



**HAL**  
open science

## Stability and strength of male-female associations in a promiscuous primate society

Alice Baniel, Guy Cowlshaw, Elise Huchard

► **To cite this version:**

Alice Baniel, Guy Cowlshaw, Elise Huchard. Stability and strength of male-female associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*, 2016, 70 (5), pp.761-775. 10.1007/s00265-016-2100-8 . hal-01950152

**HAL Id: hal-01950152**

**<https://hal.science/hal-01950152v1>**

Submitted on 20 Dec 2018

**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 Published in final edited form as:

2 *Behavioral ecology and sociobiology* 70.5 (2016): 761-775. doi:10.1007/s00265-016-2100-8

3

4 **Stability and strength of male-female associations in a**  
5 **promiscuous primate society**

6 **Alice Baniel<sup>1,2,3,§</sup>, Guy Cowlshaw<sup>3</sup>, Elise Huchard<sup>1</sup>**

7

8 **AUTHORS AFFILIATIONS**

9 <sup>1</sup> Centre d'Ecologie Fonctionnelle et Evolutive, Unité Mixte de Recherche 5175, Centre  
10 National de la Recherche Scientifique, 1919 Route de Mende, 34293 Montpellier Cedex 5,  
11 France

12 <sup>2</sup> Institut des Sciences de l'Evolution de Montpellier, Université de Montpellier, Place Eugène  
13 Bataillon, CC 065, 34095 Montpellier Cedex 5, France

14 <sup>3</sup> Institute of Zoology, The Zoological Society of London, Regent's Park, London NW1 4RY,  
15 UK

16

17 <sup>§</sup>Corresponding author: Alice Baniel, Centre d'Ecologie Fonctionnelle et Evolutive, Unité  
18 Mixte de Recherche 5175, Centre National de la Recherche Scientifique, 1919 Route de  
19 Mende, 34293 Montpellier Cedex 5, France, telephone: +33467613247, fax: + 33467613336,  
20 email address: alice.baniel@gmail.com

21

22 **ABSTRACT**

23 Close associations between adult males and lactating females occur in several promiscuous  
24 primate species. Benefits gained by males from such bonds may include increases in offspring  
25 fitness through paternal effort (the "mate-then-care" hypothesis) and/or subsequent mating  
26 opportunities with the female (the "care-then-mate" hypothesis). Heterosexual friendships  
27 between males and females have been described as tightly linked to the presence of a  
28 dependent infant, but few studies have investigated whether these associations may be longer,  
29 starting before an infant birth and lasting after its independence, and whether they may vary in  
30 strength across time and dyads. We investigated the stability and strength of heterosexual  
31 bonds in two groups of wild chacma baboons (*Papio ursinus*) to test whether male-female  
32 associations (1) last from offspring conception to independence, as expected under the mate-  
33 then-care hypothesis, (2) last after maternal cycling resumption and increase male mating  
34 success, as expected under the care-then-mate hypothesis, and (3) vary in strength depending  
35 on female reproductive state, age and rank. Our results show that most male-female bonds are  
36 already present at offspring conception, are maintained during pregnancy and lactation, and  
37 disappeared when mother resumed cycling. Moreover, heterosexual bonds were most intense  
38 during early lactation and for high-ranking females, and did not predict subsequent mating  
39 activity. Those findings favour the mate-then-care hypothesis, and confirm that male paternity  
40 assessment may, at least partially, rely on mating history. Overall, stable heterosexual  
41 friendships exist outside early lactation and last longer than previously thought, suggesting  
42 that male-female bonds could play an important and under-appreciated role on the social  
43 structure of groups in promiscuous primate societies.

44

45 **SIGNIFICANCE STATEMENT**

46 Stable male-female bonds are rare in promiscuous mammals. Baboons are unusual in this  
47 respect: tight friendships have been described between adult males and lactating females and  
48 may protect infants against infanticide, but few studies have investigated whether these  
49 associations may start before an infant's birth, or extend after its nutritional independence. We  
50 explored the stability and strength of heterosexual relationships in the chacma baboon, and  
51 found that friendships start before infant's conception, are maintained throughout pregnancy,  
52 strengthen during lactation and disappear before mothers resume cycling. Such pattern of  
53 association suggests that male-female bonds represent paternal effort, and may arise from  
54 sexual activity before and during the conceptive cycle. Most females appear permanently  
55 associated with one male regardless of their reproductive state, suggesting that heterosexual  
56 bonds play an important, and under-appreciated, role in structuring the social organization of  
57 baboon societies.

