



**HAL**  
open science

## Avoidant social style among wild crested macaque males (*Macaca nigra*) in Tangkoko Nature Reserve, Sulawesi, Indonesia

Maura Tyrrell, Carol M Berman, Julie Duboscq, Muhammad Agil, Try  
Sutrisno, Antje Engelhardt

### ► To cite this version:

Maura Tyrrell, Carol M Berman, Julie Duboscq, Muhammad Agil, Try Sutrisno, et al.. Avoidant social style among wild crested macaque males (*Macaca nigra*) in Tangkoko Nature Reserve, Sulawesi, Indonesia. *Behaviour*, 2020, 157 (5), pp.451-491. 10.1163/1568539X-bja10009 . hal-02909359

**HAL Id: hal-02909359**

**<https://hal.science/hal-02909359v1>**

Submitted on 14 Oct 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



1  
2  
3  
4 **Avoidant social style among wild crested macaque**  
5 **males (*Macaca nigra*) in Tangkoko Nature Reserve,**  
6 **Sulawesi, Indonesia**  
7  
8

9 **Maura Tyrrell<sup>a,\*</sup>, Carol M. Berman<sup>a,b</sup>, Julie Duboscq<sup>c</sup>, Muhammad Agil<sup>d</sup>,**  
10 **Try Sutrisno<sup>d</sup> and Antje Engelhardt<sup>e</sup>**  
11

12 <sup>a</sup> Graduate Program in Evolution, Ecology and Behavior, University at Buffalo, Buffalo, NY, USA

13 <sup>b</sup> Department of Anthropology, University at Buffalo, Buffalo, NY, USA

14 <sup>c</sup> UMR 7206 Eco-anthropologie, CNRS — MNHN — Paris Diderot, Musée de l’Homme, Paris, France

15 <sup>d</sup> Faculty of Veterinary Medicine, Bogor Agricultural University, Bogor, Indonesia

16 <sup>e</sup> School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK

17  
18 \*Corresponding author’s e-mail address: mauratyr@buffalo.edu

19  
20 Received 1 October 2019; initial decision 17 November 2019; revised 28 March 2020;  
21 accepted 6 April 2020

---

22  
23 **Abstract**

24 Although it is well established that female crested macaques (*Macaca nigra*) display very tolerant  
25 social styles, less is known about the extent to which crested macaque males can be character-  
26 ized by the social style concept. We examined core social style traits and other measures of social  
27 interactions in three groups of wild crested macaque males in Tangkoko Reserve, Indonesia. Com-  
28 parisons with males of other macaque species suggest that they display a mixture of tolerant and  
29 despotic indicators, a pattern inconsistent with tolerant, despotic or uniformly intermediate des-  
30 ignations. Their apparent avoidance of affiliative interactions and reconciliation involving contact  
31 suggest that their relationships also contrast with the typically affiliative and relaxed social style of  
32 female crested macaques. Rather than labeling them as distinctly tolerant or despotic, we describe  
33 the social style of crested males as ‘avoidant’, which may reflect tense relationships due to high  
34 levels of risky reproductive competition.

35 **Keywords**

36 primate males, social relationships, social style, macaques, *Macaca nigra*.

## 1. Introduction

### 1.1. Social style

Primate social structure varies markedly among group-living species, and the concept of social style has been used to describe aspects of that variation. The social style concept is based on the observation that several aspects of social structure, including dominance asymmetry, intensity of aggressive interactions, responses to aggression, kin preferences- and conflict management strategies, appear to co-vary with one another among species (Thierry, 2000, 2007). Among macaques, social styles are hypothesized to vary on a four-grade scale from extremely despotic to extremely tolerant. Extremely despotic species (grade 1) like Japanese (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*) typically exhibit intense unidirectional aggression, strong dominance asymmetry, strong preferences for kin, and low proportions of reconciled conflicts (Thierry, 2000, 2007). On the opposite end of the scale, extremely tolerant species (grade 4) like moor macaques (*Macaca maura*) and Tonkean macaques (*Macaca tonkeana*) show less intense aggression, bidirectional conflicts, weak dominance asymmetry, less intense kin preferences, and high proportions of reconciled conflicts (Thierry, 2000, 2007). In addition, in despotic societies the silent-bared teeth display, a facial expression in which the teeth are exposed by the vertical retraction of the lips, is a unidirectional submission signal consistently given by a subordinate to a dominant individual (de Waal & Luttrell, 1985), whereas in grade 4 species, the silent-bared teeth display is a bidirectional signal of friendly intention used by both dominants and subordinates that facilitates friendly interactions (Dixon, 1977; Duboscq et al., 2013; Thierry et al., 1989, 2000).

Studies of social style in macaques have focused primarily on females, because females form the permanent core of macaque groups, and because most early studies related to social style were done in captive groups that often contained only a few fully adult males (e.g., Thierry, 1985; De Waal & Ren, 1988; De Waal & Luttrell, 1989; Butovskaya, 1993; Petit et al., 1997; Demaria & Thierry, 2001). Thus male–male interactions were often omitted or lumped in with female data. This left open the question of whether the social style framework can be used to characterize macaque male–male relationships as despotic or tolerant as well. Many early researchers assumed that intense competition over fertilizations among primate males should inhibit social bonding between males and traits associated with a tolerant social

1 style in favor of aggression and overt competition (van Hooff & van Schaik, 1  
2 1992, 1994; van Schaik, 1996; van Hooff, 2000), thus limiting males to 2  
3 despotic social styles, if any. Additionally, male–male relationships may be 3  
4 expected to be weaker than female–female relationships in macaques due to 4  
5 their social organization; females are philopatric and males disperse from 5  
6 their natal groups. As a result, adult males are less likely to be related, 6  
7 and hence closely bonded, to other group males than are females, especially 7  
8 females belonging to the same matriline. Nevertheless, affiliative and cooper- 8  
9 ative relationships between males have been described in a number primate 9  
10 species, including macaques (Hill, 1994; van Hooff & van Schaik, 1994), 10  
11 suggesting that they may display a range of social styles. However, detailed 11  
12 studies of core social style traits for male–male interactions have been done 12  
13 for relatively few species (*M. arctoides*: Richter et al., 2009; *M. maura*: Riley 13  
14 et al., 2014; *M. sylvanus*: Preuschoft et al., 1998; *M. thibetana*: Berman et 14  
15 al., 2007; *M. radiata*: Cooper et al., 2007; *M. assamensis*: Cooper & Bern- 15  
16 stein, 2008); hence it is as yet unclear whether primate male social style traits 16  
17 covary as predicted by the social style concept. 17

18 It also remains unclear whether males tend to show similar or sharply dif- 18  
19 ferent social styles as their female conspecifics. Given that male and female 19  
20 infants of many primate species, including macaques, experience similar 20  
21 treatment by mothers, and that both sexes conform to particular species- 21  
22 typical patterns of interaction that may be partly constrained by inherent 22  
23 traits (i.e., social reaction norms), it may seem reasonable at first to hy- 23  
24 pothesize that they may display similar social styles. However, males and 24  
25 females are also subject to widely different selective pressures within groups; 25  
26 whereas female reproductive success is limited primarily by resource distri- 26  
27 bution, male reproductive success is limited by fertilization (Emlen & Oring, 27  
28 1977). Thus, social styles may be predicted to differ between the sexes. In- 28  
29 deed, recent studies on macaques have shown that male–male social relation- 29  
30 ships may differ markedly from those of female conspecifics. For example, 30  
31 stumptail macaque males show more despotic tendencies than their female 31  
32 counterparts, including higher proportions of intense aggression and lower 32  
33 proportions of counteraggression (Richter et al., 2009). In contrast, male Ti- 33  
34 betan macaques (Berman et al., 2004, 2007), Barbary macaques (Preuschoft 34  
35 et al., 1998), and Assamese macaques (Cooper & Bernstein, 2002, 2008; 35  
36 Schulke et al., 2010; Ostner & Schulke, 2014) all have relatively more toler- 36  
37 ant social relationships in comparison to their female counterparts. Finally, 37

1 moor macaque males appear to be similar to extremely tolerant females in 1  
2 their low rates of aggression, low proportions of intense aggression, but more 2  
3 similar to grade 2 and 3 macaques' proportions of counteraggression (Ri- 3  
4 ley et al., 2014). Additionally, a study by Palagi et al. (2014) on Tonkean 4  
5 macaques reports sex differences in patterns of consolation (affiliation be- 5  
6 tween victims and third party), highlighting the nuances between male–male 6  
7 and female–female relationships. Thus the extent to which male relationships 7  
8 resemble those of female conspecifics and the factors that may lead the sexes 8  
9 to vary are also still unclear. Here we attempt to fill some of these gaps by 9  
10 examining social relationships among adult male crested macaques (*Macaca* 10  
11 *nigra*) with an emphasis on core social style traits. By examining core social 11  
12 style traits separately in males and females, we aim to get a better overall 12  
13 understanding of differences in male and female social styles. 13

#### 14 1.2. Crested macaques 14

15 15  
16 Crested macaques are one of seven macaque species endemic to Sulawesi, 16  
17 Indonesia (Fooden 1969). While females remain in their natal groups for life 17  
18 forming matriline, males disperse after reaching sexual maturity and may 18  
19 immigrate into other groups several times throughout their lifetime (Reed 19  
20 et al., 1997; Marty et al., 2017). Wild (Duboscq et al., 2013) and captive 20  
21 crested macaque females (Petit & Thierry, 1994; Petit et al., 1997) have been 21  
22 characterized as extremely tolerant and placed in grade 4 of the social style 22  
23 scale (Thierry, 2007). Duboscq and colleagues (2013) found that wild crested 23  
24 macaque females have frequent low intensity aggression, high proportions 24  
25 of bidirectional conflicts, moderate dominance asymmetry and high concili- 25  
26 atory tendencies compared with other female macaques. When approached 26  
27 nonagonistically by other females, they are more likely to respond with af- 27  
28 filiation than agonism (Duboscq et al., 2013), after which they often remain 28  
29 in close proximity for up to several minutes (Tyrrell, personal observation). 29  
30 Finally, silent bared-teeth displays are friendly facial expressions distributed 30  
31 equally to dominants and subordinates. Male crested macaque relationships 31  
32 have not been as extensively examined as female crested macaque relation- 32  
33 ships. Captive groups have contained too few males to examine male–male 33  
34 relationships separately from females (Petit & Thierry, 1994; Petit et al., 34  
35 1997). Reed et al. (1997) were the first to focus on wild crested macaque 35  
36 males, characterizing them as hierarchical and antagonistic. Despite this 36  
37 assessment, other researchers have reported affiliative behaviour patterns 37

1 indicative of a degree of tolerance, including post conflict reconciliation 1  
2 and ritualized greetings in which males exchange affiliative gestures like 2  
3 mounting, genital-grasping, or mock biting (Dixon, 1977; Petit & Thierry, 3  
4 1994). These greetings may be similar to those observed in baboons (Smuts 4  
5 & Watanabe, 1990; Whitham & Maestripieri, 2003) and bonnet macaques 5  
6 which are hypothesized to show tolerant styles (Sugiyama, 1971; Silk, 1994). 6  
7 Thus male–male relationships appear to be more complex than originally 7  
8 thought. 8

### 9 *1.3. Socioecological and phylogenetic models* 9

10 Competing hypothetical explanations for covariation in aspects of social 10  
11 style across species have been based on socioecological factors and phy- 11  
12 logenetic/structural considerations (socioecological: Wrangham, 1980; van 12  
13 Schaik, 1989; Koenig et al., 2013; Isbell, 2017; phylogenetic/structural: Mat- 13  
14 sumura, 1999; Thierry et al., 2000, 2008; Thierry, 2004; Kamilar & Cooper, 14  
15 2015). The most current socioecological model (Sterck et al., 1997) fo- 15  
16 cuses on females and is based on the assumption that females' needs for 16  
17 resources and safety influence their distribution and the nature of their rela- 17  
18 tionships to one another. Specifically, females form groups when doing so 18  
19 facilitates gaining access to food and protection from predators and/or infan- 19  
20 tanticidal males. Once females coalesce into permanent and cohesive groups, 20  
21 food abundance and distribution are hypothesized to determine the types of 21  
22 competitive regimes females face (i.e., the level competition for food re- 22  
23 sources within and between groups). These competitive regimes in turn lead 23  
24 to variable patterns of dominance asymmetry that give rise ultimately to their 24  
25 social styles and variable levels of kin bias. In female philopatric species, 25  
26 including macaques, high within group competition is hypothesized to lead 26  
27 to despotism. However, despotic tendencies will be moderated when high 27  
28 within group competition is accompanied by high between group competi- 28  
29 tion. Although there is evidence supporting the idea that food distribution 29  
30 and the resulting feeding competition influence female social relationships 30  
31 in some ways, the socioecological model's predictions related to dominance, 31  
32 coalitions and kinship, have not been consistently supported (Matsumura, 32  
33 1999; Menard, 2004; Thierry, 2008; Clutton-Brock & Janson, 2012; Koenig 33  
34 et al., 2013; Balasubramaniam et al., 2014). 34  
35

36 The socioecological model's predictions for male–male relationships 36  
37 posit that the nature of male–male relationships depends on the level of 37

