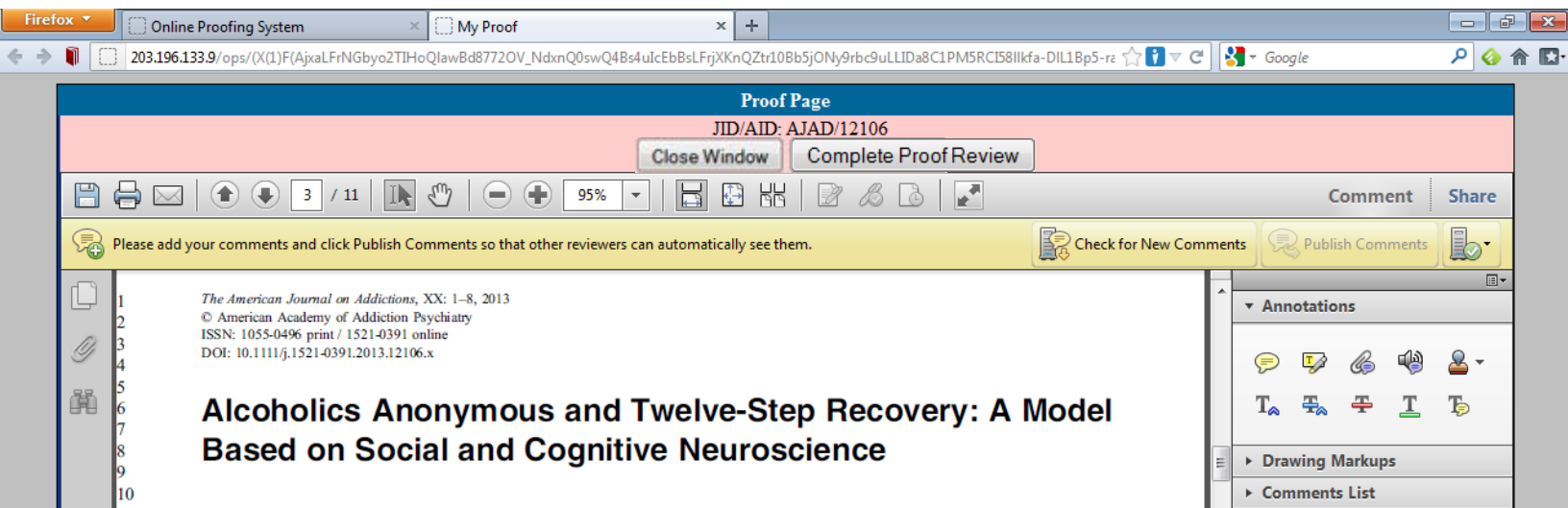


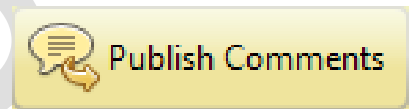
WILEY

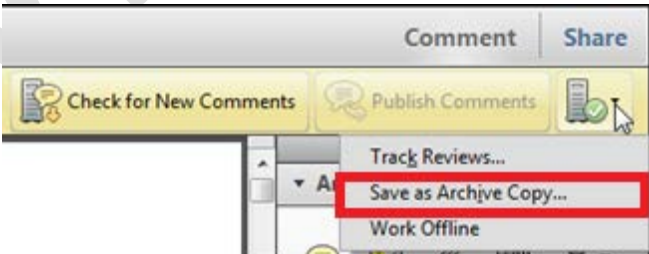
Online Proofing System

1. Corrections should be marked with the Adobe Annotation & Comment Tools below:



2. To save your proof corrections, click the 'Publish Comments' button. Publishing your comments saves the marked up version of your proof to a centralized location in Wiley's Online Proofing System. Corrections don't have to be marked in one sitting – you can publish corrections and log back in at a later time to add more.



3. When your proof review is complete we recommend you download a copy of your annotated proof for reference in any future correspondence concerning the article before publication. You can do this by clicking on the icon to the right of the 'Publish Comments' button and selecting 'Save as Archive Copy...'.


4. When your proof review is complete and you are ready to send corrections to the publisher click the 'Complete Proof Review' button that appears above the proof in your web browser window. Do not click the 'Complete Proof Review' button without replying to any author queries found on the last page of your proof. Incomplete proof reviews will cause a delay in publication. **Note: Once you click 'Complete Proof Review' you will not be able to mark any further comments or corrections.**



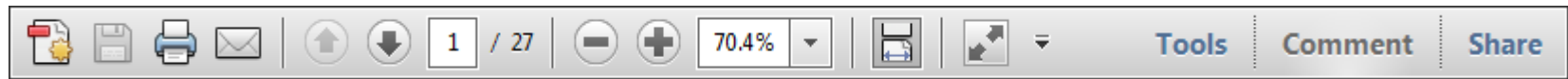
Firefox, Chrome, Safari Users

If your PDF article proof opens in any PDF viewer other than Adobe Reader or Adobe Acrobat, you will not be able to mark corrections and query responses, nor save them. To mark and save corrections, please follow these [instructions to disable the built-in browser PDF viewers in Firefox, Chrome, and Safari](#) so the PDF article proof opens in Adobe within a Firefox or Chrome browser window.

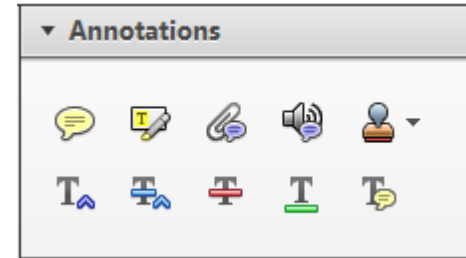
Required software to e-Annotate PDFs: Adobe Acrobat Professional or Adobe Reader (version 8.0 or above). (Note that this document uses screenshots from Adobe Reader X)

The latest version of Acrobat Reader can be downloaded for free at: <http://get.adobe.com/reader/>

Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. Replace (Ins) Tool – for replacing text.



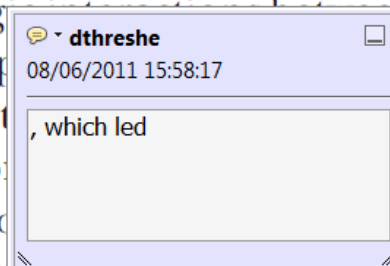
Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.

Replacement text into the blue box that appears.

standard framework for the analysis of microeconomics. Nevertheless, it also led to the emergence of strategic behavior in the number of competitors in the industry. This is that the structure of the industry, which led to the emergence of imperfect competition. The main components of the industry, which are exogenous to the industry, are important works on the industry by Shirasaka (henceforth) and we open the 'black box'.



2. Strikethrough (Del) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits and the number of competitors are zero and the number of competitors (net) values are not determined by the industry. Blanchard and Kiyotaki (1987), in their paper on perfect competition in general equilibrium, discuss the effects of aggregate demand and supply in a classical framework assuming monopoly power. The number of firms in the industry is an exogenous number of firms.

3. Add note to text Tool – for highlighting a section to be changed to bold or italic.



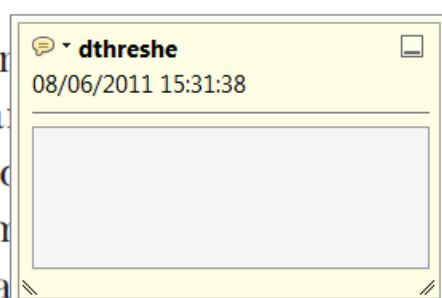
Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups consistent with the VAR evidence.

sation of the industry with well-labeled components. The number of competitors in the industry is consistent with the demand-side evidence.