58

59 **KEYWORDS:** friendship, male-female association, paternal care, mating success, chacma  
60 baboon, *Papio ursinus*

61

## 62 **ACKNOWLEDGMENTS**

63 We are thankful to the Tsaobis Baboon Project volunteers in 2013 and 2014 for invaluable  
64 help in the field, in particular to Ignacio Abadia Suanzes-Carpegna, Andrew Allan, Einat Bar-  
65 Ziv, Katie Hatton, Caitlin Miller, Frieda Shikongo, Chris Smith and Agata Staniewicz. Our  
66 thanks also go to Alecia J. Carter, Alexander Lee and Cassandra Raby for running the field  
67 site in collaboration and for helpful discussions. We are very grateful to Alexandre Courtiol  
68 who wrote the mantel test script, as well as to Christof Neumann, Anja Widdig and one  
69 anonymous reviewer for their constructive comments on an earlier version of the manuscript.  
70 Permission to work at Tsaobis Nature Park is kindly granted by the Ministry of Lands and  
71 Resettlement, thanks to the Gobabeb Research and Training Centre for affiliation, and the

72 Ministry of Environment and Tourism. We are also grateful to the Snyman and Wittreich  
73 families for permission to work on their land, and to Herman Strydom and Willem Odendaal  
74 for help in the field. This paper is a publication of the ZSL Institute of Zoology's Tsaobis  
75 Baboon Project. Contribution ISEM 2016-050.

76

## 77 INTRODUCTION

78 In group-living mammals, the quality and stability of social relationships can have important  
79 fitness consequences (Silk 2007a, b). In particular, social bonding and integration are known  
80 to influence fecundity and offspring survival (yellow baboons, *Papio cynocephalus*: Silk et al.  
81 2003; chacma baboons, *Papio ursinus*: Silk et al. 2009; feral horses, *Equus ferus caballus*:  
82 Cameron et al. 2009; bottlenose dolphins, *Tursiops* sp.: Frere et al. 2010) as well as longevity  
83 (chacma baboons: Silk et al. 2010a, Archie et al. 2014; bottlenose dolphins: Stanton and  
84 Mann 2012). In humans (*Homo sapiens*) also, social integration can influence psychological  
85 stress (DeVries et al. 2003; Rosal et al. 2004), health (Cacioppo and Hawkley 2003; Uchino  
86 2006) and survival (review in Holt-Lunstad et al. 2010).

87 Most studies have focused on the stability and benefits of same-sex relationships  
88 (Machanda et al. 2013; Archie et al. 2014), especially among members of the philopatric sex  
89 – namely females in most mammals (Handley and Perrin 2007) – who are more likely to  
90 maintain stable bonds because they co-reside for long periods with relatives (van Schaik  
91 1989; Sterck et al. 1997). However, several studies have now reported that social relationships  
92 between males and females can also have important fitness consequences for both sexes, with  
93 benefits for offspring survival (savanna baboons: Palombit 2003), female longevity (chacma  
94 baboons: Cheney et al. 2012; Archie et al. 2014) and male mating or reproductive success  
95 (rhesus macaques, *Macaca mulatta*: Kulik et al. 2011; Massen et al. 2012; Assamese  
96 macaques, *Macaca assamensis*: Ostner et al. 2013).

97 Heterosexual bonds may be particularly important in primates. First, many primates  
98 form stable groups where males and females live together year-round, in contrast to other  
99 mammals where stable male-female associations are less common (van Schaik and Kappeler  
100 1997). Second, in several polygynous primates, lactating females form preferential  
101 associations with particular males, often called "friendships" (olive baboons, *Papio anubis*:

