collect one 12-min sample daily for each group-mate following a predetermined randomized time schedule. She recorded the approaches of focal individuals to each consort partners, from >1 m to <1 m, the interpositions of the top-ranking male in response to a focal individual approaching the estrous female (he places himself between the group-mate and the female), and the displacement behaviors of focal individuals (scratching, yawning). In addition, she recorded all occurrences of mounts involving sexual partners, affiliative interferences in mounts by group members (approaching or addressing affiliative behaviors to the mating pair, *cf.* Thierry 1986), and conflicts (aggressive behavior using facial threat, vocal threat, chase, slap, grab, or bite performed by one individual, followed by another aggressive or nonaggressive response by the aggressed individual).

A. De Marco collected 80 scans and 120 min of focal samples on each of the 12 and 6 focal subjects in the Strasbourg and Rieti group, respectively, for each of the 2 swelling females in each group, and the same number during control periods.

We measured the dominance status of top-ranking males using the supplantations spontaneously occurring during observations plus those recorded during drinking competition tests (*cf.* Thierry *et al.* 1994). To assess dominance relationships we built a matrix of supplantations. We then used MatMan version 1.0 (Noldus Information Technology, Wageningen, The Netherlands) to rank individuals in a dominance hierarchy (De Marco *et al.* 2010).

Data Analysis

To verify that sexual partners were consorting, we compared the number of contact-sittings and matings occurring between them during consort and control periods using the χ^2 goodness-of-fit test. We tested the normality of data distribution via the Kolmorogov-Smirnov test before conducting repeated-measures analyses of variance. We compared consort and control periods with period as an intrasubject factor, and group and group-mate sex as intersubject factors. When data were not normally distributed we compared the interactions involving the top-ranking male across consort and control periods using the χ^2 goodness-of-fit test. We used SPSS version 16 (SPSS Inc., Chicago, IL) to run statistical tests. All probabilities were 2-tailed.

The significance level was set at 0.05. Given the number of statistical comparisons, we used the sequential Bonferroni procedure to adjust significance levels (Quinn and Keough 2002). Average values are given in the text and tables as means±SD.

Results

Consorting Partners

We verified that the estrous female and the top-ranking male were more often sitting in contact with each other at the time of consortship than during control days (Strasbourg female 1: χ^2=23.3, p<0.001; Strasbourg female 2: χ^2=9.8, p=0.003; Rieti female 1: χ^2=38.3, p<0.001; Rieti female 2: χ^2=14.3, p<0.001; Fig. 2). Similarly, most matings between the top-ranking male and the females occurred during the consort period (Strasbourg female 1: χ^2=9.1, p=0.004; Strasbourg female 2: χ^2=47.3, p< 0.001; Rieti female 1: χ^2=228.8, p<0.001; Rieti female 2: χ^2=109.1, p<0.001; Fig. 2).

Interactions Between Group-mates and Consorting Partners

Affiliative interferences in mounts involving the receptive female occurred more frequently when she was in estrus than when she was not (Strasbourg female 1: χ^2= 4.5, p=0.041; Strasbourg female 2: χ^2=93.0, p<0.001; Rieti female 1: χ^2=13.8, p< 0.001; Rieti female 2: χ^2=22.6, p<0.001; Fig. 2).

In both groups, group-mates approached the top-ranking male more frequently during consortship than during control periods, whereas they did not significantly modify their rates of approaches to the estrous female (Table I). Both male and female group-mates faced the top-ranking male more often during consortship than during control periods (Table I). Group-mates' orientation toward the estrous female also increased during consortship; the effect was stronger in male than in female group-mates (Table I).

At the time of consortship, the top-ranking male spent more time positioned between the estrous female and group-mates; the effect was stronger in the Rieti group (Table I). He also regularly interposed himself between the female and other males (Strasbourg group: mean frequency per hour per subject = 1.75±3.02; Rieti group: 1.08±0.31), whereas he performed no interposition during the control period, and none toward other females. Conflicts were more numerous between male group-mates and the top-ranking male during consortship in the Rieti group (consort: N=17, control: N=1; χ^2=14.2, p<0.001). The number of conflicts recorded in other classes of individuals were too rare to run statistical tests.