4. Add sticky note Tool – for making notes at specific points in the text.

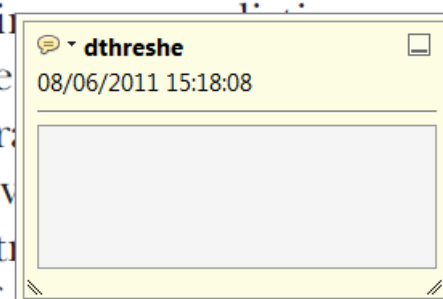


Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

industry and supply shocks. Most of the industry's output is sold in a competitive market. The number of firms in the industry is consistent with the demand-side evidence. The structure of the sector is consistent with the demand-side evidence.



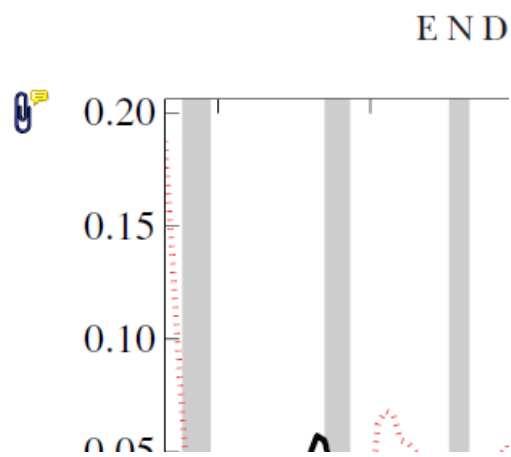
5. Attach File Tool – for inserting large amounts of text or replacement figures.



Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it

- Click on the [Attach File](#) icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.



6. Add stamp Tool – for approving a proof if no corrections are required.



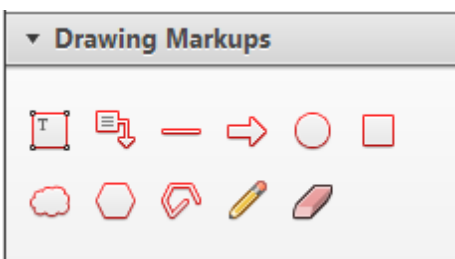
Inserts a selected stamp onto an appropriate place in the proof.

How to use it

- Click on the [Add stamp](#) icon in the Annotations section.
- Select the stamp you want to use. (The [Approved](#) stamp is usually available directly in the menu that appears).
- Click on the proof where you'd like the stamp to appear. (Where a proof is to be approved as it is, this would normally be on the first page).

of the business cycle, starting with the
 on perfect competition, constant ret
 production. In this environment goods
 extra profits and the market for marke
 he market for goods is determined by the model. The New-Key
 otaki (1987), has introduced produc
 general equilibrium models with nomin
 and market-clearing. Most of this literat

APPROVED

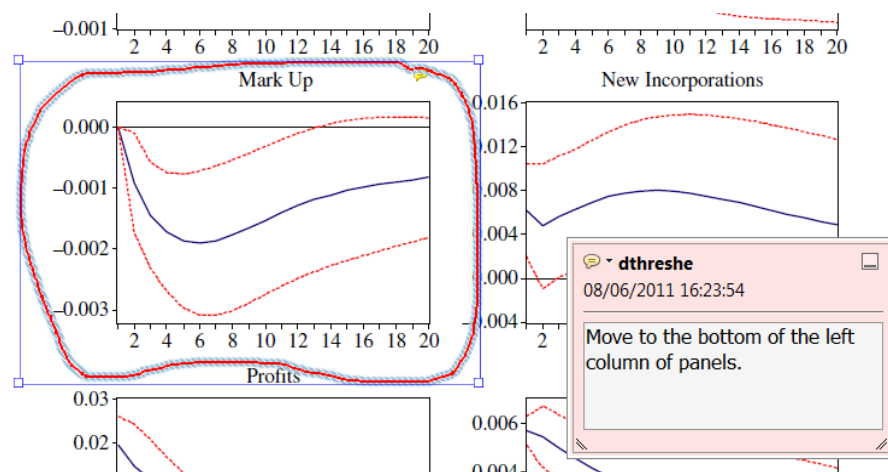


7. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

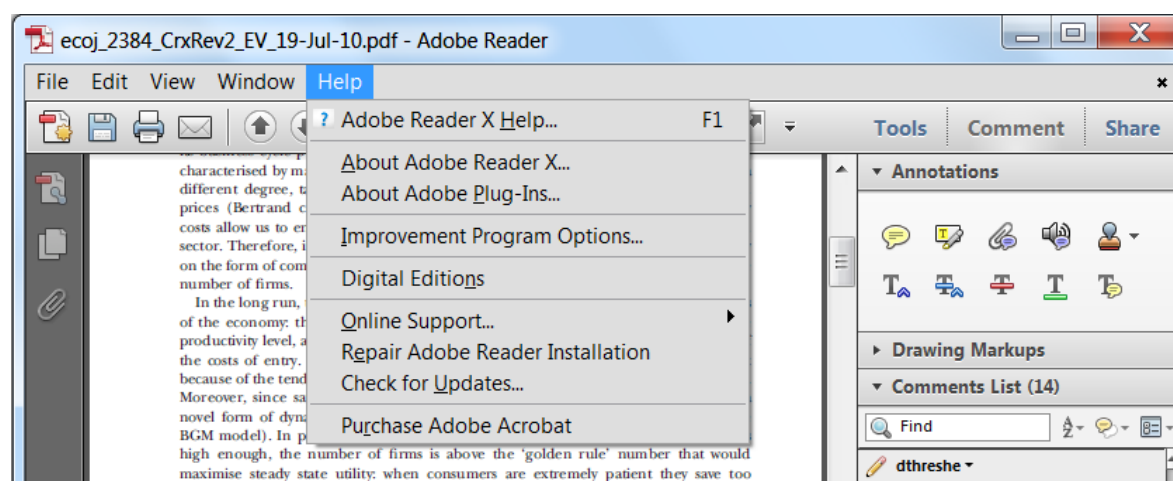
Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..


How to use it

- Click on one of the shapes in the [Drawing Markups](#) section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



For further information on how to annotate proofs, click on the [Help](#) menu to reveal a list of further options:



	Journal	MSP No.	Dispatch: July 13, 2015	CE: Sreeja
	AJP	15-0040.R2(22451)	No. of Pages: 9	PE: Marian Ato

RESEARCH ARTICLE

The Functions of Non-Reproductive Mounts Among Male Barbary Macaques (*Macaca sylvanus*)

^{Q1}LAURIANE FARAUT, ^{Q2}AMY NORTHWOOD, AND BONAVENTURA MAJOLO*

School of Psychology, University of Lincoln, Lincoln, United Kingdom

Same-sex, ^{Q2}non-reproductive mounts have been observed in a number of primate species and in various social contexts. However, the function of non-reproductive mounts is still largely unknown. We aimed to test whether non-reproductive mounts function to assert dominance and as appeasement behavior in male Barbary macaques. We analyzed post-mount behavior in 54 macaques belonging to two captive groups at Trentham Monkey Forest in Staffordshire, using 10 min post-mount/matched-control focal sessions collected either on the mounter or the mountee. In support of the dominance assertion hypothesis, the higher-ranking male within a mounting pair was more likely to be the mounter than the mountee, and to mock bite the lower-ranking male. In support of the appeasement hypothesis, the former mounting partners were more likely to exchange grooming and to have a lower frequency of self-scratching (a measure of social tension) after a non-reproductive mount than in control sessions. Our study indicates that non-reproductive mounts have different and not mutually exclusive functions and can modulate the quality of social interactions among group members. We discuss the possible factors that can affect the occurrence of non-reproductive mounts within and between species. Am. J. Primatol. 9999:1–9, 2015. © 2015 Wiley Periodicals, Inc.