102 Smuts 1985; Lemasson et al. 2008; yellow baboons: Altmann 1980; Nguyen et al. 2009;  
103 chacma baboons: Palombit et al. 1997; Huchard et al. 2010; Moscovice et al. 2010; rhesus  
104 macaques: Manson 1994; Barbary macaques, *Macaca sylvanus*: Paul et al. 1996; Ménard et  
105 al. 2001). These relationships are characterized by a high level of spatial proximity and  
106 grooming interactions between partners and are actively maintained by females (Palombit et  
107 al. 1997; Huchard et al. 2010). Their benefits to females are thought to be mainly related to  
108 infanticide avoidance, where males protect vulnerable offspring (Palombit et al. 1997;  
109 Palombit 1999; Palombit 2000; Weingrill 2000), although further benefits may include  
110 protection from non-lethal conspecific aggression (Smuts 1985; Manson 1994; Lemasson et  
111 al. 2008; Nguyen et al. 2009; Kulik et al. 2012), reduced predation risk (van Schaik and van  
112 Noordwijk 1989), stress alleviation during social instability (Beehner et al. 2005; Engh et al.  
113 2006) and promotion of male-infant associations after weaning, which can provide juveniles  
114 with support in agonistic interactions with conspecifics (Buchan et al. 2003) and foraging  
115 benefits (Charpentier et al. 2008; Huchard et al. 2013).

116         The benefits gained by males from such associations are less clear (Palombit 2000).  
117 There are two alternative, non-exclusive hypotheses. First, the “care-then-mate” hypothesis  
118 posits that males may trade protection services for reproductive opportunities (Seyfarth  
119 1978a; Smuts 1985; review in van Schaik and Paul 1996), such that friendships increase a  
120 male’s future chances of mating with his female friend. This hypothesis has received some  
121 support in olive baboons (Smuts 1985; Smuts and Gubernick 1992) and in Barbary macaques  
122 (Ménard et al. 2001), where friendships predicted mating frequency during following cycles.  
123 However, a relationship between male care-giving and subsequent mating activity has not  
124 been observed in other species (yellow baboons: Nguyen et al. 2009; chacma baboons:  
125 Weingrill 2000). Second, the “mate-then-care” hypothesis (Bales 1980; Smuts 1985;  
126 Moscovice et al. 2010) proposes that males form friendships based on their likelihood of

127 paternity, in order to protect their own reproductive investment, i.e. to protect their offspring  
128 from infanticide. This hypothesis has received greater support. Several studies found that  
129 most males had mated with their female friend during her conceptive cycle (olive baboons:  
130 Smuts 1985; yellow baboons: Nguyen et al. 2009; chacma baboons: Palombit et al. 1997;  
131 Moscovice et al. 2010) and genetic studies confirmed that males are often - but not always -  
132 the sire of the infant of their female friend (Moscovice et al. 2009; Nguyen et al. 2009;  
133 Huchard et al. 2010; Ostner et al. 2013).

134         These observations raise an important question, namely how males may assess their  
135 paternity in a promiscuous mating system. First, males might compare the phenotype of the  
136 infant to their own using facial, vocal or olfactory cues (phenotype matching, review in  
137 Widdig 2007). Alternatively, males might rely on their past mating history with the mother of  
138 the infant (Palombit et al. 1997; Moscovice et al. 2010). As male-female friendships are  
139 described to start with the birth of an infant (Palombit et al. 1997; Palombit 1999), such  
140 assessment of paternity may require complex cognitive abilities: males may have to identify  
141 which oestrus cycle corresponded to the conceptive cycle for a given infant, as well as to  
142 evaluate and remember his mating activity with the mother during that cycle, including the  
143 length of his monopolization (or the number of matings) in relation to the proximity of  
144 ovulation and the mating activity of rivals. A more parsimonious scenario is that male-female  
145 associations may not start with an infant birth but with its conception, and be subsequently  
146 maintained throughout pregnancy, though perhaps at lower intensity than following the birth  
147 because pregnant females do not face any risk of infanticide (but may still face a risk of  
148 socially-induced abortion, Alberts et al. 1992; Roberts et al. 2012). Male-female associations  
149 during pregnancy have been documented in Assamese macaques (Ostner et al. 2013) and in  
150 some baboon populations (olive baboons: Smuts 1985; chacma baboons: Weingrill 2000), but  
151 not in others (Palombit et al. 1997). It may therefore be necessary to assess the stability of



152 heterosexual relationships over longer periods, namely from infant conception to  
153 independence and beyond, as well as how their strength may vary across such periods, to  
154 better understand the function of heterosexual relationships, and the mechanisms favouring  
155 their formation.