1 competition between males, which is influenced primarily by the distribu- 1  
2 tion of females and the dynamics of female relationships (Emlen & Oring, 2  
3 1977; van Hooff & van Schaik, 1994; van Schaik, 1996; Kappeler & van 3  
4 Schaik, 2002). When females form coherent groups from which single males 4  
5 cannot exclude other males, males must compete with one another over ac- 5  
6 cess to fertile females, a resource that cannot be shared. When access to 6  
7 fertile females is monopolisable within a group, high contest competition, 7  
8 in which aggression or displacements by dominants reduces other individ- 8  
9 uals' access to resources (Janson & van Schaik, 1988; van Schaik & van 9  
10 Noordwijk, 1988), is hypothesized to interfere with the formation of affilia- 10  
11 tive and cooperative relationships between males (Van Hooff & Van Schaik, 11  
12 1992, 1994). As such, high contest competition among males should result 12  
13 in high reproductive skew in which the most dominant males copulate most 13  
14 with fertile females (van Hooff, 2000). When females are not monopolis- 14  
15 able, several males may compete by sperm competition rather than contest 15  
16 competition (Harcourt et al., 1981, Harvey et al., 1995), reducing constraints 16  
17 on affiliation and cooperation. Like females, males subject to high within 17  
18 group competition (and high reproductive skew) are hypothesized to show 18  
19 greater tolerance to one another when they also experience high levels of 19  
20 between-group competition (Van Schaik, 1996; Van Hooff, 2000). Tolerance 20  
21 in the form of reduced aggression toward subordinates by dominant indi- 21  
22 viduals during times of competition over resources may also represent a 22  
23 behavioural mechanism to prevent escalated aggressive conflicts (e.g., Bar- 23  
24 bary macaques: Preuschoft et al., 1998). In crested macaques, mating success 24  
25 and paternity are highly skewed in favour of the highest ranking males (En- 25  
26 gelhardt et al., 2017). This, along with a high degree of sexual dimorphism 26  
27 and vocal signals of dominance (Neumann et al., 2010), suggest strong con- 27  
28 test competition between males within groups. Immigrating males are often 28  
29 met with fierce resistance from resident males (Marty et al., 2017), and fre- 29  
30 quent intergroup encounters also occur (0.8/day) (Martínez Íñigo, 2018), 30  
31 suggesting high levels of between-group competition. 31

32 In contrast to the socioecological model's claim that competitive regimes 32  
33 and social relationships are shaped primarily by ecological determinants, 33  
34 other more recent models emphasize the importance of evolutionary history 34  
35 and structural linkages in shaping primate social systems. Although socioe- 35  
36 cological factors may have shaped primate social structure in the distant past, 36  
37 phylogenetic analyses suggest that current variation in female relationships 37

1 may be better explained by phylogenetic relationships than by adaptation to 1  
2 current socioecological conditions (Menard, 2004; Thierry, 2008; Clutton- 2  
3 Brock & Janson, 2012; Kamilar & Cooper, 2015). Thierry's structural model 3  
4 in particular focuses on social style traits and purports that they are inher- 4  
5 ent characteristics that are structurally inter-related, and as a result co-evolve 5  
6 (and covary) with one another across species (Thierry, 2004, 2007, 2013). 6  
7 There is increasing evidence that related species have similar social styles, 7  
8 despite differences in feeding ecology or ecological conditions (Di Fiore & 8  
9 Rendall, 1994; Thierry et al., 2000, 2008; Thierry, 2007, 2008; Balasubrama- 9  
10 niam et al., 2012, 2018) suggesting that phylogenetic history is an important 10  
11 factor in the evolution of primate social systems, particularly for Old World 11  
12 Monkeys. Although differences between groups of the same species have 12  
13 been reported, these differences are considerably smaller relative to differ- 13  
14 ences across species (Thierry et al., 2008). Nevertheless, some studies show 14  
15 intraspecific variability in social style traits across groups (e.g., Zhang & 15  
16 Watanabe, 2014) or over time (Berman & Thierry, 2010), suggesting some 16  
17 flexibility related to current conditions, including group size (Balasubrama- 17  
18 niam et al., 2011), socioeconomic sex ratios and intergroup competition (Majolo 18  
19 et al., 2009; Horiuchi et al., 2007). 19

#### 20 1.4. Covariation of social style traits 20

21 A common approach to empirically distinguish between the structural and 21  
22 socioecological models is through the concept of covariation of social style 22  
23 traits vs. the influence of external factors. The structural model explicitly 23  
24 predicts the covariation of traits, given its emphasis on the inherent link- 24  
25 age of social style traits. While the socioecological framework predicts the 25  
26 clustering of social style traits to some extent (Sterck et al., 1997; Koenig 26  
27 et al., 2013), it does not necessarily predict structural linkages or tight co- 27  
28 variation among them. Rather it predicts variation of social style traits with 28  
29 factors expected to influence competitive regimes, e.g., group size. So far, 29  
30 the concept of covariation of social style traits has received some empirical 30  
31 support, but the extent to which traits actually covary is unclear. Assigning 31  
32 females of macaque species to the grades on the extreme ends of the scale (1 32  
33 and 4) has been straightforward, as characteristics fit the predicted patterns 33  
34 with little overlap. However, placing species into the intermediate grades 34  
35 (2 and 3) has been more problematic. For example, Balasubramaniam et al. 35  
36 (2012) found that among female macaques, counteraggression behaved 36  
37 37



dichotomously rather than continuously along the scale, and some species assigned to an intermediate grade showed a mix of tolerant and despotic characteristics that did not appear to covary systematically. Moreover, some traits including those related to grooming kin bias and social network modularity (Berman & Thierry, 2010; Sueur et al., 2011; Balasubramaniam et al., 2018) were strongly related to group size. In a recent review, Balasubramaniam and colleagues (2020) suggested that such mixed results for covariation and evidence of flexibility with external conditions is consistent with the idea that covariation among social style traits was present in the distant evolutionary past of the genus, but that it has been subsequently modified by semi-independent responses to variation in current conditions.

### *1.5. Aim and predictions*

Here we aim to characterize the social style of wild crested macaque males by examining several core indicators, including aggression intensity, counteraggression, dominance asymmetry, conciliatory tendency, outcomes of nonagonistic approaches and the silent bared-teeth display. These indicators will be compared (1) with available published data for males of other macaque species, (2) with female crested macaques, using data from Duboscq and colleagues (2013) and (3) among males within the three study groups. Additional behavioural measures, including rates of nonagonistic approaches, affiliation and aggression, will be compared to female crested macaques to supplement descriptions of relationships.

If males exhibit a tolerant social style, we predict that they will display relatively low proportions of aggressive interactions involving biting, high proportions of counteraggression, low hierarchical steepness, high conciliatory tendencies, high proportions of affiliative responses to nonagonistic approaches and bidirectional silent bared-teeth displays.

If crested macaque males exhibit a despotic social style, we predict that they will display relatively high proportions of aggressive interactions involving biting, low proportions of counteraggression, high hierarchical steepness, low conciliatory tendencies, low proportions of affiliative responses to nonagonistic approaches and unidirectional silent bared-teeth displays.

If the male social style traits listed above covary closely with one another, we predict that, relative to other macaque males, all traits will consistently indicate the same social style, e.g., extremely despotic, extremely tolerant or consistently intermediate.

1 If crested macaque male social style is similar to that of tolerant crested 1  
2 females, there should be no significant differences between their measures on 2  
3 these traits and those of females. If their relationships are similarly friendly 3  
4 and relaxed as those of females, we predict similarly high rates of affiliation 4  
5 and nonagonistic approaches, and low rates of aggression. 5

6 If social style traits are primarily inherent species-characteristics rather 6  
7 than variable responses to current circumstances (e.g., variation in group 7  
8 size, male immigration rates, intensities of tourism/crop-guarding, see Meth- 8  
9 ods below), we predict that male social style traits listed above should not dif- 9  
10 fer significantly between study groups. Significant variation between groups 10  
11 in social style traits and other types of interaction would suggest responses 11  
12 to current conditions, consistent with a socioecological explanation. 12  
13

## 14 2. Methods 14

### 15 2.1. Subjects and study site 15

16  
17 Our methods follow the research guidelines of the United States and In- 17  
18 donesian governments and institutions, and the guidelines of ASAB for the 18  
19 treatment of animals in behavioural research and teaching. Our data collec- 19  
20 tion protocol was approved by the University at Buffalo's IACUC committee 20  
21 (No. ANT04074N). 21

22 Data collection took place at Tangkoko Nature Reserve in North Sulawesi, 22  
23 Indonesia (1°33' N, 125°10' E) from March 2016–February 2017, as part of 23  
24 a long-term project, the Macaca Nigra Project (MNP). The reserve is clas- 24  
25 sified as lowland rainforest with seasonal changes in rainfall, composed of 25  
26 primary and secondary forest with areas of regenerating gardens (O'Brien 26  
27 & Kinnaird, 1997). The Macaca Nigra Project ([www.macaca-nigra.org](http://www.macaca-nigra.org)) es- 27  
28 tablished the field site within the Tangkoko Reserve in Sulawesi in 2006. 28  
29 Currently three groups are fully habituated and regularly followed on foot 29  
30 by MNP staff and researchers. Two of the groups (R2 and R1) are also sub- 30  
31 jected to tourism and crop guarding, while the third (PB1) is not. 31

32 We observed the three wild, unprovisioned study groups throughout the 32  
33 duration of the project. Group R1 had a total of approximately 110 individ- 33  
34 uals, including 10–13 adult males and 33 adult females, R2 had a total of 34  
35 about 70 individuals, including 6 adult males and 27 adult females, and PB1 35  
36 had a total of about 78 individuals, including 7 adult males and 26 adult fe- 36  
37 males. Kinship among adult males was unknown. All adult individuals were 37

1 identified by scars, broken or missing fingers, facial features and/or the shape 1  
2 of the anogenital region. 2

### 3 2.2. *Data collection* 3

4  
5 MT, TS and three other field assistants followed the study groups from dawn 5  
6 to dusk (ca. 0500 h to 1730 h, WITA) daily, from March 2016 to February 6  
7 2017. We collected a total of 2595 hours of data from 28 adult males (mean: 7  
8 92.7 h/male; range: 7.4–150.3 h), using focal animal sampling (Altmann, 8  
9 1974). At the start of the study, focal males included all adult, non-natal 9  
10 males in each of the three groups (5 males from R2, 4 males from PB1, 10  
11 males from R1). Nine new males were added to the focal subject list as they 11  
12 migrated into the study groups. Three new adult males migrated into R1 and 12  
13 one new male migrated into PB1 from unhabituated groups. Three adult na- 13  
14 tal males from R2 migrated for the first time into R1, and two adult natal 14  
15 males from PB1 migrated for the first time into R1. One male migrated from 15  
16 R2 to R1, and thus has focal observations in both groups. Three additional 16  
17 adult males entered the study groups (2 in PB1 and 1 in R1) but remained 17  
18 unhabituated during the time frame of the study. Five males left R1 before the 18  
19 end of the study. The total number of male subjects observed in each group 19  
20 was 5 males from R2, 5 males from PB1 and 19 males from R1. We focused 20  
21 on male–male relationships among nonnatal males, because assessments of 21  
22 social style typically focus on nonkin dyads to distinguish social style effects 22  
23 from kin selection effects (Thierry, 2007; Thierry et al., 2008), and nonnatal 23  
24 males are less likely to be related to other males than are natal males. There- 24  
25 fore, we excluded natal males from this study. Moreover, there were too few 25  
26 adult natal males to analyse separately. We recorded aggression, affiliation, 26  
27 displacements, submissive behaviour and silent bared-teeth displays in focal 27  
28 sessions that lasted 2 h when possible (mean length: 1.8 h). Long focal fol- 28  
29 lows were useful to obtain data on males whose rates of interactions are low 29  
30 and whose movement patterns and location were less predictable than those 30  
31 of females. Identities of the actor and recipient of behaviours were recorded 31  
32 as well as the sequence of events. Each day, focal males were selected from 32  
33 a predetermined random order, and sessions were evenly distributed across 33  
34 time of day for each male (5:45 am–9 am, 9 am–12 pm, 12 pm–3 pm, 3 pm–6 34  
35 pm). We performed point-time sampling every 2 min during focal sampling 35  
36 sessions during which we recorded the identities of other males within body 36  
37 contact, one body length (0.5 m), 5 body lengths (2.5 m) and 5 m of the 37

1 focal. We also recorded the general activity of the group (whether the ma- 1  
2 jority of the group was feeding, travelling or socialising) every 10 min. Data 2  
3 were recorded directly into Toshiba Encore tablets with PTab spreadsheet 3  
4 program. We tested interobserver reliability between all pairs of observers, 4  
5 using Cohen's Kappa separately for behaviours (74–83%), focal proximity 5  
6 to other males (77–100%), group activity (range 70–100%), and individual 6  
7 identification (100%). Interobserver reliability was re-tested additional times 7  
8 throughout the study and some scores improved. 8

9 Data on female crested macaques were available for two groups R1 ( $N =$  9  
10 21) and PB1 ( $N = 15$ ), having been collected by Julie Duboscq, Jerome 10  
11 Micheletta and Dwi Yandhi Febriyanti from October 2008–May 2010 (Du- 11  
12 boscq et al., 2013). Our team and Duboscq's team followed the same data 12  
13 collection protocol and used the same behavioural definitions. Both teams 13  
14 passed interobserver reliability tests with long-term *Macaca Nigra* Project 14  
15 field assistants for individual IDs and behavioural data collection. 15

### 16 2.3. Behavioural definitions 16

17 Aggressive interactions were defined as any aggressive behaviour that was 17  
18 followed by a response from the receiver (aggression, affiliation, submis- 18  
19 sion). Aggressive behaviours were categorized as threats (aggressive vocal- 19  
20 izations such as bark, grunt, rattle, and facial expressions such as half-open 20  
21 mouth, open mouth bared teeth), noncontact attacks (stamp, lunge, chase), 21  
22 contact attacks (hit, missed hit, grab, push) or bites (Thierry et al., 2000). 22

23 A displacement was defined as a nonaggressive approach by a male within 23  
24 2.5 m while the approached male simultaneously moved away (Thierry et al., 24  
25 2000). 25

26 Affiliative interactions included friendly behaviours such as grooming, 26  
27 embracing, grasping of fur, grasping of the genitals, male–male mounting, 27  
28 any nonaggressive body contact, presentation of hindquarters and friendly 28  
29 facial expressions such as lipsmacking (Thierry et al., 2000). A grooming 29  
30 bout consisted of any continuous episode of grooming with interruptions of 30  
31 no more than 10 s. If an affiliative interaction consisted of only lipsmacking, 31  
32 it was categorized as noncontact affiliation. Interactions that included both 32  
33 contact and noncontact behaviours were scored as contact affiliation. 33

34 The silent bared-teeth display is a facial expression in which the upper 34  
35 or both lips are vertically retracted, in which with the corners of the mouth 35  
36 are drawn back, exposing the teeth and sometimes the gums (Thierry et al., 36  
37 2000). 37

1 We recorded nonagonistic approaches when a focal male approached another male within one bodylength (approximately 0.5 m), and remained in proximity for 5 s. We also recorded nonagonistic approaches within five bodylengths (approximately 2.5 m). We classified outcomes of nonagonistic approaches as positive, negative or neutral. Positive outcomes were those in which the approaching male and/or the approached male engaged in affiliation within 10 s. Negative outcomes were those in which the approached male aggressed or retreated from the approacher within 10 s. Neutral outcomes were recorded if there was no observable action/reaction from either male within 10 s.