Key words: appeasement; anxiety; Barbary macaque; dominance; mount; socio-sexual behavior

INTRODUCTION

Socio-sexual behaviors [Wickler, 1967], that is, behaviors that are sexual in form but do not have a reproductive function [e.g., hindquarter presentation: Hausfater & Takacs, 1987; hold-bottom rituals: de Waal & Ren, 1988], are common in the primate order [e.g., *Callithrix jacchus* Epplé, 1975; pigtailed macaques, *Macaca nemestrina*: Bernstein, 1980; bonobos, *Pan paniscus*: Kano, 1980; baboons, *Papio* spp.: Colmenares, 1991 ^{Q3}] and in other vertebrates [e.g., Asian elephant, *Elephas maximus*: Rees, 2004; bottlenose dolphins, *Tursiops aduncus*: Mann, 2006; bids: Poiani, 2008]. Socio-sexual behaviors can be related to homo-sexuality [e.g., Vasey, 1995] and can have an indirect reproductive function. For example, female-female mount has been hypothesized to attract the attention of males and to increase the probability of copulations [Vasey, 1995; but see: Sommer et al., 2006; Srivastava et al., 1991]. Socio-sexual behaviors may have various social functions (i.e., not directly related to reproduction), such as ritualized “greeting” or appeasement gestures, to avoid aggression and/or to “acknowledge” the dominant position of a high-rank individual [Bernstein, 1980; Colmenares, 1991 ^{Q4}; Epplé, 1975; Maestripieri, 1997; Smuts & Watanabe, 1990]. Species-specific differences have been observed in the frequency, sequence of behaviors displayed and

in the context in which socio-sexual behaviors occur [Colmenares, 1991b].

Non-reproductive mounts (NRMs) are one of the best examples of socio-sexual behaviors. NRMs can be defined as a monkey (i.e., the mounter) climbing with their feet on the hips of another animal (i.e., the mountee), or staying on the ground, and grabbing the waist of the mountee with their hands [“double-foot-clasp” posture: see Handy & Brown, 1974]. Contrary to sexual mounts, the duration of NRMs is short and the mounter does not usually show thrusting or penetration [Hanby, 1974; Reed et al., 1997]. NRMs and/or the presentation of the hindquarters often occur in response to an approach by a dominant individual [Cordischi et al., 1991; Maestripieri, 1996; Wickler, 1967], sometimes matched with genital grabbing or

*Correspondence to: Bonaventura Majolo, School of Psychology, University of Lincoln, Brayford Pool, Lincoln, Lincolnshire LN6 7TS, United Kingdom. E-mail: bmajolo@lincoln.ac.uk

Received 18 February 2015; revised 22 June 2015; revision accepted 4 July 2015

DOI: 10.1002/ajp.22451
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

touching [Reed et al., 1997]. NRMs are displayed by individuals of any age, starting from infants who are just a few months old [Goy & Wallen, 1979; Hanby & Brown, 1974; Owens, 1976; Sommer et al., 2006], and are frequently observed in a social play context [Hanby & Brown, 1974; Owens, 1976; Sommer et al., 2006; Yamagiwa 1987].

It has been frequently argued that NRMs are used to assert dominance and thus the role of the two animals would depend on their relative dominant position [dominance assertion hypothesis: Wickler, 1967]: the mounter should be more likely to be the dominant individual within the dyad than the subordinate. According to this hypothesis, NRMs may be a low risk way to confirm dominance between two animals without the need of threatening displays and their possible associated costs for both animals (in terms of escalated aggression, counter-aggression or third-party intervention). The rank-related role of animals involved in a NRM has been confirmed in homo-sexual [Akers & Conaway, 1979; Cordischi et al., 1991; Kano, 1980; Kutsukake et al., 2006; Oi, 1990; Srivastava et al., 1991] and hetero-sexual NRMs [Anthoney, 1968; Sommer et al., 2006; Maestripiéri, 1996, 2007]. Conversely, other studies have not found a relationship between relative dominance position and the rank-related role in NRMs [Bernstein, 1980; Colmenares, 1990; Hanby et al., 1971; Hanby, 1974; Owens, 1976; Reed et al., 1997; Reinhardt et al., 1986; Savage-Rumbaugh & Wilkerson, 1978; Smuts & Watanabe, 1990; Vasey et al., 1998]. The dominant individual within a dyad is more likely to mock bite their mounting partner than the contrary (mock biting was defined as an animal grabbing with their mouth the back of the neck of another animal without actually biting or causing injuries) [Maestripiéri, 1996, 1997, 2007].

NRMs appear to increase during periods of social uncertainty or tension [Hanby, 1974], for example, around limited resources involving close proximity distances [Kano, 1980]. Moreover, after the introduction of an individual to a group, agonistic interactions and NRMs were observed between resident individuals and the newly released animals within the first 5 min of release [Bernstein, 1969]. Among pigtail macaques, *Macaca nemestrina*, female-female NRMs occurred most frequently in the aftermath of an agonistic event [e.g., 80% of all mounting interactions: Oi, 1990; but see Owens, 1976; Yamagiwa, 1987]. Such post-conflict NRMs [Hanby, 1974] may be used to reconcile with the former opponents [Aureli et al., 1989; Castles et al., 1996; Cooper et al., 2007; Cords, 1992; Majolo et al., 2005; Matsumura, 1996] or as post-conflict affiliation between a former opponent and a third-party [Bernstein, 1969; Colmenares, 1991 ^{Q5}; Hanby, 1974; Kano, 1980; Majolo et al., 2009; Owens, 1976; Petit & Thierry, 1994; Smuts & Watanabe, 1990]. The tension-reduction hypothesis [Colmenares,

1990; Hausfater & Takacs, 1987; Smuts & Watanabe, 1990] predicts that NRMs play an important role in conflict management strategies, decreasing social tension and the likelihood for an animal to receive further aggression from the former opponent or a third-party [Aureli et al., 1994, 1997].

Our aim was to test two hypotheses on the function of NRMs, namely, the dominance assertion and the tension-reduction hypotheses. Since the conflict resolution function of NRMs has already been demonstrated in other studies [e.g., Aureli et al., 1989; Cords, 1992; McFarland & Majolo, 2013a], here we focused on NRMs between two males who had not been involved in an agonistic interaction within 10 min before a NRM. First, we tested whether NRMs and mock bites function to assert dominance in male macaques (dominance assertion hypothesis). If so, we predicted that the dominant animal in a dyad should be more likely to be the mounter than the mountee, and to be more likely to mock bite when being the mounter than the subordinate animal. Moreover, we predicted that such difference should become more evident when the rank distance between males is large and when males are more distantly related. Second, we tested the function of NRMs as appeasing behavior (tension-reduction hypothesis): we predicted that the occurrence of aggression and of self-directed behavior [i.e., self-scratching, a behavioral indicator of social tension; Maestripiéri et al., 1992] should be reduced in the first minutes after a NRM than in control condition (no NRM) and grooming between former NRM partners should increase. We tested these two hypotheses in male Barbary macaques (*M. sylvanus*), a species where NRMs have been previously observed [Deag, 1980]. This species lives in multimale-multifemale social groups and is characterized by a relatively high level of social tolerance [Thierry, 2007]. Male-male affiliation is common in Barbary macaques, including between unrelated males, agonistic interactions rarely escalate into severe aggression, and dominance hierarchy is usually less linear than among females [Kaburu et al., 2012; McFarland & Majolo, 2013b; Thierry, 2007; Thierry et al., 2008; Young et al., 2014]. As such, this species is likely to assert dominance through NRMs without the need of overt aggression.