156         Here, we analyse the stability and strength of male-female associations in wild chacma  
157 baboons. Chacma baboons live in large multimale multifemale societies where females are  
158 philopatric and establish stable, linear and heritable dominance hierarchies, in which  
159 daughters rank below their mother (Seyfarth 1976; Bergman et al. 2003). As in most baboon  
160 societies, male chacma baboons compete to access dominance, which rules access to mating  
161 opportunities (Bulger 1993; Weingrill et al. 2003). High-ranking males mate guard oestrous  
162 females by forming ‘consortships’ during which they maintain close spatial proximity and  
163 monopolize sexual access at the most likely time of ovulation (Bulger 1993; Weingrill et al.  
164 2003). Infanticide risk is high in chacma baboons, which may, in turn, promote the formation  
165 of heterosexual associations in the first year of infant life, when its vulnerability is high  
166 (Palombit 2003). Lactating females are primarily responsible for the maintenance of such  
167 social bonds (Palombit et al. 1997; Huchard et al. 2010) and compete over access to male  
168 partners, as higher-ranking females form stronger bonds with the dominant male (Seyfarth  
169 1978) and high-ranking mothers actively prevent lower-ranking mothers from gaining access  
170 to their male friends (Palombit et al. 2001).

171         This study has three objectives. First, we assess the stability of male-female bonds  
172 across female reproductive states to test whether male-female relationships last from offspring  
173 birth to the resumption of maternal cycling and/or to next conception, as predicted by the  
174 care-then-mate hypothesis, or alternatively from offspring conception to independence, as  
175 predicted by the mate-then-care hypothesis. Second, we assess whether females or males are  
176 primarily responsible for the maintenance of close proximity between friends throughout

177 female reproductive states. We expected males to be responsible for proximity maintenance  
178 when females were sexually receptive and then a role reversal, with females maintaining  
179 proximity during pregnancy and lactation, as females may get more benefits than males from  
180 these associations during these stages. Third, we examine how the strength of spatial  
181 associations between males and females varies across the successive reproductive states of a  
182 female. We predict that heterosexual bonds would be the tightest during early lactation (0-6  
183 months) when the infant is presumably at the highest risk of infanticide (Palombit et al. 2000;  
184 Palombit 2003), would weaken or stop as the infant becomes less vulnerable to infanticide  
185 (>6 months and until weaning), and would be weak during pregnancy when there is no risk of  
186 infanticide. The strength of heterosexual associations may however also vary across dyads,  
187 based on male and female rank. If females compete over male proximity, higher-ranking  
188 females may maintain more stable bonds, while higher-ranking males who are most  
189 successful at monopolizing females may have higher paternity certainty and display stronger  
190 associations with females subsequently.

191

## 192 **Materials & Methods**

### 193 *Field site and study subjects*

194 We studied a population of wild chacma baboons living at Tsaobis Nature Park, on the edge  
195 of the Namib desert, Namibia (22°22'S 15°44'E) (for detailed information on the field site and  
196 population, see Cowlshaw 1997). Data were collected in June-October 2013 and May-  
197 November 2014 on two large groups of baboons: J group (2013: 7-10 males, 17 females, 29-  
198 32 juveniles; 2014: 7-8 males, 18 females, 35 juveniles) and L group (2013: 9-11 males, 18-  
199 19 females, 31-33 juveniles; 2014: 9 males, 17-19 females, 29 juveniles). All adults were  
200 individually recognizable and fully habituated to observation at close range. Age (in years)  
201 was estimated from a combination of known birth dates and dental patterns of tooth eruption

202 and wear, examined during prior captures (Huchard et al. 2009). Only adults were included in  
203 the study. Males were considered adult when they reached eight years of age (Alberts and  
204 Altmann 1995) and females when they reached menarche (Altmann and Alberts 2003).  
205 Female parity (nulliparous, primiparous, multiparous) was taken from life-history data.  
206 The reproductive state of each female was monitored on a daily basis and categorized  
207 according to a chronology followed from the last cycle before birth (the conceptive cycle) to  
208 the first cycle after birth. First, we considered the "swollen" period of the conceptive cycle  
209 during which females were sexually receptive with a perineal swelling ("SWc"). Conceptive  
210 cycles were distinguished from non-conceptive cycles *a posteriori*, identified as the last cycle  
211 preceding pregnancy. To test the care-then-mate hypothesis, we further included all  
212 documented swollen periods of a particular interbirth interval. Pregnancy ("P") was  
213 determined *a posteriori* and encompassed the six months separating the conceptive cycle from  
214 an infant birth. Lactation referred to the entire period during which females had a dependent  
215 infant and were not cycling and was split between the first six months of lactation ("L1") and  
216 the rest of lactation ("L2"). Finally, "SW1" refers to the first swollen period after lactational  
217 amenorrhea when females resume cycling.