#### 11 *2.4. Data analysis*

12 We used only dyadic interactions between males during focal observations in the analysis. If more than one behaviour of the same category (i.e., affiliative, aggressive) were performed in succession between 2 individuals (within 10 s), those behaviours were considered to be a single episode and were reported as a single interaction. If both agonistic and affiliative behaviours were exchanged within the same episode, the episode was scored as an agonistic interaction. Rates of behaviours (the total number of behavioural events performed by the focal subject divided by the total number of hours the focal subject was observed) and percentages of total behaviours (proportions of specific categories of behaviours out of all affiliative/aggressive behaviours) were calculated for each male. From these, group means and standard errors were derived.

##### 25 *2.4.1. Aggression*

26 We calculated the percentages of total aggressive interactions that involved biting, contact attacks, noncontact attacks and threats. If multiple aggressive behaviours were exchanged between individuals within the same episode, the behaviour of highest intensity was used to classify the interaction (bite > contact attack > noncontact attack > threat). Counteraggression was calculated as the percentage of aggressive interactions in which the recipient of aggression responded with aggression within 10 seconds.

##### 33 *2.4.2. Affiliation*

34 The quality of affiliative interactions was assessed by calculating the percentage of total affiliative interactions involving body contact (e.g., mount, embrace, touch, grasp, grooming) for each male. Grooming rates were calculated for each male as the number of grooming bouts divided by the total

1 observation hours for that male. A grooming bout consisted of immediately 1  
2 consecutive grooming episodes between two individuals that stopped and 2  
3 restarted within 10 seconds of each other. 3

#### 4 2.4.3. Conciliatory tendency 4

5 The PC-MC method (de Waal & Yoshihara, 1983) was used to test for the occurrence 5  
6 of post-conflict affiliation. A post-conflict observation period (PC) 6  
7 started immediately after an aggressive interaction ended between the focal 7  
8 male and an opponent male and lasted 5 min (per de Waal & Yoshihara, 8  
9 1983). All aggressive and affiliative behaviours exchanged between the focal 9  
10 male and the opponent were recorded. If aggression re-occurred within the 10  
11 PC, it was discarded and restarted once the new aggression ended. Matched- 11  
12 control periods (MC) were extracted from focal data to compare the timing 12  
13 of the first affiliative contact in the PC and in the corresponding MC (Aureli, 13  
14 1992). For each PC, a 5-min MC period was chosen based on the following 14  
15 criteria: the same opponent was within 5 m at the start of the MC, the op- 15  
16 ponents had not participated in aggression or affiliative interactions within 16  
17 2 min of the start of the MC, and the general group activity was the same 17  
18 as in the PC. MC periods were within one month of the PC, when possible. 18  
19 If the first affiliative interaction between former opponents occurred earlier 19  
20 in the PC than MC, the pair was labelled ‘attracted’. If the first affiliative 20  
21 interaction occurred earlier in the MC than PC, or if it occurred in the MC 21  
22 but not in the PC, the pair was labelled ‘dispersed’. If affiliation occurred 22  
23 at the same time in the PC and MC periods, or in neither PC nor MC pe- 23  
24 riods, the pair was labelled ‘neutral’. The corrected conciliatory tendency 24  
25 (CCT) was calculated in two ways: using contact affiliation only and using 25  
26 all affiliation (both contact and noncontact). CCTs were calculated for each 26  
27 individual with at least 2 PC–MC pairs as: (the number of attracted pairs – 27  
28 number of dispersed pairs)/(total number of PC–MC pairs) (Veenema et al., 28  
29 1994) for each individual, and then as a group mean. 29  
30

#### 31 2.4.4. Dominance hierarchy 31

32 Dominance hierarchies were constructed from the direction of displacements 32  
33 during stable periods (e.g., periods with no male migrations). We calculated 33  
34 the linearity index  $h'$ , which corrects for unknown relationships (de Vries, 34  
35 1995) and determined the rank order of individuals using the dominance 35  
36 matrix created by the I & SI method (Matman 1.0). *Hierarchical steepness*, a 36  
37 measure of the extent to which an individual can exercise a negative influence 37

1 on another individual (De Vries et al., 2006), was calculated using the slope 1  
2 of individual normalized David scores (Gammell et al., 2003). David scores 2  
3 were calculated using actor-receiver matrices based on dyadic aggressive 3  
4 interactions with a clear winner and loser (i.e., the receiver of aggression 4  
5 responded submissively by avoiding or fleeing). Steepness values range from 5  
6 0, indicating no differences in the relative abilities to win aggressive contests 6  
7 across adjacently-ranked individuals, to 1, which indicates the maximum 7  
8 differences in such abilities to win aggressive contests. We report  $D_{ij}$  dyadic 8  
9 dominance indices, which correct for chance observations by taking into 9  
10 account the frequency of interactions, and  $P_{ij}$  indices which do not correct 10  
11 for interaction frequency (De Vries et al., 2006; Balasubramaniam et al., 11  
12 2013). 12

#### 13 2.4.5. *Silent-bared teeth display* 13

14 To determine the directionality of the silent bared-teeth display, we calcu- 14  
15 lated the up-down index ( $u/(u + d)$ ) for each individual (Castles et al., 1996), 15  
16 in which  $u$  is the number of displays directed toward a higher ranking indi- 16  
17 vidual and  $d$  is the number of displays directed to a lower ranking individual. 17  
18 An index of 0.5 indicates that there is no tendency for silent-bared teeth 18  
19 display to be directed up or down the hierarchy. An index higher than 0.5 19  
20 indicates a tendency for the silent-bared teeth display to be directed up the 20  
21 hierarchy, while an index below 0.5 indicates a tendency for the display to be 21  
22 directed down the hierarchy (Castles et al., 1996). We performed binomial 22  
23 tests for each individual to determine whether the index differed significantly 23  
24 from 0.5. 24  
25

#### 26 2.5. *Comparisons with other macaque males* 26

27 To compare male crested macaques with male macaques belonging to other 27  
28 species, we plotted crested male scores (mean across all individuals) along 28  
29 with published scores for other species. Due to the scarcity of comparable 29  
30 data, we were able to do this only for some social style measures. We in- 30  
31 cluded studies done both in the wild and in captivity. Since so few studies 31  
32 have examined male social style traits and made direct comparisons with fe- 32  
33 males (e.g., Cooper & Bernstein, 2008, Richter et al., 2009), social style 33  
34 grades have typically not been assigned separately to males. Thus, male 34  
35 macaque social style values are marked with symbols according to the so- 35  
36 cial style grades assigned to the females of the same species (Figures 2–4). 36  
37

## 2.6. Statistical analyses

Analyses were performed in R 3.4.1 (R Core Team, 2017) using the R Stats Package and lme4 Package. Wilcoxon signed-ranks test were used to compare proportions of attracted vs. dispersed PC-MC pairs and to compare individuals' silent bared-teeth display up/down indices to neutral scores of 0.5. We used linear regression models (LMs) to compare social style characteristics of crested macaque males across the three groups, and linear mixed models (LMMs) to compare the males with crested macaque females, controlling for group and rank. Our models satisfied general assumptions of linear regression models including non-multicollinearity (all VIF values  $\leq 2$ ), homoscedasticity (Non-Constant Error Variance test), no autocorrelation (Durbin-Watson test) and normality of residuals (Shapiro-Wilk test) (Field et al., 2012). To assess whether the social style characteristics and social interaction rates of males of different groups differed from each other, an LM was performed for each of the following dependent variables: rate of overall aggression, percentage of counteraggression, percentage of biting aggression, percentage of non-biting contact attacks, percentage of threat aggression, rate of overall affiliation, percentage of contact affiliation, rate of grooming, rate of nonagonistic approach within one and five bodylengths and percentage of positive/negative/neutral outcomes of approaches within one and five bodylengths. 'Group' was included as a fixed effect, and 'rank' was included as a control variable. Interactions between group and rank were removed from the model since they were insignificant for every dependent variable. To assess whether male social style characteristics differed significantly from those of females belonging to the same groups, we performed an LMM for each of the above listed dependent variables (except for rate of approach within 5 bodylengths and percentage of outcomes of approaches within 5 bodylengths, since these data were not available for the females). We entered sex as a fixed factor, group as a random factor and rank as a control. Where necessary to satisfy the assumptions of normality for both sets of analyses, the dependent variables were transformed using square root or cubed root transformations before analysis. In a few cases in which transformations were not sufficient to reach normality, we used nonparametric tests (Mann-Whitney  $U$  or Kruskal-Wallis one-way ANOVA) to confirm the results of the LM and LMM tests. In all cases, the results of the LM and LMMs and nonparametric tests were consistent. Hence we report only the results of the LMs and LMMs.



### 3. Results

For all rates and percentages of behaviours reported,  $N = 29$  males, unless otherwise noted.

#### 3.1. Aggression

We recorded a total of 1483 aggressive interactions during the study. Overall, males engaged in aggression at an average rate of 0.55 interactions/h, with group means ranging between 0.23–0.70 interactions/h (Table 1). The majority of aggressive interactions consisted of threats (1058 or 71.3% of all aggressive interactions). Biting was extremely rare and only occurred 2 times (0.13% of total aggression). Attacks involving physical contact other than biting were also rare (40 interactions or 2.7% of total aggression), whereas noncontact attacks occurred 383 times (25.8% of aggressive interactions). Counteraggression occurred 43 times (2.9% of all aggressive conflicts).

#### 3.2. Affiliation and approach

We recorded a total of 3483 affiliative interactions during the study. Males engaged in affiliative behaviours at a mean rate of 1.54 interactions/h, with group means ranging from 0.69–1.97 interactions/h (Table 1). Grooming was extremely rare between males, occurring about once every 66 h. Other types of affiliation involving body contact occurred 1279 times, making up 37.8% of all affiliative interactions.

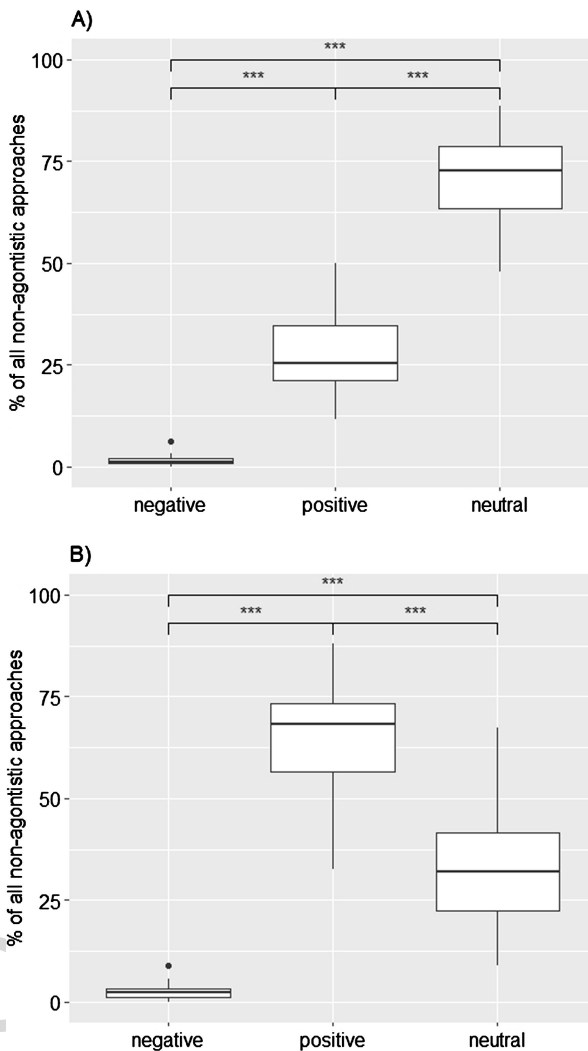
Males approached other males within five bodylengths nonagonistically at a mean rate of  $1.15 \pm 0.13$  (mean  $\pm$  SE) times/h for a total of 6048 approaches. A large majority of outcomes of these approaches were neutral (no response) (4434; mean = 70.5%; see Figure 1A). Nonagonistic approaches within one bodylength were relatively rare (total = 2168), occurring at mean rate of  $0.45 \pm 0.05$  (mean  $\pm$  SE) times/h, but when they did occur, the majority of outcomes were positive (1340; mean = 65.1%; see Figure 1B). Most positive outcomes (71%) involved brief exchanges (about 5–10 s) of body contact affiliation such as genital grasp, mount, embrace, mock bite or other friendly touch, after which the males did not remain in close proximity.