METHODS

Study Site and Subjects

This study was conducted on two semi-free ranging groups of Barbary macaques living in a 60 acre outdoor enclosure at the Trentham Monkey Forest in Staffordshire, Great Britain (<http://www.trentham-monkey-forest.com>). Monkeys in the forest are fed every morning with fruits, vegetables, and seeds (water is available *ad libitum*). Seeds are

1 scattered during the day and the monkeys also rely
 2 on natural food sources (e.g., leaves, grass, nuts, and
 3 insects) they find in the park.

4 Data were collected on 54 adult (i.e., >7 years
 5 old) or sub-adult [i.e., between 7 and 4-years-old;
 6 Deag, 1980] macaque males. Twenty-six males
 7 (19 adults and 7 sub-adults) belonged to the
 8 “German” group (so named because founder mem-
 9 bers of this group came from Affenberg Salem
 10 Monkey Mountain, Germany), a group composed of
 11 a total of 57 individuals at the time of the data
 12 collection. Twenty-eight males (24 adults and 4 sub-
 13 adults) belonged to the “French” group (so named as
 14 founder members of this group came from the
 15 Montagne des Singes at Kintzheim, France) which
 16 was composed of 78 individuals. Both study groups
 17 were established in the park in 2005. All the age
 18 classes (infant, juvenile, sub-adult, and adult) of
 19 both sexes were present in the two study groups;
 20 age and maternal kinship of the study animals were
 21 known from back records.

22 This study complies with protocols approved by
 23 the Ethics Committee of the School of Psychology,
 24 University of Lincoln. Moreover, this study adheres
 25 to the legal requirements of Great Britain and to the
 26 American Society of Primatologists Principles for the
 27 Ethical Treatment of Non-Human Primates.

28 29 Data Collection

30 Data were collected daily between 10.00 and
 31 17.30, from June to October 2009 on the “German”
 32 group and from March to May 2014 on the “French”
 33 group. No data were collected during weekends or
 34 bank holidays due to the high number of visitors.

35 We used an adapted version of the “post-conflict-
 36 matched-control” method proposed by de Waal and
 37 Yoshihara [1983] to analyze post-mount behavior.
 38 Every time a NRM was observed, a 10 min post-
 39 mount (PM) focal session was run on the mounter or
 40 the mountee as soon as the mount ended. We ran a
 41 PM focal session only on NRMs that were not
 42 preceded, in the 10 min before a given NRM, by an
 43 agonistic interaction involving the focal animal and/
 44 or his NRM partner. Since at the park visibility of the
 45 animals is very good, we could effectively monitor the
 46 occurrence of agonistic interactions and NRMs
 47 without missing important details. During PM focal
 48 sessions, we recorded the identity of each male
 49 involved, their role during the NRM (mounter or
 50 mountee) and whether the mounter mock bite
 51 [Maestriperi, 2007] the mountee or not. When
 52 collecting focal sessions, we tried to balance the
 53 number of sessions run on the mounter or the
 54 mountee across dyads and study animals. At the
 55 start of each PM session we recorded the context in
 56 which the NRM occurred, that is, whether the
 57 mounter and mountee were socializing/resting
 58 (without being involved in an agonistic interaction)

or they were feeding/foraging before/after the NRM.
 When a male attempted to reject a NRM from
 another animal, by running away from the potential
 mounter, the NRM was considered to be unsuccess-
 ful: no PM data were collected and data on that NRM
 were discarded (discarded NRMs represented 3.8% of
 all NRMs observed). During PM focal sessions, we
 also recorded the duration of grooming interactions
 between the focal animal and the mounter/mountee
 [Hanby & Brown, 1974]. Finally, we recorded all of
 the occurrences of self-scratching to non-invasively
 assess social tension in the study animals. Two
 occurrences of self-scratching had to be separated by
 a minimum of 5 sec to be considered two separate
 events [Majolo et al., 2009]. If another NRM,
 involving the focal animal and his previous mounting
 partner or another male, occurred during an ongoing
 PM session, the PM focal was extended for additional
 10 min, giving us data for two PM focals. However,
 two NRMs had to be separated by more than 8 min to
 be considered two separate PM focals; if two NRMs
 occurred ≤ 8 min from one another, the first PM focal
 was discarded and only the second PM focal (i.e.,
 based on the second NRM observed) was included in
 the analyses. PM focals, based on NRMs involving
 the same focal animal and occurring between 8 and
 10 min from one another, represented 2.5% of the PM
 focals analyzed in this study.

On the next possible day after a given PM session
 (within 1 week from the matched PM), a matched-
 control (MC) session was run on the same focal
 animal and collecting the same data. We matched the
 context (i.e., socializing/resting versus feeding/forag-
 ing; see above) and the distance in meters between
 former mounter and mountee at the start of the PM
 and MC (we allowed for a maximum of 10 m
 difference for the distance between mounter and
 mountee between PM and MC). MC sessions were
 used to extract baseline frequencies and durations
 for the recorded behaviors and compared to data
 extracted from matched PMs.

We collected *ad libitum* data [Altmann, 1974] on
 the outcome of displacement and aggressive interac-
 tions between two males (i.e., not involving third
 parties) and with a clear cut result (i.e., one animal
 being the aggressor and the other, the target of
 aggression, displaying submission). We recorded the
 following aggressive behaviors: displacement, threat
 (i.e., open-mouth display or aggressive call), chase, and
 agonistic body contacts [Fischer & Hammerschmidt,
 2002; Hesler & Fischer, 2007]. In addition, We recorded
 five submissive behaviors: displacement, crouch sub-
 mission, teeth-chattering, silent-bared teeth display,
 fear scream, and flee [Fischer & Hammerschmidt,
 2002; Wiper & Semple, 2007]. A total of 783 dyadic
 agonistic behaviors were recorded (mean number of
 agonistic behavior per monkey \pm SE = 26.3 ± 20.3); we
 did not observe any agonistic behavior in 5.6% of the
 total male-male dyads.

Data Analysis

We used MatMan 1.1 [Noldus Information Technology, Wageningen, the Netherlands; De Vries et al., 1993] to determine the dominance rank of each focal male. We observed no rank reversal during the course of our data collection and the dominance hierarchy in the two study groups was stable. The linearity index was 0.29 for the male dominance hierarchy in the German group (directional consistency index = 0.69) and 0.34 for the French group (directional consistency index = 0.64). To reliably analyze the role of dominance rank of the two mounting partners on NRMs and subsequent behavior, we excluded from the analyses data on three PM-MC pairs, as they had been collected on males whose relative rank position within the dyad was uncertain.