218

### 219 ***Behavioural observations***

220 Observers on foot followed both groups daily from dawn to dusk, conducting focal animal  
221 sampling (Altmann 1974) on all adult males and females. All observers (except AB) were  
222 blind with respect to the research questions. Focal follows lasted 60 minutes on average  
223 (mean focal length $\pm$ sd: 58.6 $\pm$ 7.2min, range: 23-97min) and were spread equally across the  
224 day (split into four three-hour time blocks) for each individual. The focal individual was  
225 chosen in a semi-random manner, in order to balance observation time equally across  
226 individuals, and, for females, across reproductive states, and was only sampled once per day.

227 A total of 903 focal observations of 75 females were included in the analysis (here the  
228 statistical unit 'female' is a female in a particular reproductive state) distributed across the  
229 following reproductive states: pregnant (N=496 observations of 37 females, range: 4-23,  
230 mean±sd: 13.4±4.8), early lactating (N=239 observations of 20 females, range: 5-18,  
231 mean±sd: 12.0±4.3) and late lactating (N=168 observations of 18 females, range: 4-15,  
232 mean±sd: 9.3±3.3). A total of 538 focal observations of 24 males were collected (number of  
233 observations per male: range: 10-37, mean±sd: 22.4±8.6). During focal observations, we  
234 continuously recorded all agonistic interactions (supplants, displacements, attacks, threats, see  
235 Huchard and Cowlishaw (2011) for definitions), and social and sexual interactions (including  
236 grooming bouts and copulations), along with the identity of the other individuals involved and  
237 the direction of the interaction. We also noted all approaches and leaves between adult males  
238 and females within 1 meter. During female focal follows, we also recorded proximity scans  
239 every five minutes to note the identity and distance of the nearest male neighbour.

240 In addition, throughout the day, we collected *ad libitum* agonistic interactions and  
241 grooming bouts, again with the identity of individuals involved. Observers moved regularly  
242 through the group to look for focal individuals which ensured that the *ad lib* grooming data  
243 provided an unbiased representation of overall grooming interactions. Consortships were  
244 defined as periods when swollen females were constantly followed by a male who mated  
245 exclusively with them (Alberts et al. 1996). Presence and changes in consortships were  
246 monitored *ad lib* on a daily basis.

247 Adult ranks were established using both *ad lib* and focal observations of agonistic  
248 interactions with the Elo-rating procedure (Albers and de Vries 2001) implemented in the R  
249 package EloRating (version 0.43) (Neumann et al. 2011). We computed separate female and  
250 male hierarchies and obtained a score for each individual for each day of observation. To  
251 obtain comparable ratings across the study period, we derived a daily standardized rank by

252 scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the  
253 minimal score and thus the lowest ranking individual) and 1 (corresponding to the maximal  
254 score and the highest ranking individual).

255 During the study period, the rate of alpha male takeover and male immigration were  
256 high in both groups (1 and 4 immigration events in J group in 2013 and 2014 respectively; 6  
257 and 1 immigration events in L group in 2013 and 2014 respectively), leading to some  
258 instability into male dominance hierarchies (see Fig. S1-S4 in Online resource). Concerning  
259 J group, dominance hierarchy was stable in 2013 with the same alpha male for the entire study  
260 period (Fig. S1), while 2014 was very unstable with five males competing constantly for  
261 dominance and alternating in reaching the alpha male status (Fig. S2). Concerning L group, in  
262 2013 the alphas lost his dominance in July 2013, then another resident male reached alpha  
263 status but concomitantly two new males immigrated and rised in rank, causing high instability  
264 in the hierarchy (Fig. S3). In 2014, the dominance was contested among three males who  
265 alternated as alpha males, then one new male immigrated toward the end of the study period  
266 and reached dominance (Fig. S4).

267

## 268 *Data analysis*

### 269 *1. Stability of male-female associations across reproductive states*

270 We assessed the stability of male-female preferential associations across the consecutive  
271 reproductive states of each female, in order to test (1) whether females remain associated to  
272 the most likely father of their offspring from its conception to its independence (as predicted  
273 by the mate-then-care hypothesis), or alternatively, (2) whether male-female relationships  
274 predict the male's chances of subsequently consorting with her and/or increase his likelihood  
275 of siring her next offspring (as predicted by the care-then-mate hypothesis).