#### 3.3. Silent bared-teeth display

We analysed 494 silent-bared teeth displays ( $R_1 = 370$ , mean = 19/male, range = 0–57;  $R_2 = 46$ , mean = 9/male, range = 0–15; PB1 = 78, mean = 15/male, range = 0–32). Of them, 367 (74%) were directed down, and 127

**Table 1.** Summary of crested macaque male behavioural traits from the three study groups.

|   | R <sub>1</sub> , N = 19 males | R <sub>2</sub> , N = 5 males | PB <sub>1</sub> , N = 5 males | All males, N = 29 |
|---|-------------------------------|------------------------------|-------------------------------|-------------------|
| <b>Aggression (means across individuals ± SE)</b>             |                               |                              |                               |                   |
| All aggression (rate/h)                                       | 0.70 ± 0.08                   | 0.23 ± 0.08                  | 0.31 ± 0.09                   | 0.55 ± 0.07       |
| Bites (%)   | 0.0 ± 0.0                     | 0.7 ± 0.7                    | 0.0 ± 0.0                     | 0.1 ± 0.1         |
| Contact attacks (%)   | 4.1 ± 1.7                     | 1.4 ± 1.4                    | 0.5 ± 0.5                     | 3.0 ± 1.2         |
| Noncontact attacks (%)  | 32.4 ± 3.5                    | 44.7 ± 7.5                   | 21.9 ± 3.8                    | 32.7 ± 2.9        |
| Threats (%)   | 63.5 ± 4.5                    | 53.2 ± 8.1                   | 77.6 ± 3.5                    | 64.2 ± 0.03       |
| Counter-aggression (%)  | 4.2 ± 1.7                     | 3.1 ± 2.1                    | 4.4 ± 3.2                     | 4.1 ± 1.3         |
| <b>Affiliation (means across individuals ± SE)</b>            |                               |                              |                               |                   |
| Overall rate (interactions/h)                                 | 1.97 ± 0.17                   | 0.75 ± 0.23                  | 0.69 ± 0.07                   | 1.54 ± 0.16       |
| Contact affiliation (% of total affiliation)                  | 36.3 ± 2.0                    | 50.2 ± 2.7                   | 31.8 ± 4.2                    | 37.9 ± 2.9        |
| Grooming rate (bouts/h)                                       | 0.02 ± 0.008                  | 0.005 ± 0.004                | 0.007 ± 0.003                 | 0.015 ± 0.005     |
| <b>Non-agonistic approach (means across individuals ± SE)</b> |                               |                              |                               |                   |
| Rate of approach within 5 bodylengths                         | 1.46 ± 0.16                   | 0.61 ± 0.02                  | 0.57 ± 0.09                   | 1.15 ± 0.13       |
| Positive outcome (% of total approaches)                      | 28.4 ± 2.2                    | 30.4 ± 6.7                   | 24.2 ± 1.3                    | 28.0 ± 1.8        |
| Negative outcome (% of total approaches)                      | 1.5 ± 0.3                     | 1.4 ± 0.4                    | 1.5 ± 0.5                     | 1.5 ± 0.2         |
| Neutral outcome (% of total approaches)                       | 70.0 ± 2.4                    | 68.2 ± 7.1                   | 74.4 ± 1.6                    | 70.4 ± 2.0        |
| Rate of approach within 1 bodylength                          | 0.56 ± 0.07                   | 0.28 ± 0.05                  | 0.22 ± 0.04                   | 0.45 ± 0.05       |
| Positive Outcome (% of total approaches)                      | 66.6 ± 3.3                    | 61.1 ± 7.8                   | 63.8 ± 3.5                    | 65.1 ± 2.6        |
| Negative Outcome (% of total approaches)                      | 2.2 ± 0.5                     | 3.0 ± 0.9                    | 2.8 ± 0.9                     | 2.4 ± 0.4         |
| Neutral Outcome (% of total approaches)                       | 31.2 ± 3.5                    | 35.9 ± 8.4                   | 33.4 ± 3.9                    | 32.5 ± 2.7        |
| Silent bared-teeth display (Up/Down Index)                    | 0.30 ± 0.05                   | 0.04 ± 0.04                  | 0.25 ± 0.12                   | 0.25 ± 0.05       |



**Figure 1.** Proportions of types of outcomes following nonagonistic approaches between males within five bodylengths (A) and one bodylength (B). (Medians, interquartiles (error bars), 1.5 interquartile ranges and outliers). \*\*\*  $p < 0.001$ , Mann-Whitney  $U$  test.

(26%) were directed up the hierarchy (mean  $\pm$  SE:  $29 \pm 5\%$ ,  $N = 28$  males). The overall up/down index was 0.26, with group means ranging from 0.04–0.30 (Table 1). Individual index scores for males with at least 5 silent-bared teeth displays were significantly different from a neutral score of 0.5

(Wilcoxon signed-ranks:  $V = 16$ ,  $N = 24$ ,  $p < 0.001$ ), indicating a significant overall tendency for males to direct the display down the hierarchy. However, this tendency was neither displayed by all males nor wholly consistent among individual males, as would have been indicated by individual zero scores. Twenty-one individuals had up/down indices of less than 0.5, two had indices of more than 0.5, and one had an index of exactly 0.5. Separate binomial tests for each individual indicated that 13 of 24 (54%) of males displayed up/down indices significantly lower than 0.5 ( $p < 0.05$ ).

### 3.4. Conciliatory tendency

Out of a total of 540 PC-MC pairs ( $R_1$ : 428 pairs,  $R_2$ : 41 pairs,  $PB_1$ : 71 pairs), 92 were attracted, 42 were dispersed and 306 were neutral, yielding an overall CCT of 27.8%. Group means were calculated from individuals CCT's ( $R_1$ : 28.8, ( $N = 15$ ) males;  $R_2$ : 29.9%, ( $N = 4$ ), and  $PB_1$ : 27.2% ( $N = 5$ ). In  $R_1$ , individuals had significantly higher proportions of attracted pairs than dispersed pairs (Wilcoxon signed-ranks test,  $R_1$ :  $V = 91$ ,  $p = 0.002$ ), indicating that individuals engaged in affiliation at higher rates after aggression than at other times. All males in  $R_2$  and  $PB_1$ , with one exception, also had higher proportions of attracted than dispersed pairs, but Wilcoxon signed-ranks tests did not reach significance ( $R_2$ :  $V = 10$ ,  $p = 0.10$ ;  $PB_1$ :  $V = 10$ ,  $p = 0.10$ ).

### 3.5. Dominance hierarchies

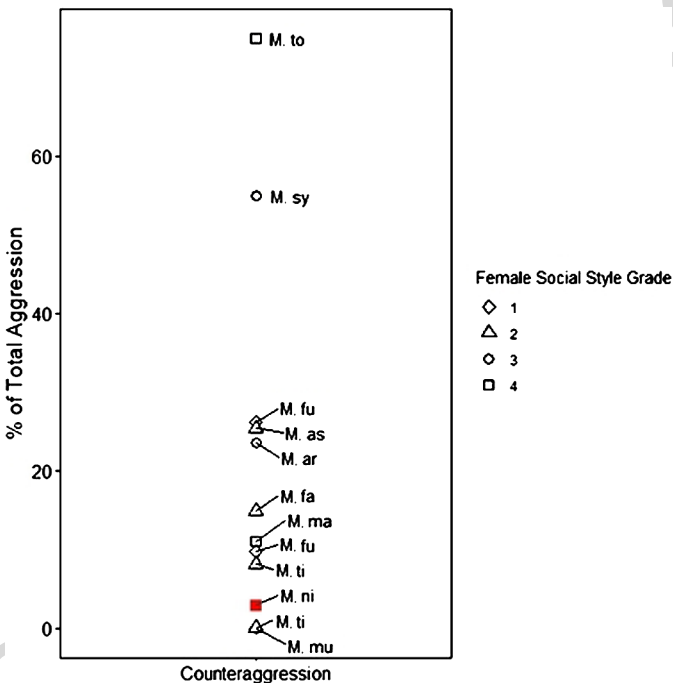
$R_1$  displayed a significantly linear dominance hierarchy ( $R_1$ :  $h' = 0.58$ ,  $N = 13$ ,  $p = 0.002$ ). Although  $h'$  was relatively high in the other two groups, it did not reach significance most likely due to small sample sizes ( $R_2$ :  $h' = 0.85$ ,  $N = 5$ ,  $p = 0.23$ ;  $PB_1$ :  $h' = 0.83$ ,  $N = 5$ ,  $p = 0.11$ ); there were no inconsistencies in either group, and no two-way relationships in  $PB_1$ . Hierarchies were moderately steep (Table 2).  $p_{ij}$  steepness scores were slightly higher than  $D_{ij}$  scores, but still in the moderately steep range. For both measures,  $PB_1$  displayed the lowest score, and  $R_2$  the highest.

### 3.6. Comparisons with other macaque males

The percentage of aggression followed by counteraggression among macaque males ( $N = 10$  species, 12 groups) ranged from 0 to 75%, with the majority of species under 27% (Figure 2). Compared to other macaque

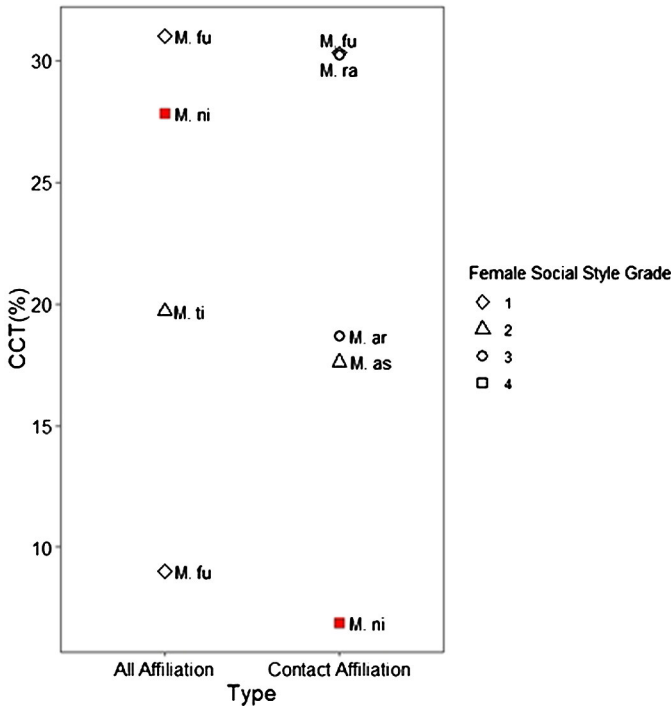
**Table 2.**  
Steepness values using  $D_{ij}$  and  $p_{ij}$  scores.

| Group           | $D_{ij}$ scores | $p_{ij}$ scores | $N_{Interactions}$ |
|-----------------|-----------------|-----------------|--------------------|
| R <sub>1</sub>  | 0.33            | 0.42            | 360                |
| PB <sub>1</sub> | 0.31            | 0.40            | 57                 |
| R <sub>2</sub>  | 0.54            | 0.68            | 48                 |



**Figure 2.** Comparison of percentages of aggression followed by counteraggression across macaque males.\* Indicates captive group. (From top to bottom) *M. tonkeana*\* (Thierry, 1985); *M. sylvanus* (Thierry & Aureli, 2006); *M. fuscata*\* (Petit et al., 1997); *M. assamese* (Cooper & Bernstein, 2008); *M. arctoides* (Richter et al., 2009); *M. fascicularis*\* (Thierry, 1985); *M. maura* (Riley et al., 2014); *M. fuscata* (Thierry, 1990)\*; *M. thibetana* (Berman et al., 2004, period I); *M. nigra* (this study); *M. thibetana* (Berman et al., 2004, period II); *M. mulatta*\* (Thierry, 1985). Female social style grades based on Thierry (2007).

males, crested macaque males had the lowest levels of counteraggression (2.9%), after despotic rhesus (0%) and Tibetan macaque males (0%), consistent with a relatively despotic style.

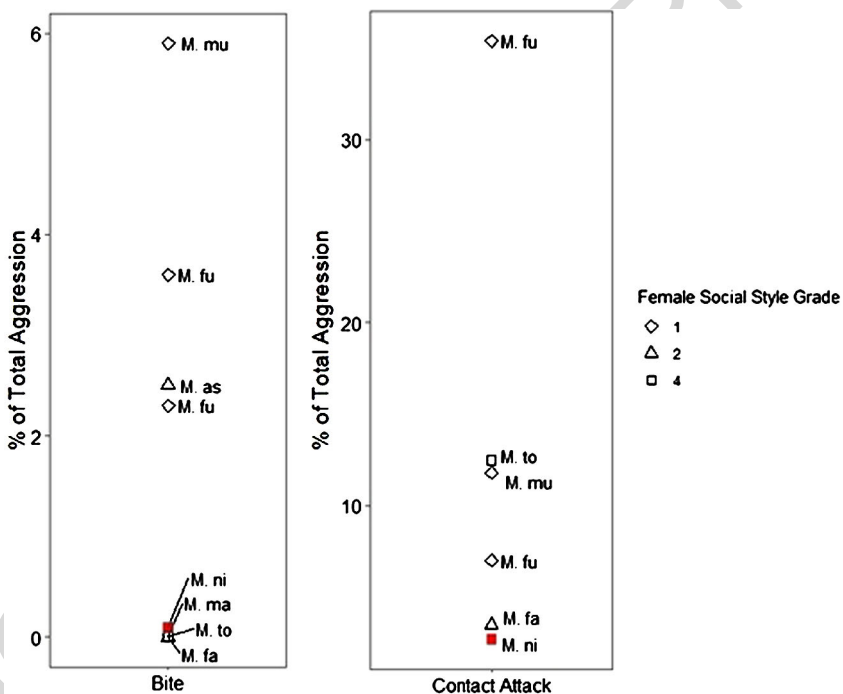


**Figure 3.** Comparison of conciliatory tendencies across macaque males. \* Indicates captive group. All Affiliation: CCT's calculated by using all types of affiliation (From top to bottom): *M. fuscata* (Majolo et al., 2005); *M. nigra* (this study); *M. thibetana* (Berman et al., 2004); *M. fuscata*\* (Schino et al., 1998); Contact Affiliation: CCT's calculated by using contact affiliation only (From top to bottom: *M. fuscata*\* (Petit et al., 1997); *M. radiata* (Cooper et al., 2007); *M. arctoides* (De la O et al., 2013); *M. assamensis* (Cooper & Bernstein, 2008); *M. nigra* (this study). Female social style grades based on Thierry (2007).