Data analyses were based on a total of 235 PM-MC pairs (81 PMs-MCs in 2009 and 154 PMs-MCs in 2014), 117 PMs-MCs from the mouter and 118 PMs-MCs from the mountee. We collected PM-MC focal data on 138 different male-male dyads; each of the 54 study males was represented in at least one PM-MC session (mean PMs-MCs per study male \pm SE = 4.4 ± 3.0).

We extracted data on maternal kinship from the Park's back records in order to test whether kinship modulated the effect that NRMs could have on aggression, affiliation and social tension. A total of 16.6% of the study dyads were formed by genetically related males (i.e., 4.25% of study dyads had $r = 0.5$; 1.7% of dyads had $r = 0.25$; 4.25% of dyads had $r = 0.125$; 4.7% of dyads had $r = 0.03$; 1.7% of dyads had $r = 0.015$).

Dominance Assertion

In order to test whether NRMs and mock bites function to assert dominance in male macaques, we first ran a binomial test to determine whether the mouter was more likely to rank higher than the mountee or not. Moreover, we ran a generalized linear mixed model (GLMM) with a binomial distribution where our dependent variable was the rank of the mouter (categorical: whether the mouter was the higher-ranking individual of the dyad or not) and the independent variables were the absolute rank difference between mounting partners and their kin relationship (continuous; see above). Within our study dyads, males who were more closely genetically related to each other had a smaller absolute rank distance (GLMM: coefficient \pm SE = -0.41 ± 0.11 , $Z = -3.64$, $P < 0.001$, $N = 235$). In order to control for co-linearity between these two variables, each GLMM in this study was run three times, one GLMM for the full model (all independent variables included together) and two "control" GLMMs where only the relationship of, respectively, the absolute rank difference between mounting partners, or their kin relationship with the

dependent variable, was tested. Below we report the full model for each GLMM and we only report the results of these two "control" GLMMs if the significance of absolute rank difference or their kin relationship differed between the full and control GLMM.

We ran a GLMM where the occurrence of mock bite from the mouter to the mountee (categorical: yes or no) was the dependent variable and the rank of the mouter (categorical; see above), the absolute rank difference between mounting partners and their kin relationship were the independent variables. In these GLMMs we entered the ID of the focal animal as a random factor to control for pseudo-replication of the data (as the same animals were sampled more than once [Pinheiro & Bates, 2000]).

For the dominance assertion and appeasement behavior hypotheses, we ran a series of preliminary GLMMs where we entered, together with the variables described above or in the next section, age of the males (adult or sub-adult) in each dyad and context where the NRM occurred. Since age and context had a non-significant effect in all of these GLMMs (age: average $P > 0.27$; context: average $P > 0.49$), we excluded these two variables from the analyses presented below.

Appeasement Behavior

We ran three GLMMs to test the appeasement function of NRMs by comparing the behavior of our focal animals between PMs and MCs. First, we ran a GLMM where the dependent variable was the occurrence of aggression between former mounting partners (categorical, yes or no) in each PM or MC ($N = 470$; 235 PMs plus 235 MCs). In this GLMM the independent variables were: condition (categorical: PM vs. MC session), absolute rank difference between mounting partners and their kin relationship (continuous). Second, we ran two GLMMs where the dependent variables were, respectively, the duration of grooming exchanged between former mounting partners (in seconds; continuous) or the frequency of self-scratching (events/minute; continuous). Studies on conflict resolution have shown that affiliation between former opponents and increase/decrease of social tension are more likely to occur (or to be more frequent) in the ^{Q6}1st–3rd minutes after a conflict [e.g., Aureli et al., 1989; Majolo et al., 2005]. Therefore, in order to test if NRMs affected the duration of affiliation or the frequency of self-scratching after a mount, these two GLMMs were run using data collected on each minute of a PM or MC as data points (i.e., 10 data points for each PM or MC; $N = 4,700$). In these two GLMMs we entered the following independent variables: condition (categorical: PM vs. MC session), minute (ranging from the 1st to the 10th minute of a PM or MC), absolute rank difference between mounting partners and their kin

relationship (continuous). Note that we did not analyze the timing of aggression between former mounting partners in order to avoid running a zero-inflated analysis, as we never observed more than one aggressive interaction per PM or MC. Moreover, we could not run two different analyses for grooming given or received by the mouter/mountee as sample size for grooming interactions in PMs/MCs was too small. In the GLMM on self-scratching we entered role of the focal male (categorical: mouter or mountee) as an additional independent variable. Since in these three GLMMs (i.e., on aggression, grooming and self-scratching) we compared PMs to MCs, we entered the ID of each PM-MC pair as a random factor nested into the ID of the focal animal. All analyses were run using Stata version 12.0 (Stata-Corp. 2011).

RESULTS

Dominance Assertion

The higher-ranking animal within each dyad was more likely to be the mouter than expected by chance (binomial test: $P < 0.05$; $N = 228$): in 135 (59.3%) NRMs the higher-ranking male was the mouter whereas in 93 (40.7%) NRMs the lower-ranking male was the mouter. The higher-ranking male of the dyad was more likely to be the mouter than the mountee the less genetically related the two males were (GLMM: coefficient \pm SE = -0.28 ± 0.12 , $Z = -2.35$, $P < 0.05$). Moreover, we found a positive relationship between absolute rank difference and rank of the mouter (coefficient \pm SE = 0.10 ± 0.05 , $Z = 1.96$, $P = 0.05$, $N = 235$): the larger the absolute rank distance between two males the more likely the higher-ranking male was to be the mouter. However, this relationship became marginally non-significant in the control GLMM (coefficient \pm SE = 0.01 ± 0.05 , $Z = 1.84$, $P = 0.07$, $N = 235$).

Mock bites were more likely to occur when the mouter was the higher-ranking male of the dyad than the lower-ranking male (GLMM: coefficient \pm SE = 1.76 ± 0.40 , $Z = 4.42$, $P < 0.001$, $N = 235$). Among the 64 NRMs in which the mouter mock bit the mountee, 54 (84.4%) mock bites were displayed by the higher-ranking male of the dyad versus 10 (15.6%) mock bites displayed by the lower-ranking male. Absolute rank distance between the mounting partners (GLMM: coefficient \pm SE = -0.00 ± 0.03 , $Z = -0.11$, $P = 0.92$) and their genetic relationship (GLMM: coefficient \pm SE = 0.05 ± 0.07 , $Z = 0.68$, $P = 0.50$) did not have a significant effect on the occurrence of mock bites.

Appeasement Behavior

The occurrence of aggression between former mounting partners was not significantly different between PM and MC sessions (GLMM: coefficient \pm

SE = 0.00 ± 0.71 , $Z = 0.01$, $P = 0.99$, $N = 470$). Aggression was observed in 37 PMs and 35 MCs. Moreover, the occurrence of aggression was not affected by the absolute rank distance of the two males (coefficient \pm SE = 0.04 ± 0.10 , $Z = 0.45$, $P = 0.65$). However, aggression was more likely to occur between males with a higher degree of genetic relatedness (GLMM: coefficient \pm SE = 2.71 ± 0.98 , $Z = 2.76$, $P < 0.01$).