276

277 Identification of the most likely father

278 Following previous studies (Smuts 1985; Nguyen et al. 2009; Moscovice et al. 2010), we  
279 defined the most likely father of an infant as the male who mate-guarded the female during  
280 the fertile period of her conceptive cycle, defined as the five days preceding the day of  
281 detumescence when the probability of ovulation is maximal (Higham et al. 2008; Daspre et al.  
282 2009). On 56 fully observed cycles, sexual receptivity lasted  $22.1 \pm 5.5$  days (mean $\pm$ sd) on  
283 average (range: 13-43) and the number of consort males per swollen cycle was  $1.1 \pm 0.6$   
284 (mean $\pm$ sd) (range: 0-2). Consortships lasted  $8.8 \pm 6.0$  days (mean $\pm$ sd) on average (range: 0.5-  
285 32, N=48 cycles). On 74 cycles observed during the fertile period (i.e. 5 days before  
286 detumescence), the number of consort males during the fertile period was  $0.99 \pm 0.6$  (mean $\pm$ sd)  
287 (range: 0-2) and consortships during the fertile period lasted  $3.9 \pm 1.5$  days (mean $\pm$ sd) (range:  
288 0.5-5, N=60 cycles). As a result, only one male monopolized the female during the fertile  
289 cycle in most cycles and assignments of most likely father were straightforward. On 3/26  
290 conceptive cycles, two males consorted with a female consecutively during the fertile period.  
291 However, the time spent in consortship was always very biased toward one male (mean  
292 percentage of monopolization by the main male $\pm$ sd:  $83\% \pm 11\%$ ) so we selected that male as  
293 the most likely father.

294

295 Identification of the male friend

296 During pregnancy, early lactation and late lactation, we identified the male friend of each  
297 female from the dyadic proximity and grooming scores with all males in the group, as  
298 follows.

299 *Grooming.* A grooming allocation index quantified grooming given by females to  
300 males and relied on a combination of *ad lib* and male and female focal observations (see  
301 Table S1 in the Online Resource for sample sizes). Grooming bouts involving the same dyad

302 were discarded if they occurred within 30 minutes of a previous bout, in order to ensure  
303 independency among bouts. The strength of connection of a male-female dyad was estimated  
304 as the share of grooming that a female allocated to a particular male, calculated as the number  
305 of grooming bouts that a female gives to a male divided by the total number of grooming  
306 bouts given by that female to any male during the period when this male was resident in the  
307 group. This index controls for variation across females in the total time spent socializing with  
308 males, as well as for variation across males in the time spent in the group.

309 *Spatial proximity.* A spatial proximity index was calculated using female focal  
310 observations only (see Table S1 in the Online Resource for sample sizes). Every five minutes,  
311 scans recorded the identity and distance of the nearest adult male. The strength of connection  
312 of a male-female dyad was calculated as the number of scans where the male was the female's  
313 nearest neighbour divided by the total number of informative scans (i.e., for which the nearest  
314 neighbour is identified) collected for that female over the time period during which the male  
315 was resident in the group. In a few scans (0.3 %), two adult males were equally distant. These  
316 scans were counted in the dyadic index of both males. At Tsaobis, visibility is most of the  
317 time excellent, and facilitates the collection of accurate proximity data. Male nearest  
318 neighbours were on average at  $14.0 \pm 13.9$  meters (mean $\pm$ sd, range: 0-150m) from females.  
319 The mean percentage ( $\pm$ sd) of informative scans per focal observation was 71.8% ( $\pm$ 8.7%).  
320 Other, non-informative scans were omitted by observers, or impossible to collect because of  
321 poor visibility conditions, or because the focal individual was isolated from the rest of the  
322 group.

323 For both indices, we favoured the use of relative over absolute measures of  
324 heterosexual associations (i.e., we calculated female allocation of grooming and proximity  
325 toward each male, rather than absolute frequency of grooming or time spent in proximity of  
326 each male) in order to identify the favourite male(s) social partner of females while

327 controlling for differences in sociality among females (some females may be more social than  
328 others). We assessed the significance of the Pearson correlation between grooming and  
329 proximity indices of all heterosexual dyads using a Mantel test and 1000 permutations. The  
330 test compares the observed Pearson correlation between the matrices of proximity and  
331 grooming to the simulated correlation (where dyadic values are randomized 1000 times within  
332 a female).