Activities and Interactions of Group-mates

Whereas the duration of feeding did not change significantly across periods, monitoring increased significantly during consortship (Table II). Group-mates spent less time sleeping and manipulating, the latter effect being stronger in males compared to females, and in the Rieti group compared to the Strasbourg group (Table II). We found no significant differences between consortship and nonconsortship periods for displacement behaviors (Table II). We did not find any significant

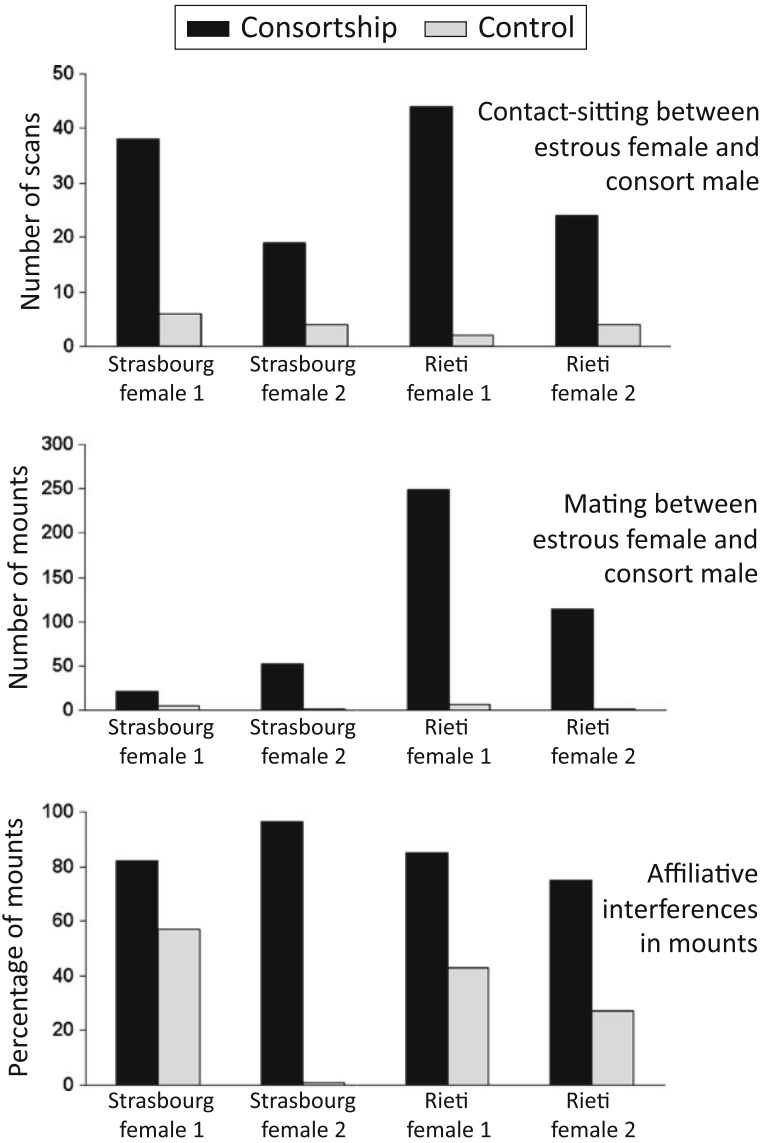

Fig. 2 Contact-sitting and mating between the 2 focal estrous females and the consorting male, and affiliative interferences in mounts during consort and control periods in the 2 focal groups.

differences between periods in the rates of conflicts occurring between group-mates in either groups (Strasbourg: consort: N=15, control: N=24, χ^2=2.08, p=0.200; Rieti: consort: N=18, control: N=8, χ^2=3.85, p=0.076).