Male macaque conciliatory tendencies (CCT scores) ranged from 6.9–30.3% (Figure 3). Direct comparisons between macaque male conciliatory tendencies were difficult because studies included different age classes (subadult and adults vs. adults only) and used different affiliation criteria (all types of affiliation vs. contact affiliation only). In order to compare studies that used both affiliation criteria, we calculated crested macaque scores both ways and compared them separately with similar scores for other species. Noncontact affiliation consisted almost entirely of lipsmacking for crested males. Crested macaque male CCT score involving all types of affiliation (27.8%) was relatively high compared with other males ( $N = 3$  species, 4 groups) (Figure 3). However, when only contact affiliation was considered,

1 male crested macaque CCT score (6.9%) was the lowest of all macaque 1  
 2 males ( $N = 5$  species, 5 groups) (Figure 3), and comparable to extremely 2  
 3 despotic females, suggesting that crested macaque males engage in post- 3  
 4 conflict affiliation, but do so primarily by lipsmacking rather than via body 4  
 5 contact. 5

6 Among macaque males, the percentage of total aggression involving bit- 6  
 7 ting was generally low (range 0–5.9%) ( $N = 7$  species, 8 groups) (Figure 4). 7  
 8 Even so, crested macaque males had an extremely low level of biting com- 8  
 9 pared to other males. Similarly, the percentage of contact attacks for crested 9  
 10



31 **Figure 4.** Comparison of aggression intensity across macaque males. \* Indicates captive 31  
 32 group. (A) Percentage of biting out of total aggression. From top to bottom: *M. mulatta*\* 32  
 33 (Thierry, 1985); *M. fuscata*\* (Petit et al., 1997); *M. assamensis* (Cooper & Bernstein, 2008); 33  
 34 *M. fuscata* (Majolo et al., 2005); *M. nigra* (this study); *M. maura* (Riley et al., 2014); *M.* 34  
 35 *tonkeana*\* (Thierry, 1985); *M. fascicularis*\* (Thierry, 1985). (B) Percentage of contact ag- 35  
 36 gression out of total aggression. *M. fuscata*\* (Petit et al., 1997); *M. tonkeana*\* (Thierry, 1985); 36  
 37 *M. mulatta*\* (Thierry, 1985); *M. fuscata* (Majolo et al., 2005); *M. fascicularis*\* (Thierry, 37  
 1985); *M. nigra* (this study). Female social style grades based on Thierry (2007).

macaque males (2.7%) was the lowest among other macaque male studies (range 3.5–35.4%) (Fig 4).

Taken together, these comparisons suggest that crested macaque male social style traits do not covary in a manner predicted by the social style hypothesis. Crested macaque male counteraggression is very low compared with other male macaques, i.e., on the more despotic end of the social style scale. However, aggression intensity and CCT (involving all types of affiliation) is high compared to other male macaques, i.e., on the more tolerant end of scale.

### 3.7. Comparisons with crested macaque females

Linear mixed models showed that sex is a significant predictor for all social style measures (Table 3, Table A1 in the Appendix). R1 and PB1 males had lower conciliatory tendencies and percentages of counteraggression, bites

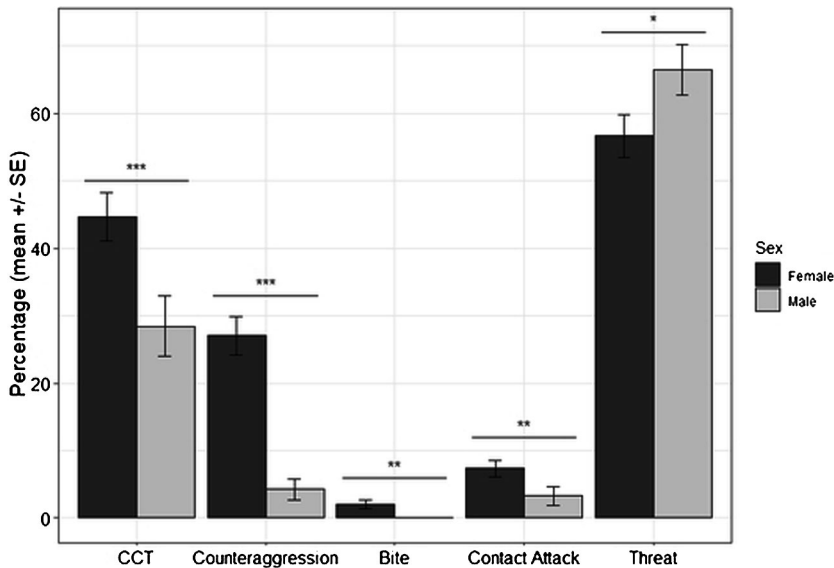
**Table 3.**

Results of linear mixed models comparing behavioral measures of males and females from groups R<sub>1</sub> and PB<sub>1</sub>.

|                                       | Estimate | SE   | <i>t</i> | <i>p</i> |
|---------------------------------------|----------|------|----------|----------|
| Social style measures                 |          |      |          |          |
| Outcome variable                      |          |      |          |          |
| CCT                                   | −0.16    | 0.05 | −2.94    | 0.00***  |
| % Counteraggression                   | −3.59    | 0.42 | −8.51    | 0.00***  |
| % Bite                                | −2.37    | 0.74 | −3.20    | 0.00***  |
| % Contact attack                      | −1.19    | 0.39 | −3.05    | 0.00***  |
| % Threat                              | 12.02    | 4.71 | 2.56     | 0.01**   |
| Approaches within 1 bodylength        |          |      |          |          |
| % Positive outcome                    | 34.33    | 2.33 | 14.76    | 0.00***  |
| % Negative outcome                    | −0.90    | 0.23 | −3.82    | 0.00***  |
| % Neutral outcome                     | −30.27   | 2.42 | −12.53   | 0.00***  |
| Other measures of social interactions |          |      |          |          |
| Outcome variable                      |          |      |          |          |
| Rate of overall aggression            | 0.13     | 0.04 | 2.95     | 0.00***  |
| Rate of overall affiliation           | −0.37    | 0.07 | −5.60    | 0.00***  |
| Rate of grooming                      | −1.19    | 0.11 | −10.52   | 0.00***  |
| % Body contact affiliation            | −4.58    | 2.04 | −2.25    | 0.02*    |
| Rate of approach (1 bodylength)       | −4.84    | 0.30 | −16.23   | 0.00***  |

Estimates are in reference to the fixed effect sex (male). Significant results are marked with asterisks.





**Figure 5.** Comparison of crested macaque male and female social style measures: conciliatory tendencies, counteraggression, and percentages of biting, contact attacks and threats out of total aggression. Mann-Whitney  $U$  tests significance values: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

and contact attacks than R1 and PB1 females, and higher percentages of threat aggression (Figure 5). They also had higher percentages of positive outcomes and lower percentages of both negative outcomes and neutral outcomes to nonagonistic approaches within one bodylength than females (Table 3). In addition, males had higher overall rates of aggression, lower rates of nonagonistic approaches within one bodylength than females (Table 3), and lower overall rates of affiliation than females. Finally, they engaged in less grooming and other affiliation involving body contact than females.

### 3.8. Group comparisons

Males in different social groups displayed similar social style traits: conciliatory tendencies, percent counteraggression and aggression intensity, including percent biting and contact attacks (Table 4, Figure 6ab, Table A2 in the Appendix). Following nonagonistic approaches within five bodylengths, they displayed similar percentages of positive, negative and neutral outcomes (Table 4). Similar percentages of positive, negative and neutral outcomes were also displayed following nonagonistic approaches within one bodylength

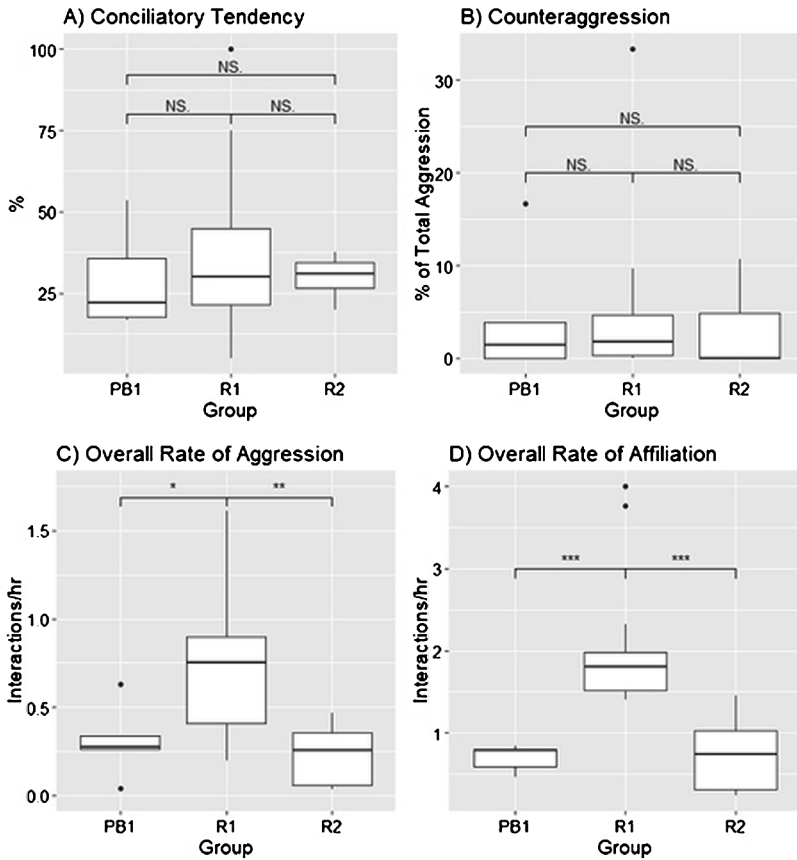
**Table 4.**  
Results of linear regression models comparing interaction in different groups.

| Dependent variable                            | PB1 vs. R1 |          | PB1 vs. R2 |          | R1 vs. R2 |          |
|---|------------|----------|------------|----------|-----------|----------|
|   | Estimate   | <i>p</i> | Estimate   | <i>p</i> | Estimate  | <i>p</i> |
| <b>Social style measures</b>                  |            |          |            |          |           |          |
| CCT   | 0.03       | 0.79     | 0.10       | 0.54     | -0.16     | 0.88     |
| % Counteraggression                           | -0.07      | 0.64     | 0.08       | 0.68     | 0.14      | 0.33     |
| % Bite  | 0.00       | 0.89     | 0.01       | 0.10     | 0.01      | 0.06     |
| % Contact attack                              | 0.12       | 0.08     | 0.02       | 0.81     | -0.10     | 0.15     |
| % Threat                                      | -0.15      | 0.07     | -0.29      | 0.01**   | -0.13     | 0.12     |
| <b>Approach — five bodylengths</b>            |            |          |            |          |           |          |
| % Positive outcome                            | 4.47       | 0.39     | 6.26       | 0.33     | 1.79      | 0.73     |
| % Negative outcome                            | 0.12       | 0.69     | -0.02      | 0.96     | -0.14     | 0.64     |
| % Neutral outcome                             | -4.63      | 0.41     | -6.16      | 0.38     | -1.54     | 0.79     |
| <b>Approach — one bodylength</b>              |            |          |            |          |           |          |
| % Positive outcome                            | 2.31       | 0.74     | -2.68      | 0.77     | -4.99     | 0.50     |
| % Negative outcome                            | -0.15      | 0.73     | 0.06       | 0.91     | 0.21      | 0.63     |
| % Neutral outcome                             | -1.82      | 0.82     | 2.49       | 0.80     | 4.31      | 0.58     |
| <b>Other measures of social interactions</b>  |            |          |            |          |           |          |
| Rate of overall aggression                    | 0.34       | 0.00***  | -0.08      | 0.39     | -0.43     | 0.00***  |
| Rate of overall affiliation                   | 0.58       | 0.00***  | -0.01      | 0.97     | -0.58     | 0.00***  |
| Rate of grooming                              | 0.04       | 0.43     | 0.01       | 0.88     | -0.03     | 0.55     |
| % Body contact affiliation                    | 0.03       | 0.44     | 0.18       | 0.00***  | 0.15      | 0.00***  |
| Rate of nonagonistic approach (1 bodylength)  | 0.32       | 0.01**   | 0.06       | 0.69     | -0.26     | 0.04*    |
| Rate of nonagonistic approach (5 bodylengths) | 0.87       | 0.01**   | 0.04       | 0.91     | -0.83     | 0.01**   |

Significant results are marked with asterisks.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37



**Figure 6.** Group comparisons of two male social style measures (conciliatory tendency (A) and counteraggression (B)), overall rate of aggression (C) and affiliation (D). (Median, interquartiles (error bars), 1.5 interquartile ranges and outliers). \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ , Mann–Whitney  $U$ -test.

(Table 4). The only exception was for percent threats, a form of mild aggression, which was significantly lower in R<sub>2</sub> than PB<sub>1</sub>. In contrast, males displayed more marked group differences in rates of (1) overall aggression, (2) nonagonistic approaches within one bodylength and five bodylengths, and (3) affiliative behaviours: overall affiliative behaviour, contact affiliation, but not grooming (Table 4, Figure 6cd, Appendix Table II). R<sub>1</sub> had significantly higher rates of overall affiliation, aggression, and nonagonistic approaches than PB<sub>1</sub> and R<sub>2</sub>. R<sub>2</sub> had a higher percentage of contact affiliation than R<sub>1</sub> and PB<sub>1</sub>.