333 For each behavioural index, we investigated if one or two males had an outstandingly  
334 high score compared to other males, hereafter referred as the “preferred male(s)”. We ranked  
335 males from the highest to the lowest score, then calculated the ratio of the highest index  
336 divided by the second highest index and the ratio of the second highest index divided by the  
337 third highest index. If the first ratio was higher than two (i.e. the male with the highest index  
338 had twice as many interactions with the female than the second male), we assigned only one  
339 preferred male - the one with the highest score - to the female. If the second ratio was also  
340 higher than two, we assigned two preferred males - the ones with first and second highest  
341 indices - to the female. Otherwise, we considered that the female had no preferred male for  
342 this reproductive state. Thus, females could have one, two or no preferred male(s) if no male  
343 had a highly differentiated score compared to the others. Then, we compared the preferred  
344 male(s) designated by each behavioural index and considered as "male friend" the male that  
345 was preferred according to both grooming and proximity indices (see Supplementary text in  
346 the Online Resource for more details regarding male friend attribution, including cases of  
347 discrepancy between the preferred male(s) assigned by each index). Several females had more  
348 than one offspring during the study period and observations of the same female in a different  
349 interbirth interval were considered separately, as the male associate may likely change in  
350 different interbirth intervals.

351



352 Test of the stability of male-female association between consecutive reproductive states

353 *Test of the mate-then-care hypothesis.* We assessed whether females remain associated  
354 with the most likely father of their offspring from conception to pregnancy (SWc-P) and with  
355 the same male friend from pregnancy to lactation (P-L) of the same interbirth interval. For the  
356 latter, we pooled females in both early and late lactation due to sample size limitation. We  
357 tested whether the identity of the most likely father/male friend remained consistent in the  
358 second state relative to the first state using two-tailed permutation tests. We only included  
359 cases where the most likely father/male friend of the first reproductive state was still in the  
360 group during the second reproductive state of the female. For each female, we created a pool  
361 of males that were present in the two reproductive states of interest and assigned 1 to the most  
362 likely father/male friend of each state. We randomized 50,000 times the identities of the most  
363 likely father/male friend in one state, computed the random distribution of the proportion of  
364 females associated with the same male across both reproductive states, and compared it to the  
365 observed proportion (i.e. based on the original data). The exact two-tailed p-value was  
366 computed as the proportion of cases displaying a higher or lower value than the observed  
367 correlation on the upper or lower tail of the simulated distribution, respectively.

368 *Test of the care-then-mate hypothesis.* We used two complementary approaches. First,  
369 we tested whether friendships predict male consortships during any future cycle of the next  
370 interbirth interval. We used all cycles for which the identity of the previous male friend was  
371 known, and for which he was still present in the group. For each cycle of each female and for  
372 each male, we recorded whether he mate-guarded the female or not (regardless of whether it  
373 was during the fertile period), and analysed variation in this variable using a generalized  
374 linear mixed-effect model with a binomial error structure and logit link function. Fixed effects  
375 included a categorical variable "Previous friend? (yes/no)", male rank (averaged across the

376 period considered) and group membership. Random factors included the identity of the cycle,  
377 female and male.

378 For all mixed models in our study, the statistical significance of the full model was  
379 assessed by comparing its fit with the respective null model (containing only the random  
380 factors) using a log-likelihood ratio test (LRT). Given the significance of the full model, the  
381 significance of the fixed factors was tested using a LRT test (assuming an asymptotic chi-  
382 square distribution of the test statistic), and using the full model (to avoid problems arising  
383 from stepwise model selection procedures: Whittingham et al. 2006; Mundry and Nunn  
384 2009). We further computed the 95% confidence intervals (using the `confint.merMod`  
385 function) of fixed factors (for multilevel categorical variables, confidence intervals were used  
386 to test the significance of each level of the variable by checking that they did not cross zero).  
387 To test for all differences between levels of a multilevel categorical variable, we changed the  
388 reference category sequentially (Pinheiro and Bates 2000). Model stability was assessed by  
389 randomly splitting the dataset in two and running the same GLMMs on the two subsets in  
390 order to check the robustness of estimates and significance of fixed effects (results not  
391 shown). All GLMMs were run using the `lme4` package (Bates et al. 2014) in R version 1.1-7  
392 (R Core development Team 2015).