Discussion

This is the first study demonstrating that the behavior of group members is modified at the time of sexual consortship in primates. The close association between sexual

Table I Comparison of interactions between sexual partners and male or female group-mates during consort and control periods

Behavior	Consort				Control				Factors							
	Strasbourg group		Rieti group		Strasbourg group		Rieti group		Period		Period * group		Period * sex		Period * sex * group	
	Male	Female	Male	Female	Male	Female	Male	Female	$F_{1,14}$	p value	$F_{1,14}$	p value	$F_{1,14}$	p value	$F_{1,14}$	p value
Group-mate approach to top-ranking male[a]	7.00±3.62	7.17±3.38	5.75±0.50	7.33±3.51	3.96±1.81	6.54±2.12	3.08±0.80	4.17±1.15	8.4	0.012*	0.4	0.520	0.3	0.568	0.8	0.389
Group-mate approach to estrous female[a]	7.29±3.78	7.96±1.97	6.08±0.29	7.17±2.52	4.75±1.36	7.67±1.02	4.0±0.90	4.50±1.22	3.5	0.083	0.01	0.900	0.9	0.347	0.2	0.688
Group-mate head orientation toward top-ranking male[b]	47.33±23.25	42.5±7.97	69.67±10.5	53.33±0.57	34.0±7.15	43.0±5.33	45.0±4.36	37.67±2.31	20.0	0.001*	5.3	0.036	3.7	0.075	0.2	0.691
Group-mate head orientation toward estrous female[b]	49.33±23.64	48.5±9.27	71.0±10.53	53.33±1.52	29.17±3.43	44.17±8.47	36.33±2.31	48.67±8.39	20.2	0.001*	1.1	0.314	10.4	0.006*	1.0	0.335
Position of top-ranking male[b]	72.0±3.16	64.83±6.24	76.0±4.0	67.67±5.51	22.83±2.64	19.17±2.64	16.33±0.57	8.67±0.57	1538	<0.001*	19.2	0.001*	0.1	0.457	0.3	0.611

We used repeated-measures ANOVA; values with asterisks remain significant with the sequential Bonferroni procedure for multiple testing: 5 tests within columns

[a] Frequency per hour

[b] Percentage of scans

Table II Comparison of group-mates' activities and displacement behaviors during consort and control periods

Behavior	Consort				Control				Factors							
	Strasbourg group		Rieti group		Strasbourg group		Rieti group		Period		Period * group		Period * sex		Period * sex * group	
	Male	Female	Male	Female	Male	Female	Male	Female	$F_{1,14}$	p value	$F_{1,14}$	p value	$F_{1,14}$	p value	$F_{1,14}$	p value
Feeding[b]	4.62±3.57	2.82±2.27	7.71±1.30	11.7±2.6	5.56±3.65	2.63±2.77	10.2±0.7	12.2±3.2	3.4	0.087	1.3	0.282	2.3	0.153	0.2	0.685
Manipulating[b]	7.96±3.87	9.0±5.4	13.5±1.6	15.0±13.9	11.6±5.3	3.78±2.49	25.9±0.9	21.0±11.5	23.7	<0.00*	34.0	<0.001*	19.4	0.001*	0.5	0.477
Monitoring[b]	66.9±11.5	61.9±9.1	59.2±4.7	40.2±7.8	53.7±8.37	65.5±10.7	43.9±3.5	34.1±3.7	13.5	0.003*	5.6	0.033	8.8	0.032	0.1	0.714
Sleeping[b]	3.36±1.18	4.61±1.85	1.88±1.65	1.46±2.53	3.99±2.46	6.39±2.82	6.68±0.75	5.23±4.84	12.2	0.004*	3.8	0.080	0.01	0.972	0.5	0.50
Scratching[a]	14.3±3.4	10.0±2.8	9.91±5.74	8.50±4.77	15.2±7.5	10.3±3.4	12.5±4.1	10.6±2.5	2.2	0.162	0.8	0.390	0.1	0.788	0	0.983
Yawning[a]	1.75±1.82	0.04±0.10	3.33±2.47	0.67±1.15	1.75±1.08	0.13 ± 0.21	2.58 ± 1.63	0.17 ± 0.29	1.2	0.300	1.5	0.239	0.1	0.763	0.02	0.880