The duration of grooming exchanged between former mounting partners was longer in PM than in MC sessions (GLMM: coefficient \pm SE = -3.02 ± 0.65 , $Z = -4.64$, $P < 0.001$, $N = 4,700$; Fig. 1). Minute of the PM or MC session (coefficient \pm SE = -0.00 ± 0.12 , $Z = -0.01$, $P = 0.99$), absolute rank distance between mounting partners (coefficient \pm SE = 0.06 ± 0.58 , $Z = 0.92$, $P = 0.92$) and their genetic relationship (coefficient \pm SE = -0.97 ± 1.34 , $Z = -0.73$, $P = 0.47$) did not affect the duration of grooming exchanged.

Supporting our prediction, the frequency of self-scratching was significantly lower in PM than MC sessions (GLMM: coefficient \pm SE = 0.04 ± 0.02 , $Z = 2.43$, $P < 0.05$, $N = 4,700$; Fig. 2). Moreover, the frequency of self-scratching decreased the more minutes had passed since the start of the focal sessions (coefficient \pm SE = -0.01 ± 0.03 , $Z = -1.93$, $P = 0.05$). Conversely, the frequency of self-scratching was not affected by the rank distance between mounting partners (coefficient \pm SE = 0.00 ± 0.00 , $Z = 0.28$, $P = 0.79$), their genetic relationship (coefficient \pm SE = -0.01 ± 0.01 , $Z = -1.70$, $P = 0.09$) or the mouter/mountee role of the focal animal (coefficient \pm SE = 0.02 ± 0.03 , $Z = 0.57$, $P = 0.57$). It is possible that self-scratching was lower in PM than in MC sessions as former mounting partners were engaged in grooming. In order to control for the possible effect of grooming on self-scratching, we re-ran the previous GLMM excluding paired PM-MC sessions in

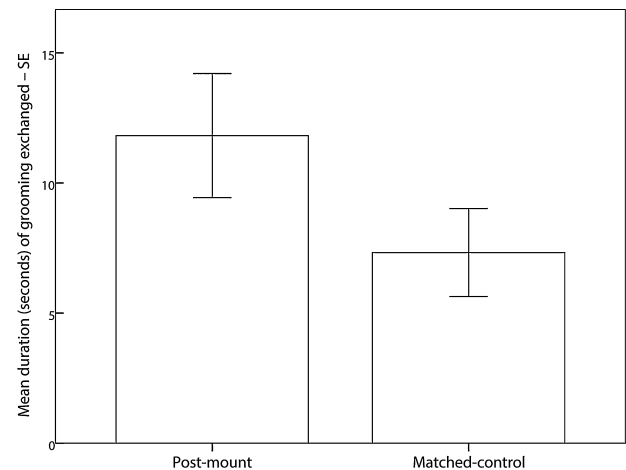


Fig. 1. Duration (seconds) of grooming exchanged between former mounting partners in Post-Mount or Matched-Control sessions.

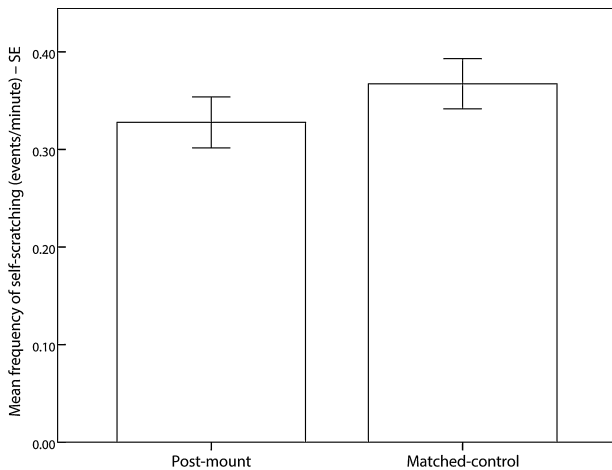


Fig. 2. Frequency (events/minute) of self-scratching in Post-Mount or Matched-Control sessions.

which the focal animal was exchanging grooming with the former mounting partner (in the PM and/or MC). Confirming the previous analysis, self-scratching was significantly lower in PM than in MC sessions (coefficient \pm SE = 0.04 ± 0.02 , $Z = 2.07$, $P < 0.05$).

DISCUSSION

The intensity of agonistic interactions is often low in male Barbary macaques and males can form strong social relationships with one another that give fitness benefits [Young et al., 2014]. Gestures and signals that modulate the frequent social interactions among males and that assert dominance are expected to be common in this species. We found evidence in support of the dominance assertion and appeasement functions of NRMs in male Barbary macaques. The higher-ranking male of the mounting pair was more likely to be the mounter than the mantee, and to mock bite the mounting partner more than the lower-ranking male. Moreover, males exchanged longer grooming bouts with one another and had lower frequency of self-scratching soon after a NRM than in control conditions. Therefore, NRMs allow Barbary macaque males to assert dominance, facilitate grooming exchange and reduce social tension without the risk of escalated aggression, even if NRMs require close proximity between males. As such, NRMs appear to be an effective but lower risk strategy to modulate social interactions than aggressive displays. Our results support the hypothesis that primates use NRMs as a non-aggressive indicator of dominance [Altmann, 1962] and are in agreement with previous research on this topic [Anthony, 1968; Cordischi et al., 1991; Kano, 1980; Maestriperi, 1996, 2007; Oi, 1990; Sommer et al., 2006; Wickler, 1967]. The higher-ranking male of the mounting pair was more likely to be the

mounter the larger the absolute rank distance between two males and the less genetically related they were. Therefore, NRMs are particularly important as a way to assert dominance the larger the rank distance between two males. Interestingly, closely related males were more likely to be close in rank, suggesting that kinship can affect dominance rank in macaque males as it does among females [Aureli et al., 1997]. Such an effect of kinship may be due to maternal effects (mothers supporting their infants against other group members), coalitions between genetically-related males [Young et al., 2014], or a combination of both, and may become more evident in captivity where male dispersal is only possible via targeted management practices (i.e., removal from, or introduction of new animals to a group).

Although we found support for the dominance assertion function of NRMs, during the course of the study it was not uncommon to record a subordinate individual mounting a dominant male. This was not surprising, given the frequent male-male interactions in the Barbary macaque. Moreover, NRMs can have other functions than dominance assertion [e.g., Maestriperi, 1997; Smuts & Watanabe, 1990]. For example, NRMs can favor bonding between two animals and/or represent homo-sexual behavior, which may not involve an effect of rank on the mounting roles of the two males. The quality of social relationship between two males is likely to affect how frequently males engage in NRMs and how consistently the dominant male of the dyad has the role of the mounter. Unfortunately, we could not collect baseline data on the frequency of affiliation and NRMs in our study; thus, we could not test whether relationship quality between two males has a positive effect on the frequency of NRMs or not.

Mock bites are thought to be ritualized aggressive behavior [Demaria & Thierry, 1989] usually displayed by high-ranking individuals towards subordinates [Maestriperi, 1996]. A recent comparative study [Maestriperi, 2007] on three macaque species with different dominance style—rhesus (*Macaca mulatta*), pig-tailed (*M. nemestrina*), and stump-tailed macaque (*M. arctoides*)—showed variation in the frequency of mock bites across species. In agreement with our results, mock bites were displayed significantly more often by higher-ranking individuals than lower-ranking ones in all of the three species. However, the frequency of mock bites was different according to the degree of social tolerance of each species: the more tolerant species (stump-tailed macaque) displayed a higher frequency of mock bites than the more despotic rhesus and pig-tailed macaques [Maestriperi, 2007].