#### 4. Discussion

Although it is well established that female crested macaques display extremely tolerant social styles, male crested macaques have been inconsistently characterized as both tolerant and extremely hostile. We examined core social style traits and other measures of social interaction in adult males in three groups of wild crested macaque males in order to characterize their relationships with one another and to ask whether they are consistent with a particular social style (despotic, tolerant or intermediate). We found that males displayed a mixture of tolerant and despotic social style indicators, rather than displaying all indicators consistently on one end of the social style scale, or consistently intermediate. These findings are not consistent with the notion of covariation among social style traits. Relative to other males, crested macaque males had extremely low percentages of biting and other types of contact aggression, typical of tolerant species, but they also had extremely low levels of counteraggression, typical of despotic species. In general, male counteraggression did not appear to correspond to the social style grade assigned to females; although the two highest scores were for species with tolerant females, male scores for species with females in grades 1, 2 and 4 had broadly overlapping ranges. Although we did not limit our measure of counteraggression to nonfood or nonmating contexts, as some captive studies have done, instances of counteraggression were very infrequent in all contexts. When lipsmacking was counted as an affiliative gesture, conciliatory tendencies were high compared to other males, typical of tolerant species, but when they were not counted as affiliative, conciliatory tendencies were extremely low, typical of despotic species. Nevertheless, either way, crested males displayed a mix of tolerant and despotic traits. Additionally, males had moderate levels of hierarchical steepness, and they tended to direct the silent-bared teeth display down the dominance hierarchy. As expected for sexes that are subject to differing selective pressures, males also differed significantly in social style traits and other types of social interactions when compared to females from the same social groups. Compared to females, males had lower conciliatory tendencies (counting lipsmacking for both sexes) and lower percentages of counteraggression, suggesting less tolerance, but also lower percentages of biting and other contact aggression, suggesting more tolerance. Moreover, males showed much lower overall rates of nonagonistic approaches and affiliation than females and almost no grooming. Their low levels of affiliative interaction and their avoidance of

1 reconciliation involving contact, suggest that their relationships do not re- 1  
2 flect the typically affiliative and relaxed nature of female crested macaque 2  
3 relationships or those of other tolerant species. We hypothesize that the ap- 3  
4 parent tolerance among male crested macaques may be better described as 4  
5 avoidance due perhaps to tension over high levels of risky reproductive com- 5  
6 petition. We develop this hypothesis below as we discuss our findings in 6  
7 more detail. 7

8 Past studies have dealt with evidence of mixed tolerant and despotic 8  
9 traits, including extreme scores in both directions, in at least two ways. 9  
10 Early studies (Castles et al., 1996; Cooper & Bernstein, 2002; Berman et 10  
11 al., 2004; Thierry, 2007) placed them in intermediate positions on the so- 11  
12 cial style scale, even though the covariation hypothesis predicts consistently 12  
13 intermediate traits. However more recent studies and reviews (Balasubra- 13  
14 maniam et al., 2020; Berman et al., 2007; Kaburu & Newton-Fisher, 2015) 14  
15 have proposed more nuanced interpretations, for male social styles in par- 15  
16 ticular. These studies suggest that signs of male–male social tolerance can 16  
17 emerge from despotic dominance styles and may represent an adaptive out- 17  
18 growth of within-group competition that allows males to avoid injury and/or 18  
19 enhance their competitive abilities by displaying tolerance to other males. 19  
20 For example, male chimpanzees display characteristics typical of a despotic 20  
21 social style (steep dominance hierarchies in many communities and high re- 21  
22 productive skew), yet they also show signs of a more relaxed dominance 22  
23 style; dominants show tolerance to subordinates and provide agonistic sup- 23  
24 port, and grooming relationships are highly reciprocal (Kaburu & Newton- 24  
25 Fisher, 2015). Kaburu & Newton-Fisher (2015) coined the term ‘egalitarian 25  
26 despots’ to describe male chimpanzees with this seemingly contradictory 26  
27 mix of traits. Displays of tolerance by male chimpanzees are hypothesized 27  
28 to be dependent on sociodemographic factors (i.e., the number of males 28  
29 aged 20–30 years in the group), rather than an inherent characteristic of the 29  
30 species (Kaburu & Newton-Fisher, 2015). In groups with a high number of 30  
31 equally matched male competitors, despotism was constrained and hierarchi- 31  
32 cal steepness tended to be lower (Kaburu & Newton-Fisher, 2015). Similarly, 32  
33 Tibetan macaque males have a mix of despotic and tolerant traits. Low per- 33  
34 centages of counteraggression, the use of the silent-bared teeth display as 34  
35 a submissive signal and a high degree of competition over fertile females 35  
36 point to highly asymmetric dominance relationships (Li, 1999; Berman et 36  
37 al., 2004), but the males also show affiliative behaviours that are associated 37

1 with tolerant species, including moderate conciliatory tendencies, ritualized 1  
2 greetings and triadic interactions involving infants that facilitate friendly in- 2  
3 teractions and social bonding between males (Ogawa, 1995). Furthermore, 3  
4 high ranking males may increase tolerance towards lower ranking males as a 4  
5 way to discourage revolutionary alliances (Berman et al., 2007). Taking af- 5  
6 ter Kaburu & Newton-Fisher’s description of male chimpanzee relationships, 6  
7 Balasubramaniam et al. (2020) refer to Tibetan macaque males as ‘tolerant 7  
8 despots’ to describe the emergence of tolerance despite evidence of despo- 8  
9 tism. 9

10 Finally, Barbary macaque males exhibit social style traits on both ends 10  
11 of the continuum. Barbary macaque males intensely compete over females 11  
12 but have apparently tolerant relationships in that they rarely engage in overt 12  
13 aggression outside of the mating season, lack formalized submissive sig- 13  
14 nals and engage in affiliative interactions (Paul et al., 1996; Preuschoft et 14  
15 al., 1998; Berghänel et al., 2011). In competitive situations, they tend to ig- 15  
16 nore and avoid each other rather than behave aggressively (Preuschoft et al., 16  
17 1998). However, when physical aggression does break out among males, it 17  
18 can result in severe injuries. Thus, the apparent tolerance between males ap- 18  
19 pears to be a result of a stalemate between dangerous males. Avoidance may 19  
20 be viewed as an important de-escalation tactic to deal with intense within- 20  
21 a general avoidance of all types of interactions, in that they have very low 21  
22 rates of affiliation, including behaviours such as grooming and other friendly 22  
23 body contacts, as well as low rates of aggressive behaviours compared to fe- 23  
24 male conspecifics (Richter et al., 2009). Male–male avoidance in stumptail 24  
25 macaques, like Barbary macaques, is hypothesized to prevent conflicts and 25  
26 serious injuries. This idea of avoidance as a strategy may also have relevance 26  
27 for crested macaque male relationships. In addition to our findings of a mix 27  
28 of extreme and intermediate social style scores, they face high within-group 28  
29 competition over fertile females in which the highest-ranking males sire the 29  
30 majority of offspring (Engelhardt et al., 2017). Although biting and contact 30  
31 aggression was rarely observed during focal sessions, serious injuries have 31  
32 been observed resulting from fights between males, especially when males 32  
33 migrate into new groups (Marty et al., 2016, 2017; personal observation). As 33  
34 such, we suggest that tolerance in crested macaque males may not be based 34  
35 on friendliness and relaxed relationships, but may be better described as an- 35  
36 other pattern of avoidance, similar to those seen in male stumptail macaques 36  
37 and Barbary macaques. 37

1 The argument that the apparent tolerance displayed by crested macaque 1  
2 males does not emerge from social tolerance per se or affiliative tenden- 2  
3 cies, but rather from tendencies to avoid social contact, is highlighted when 3  
4 comparing them to females, whose relationships have been consistently de- 4  
5 scribed as friendly and relaxed. For example, although males had signifi- 5  
6 cantly higher rates of aggression than females, they had significantly lower 6  
7 percentages of biting and contact aggression, but higher proportions of threat 7  
8 aggression, involving no contact. This suggests, that although males engaged 8  
9 in a substantial amount of hostile behaviour, they avoided actual contact 9  
10 during aggressive interactions. In addition, males had significantly lower 10  
11 conciliatory tendencies and counteraggression than females, suggesting that 11  
12 they were less able to manage aggression through post conflict affiliation 12  
13 and less willing to challenge aggressors. Moreover, when they engaged in 13  
14 post conflict affiliation, they primarily did so using lipsmacking and rarely 14  
15 with affiliative contact. Rates of nonagonistic approach and affiliative in- 15  
16 teraction also suggest avoidance in males. In contrast to females, rates of 16  
17 close approach and affiliation among males were very low. Although nonag- 17  
18 onistic approaches led on most occasions to an affiliative act involving brief 18  
19 contact, in general males used predominantly noncontact modes of affilia- 19  
20 tion when they did engage affiliatively. As with post conflict affiliation, 20  
21 lipsmacking was the most common affiliative behaviour used by males in 21  
22 these contexts, and unlike females, they typically did not remain within one 22  
23 bodylength for more than 5–10 s. Also unlike females who groomed at high 23  
24 rates, males engaged in virtually no grooming of one another. Although rates 24  
25 of grooming and proximity may be influenced by a variety of factors, making 25  
26 it difficult to compare directly, crested male rates of grooming and proximity 26  
27 contrast even with those of extremely despotic male macaques, suggesting 27  
28 a distinction between despotism per se and avoidance. For example, Hori- 28  
29 uchi (2007) reported individual mean grooming rates/h in despotic Japanese 29  
30 macaque males of 0.07 at Shimokita Peninsula and 0.8 at Yakushima vs. 30  
31 0.015 in our subjects. Similarly, Drickamer (1976) reported per dyad groom- 31  
32 ing rates/h among male rhesus on Cayo Santiago of 0.016 vs. <0.001 in 32  
33 our subjects (see also Kaufman, 1967). Finally, our data suggest that crested 33  
34 male dyads appear to spend a smaller proportion of time within 5 m of each 34  
35 other than Japanese macaque males (0.017 vs. 0.022) (dyadic proximity ra- 35  
36 tio estimated from graph; Kawazoe, 2016). Given their mix of despotic and 36  
37 37

1 tolerant characteristics, labels of a distinctly ‘tolerant’ or ‘despotic’ or ‘inter- 1  
2 mediate’ social style do not seem an appropriate fit for crested males. Due to 2  
3 signs of avoidance of contact, and in light of their intense competition over 3  
4 females, a more fitting description of their social style may be ‘avoidant’. 4  
5 The use of the term ‘avoidant’ distinguishes crested macaque males from 5  
6 males described as ‘egalitarian or tolerant despots’ (i.e., chimpanzees and 6  
7 Tibetan macaques) whose tolerance appears to be more calmly bestowed by 7  
8 dominants on subordinates. Whether or not male crested macaques also use 8  
9 tolerance strategically or selectively like chimpanzees and Tibetan macaque 9  
10 males is as yet unknown. 10

11 In addition to several core social style traits, we also examined the use 11  
12 of the silent bared-teeth display in crested macaque males and found that 12  
13 it differs from macaque species on both extreme ends of the social style 13  
14 scale. Thus its function appears to differ from either despotic or tolerant 14  
15 macaque species. The strong tendency for crested macaque males to direct 15  
16 the silent-bared teeth display down the hierarchy raises the hypothesis that 16  
17 it may communicate dominant status in adult males. However, if so, it is 17  
18 not a formal signal of dominance, because it is not consistently directed by 18  
19 dominants to subordinates. On the other hand, it may be that it functions as 19  
20 a friendly expression as it does in females, but that unlike females, dominant 20  
21 partners are more likely to initiate the display with subordinate partners than 21  
22 vice-versa, perhaps to communicate a benign intent towards subordinates. At 22  
23 this point, whether it conveys a message related to dominance per se or not 23  
24 is unclear. A more detailed examination of the context and function of the 24  
25 display in crested macaque males is forthcoming. 25  
26

27 A recent hypothetical evolutionary explanation for the occurrence of 27  
28 species with mixed despotic and tolerant traits is based on phylogenetic and 28  
29 comparative analyses of social style traits as well as evidence that some traits 29  
30 are influenced by more recent socioecological conditions (Balasubramaniam 30  
31 et al., in 2020). It suggests that patterns of covariation (and the lack thereof) 31  
32 among macaque species is consistent with the idea that covariation among 32  
33 social style traits was present in the distant evolutionary past of the genus, 33  
34 but that it has been subsequently modified by semi-independent responses to 34  
35 variation in current conditions. Specifically, it cites evidence for co-variation 35  
36 between some social style traits and social style grade across some macaques 36  
37 in different phylogenetic lineages, but not across species within the same 37



1 lineage. In addition, it points out that some social style traits also vary be- 1  
2 tween groups within species (e.g., Zhang & Watanabe, 2014) and that some 2  
3 traits are more strongly influenced by varying external circumstances such as 3  
4 group size (Balasubramaniam et al., 2018) and human disturbance (Berman 4  
5 et al., 2004) than by phylogeny. Assuming that this hypothesis is correct, we 5  
6 speculate below about particular current circumstances that could have an in- 6  
7 fluence on crested macaque male social style traits. Like Tibetan macaques, 7  
8 our crested macaque study groups were subject to disturbance by tourism 8  
9 (Berman et al., 2004, 2007) as well as by crop-guarding, factors that may 9  
10 have either led to more despotism due to high levels of stress, or to more 10  
11 tolerance in response to an external threat. While human disturbance may 11  
12 have had a general effect on the crested macaque population, it did not ap- 12  
13 pear to affect groups differentially, as might be expected. One of the study 13  
14 groups, PB1, experienced minimal levels of tourism and crop guarding com- 14  
15 pared with the other two groups. Yet, there were no differences in social 15  
16 style traits among the three groups, results that are consistent with most other 16  
17 studies of intraspecific group differences in social style traits (Thierry et al., 17  
18 2008; but see Horiuchi, 2007; Majolo et al., 2009; Zhang & Watanabe, 2014). 18  
19 Larger group size is hypothesized to lead to despotic styles due to increased 19  
20 contest competition over resources (Koenig et al., 2013; Sterck et al., 1997; 20  
21 van Schaik, 1989) and/or increased temporal constraints (Berman & Thierry, 21  
22 2010; Dunbar, 1992). The groups varied in size from 33 adults in PB1 and 22  
23 R2 to about 45 adults in R1, without differing in social style traits, although 23  
24 group size may have played a role in the differences in rates of social af- 24  
25 filiation, aggression and nonagonistic approaches that we found; R1 males 25  
26 showed higher rates of affiliation, aggression and nonagonistic approaches 26  
27 than the other two groups. 27

28 High levels of intergroup competition have also been hypothesized to 28  
29 lead to tolerant behaviour among species also living under conditions of 29  
30 high within-group competition (Sterck et al., 1997; Horiuchi, 2007; Majolo 30  
31 et al., 2009). Given that crested macaque males experience high reproduc- 31  
32 tive skew within groups (Engelhardt et al., 2017) as well as frequent in- 32  
33 tergroup encounters and attempts at male immigration (Marty et al., 2016, 33  
34 2017; Martínez Íñigo, 2018), this explanation may also apply generally to 34  
35 the population. However, again it does not appear to apply to group differ- 35  
36 ences in social style traits which did not vary between social groups, in spite 36  
37 of the fact that R1 experienced higher rates of intergroup encounters and 37