We used repeated-measures ANOVA; values with asterisks remain significant with the sequential Bonferroni procedure for multiple testing: 6 tests within columns

[a] Frequency per hour

[b] Percentage of scans

partners influenced the social interactions, activities, and interindividual distances of group-mates significantly. As found in a previous study (Aujard *et al.* 1998), top-ranking males also spent more time in contact-sitting with receptive females and more frequently copulated with them.

Our first prediction was supported, i.e., that group-mates would pay special attention to sexual partners. Not only was the proportion of affiliative interferences in mating between the top-ranking male and the estrous female higher during consortship than in control periods, but also the consort pair attracted the attention of other group members. In general, group-mates were more frequently oriented toward the top-ranking male and the female at the time of consortship and they approached the top-ranking male more often. Different individuals could have different motivations for paying attention to sexual partners. For instance, adult males could be waiting for mating opportunities if the female escapes the attention of the top-ranking male. On the other hand, group-members interfered in mounts more often at the time of consortship than at other times. It is known that immature individuals interfere more often than older group members, especially when their mother is involved (Thierry 1986). Here they watched and followed the behaviors of sexual partners, being in a position to learn about mate guarding and mating.

The previous results are particularly interesting in view of the fact that the top-ranking male performed mate guarding by spending more time positioned between the female and group-mates during consortship, and by actively interposing himself between her and approaching group-mates, especially when the latter were males. Rates of conflicts between him and other males remained relatively low at the time of consortship, but they increased in 1 of the 2 groups, consistent with our second prediction.

It is a general finding that females increase their locomotory activity and reduce foraging during the periovulatory period (Aujard *et al.* 1998; Bercovitch 1983; Dixson 1998). Mate guarding and aggression are also associated with costs for dominant males in terms of time and energy expenditure, as reported in savannah baboons (*Papio* sp.: Alberts *et al.* 1996; Bercovitch 1983). Although the amount of sexual effort in lower-raking males is weaker than those of the top-ranking one in Japanese macaques (*Macaca fuscata*: Matsubara, 2003), our results in captive Tonkean macaques show that the daily activities of other group members—adults and subadults—can be significantly affected regardless of their sex. In accordance with our third prediction, group-mates spent less time sleeping or manipulating the environment, and they devoted more time to monitoring during consortship. Thus, the consort period could incur costs for other group members, even those not directly involved in sexual competition.

Contrary to our fourth prediction, group-mates did not exhibit signs of stress during sexual consortship. Because the rates of conflict remained relatively low, and thus the likelihood of injuries, it may be that mate guarding did not make group-mates more anxious than usual. In a previous study in Tonkean macaques, we found higher rates of affiliation between group-mates having observed a conflict, although they display low levels of scratching and yawning (De Marco *et al.* 2010). Compared to other macaque species, Tonkean macaques are characterized by relaxed dominance (Thierry 2010; Thierry *et al.* 1994). Agonistic interactions usually remain at low levels of intensity, third parties can stop aggression by addressing

appeasement signals to opponents, and a majority of conflicts are followed by reconciliation (Demaria and Thierry 2001; Petit and Thierry 1994; Thierry 1985). An alternative explanation would be that scratching and yawning are not reliable indices of anxiety in Tonkean macaques. Different measures of anxiety will be necessary to know whether Tonkean macaque group-mates are particularly able to cope with the stressful situation induced by sexual competition.