Asserting dominance through NRMs, mock bites and other non-aggressive behavior, is potentially less costly for the animals involved, as the risk of aggression, counter-aggression, and their negative effect on stress level, is reduced [but see:

de Waal & Ren, 1988]. Indeed, we found no increase of aggression following NRMs and no significant effect of absolute rank distance on mock bites. NRMs are thought to be the most common non-aggressive way to assert dominance in the genus *Macaca* [Maestripiéri, 1997]. However, inconsistencies in the form and function of NRMs across studies on the same species suggest that NRMs can be affected by proximate factors (such as group size, number of prime and post-prime males in a group, or the stability of the dominance hierarchy over time) as much as species-specific differences in the behavioral repertoire or dominance style (see above). For example, in captive Japanese macaques (*M. fuscata*) Cordischi et al. [1991] found an association between dominance rank and mounter/mountee role of the animals contrary to what was found in another study on the same species [Hanby et al., 1971]. These two captive groups differed in the number of males and thus in group composition and operational sex ratio. Moreover, in a captive group of pigtailed macaques, where a dominance reversal between the alpha and beta males had recently occurred, high-ranking males were more likely to be the mounter in NRMs [Tokuda et al., 1968]. Conversely, in another captive group of pigtailed macaques where male dominance hierarchy was stable, no effect of rank on the mounter/mountee role of the males was found [Oi, 1990].

NRMs also function as appeasement behavior: the former mounting partners were more likely to exchange grooming, and they had a lower frequency of self-scratching after a NRM than in control sessions (this latter result being independent from the occurrence of grooming). NRMs have often been considered a form of reconciliation and third-party affiliation in studies on conflict resolution [e.g., Aureli et al., 1989; Call et al., 2002; Cooper et al., 2007; Cords, 1992; Majolo et al., 2005; McFarland & Majolo, 2013a]. For example, according to the self-protection hypothesis [Call et al., 2002], an increase of socio-sexual behaviors from third-party toward victims of aggression decreases the risk of re-directed aggression from victims to third parties. However, our study showed that NRMs can reduce social tension and favor grooming exchange outside the aftermath of a conflict. The function of greetings in male baboons (*Papio anubis*) support this hypothesis [Smuts & Watanabe, 1990]. Indeed, the exchange of NRMs and/or other socio-sexual gestures between adult males reinforces dominance relationships, and thus increases the tolerance and may prevent or mitigate conflicts in case of uncertainty about a partner's intention. NRMs can thus play an important role in the establishment and maintenance of social relationships between group members. Our methodological approach did not allow us to analyze whether NRMs are more likely to occur during periods of social tension or within some specific dyads

(e.g., between kin or males having a strong social relationship). Future studies should thus test whether differences in the occurrence of NRMs across dyads are related to the differences in quality of social relationships between males, kinship, context-dependent or life history variables. Moreover, the reduction of social tension level occurred regardless to the role of the focal animal in the NRM (mounter or mountee) and it was not dependent on the mounting partners exchanging grooming. The prevalence of socio-sexual behaviors could be explained by the relative brief nature of the exchange compared to grooming interactions [Colmenares, 1990; Hohmann & Fruth, 2000; Whitham & Maestripiéri, 2003]. These behaviors could be more effective in reassuring the partner when rapid, low-consuming and low-risk activities are needed in order to reduce social tension.

In conclusion, socio-sexual behaviors may have different, not mutually exclusive functions and play an important role in modulating social interactions. The majority of research on socio-sexual behaviors has been conducted on Cercopithecidae [e.g., Maestripiéri, 2007; Oi, 1990; Sommer et al., 2006] and apes [e.g., Hohmann & Fruth, 2000; Okamoto & Agetsuma, 2001] and data on different genera and families would be necessary to determine the evolutionary history and function of socio-sexual behaviors in the primate order.

ACKNOWLEDGMENTS

We would like to thank Ellen Merz and Guillaume de Turckheim for permission to run the study. We would also like to thank the personnel of Trentham Monkey Forest for facilitating and supporting our study; in particular, we are grateful to Sue Wiper for her valuable contribution to this study and advice during the data collection. We are grateful to Dr. Paul Garber and to two anonymous reviewers for useful comments that greatly improved our manuscript.

REFERENCES

- Akers JS, Conaway CH. 1979. Female homosexual behavior in *Macaca mulatta*. Archives of Sexual Behavior 8:63–80.
- Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.
- Anthony T. 1968. The ontogeny of greeting, grooming, and sexual motor patterns in captive baboons (*Papio cynocephalus*). Behaviour 31:399–412.
- Aureli F, van Schaik CP, van Hoof JARAM. 1989. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology 51:39–51.
- Aureli F, Das M, Verleur D, van Hoof JARAM. 1994. Postconflict social interactions among Barbary macaques (*Macaca sylvanus*). International Journal of Primatology 15:471–485.
- Aureli F, Das M, Veenema HC. 1997. Differential kinship effect on reconciliation in three species of macaques (*Macaca*