1 male migration than the other two groups. Finally, near equal sex ratios have 1  
2 been suggested to promote cooperation, affiliation and tolerance in macaque 2  
3 males, for example, in Barbary, Assamese, Tibetan, and bonnet macaques 3  
4 (Silk, 1994; Preuschoft & Paul, 2000; Cooper & Bernstein, 2002; Adisehan 4  
5 et al., 2011; see also Horiuchi, 2007). However, this explanation is not likely 5  
6 to apply to this population given that male to female sex ratios were low 6  
7 among all the groups ( $R_1 = 0.30\text{--}0.39$ ;  $R_2 = 0.22$ ;  $PB_1 = 0.27$ ). Clearly 7  
8 further research is needed to examine the influence of each of these factors 8  
9 and other factors not considered here, and to evaluate whether they can exert 9  
10 population level influences on social style traits, without leading necessarily 10  
11 to intergroup variation (see Balasubramaniam et al., 2014). 11

12 In summary, this study suggests that the avoidant relationships of male 12  
13 crested macaques do not fit neatly onto the four-grade social style scale. Un- 13  
14 like their female counterparts who display consistently tolerant traits and 14  
15 relaxed and friendly affiliative relationships, male–male relationships are 15  
16 marked by a combination of despotic traits, tolerant traits and low socia- 16  
17 bility. Although males do not engage in high rates of contact aggression with 17  
18 each other, they have tense, competitive relationships marked by avoidance 18  
19 of all types of interaction. Such combinations of social style traits, along 19  
20 with social avoidance may represent more nuanced relationship qualities that 20  
21 emerge when competing males attempt to use tolerance to avoid the costs of 21  
22 competition or other external circumstances. 22

23 In addition to illustrating the avoidant tendencies of males, our results add 23  
24 to the growing realization that males should not be assumed to have similar 24  
25 social styles as the females of the same species; males of several species do 25  
26 not exhibit social style measures predicted by the grade assigned to females. 26  
27 Instead, social style traits should be examined in males and females sepa- 27  
28 rately. Additional measures other than traditional social style indicators may 28  
29 be necessary to get more accurate and general depictions of relationships 29  
30 between males (e.g., affiliative behaviour, ritualized greetings, coalitionary 30  
31 support). Finally, more comparative studies investigating male social rela- 31  
32 tionships are needed to fill in the gaps of our knowledge of the evolution of 32  
33 male social styles. 33

### 34 **Acknowledgements** 34

35 We thank the Indonesian State Ministry of Research and Technology (RIS- 35  
36 TEK), the Directorate General of Forest Protection and Nature Conservation 36  
37 37

(PHKA) and the Department for the Conservation of Natural Resources (BKSDA) for permission to conduct research in Tangkoko Nature Reserve. We are grateful to Enggar Oktaviyanti, Diah Fitri Ekarini and Santi Julianti for help with data collection. We thank Stephan Lentley for administrative support, Dwi Yandhi Febriyanti and the *Macaca nigra* Project staff for support in the field. We are grateful to two anonymous reviewers for their comments and suggestions that greatly improved the manuscript, as well as Bernard Thierry and Krishna Balasubramaniam for helpful comments and suggestions on an earlier version of the manuscript. This project was funded by the Leakey Foundation, National Geographic Waitt Program (grant no. 4241-6), American Society of Primatologists, International Society of Primatologists, Animal Behavior Society, Nacey Maggioncalda Research Foundation (grant No. 415483), Mark Diamond Research Fund (grant No. SU-15-14) and the University at Buffalo College of Arts and Sciences Dissertation Writing Grant.

## References

- Adishesan, A., Adishesan, T. & Isbell, L.A. (2011). Affiliative relationships and reciprocity among adult male Bonnet macaques (*Macaca radiata*) at Arunachala Hill, India. — *Am. J. Primatol.* 73: 1107-1113.
- Altman, J. (1974). Observational study of behaviour sampling methods. — *Behaviour* 49: 227-267.
- Aureli, F. (1992). Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). — *Behav. Ecol. Sociobiol.* 31: 329-337.
- Balasubramaniam, K.N., Beisner, B.A., Berman, C.M., De Marco, A., Duboscq, J., Koirala, S., Majolo, B., MacIntosh, A.J., McFarland, R., Molesti, S., Ogawa, H., Petit, O., Schino, G., Sosa, S., Sueur, C., Thierry, B., de Waal, F.B.M. & McCowan, B. (2018). The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. — *Am. J. Primatol.* 80: 1-15.
- Balasubramaniam, K.N., Berman, C.M., De Marco, A., Dittmar, K., Majolo, B., Ogawa, H., Thierry, B. & De Vries, H. (2013). Consistency of dominance rank order: a comparison of David's scores with I&SI and Bayesian methods in macaques. — *Am. J. Primatol.* 75: 959-971.
- Balasubramaniam, K.N., Berman, C.M., Ogawa, H. & Li, J. (2011). Using biological markets principles to examine patterns of grooming exchange in *Macaca thibetana*. — *Am. J. Primatol.* 73: 1269-1279.
- Balasubramaniam, K.N., Dittmar, K., Berman, C.M., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F.B.M. (2012). Hierarchical steepness, counter-aggression, and macaque social style scale. — *Am. J. Primatol.* 74: 915-925.

- 1 Balasubramaniam, K.N., Dunayer, E.S., Gilhooly, L.J., Rosenfield, K.A. & Berman, C.M. 1  
 2 (2014). Group size, contest competition, and social structure in Cayo Santiago rhesus 2  
 3 macaques. — Behaviour. 151: 1759-1798. 3
- 4 Balasubramaniam, K.N., Ogawa, H., Li, J.H., Ionica, C. & Berman, C.M. (2020). Tibetan 4  
 5 macaque social style: covariant and quasi-independent evolution. — In: The behavioral 5  
 6 ecology of the Tibetan macaque (Li, J.H., Sun, L. & Kappeler, P., eds). Fascinating life 6  
 7 sciences. Springer, Cham, p. 141-169. 7
- 8 Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. (2011). Social bonds predict future 8  
 9 cooperation in male Barbary macaques, *Macaca sylvanus*. — Anim. Behav. 81: 1109- 9  
 10 1116. 10
- 11 Berman, C.M., Ionica, C. & Li, J. (2007). Supportive and tolerant relationships among male 11  
 12 Tibetan macaques at Huangshan, China. — Behaviour 144: 631-661. 12
- 13 Berman, C.M., Ionica, C.S. & Li, J. (2004). Dominance style among *Macaca thibetana* on 13  
 14 Mt. Huangshan, China. — Int. J. Primatol. 25: 1283-1312. 14
- 15 Berman, C.M. & Thierry, B. (2010). Variation in kin bias: species differences and time 15  
 16 constraints in macaques. — Behaviour 147: 1863-1887. 16
- 17 Butovskaya, M. (1993). Kinship and different dominance styles in groups of three species 17  
 18 of the genus macaca (*M. arctoides*, *M. mulatta*, *M. fascicularis*). — Folia Primatol. 60: 18  
 19 210-224. 19
- 20 Castles, D.L., Aureli, F. & De Waal, F.B.M. (1996). Variation in conciliatory tendency and 20  
 21 relationship quality across groups of pigtail macaques. — Anim. Behav. 52: 389-403. 21
- 22 Clutton-Brock, T. & Janson, C. (2012). Primate socioecology at the crossroads: past, present, 22  
 23 and future. — Evol. Anthropol. 21: 136-150. 23
- 24 Cooper, M.A., Aureli, F. & Singh, M. (2007). Sex differences in reconciliation and post- 24  
 25 conflict anxiety in Bonnet macaques. — Ethology 113: 26-38. 25
- 26 Cooper, M.A. & Bernstein, I.S. (2002). Counter aggression and reconciliation in Assamese 26  
 27 macaques (*Macaca assamensis*). — Am. J. Primatol. 56: 215-230. 27
- 28 Cooper, M.A. & Bernstein, I.S. (2008). Evaluating dominance styles in Assamese and rhesus 28  
 29 macaques. — Int. J. Primatol. 29: 225-243. 29
- 30 De la O, C., Mevis, L., Richter, C., Malaivijitnond, S., Ostner, J. & Schulke, O. (2013). 30  
 31 Reconciliation in male stump-tailed macaques (*Macaca arctoides*): intolerant males care 31  
 32 for their social relationships. — Ethology 119: 39-51. 32
- 33 de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing un- 33  
 34 known or tied relationships. — Anim. Behav. 50: 1375-1389. 34
- 35 de Vries, H., Stevens, J.M.G. & Vervaecke, H. (2006). Measuring and testing the steepness 35  
 36 of dominance hierarchies. — Anim. Behav. 71: 585-592. 36
- 37 de Waal, F.B.M. & Luttrell, L.M. (1985). The formal hierarchy of rhesus macaques: an 37  
 investigation of the bared-teeth display. — Am. J. Primatol. 9: 73-85. 37
- 38 de Waal, F.B.M. & Luttrell, L.M. (1989). Toward a comparative socioecology of the genus 38  
 39 *Macaca*: different dominance styles in rhesus and stump-tail monkeys. — Am. J. Primatol. 39  
 40 19: 83-109. 40
- 41 de Waal, F.B.M. & Ren, R.M. (1988). Comparison of the reconciliation behavior of stump-tail 41  
 42 and rhesus macaques. — Ethology 78: 129-142. 42

- 1 de Waal, F.B.M. & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus 1  
2 monkeys. — Behaviour 85: 224-241. 2
- 3 Demaria, C. & Thierry, B. (2001). A comparative study of reconciliation in rhesus and 3  
4 Tonkean macaques. — Behaviour. 138: 397-410. 4
- 5 Di Fiore, A. & Rendall, D. (1994). Evolution of social organization: a reappraisal for primates 5  
6 by using phylogenetic methods. — Proc. Natl. Acad. Sci. USA 91: 9941-9945. 6
- 7 Dixson, A.F. (1977). Observations on the displays, menstrual cycles and sexual behaviour of 7  
8 the “Black ape” of Celebes (*Macaca nigra*). — J. Zool. 182: 63-84. 7
- 8 Drickamer, L. (1976). Quantitative observations of grooming behavior in free-ranging 8  
9 *Macaca mulatta*. — Primates 17: 323-335. 9
- 10 Dubosq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B. & Engelhardt, A. (2013). Social 10  
11 tolerance in wild female crested macaques (*Macaca nigra*) in Tangkoko-Batuangus Nature 11  
12 Reserve, Sulawesi, Indonesia. — Am. J. Primatol. 75: 361-375. 12
- 13 Dunbar, R.I.M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. — 13  
14 Behav. Ecol. Sociobiol. 31: 35-49. 13
- 14 Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating 14  
15 systems. — Science 197: 215-233. 15
- 16 Engelhardt, A., Muniz, L., Perwitasari-Farajallah, D. & Widdig, A. (2017). Highly polymor- 16  
17 phic microsatellite markers for the assessment of male reproductive skew and genetic 17  
18 variation in critically endangered crested macaques (*Macaca nigra*). — Int. J. Primatol. 18  
19 38: 672-691. 19
- 20 Field, A., Miles, J. & Field, Z. (2012). Discovering statistics using R. — Sage, London. 20
- 21 Fooden, J. (1969). Taxonomy and evolution of the monkeys of Celebes (Primates: Cercop- 21  
22 ithecidae). — Karger, Basel. 21
- 22 Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M. & Hayden, T.J. (2003). David’s 22  
23 score: a more appropriate dominance ranking method than Clutton-Brock et al.’s index. — 23  
24 Anim. Behav. 66: 601-605. 24
- 25 Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981). Testis weight, body weight 25  
26 and breeding system in primates. — Nature 293: 55-57. 26
- 27 Harvey, P.H., Purvis, A. & Liles, L. (1995). Sperm competition: mating system, not breeding 27  
28 system, affects testes size of primates. — Funct. Ecol. 9: 468-476. 27
- 28 Hill, D.A. (1994). Affiliative behaviour between adult males of the genus macaca. — Be- 28  
29 haviour 130: 293-308. 29
- 30 Horiuchi, S. (2007). Social relationships of male Japanese macaques (*Macaca fuscata*) in 30  
31 different habitats: a comparison between Yakushima island and Shimokita peninsula pop- 31  
32 ulations. — Anthropol. Sci. 115: 63-65. 32
- 33 Isbell, L.A. (2017). Socioecological model. — In: The international encyclopedia of prima- 33  
34 tology, 1 (Bezanson, M., MacKinnon, K.C., Riley, E., Campbell, C.J., Nekaris, K.A.I., 34  
35 Estrada, A., Di Fiore, A.F., Ross, S., Jones-Engel, L.E., Thierry, B., Sussman, R.W., Sanz, 35  
36 C., Loudon, J., Elton, S. & Fuentes, A., eds). Wiley Online Library, London. 35
- 36 Janson, C. & Van Schaik, C.P. (1988). Recognizing the many faces of primate food competi- 36  
37 tion: methods. — Behaviour 105: 165-186. 37