In chacma baboons and Barbary macaques, listening to vocalizations emitted by sexual partners provides adult males with information about their interactions (Crockford *et al.* 2007; Pfefferle *et al.* 2008). Our study in Tonkean macaques adds that not only direct competitors but also other conspecifics closely monitor the behaviors of sexual partners. Given the cognitive abilities of monkeys, it is likely that bystanders can pick up on multiple cues through observation and take decisions accordingly (McGregor 2005; Valone 2007). The present results are drawn from 2 small groups, and further sampling will be needed to increase statistical power. Future research should investigate whether the present conclusions are applicable to wild animals, and determine which behavioral cues are informative for bystanders.

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References

Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging activity of male baboons. *Animal Behaviour, 51*, 1269–1277.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*, 227–265.

Aujard, F., Heistermann, M., Thierry, B., & Hodges, J. K. (1998). Functional significance of behavioral, morphological and endocrine correlates across the ovarian cycle in semi-free ranging female Tonkean macaques. *American Journal of Primatology, 46*, 285–309.

Bercovitch, F. B. (1983). Time budgets and consortships in olive baboons (*Papio anubis*). *Folia Primatologica, 41*, 180–190.

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science, 302*, 1234–1236.

Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Interactions in male baboons: the importance of both males' testosterone. *Behavioral Ecology and Sociobiology, 59*, 480–489.

Bovet, D., & Washburn, D. A. (2003). Rhesus macaques categorise conspecifics according to their dominance relations. *Journal of Comparative Psychology, 117*, 400–405.

Cerda-Molina, A. L., Hernández-López, L., Rojas-Maya, S., Murcia-Mejia, R., & Mondragón-Ceballos, R. (2006). Male-induced sociosexual behavior by vaginal secretions in *Macaca arctoides*. *International Journal of Primatology, 27*, 791–807.

Cheney, D. L., & Seyfarth, R. M. (Eds.). (1990). *How monkeys see the world*. Chicago: University of Chicago Press.

Clutton-Brock, T. H., & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour, 49*, 1345–1365.

Crockford, C., Witting, R. M., Seyfarth, R. M., & Cheney, D. L. (2007). Baboons eavesdrop to deduce mating opportunities. *Animal Behaviour, 73*, 885–890.

Dasser, V. (1988). A social concept in Java monkeys. *Animal Behaviour, 36*, 225–230.

De Marco, A., Cozzolino, R., Dessì-Fulgheri, F., & Thierry, B. (2010). Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (*Macaca tonkeana*). *Animal Behaviour, 80*, 197–203.

Demaria, C., & Thierry, B. (2001). A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour, 138*, 397–410.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour, 66*, 551–560.

Dixson, A. F. (1998). *Primate sexuality*. Oxford: Oxford University Press.

Domb, L. G., & Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature, 410*, 204–206.

Drapier, M., Ducoing, A. M., & Thierry, B. (1999). An experimental study of collective performance at a foraging task in Tonkean macaques. *Behaviour, 136*, 99–117.

Drapier, M., Chauvin, C., & Thierry, B. (2002). Tonkean macaques find food sources from cues conveyed by group-mates. *Animal Cognition, 5*, 159–165.

Emery, M. A., & Whitten, P. L. (2003). Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology, 54*, 340–351.

Hausfater, G. (1975). *Dominance and reproduction in baboons*. Basel: Karger.

Hdry, S. B., & Whitten, P. L. (1987). Patterning of sexual activity. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 370–384). Chicago: University of Chicago Press.

Higham, J. P., MacLarnon, A. M., Ross, C., Heistermann, M., & Semple, S. (2008). Baboon sexual swellings: Information content of size and color. *Hormones and Behavior, 53*, 452–462.

Higham, J. P., Semple, S., MacLarnon, A. M., Heistermann, M., & Ross, C. (2009). Female reproductive signaling, and male mating behavior, in the olive baboon. *Hormones and Behavior, 55*, 60–67.

Huffman, M. A. (1987). Consort intrusion and female mate choice in Japanese macaques (*Macaca fuscata*). *Ethology, 75*, 221–234.

Judge, P. G., & Mullen, S. (2005). Quadratic postconflict affiliation among bystanders in a hamadryas baboon group. *Animal Behaviour, 69*, 1345–1355.