- fascicularis*, *M. fuscata*, and *M. sylvanus*). *Journal of Comparative Psychology* 111:91–99.
- Bernstein IS. 1969. Introductory techniques in the formation of pigtail monkey troops. *Folia Primatologica* 10:1–19.
- Bernstein IS. 1980. Activity patterns in a stump-tail macaque group (*Macaca arctoides*). *Folia Primatologica* 33:20–45.
- Call J, Aureli F, de Waal FBM. 2002. Postconflict third-party affiliation in stump-tailed macaques. *Animal Behaviour* 63:209–216.
- Castles DL, Aureli F, de Waal FBM. 1996. Variation in conciliatory tendency and relationship quality across groups of pigtail macaques. *Animal Behaviour* 52:389–403.
- Colmenares F. 1990. Greeting behaviour in male baboon, I: communication, reciprocity and symmetry. *Behaviour* 113:81–116.
- ~~Colmenares F. 1991a. Greeting, aggression, and coalitions between male baboons: demographic correlates. *Primates* 2:453–463.~~
- Colmenares F. 1991. Greeting behaviour between male baboons: oestrous females, rivalry and negotiation. *Animal Behaviour* 41:49–60.
- Cooper MA, Aureli F, Singh M. 2007. Sex differences in reconciliation and post-conflict anxiety in bonnet macaques. *Ethology* 113:26–38.
- Cordischi C, Cozzolino R, Aureli F, Scucchi S. 1991. Influence of context on mounting and presenting among mature male Japanese macaques. *Folia Primatologica* 56:211–213.
- Cords M. 1992. Post-conflict reunions and reconciliation in long-tailed macaques. *Animal Behaviour* 44:57–61.
- Deag JM. 1980. Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour* 75:54–81.
- Demaria C, Thierry B. 1989. Lack of effects of environmental changes on agonistic behaviour patterns in a stabilizing group of stump-tailed macaques (*Macaca arctoides*). *Aggressive Behavior* 15:353–360.
- Epplé G. 1975. The behavior of marmoset monkeys (*Callithricidae*). In: Rosenblum LA, editor. *Primate behavior*. New York: Academic Press. p 195–239.
- Fischer J, Hammerschmidt K. 2002. An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica* 73:32–45.
- Goy RW, Wallen K. 1979. Experiential variables influencing play, foot-clasp mounting and adult sexual competence in male rhesus monkeys. *Psychoneuroendocrinology* 4:1–12.
- Hanby JP. 1974. Male-male mounting in Japanese monkeys (*Macaca fuscata*). *Animal Behaviour* 22:836–849.
- Hanby JP, Brown CE. 1974. The development of sociosexual behaviour in Japanese macaques. *Behaviour* 49:152–196.
- Hanby JP, Robertson LT, Phoenix CH. 1971. Sexual behaviour in a confined troop of Japanese macaques. *Folia Primatologica* 16:123–143.
- Hausfater G, Takacs D. 1987. Structure and function of hindquarter presentations in yellow baboons (*Papio cynocephalus*). *Ethology* 74:297–319.
- Hohmann G, Fruth B. 2000. Use and function of genital contacts among female bonobos. *Animal Behaviour* 60:107–120.
- Kaburu SSK, MacLarnon A, Majolo B, Qarro M, Semple S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology* 47:74–79.
- Kano T. 1980. Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: a preliminary report. *Journal of Human Evolution* 9:255–260.
- Kutsukake N, Suetsugu N, Hasegawa T. 2006. Pattern, distribution, and function of greeting behavior among black-and-white colobus. *International Journal of Primatology* 27:1271–1291.
- Maestripiéri D. 1996. Social communication among captive stump-tailed macaques (*Macaca arctoides*). *International Journal of Primatology* 17:785–802.
- Maestripiéri D. 1997. Gestural communication in macaques: usage and meaning of nonvocal signals. *Evolution of Communication* 1:193–222.
- Maestripiéri D. 2007. Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*): use of signals in relation to dominance and social context. In: Liebal K, Müller C, Pika S, editors. *Gestural communication in nonhuman and human primates*. Amsterdam/Philadelphia: John Benjamins. p 51–66.
- Maestripiéri D, Schino G, Aureli F, Troisi A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour* 44:967–979.
- Majolo B, Ventura R, Koyama NF. 2005. Postconflict behavior among male Japanese macaques. *International Journal of Primatology* 26:321–336.
- Majolo B, Ventura R, Koyama NF. 2009. Anxiety level predicts post-conflict behaviour in wild Japanese macaques (*Macaca fuscata yakui*). *Ethology* 115:986–995.
- Mann J. 2006. Establishing trust: socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In: Sommer V, Vasey PL, editors. *Homosexual behaviour in animals*. Cambridge University Press. p 107–130.
- Matsumura S. 1996. Postconflict affiliative contacts between former opponents among wild moor macaques (*Macaca maurus*). *American Journal of Primatology* 38:211–219.
- McFarland R, Majolo B. 2013a. The importance of considering the behavioral form of reconciliation in studies of conflict resolution. *International Journal of Primatology* 34:15–29.
- McFarland R, Majolo B. 2013b. Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters* 9:20130428.
- Oi T. 1990. Patterns of dominance and affiliation in wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *International Journal of Primatology* 11:339–356.
- Okamoto K, Agetsuma N. 2001. Greeting behavior during party encounters in captive chimpanzees. *Primates* 42:161–165.
- Owens NW. 1976. The development of sociosexual behaviour in free-living baboons, *Papio anubis*. *Behaviour* 57:241–259.
- Poiani A. 2008. Same-sex mounting in birds: comparative test of a synthetic reproductive skew model of homosexuality. *The Open Ornithology Journal* 1:36–45.
- Reed C, O'Brien TG, Kinnaird MF. 1997. Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology* 18:247–260.
- Rees PA. 2004. Some preliminary evidence of the social facilitation of mounting behavior in a juvenile bull Asian elephant (*Elephas maximus*). *Journal of Applied Animal Welfare Science* 7:49–58.
- Reinhardt V, Reinhardt A, Bercovitch FB, Goy RW. 1986. Does intermale mounting function as a dominance demonstration in rhesus monkeys? *Folia Primatologica* 47:55–60.
- Smuts BB, Watanabe JM. 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *International Journal of Primatology* 11:147–172.
- Sommer V, Schauer P, Kyriazis D. 2006. A wild mixture of motivations: same-sex mounting in Indian langur monkeys. In: Sommer V, Vasey PL, editors. *Homosexual behaviour in animals: An evolutionary Perspective*, Vol. 9. New York: Cambridge University Press. p 238–272.
- Srivastava A, Borries C, Sommer V. 1991. Homosexual mounting in free-ranging female Hanuman langurs (*Presbytis entellus*). *Archives of Sexual Behavior* 20:487–512.

- 1 Tokuda K, Simons RC, Jensen GD. 1968. Sexual behavior in a
2 captive group of pigtailed monkeys (*Macaca nemestrina*).
3 *Primates* 9:283–294.
- 4 Thierry B. 2007. Unity in diversity: lessons from macaque
5 societies. *Evolutionary Anthropology: Issues, News, and*
6 *Reviews* 16:224–238.
- 7 Thierry B, Aureli F, Nunn CL, Petit O, Abegg C, de Waal
8 FBM. 2008. A comparative study of conflict resolution in
9 macaques: insights into the nature of trait covariation.
10 *Animal Behaviour* 75:847–860.
- 11 Vasey PL, Bernard C, Gauthier C. 1998. Mounting interaction
12 between female Japanese macaques: testing the influence of
13 dominance & aggression. *Ethology* 104:387–398.
- 14 Vasey PL. 1995. Homosexual behavior in primates: a review of
15 evidence & theory. *International Journal of Primatology*
16 16:173–204.
- 17 De Vries H, Netto WJ, Hanegraff PLH. 1993. Matman: a
18 program for the analysis of sociometric matrices and
19 behavioural transition matrices. *Behaviour* 125:157–175.
- 20 De Waal FBM, Ren RM. 1988. Comparison of the reconcilia-
21 tion behavior of stump-tail and rhesus macaques. *Ethology*
22 79:129–142.
- 23 De Waal FBM, Yoshihara D. 1983. Reconciliation and redir-
24 ected affection in rhesus monkeys. *Behaviour* 85:224–241.
- 25 Whitham JC, Maestripieri D. 2003. Primate rituals: the
26 function of greetings between male Guinea baboons.
27 *Ethology* 109:847–859.
- 28 Wickler W. 1967. Sociosexual signals and their intra-specific
29 imitation among primates. In: Morris D, editor. *Primate*
30 *ethology*. New Jersey, U.S.: Aldine Tra. New Brunswick.
31 p 69–147.
- 32 Yamagiwa J. 1987. Group of Virunga mountain gorillas
33 (*Gorilla gorilla beringei*). *Primates* 28:1–30.
- 34 Young C, Majolo B, Heistermann M, Schülke O, Ostner J.
35 2014. Responses to social and environmental stress are
36 attenuated by strong male bonds in wild macaques.
37 *Proceedings of the National Academy of Sciences of the*
38 *United States of America* 111:18195–18200.
- 39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59

AUTHOR QUERY FORM






JOURNAL: AMERICAN JOURNAL OF PRIMATOLOGY

Article: ajp22451

Dear Author,

During the copyediting of your paper, the following queries arose. Please respond to these by annotating your proofs with the necessary changes/additions using the E-annotation guidelines attached after the last page of this article.

We recommend that you provide additional clarification of answers to queries by entering your answers on the query sheet, in addition to the text mark-up.

Query No.	Query	Remark
Q1	Please confirm that given names (red) and surnames/ family names (green) have been identified correctly.	
Q2	Please check the order of section headings.	
Q3	Please indicate whether it is Colmenares, 1991 a or b.	
Q4	Please indicate whether it is Colmenares, 1991 a or b.	
Q5	Please indicate whether it is Colmenares, 1991 a or b.	
Q6	Please check the change made for correctness.	