- 1 Kaburu, S.S.K. & Newton-Fisher, N.E. (2015). Egalitarian despots: hierarchy steepness, reci- 1  
2 procity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. — Anim. 2  
3 Behav. 99: 61-71. 3
- 4 Kamilar, J. & Cooper, N. (2015). Phylogenetic signal in primate behaviour, ecology and life 4  
5 history. — Philos. Trans. Roy. Soc. B: Biol. Sci. 368: 20120341. 5
- 6 Kappeler, P.M. & Van Schaik, C.P. (2002). Evolution of primate social systems. — Int. J. 6  
7 Primatol. 23: 707-740. 7
- 8 Kaufman, J.H. (1967). Social relations of adult males in a free-ranging band of rhesus mon- 8  
9 keys. — In: Social communication among primates (Altmann, S., ed.). University of 9  
10 Chicago Press, Chicago, IL, p. 73-98. 10
- 11 Kawazoe, T. (2016). Association patterns and affiliative relationships outside a troop in wild 11  
12 male Japanese macaques, *Macaca fuscata*, during the non-mating season. — Behaviour 12  
13 153: 69-89. 13
- 14 Koenig, A., Scarry, C.J., Wheeler, B.C. & Borries, C. (2013). Variation in grouping patterns, 14  
15 mating systems and social structure: what socio-ecological models attempt to explain. — 15  
16 Philos. Trans. Roy. Soc. B: Biol. Sci. 368: 20120348. 16
- 17 Li, J. (1999). The Tibetan macaque society: a field study. — Anhui University Press, Hefei. 17
- 18 Majolo, B., Ventura, R. & Koyama, N. (2005). Postconflict behavior among male Japanese 18  
19 macaques. — Int. J. Primatol. 26: 321-336. 19
- 20 Majolo, B., Ventura, R., Koyama, N., Hardie, S.M., Jones, B.M., Knapp, L.A. & Schino, G. 20  
21 (2009). Analysing the effects of group size and food competition on Japanese macaque 21  
22 social relationships. — Behaviour 146: 113-137. 22
- 23 Martínez Íñigo, L. (2018). Intergroup interactions in crested macaques (*Macaca nigra*): 23  
24 factors affecting intergroup encounter outcome and intensity. — Doctoral dissertation, 24  
25 University of Lincoln, Lincoln, NE. 25
- 26 Marty, P.R., Hodges, K., Agil, M. & Engelhardt, A. (2016). Determinants of immigration 26  
27 strategies in male crested macaques (*Macaca nigra*). — Sci. Rep. 6: 32028. 27
- 28 Marty, P.R., Hodges, K., Agil, M. & Engelhardt, A. (2017). Alpha male replacements and 28  
29 delayed dispersal in crested macaques (*Macaca nigra*). — Am. J. Primatol. 79: e22448. 29
- 30 Matsumura, S. (1999). Evolution of “egalitarian” and “despotic” social systems among 30  
31 macaques. — Primates 40: 23-31. 31
- 32 Menard, N. (2004). Do ecological factors explain variation in social organization?. — In: 32  
33 Macaque societies: a model for the theory of social organization (Thierry, B., Singh, M. 33  
34 & Kaumanns, W., eds). Cambridge University Press, Cambridge, p. 237-261. 34
- 35 Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D. & Engelhardt, E. 35  
36 (2010). Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a 36  
37 tolerant species. — Anim. Behav. 79: 179-183. 37
- 38 O’Brien, T.G. & Kinnaird, M.F. (1997). Behavior, diet, and movements of the Sulawesi 38  
39 crested black macaque (*Macaca nigra*). — Int. J. Primatol. 18: 321-351. 39
- 40 Ogawa, H. (1995). Recognition of social relationships in bridging behavior among Tibetan 40  
41 macaques (*Macaca thibetana*). — Am. J. Primatol. 35: 305-310. 41
- 42 Ostner, J. & Schulke, O. (2014). The evolution of social bonds in primate males. — Behaviour 42  
43 151: 871-906. 43

- 1 Palagi, E., Dall'Olivo, S., Demuru, E. & Stanyon, R. (2014). Exploring the evolutionary 1  
2 foundations of empathy: consolation in monkeys. — *Evol. Hum. Behav.* 35: 341-349. 2
- 3 Paul, A., Kuester, J. & Arnemann, J. (1996). The sociobiology of male-infant interactions in 3  
4 Barbary macaques, *Macaca sylvanus*. — *Anim. Behav.* 51: 155-170. 4
- 5 Petit, O., Abegg, C. & Thierry, B. (1997). A comparative study of aggression and concilia- 5  
6 tion in three cercopithecine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). — 6  
7 *Behaviour*. 134: 415-432. 7
- 8 Petit, O. & Thierry, B. (1994). Reconciliation in a group of black macaques, *Macaca nigra*. — 8  
9 *Dodo* 30: 89-95. 9
- 10 Preuschoft, S. & Paul, A. (2000). Dominance, egalitarianism, and stalemate: an experimental 10  
11 approach to male–male competition in Barbary macaques. — In: *Primate males: causes* 11  
12 *and consequences of variation in group composition* (Kappeler, P.M., ed.). Cambridge 12  
13 University Press, Cambridge, p. 205-216. 13
- 14 Preuschoft, S., Paul, A. & Kuester, J. (1998). Dominance styles of female and male Barbary 14  
15 macaques (*Macaca sylvanus*). — *Behav. Ecol. Sociobiol.* 135: 731-755. 15
- 16 R Development Core Team (2017). R: a language and environment for statistical comput- 16  
17 ing. — R Foundation for Statistical Computing, Vienna. Available online at [http://www.](http://www.R-project.org/) 17  
18 [R-project.org/](http://www.R-project.org/). 18
- 19 Reed, C., Brien, T.G.O. & Kinnaird, M.F. (1997). Male social behavior and dominance 19  
20 hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). — *Int. J. Primatol.* 18: 20  
21 247-260. 21
- 22 Richter, C., Mevis, L., Malaivijitnond, S., Schülke, O. & Ostner, J. (2009). Social relation- 22  
23 ships in free-ranging male *Macaca arctoides*. — *Int. J. Primatol.* 30: 625-642. 23
- 24 Riley, E.P., Sagnotti, C., Carosi, M. & Putu Oka, N. (2014). Socially tolerant relationships 24  
25 among wild male moor macaques (*Macaca maura*). — *Behaviour* 151: 1021-1044. 25
- 26 Schino, G., Rosati, L. & Aureli, F. (1998). Intragroup variation in conciliatory tendencies in 26  
27 captive Japanese macaques. — *Behaviour*. 135: 897-912. 27
- 28 Schulke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. (2010). Social bonds enhance repro- 28  
29 ductive success in male macaques. — *Curr. Biol.* 20: 2207-2210. 29
- 30 Silk, J.B. (1994). Social relationships of male Bonnet macaques: male bonding in a matrilineal 30  
31 society. — *Behaviour* 130: 271-291. 31
- 32 Smuts, B.B. & Watanabe, J.M. (1990). Social relationships and ritualized greetings in adult 32  
33 male baboons. — *Int. J. Primatol.* 11: 147-172. 33
- 34 Sterck, E.H.M., Watts, D.P. & Van Schaik, C.P. (1997). The evolution of female social relation- 34  
35 ships in nonhuman primates. — *Behav. Ecol. Sociobiol.* 41: 291-309. 35
- 36 Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K. & Thierry, B. (2011). A com- 36  
37 parative network analysis of social style in macaques. — *Anim. Behav.* 82: 845-852. 37
- 38 Sugiyama, Y. (1971). Characteristics of the social life of Bonnet macaques (*Macaca radi-  
39 ata*). — *Primates* 12: 247-266. 39
- 40 Thierry, B. (1985). Patterns of agonistic interactions in three species of macaque (*Macaca  
41 mulatta*, *M. fascicularis*, *M. tonkeana*). — *Aggr. Behav.* 11: 223-233. 41
- 42 Thierry, B. (1990). The state of equilibrium among agonistic behavior patterns in a group of 42  
43 Japanese macaques (*Macaca fuscata*). — *C. R. Acad. Sci. Série III: Sci. Vie* 310: 35-40. 43

- 1 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. — 1  
 2 In: Natural conflict resolution (Aureli, F. & de Waal, F.B.M., eds). University of California 2  
 3 Press, Berkeley, CA, p. 106-128. 3
- 4 Thierry, B. (2004). Social epigenesis. — In: Macaque societies: a model for the study of 4  
 5 social organization (Thierry, B., Singh, M. & Kaumanns, W., eds). Cambridge University 5  
 6 Press, Cambridge, p. 267-290. 6
- 7 Thierry, B. (2007). Unity in diversity: lessons from macaque societies. — *Evol. Anthropol.* 7  
 8 16: 224-238. 7
- 8 Thierry, B. (2008). Primate socioecology, the lost dream of ecological determinism. — *Evol.* 8  
 9 *Anthropol.* 17: 93-96. 9
- 10 Thierry, B. (2013). Identifying constraints in the evolution of primate societies. — *Philos.* 10  
 11 *Trans. R. Soc. B.* 368: 20120342. 11
- 12 Thierry, B. & Aureli, F. (2006). Barbary but not barbarian: social relations in a tolerant 12  
 13 macaque. — In: *Biology and behaviour of Barbary macaques* (Hodges, J.K., ed.). Not- 13  
 14 tingham University Press, Nottingham, p. 1-18. 14
- 15 Thierry, B., Aureli, F., Nunn, C.L., Petit, O., Abegg, C. & de Waal, F.B.M. (2008). A compar- 15  
 16 ative study of conflict resolution in macaques: insights into the nature of covariation. — 16  
 17 *Anim. Behav.* 75: 847-860. 16
- 17 Thierry, B., Bynum, E.L., Baker, S., Kinnaird, M.F. & Matsumura, S. (2000). The social 17  
 18 repertoire of Sulawesi macaques. — *Prim. Res.* 16: 203-226. 18
- 19 Thierry, B., Demaria, C., Preuschoft, S. & Desportes, C. (1989). Structural convergence be- 19  
 20 tween silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque 20  
 21 (*Macaca tonkeana*). — *Folia Primatol.* 52: 178-184. 21
- 22 Van Hooff, J.A.R.A.M. (2000). Relationships among non-human primate males: a deductive 22  
 23 framework. — In: *Primate males: causes and consequences of variation in group compo-* 23  
 24 *sition* (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 183-191. 23
- 24 Van Hooff, J.A.R.A.M. & van Schaik, C.P. (1992). Cooperation in competition: the ecology 24  
 25 of primate bonds. — In: *Coalitions and alliances in humans and other animals* (Harcourt, 25  
 26 A.H. & De Waal, F.B.M., eds). Oxford University Press, New York, NY, p. 357-389. 26
- 27 Van Hooff, J.A.R.A.M. & Van Schaik, C.P. (1994). Male bonds: affiliative relationships 27  
 28 among nonhuman primate males. — *Behaviour.* 130: 309-337. 27
- 28 Van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. — In: 28  
 29 *Comparative socioecology* (Standen, V. & Foley, R.A., eds). Blackwell Scientific, Oxford, 29  
 30 p. 195-218. 30
- 31 Van Schaik, C.P. (1996). Social evolution in primates: the role of ecological factors and male 31  
 32 behaviour. — *Proc. Br. Acad.* 88: 9-31. 32
- 33 Van Schaik, C.P. & van Noordwijk, M.A. (1988). Scramble and contest in feeding competi- 33  
 34 tion among female long-tailed macaques (*Macaca fascicularis*). — *Behaviour* 105: 77-98. 34
- 35 Veenema, H.C., Das, M. & Aureli, F. (1994). Methodological improvements for the study of 35  
 36 reconciliation. — *Behav. Proc.* 31: 29-38. 35
- 36 Whitham, J.C. & Maestriperieri, D. (2003). Primate rituals: the function of greetings between 36  
 37 male Guinea baboons. — *Ethology* 109: 847-859. 37



1 Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. — *Behaviour* 75: 262-300. 1

2 Zhang, P. & Watanabe, K. (2014). Intraspecies variation in dominance style of *Macaca* 2  
3 *fuscata*. — *Primates* 55: 69-79. 3

4  
5  
6 **Table A1.**

7 Model statistics of linear mixed models comparing male and female crested macaques from 7  
8 groups R1 and PB1. 8

9

| 10 Outcome variable                      | $F_{(1,56)}$ | $p$     | Marginal $R^2$ | Conditional $R^2$ |
|--|--------------|---------|----------------|-------------------|
| 11 Social style measures                 |              |         |                |                   |
| 12 CCT                                   | 8.66         | 0.00*** | 0.13           | 0.13              |
| 13 % Counteraggression                   | 72.34        | 0.00*** | 0.57           | 0.57              |
| 14 % Bite                                | 10.23        | 0.00*** | 0.15           | 0.23              |
| 15 % Contact Attack                      | 9.32         | 0.00*** | 0.15           | 0.21              |
| 16 % Threat                              | 6.53         | 0.01**  | 0.19           | 0.19              |
| 16 Approaches within 1 bodylength        |              |         |                |                   |
| 17 % Positive outcome                    | 217.76       | 0.00*** | 0.81           | 0.81              |
| 18 % Negative outcome                    | 11.11        | 0.00*** | 0.16           | 0.40              |
| 19 % Neutral outcome                     | 156.94       | 0.00*** | 0.76           | 0.76              |
| 20 Other measures of social interactions |              |         |                |                   |
| 21 Rate of overall aggression            | 8.73         | 0.00*** | 0.12           | 0.40              |
| 22 Rate of overall affiliation           | 31.32        | 0.00*** | 0.27           | 0.52              |
| 23 Rate of grooming                      | 110.68       | 0.00*** | 0.66           | 0.66              |
| 23 % Body contact affiliation            | 5.06         | 0.03*   | 0.11           | 0.11              |

24

25 Significant results are marked with asterisks. 25

26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37

**Table A2.**

Model statistics of linear regression models comparing interactions in different groups.

| Dependent variable                            | $F_{(3,25)}$ | Adjusted $R^2$ | $p$     |
|---|--------------|----------------|---------|
| <b>Social style measures</b>                  |              |                |         |
| CCT ( $F_{(3,20)}$ )                          | 0.58         | −0.06          | 0.63    |
| % Counteraggression                           | 1.22         | 0.02           | 0.32    |
| % Bite  | 1.43         | 0.04           | 0.26    |
| % Contact Attack                              | 1.54         | 0.05           | 0.23    |
| %Threat                                       | 3.20         | 0.19           | 0.04    |
| <b>Approach — 5 bodylengths</b>               |              |                |         |
| % Positive outcome                            | 0.37         | −0.08          | 0.77    |
| % Negative outcome                            | 0.61         | −0.04          | 0.61    |
| % Neutral outcome                             | 0.33         | −0.08          | 0.80    |
| <b>Approach — 1 bodylength</b>                |              |                |         |
| % Positive outcome                            | 0.26         | −0.09          | 0.85    |
| % Negative outcome                            | 0.46         | −0.06          | 0.71    |
| % Neutral outcome                             | 0.16         | −0.10          | 0.92    |
| <b>Other measures of social interaction</b>   |              |                |         |
| Rate of overall aggression                    | 21.37        | 0.69           | 0.00*** |
| Rate of overall affiliation                   | 13.73        | 0.58           | 0.00*** |
| Rate of grooming                              | 1.64         | 0.06           | 0.21    |
| % Body contact affiliation                    | 7.40         | 0.41           | 0.00*** |
| Rate of nonagonistic approach (1 bodylength)  | 4.16         | 0.26           | 0.02*   |
| Rate of nonagonistic approach (5 bodylengths) | 13.73        | 0.58           | 0.00*** |

Significant results are marked with asterisks.