Koyama, N. F., & Dunbar, R. I. M. (1996). Anticipation of conflict chimpanzees. *Primates, 76*, 79–86.

Maestripieri, D., & Roney, J. R. (2005). Primate copulation calls and postcopulatory female choice. *Behavioral Ecology, 16*, 106–113.

Manson, J. H. (1994). Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour, 48*, 473–475.

Masataka, N., & Thierry, B. (1993). Vocal communication of Tonkean macaques in confined environments. *Primates, 34*, 169–180.

Matsubara, M. (2003). Costs of mate guarding and opportunistic mating among wild male Japanese macaques. *International Journal of Primatology, 24*, 1057–1075.

Mayagoitia, L., Santillan-Doherty, A. M., Lopez-Vergara, L., & Mondragon-Ceballos, R. (1993). Ethology. *Ecology and Evolution, 5*, 435–446.

McGregor, P. K. (Ed.). (2005). *Animal communication networks*. Cambridge: Cambridge University Press.

Michael, R. P., & Keverne, E. (1968). Pheromones in the communication of sexual status in primates. *Nature, 218*, 746–749.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded signal hypothesis. *Animal Behaviour, 58*, 229–246.

Pagel, M. (1994). The evolution of conspicuous advertisement in Old World monkeys. *Animal Behaviour, 47*, 1333–1341.

Petit, O., & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour, 48*, 1427–1436.

Pfefferle, D., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Male Barbary macaques eavesdrop on mating outcome: a playback study. *Animal Behaviour, 75*, 1885–1891.

Plavcan, J. M. (2004). Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates* (pp. 230–252). Cambridge: Cambridge University Press.

Polizzi di Sorrentino, E., Schino, G., Visalberghi, E., & Aureli, F. (2010). What time is it? Coping with expected feeding time in capuchin monkeys. *Animal Behaviour, 80*, 117–123.

Pradhan, G. R., Engelhardt, A., & van Schaik, C. P. (2006). The evolution of female copulation calls in primates: a review and a new model. *Behavioral Ecology and Sociobiology, 59*, 333–343.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Silk, J. B. (1999). Male bonnet macaques use information about third party rank relationships to recruit allies. *Animal Behaviour, 58*, 45–51.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior, 22*, 1–63.

Snowdon, C. T. (2004). Sexual selection and communication. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates* (pp. 57–70). Cambridge: Cambridge University Press.

Thierry, B. (1985). Patterns of agonistic interactions in three species of macaque (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*). *Aggressive Behavior, 11*, 223–233.

Thierry, B. (1986). Affiliative interference in mounts in a group of Tonkean macaques (*Macaca tonkeana*). *American Journal of Primatology, 14*, 89–97.

Thierry, B. (2010). The macaques: a double-layered social organization. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 229–241). Oxford: Oxford University Press.

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C., & Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In J. J. Roeder, B. Thierry, J. R. Anderson, & N. Herrenschmidt (Eds.), *Current primatology* ((pp, Vol. 2, pp. 103–117). Strasbourg: Université Louis Pasteur.

Thierry, B., Heistermann, M., Aujard, F., & Hodges, J. K. (1996). Long-term data on basic reproductive parameters and evaluation of endocrine, morphological and behavioral measures for monitoring reproductive status in a group of semi-free ranging Tonkean macaques (*Macaca tonkeana*). *American Journal of Primatology, 39*, 47–62.

Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour, 55*, 1063–1069.

Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others, a review of public information use. *Behavioral Ecology and Sociobiology, 62*, 1–14.

van Schaik, C. P., Pradhan, G. R., & van Noordwijk, M. A. (2004). Mating conflict in primates: Infanticide, sexual harassment and female sexuality. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates* (pp. 131–150). Cambridge: Cambridge University Press.

Wood, J. N., Glynn, D. D., Phillips, B. C., & Hauser, M. D. (2007). The perception of rational, goal-directed action in nonhuman primates. *Science, 317*, 1402–1405.