393 Second, we restricted the previous dataset to conceptive cycles only, to test whether  
394 male friends were the most likely fathers of their next offspring. We only included cases  
395 where the previous friend was still in the group after the female had resumed cycling. Here,  
396 there was only one cycle per female and a limited sample size, so that the significance of the  
397 stability of male-female associations across reproductive states (Previous friend-SWc) was  
398 assessed using two-tailed permutation tests as detailed above, rather than GLMMs.

399

400 ***2. Maintenance of proximity with male friend across female reproductive states***

401 We subsequently investigated, for each male-female association in each reproductive state  
402 (i.e., between each female and her consort during periods of sexual receptivity, and between  
403 each female and her male friend during pregnancy, early lactation and late lactation), who was  
404 primarily responsible for maintaining spatial proximity (within 1m) and whether their roles  
405 changed according to female reproductive state. Using focal observations from both females  
406 and males, we extracted the number of approaches and leaves within 1m that were initiated by  
407 the male associate (consort or friend) or by the female and computed a ‘Hinde’s index’ for  
408 each dyad, calculated as the percentage of approaches minus the percentage of leaves initiated  
409 by the female and directed toward her male associate (Hinde and Atkinson 1970; Hinde and  
410 Proctor 1977). The Hinde’s index ranges from -100 (male is totally responsible for  
411 maintaining proximity) to +100 (female is totally responsible for maintaining proximity), and  
412 was calculated only for dyads for which a minimum of 20 approach-leave interactions were  
413 available in a given reproductive state of the female (mean±sd:61.7±38.2 interactions per  
414 dyad, range: 21-199, N=60 dyads). We tested whether the average of Hinde’s index values for  
415 a particular reproductive state differed from zero using a one sample t-test.

416

### 417 ***3. Strength of heterosexual associations depending on female reproductive state***

418 We finally investigated variation in the strength of male-female preferential  
419 associations in relation to changes of reproductive state. We ran two mixed-effect models  
420 which aimed at investigating variation in the frequency of association (1) between a female  
421 and the most likely father of her offspring (i.e. her consort during the conceptive cycle) and  
422 (2) between a female and her male friend. The response variables of the models were binary  
423 and recorded, for each scan of a female focal observation, whether or not the nearest male  
424 neighbour was (1) the likely father or (2) the male friend. Models were run with a binomial  
425 error structure and logit link function. In both models, the fixed effects included female

426 reproductive state, female dominance rank, female parity, male dominance rank, group  
427 identity and year. Random effects included female identity, male identity and focal follow. In  
428 the first model, we were interested in measuring variation in the strength of male-female  
429 associations from conception, so the different levels of our variable “reproductive state”  
430 included the swollen period of the conceptive cycle (including periods outside consortship),  
431 pregnancy, early and late lactation. In contrast, in the second model, the male friend of a  
432 female was not always the same across her successive reproductive state but we measured  
433 variation in association with the male designated as her friend for any particular reproductive  
434 state. These models were run as described above.

435

## 436 **RESULTS**

### 437 *1. Stability of male-female associations across reproductive state*

#### 438 Identification of the behavioural male friend

439 The distribution of grooming and proximity indices among males, when ranked from the  
440 highest to the fifth highest score, revealed that the strongest gap lies between the first and  
441 second male within each index, while differences among subsequent males are considerably  
442 weaker (Fig. 1a). This indicates that most pregnant and lactating females have a particularly  
443 strong relationship with one male. One or two preferred male(s) were assigned to 96% of  
444 females with the grooming index, and one or two male(s) were assigned to 61% of females  
445 with the proximity index (see Table S2 in the Online Resource); other females did not have  
446 any preferred male. Grooming and proximity indices were highly positively correlated across  
447 dyads (Mantel test with Pearson correlation:  $r=0.83$ ,  $N=67$  females,  $p=0.001$ ). As a result,  
448 both indices were very congruent and assigned the same male in 97% of cases (see Online  
449 Resources for more details). After the consensus between the two indices, all females had  
450 only one male friend (i.e. there was no case where the same two males were considered as

451 preferred by both indices). Overall, we defined one male friend for 83% of females (N=67 out  
452 of 81), including 83% of pregnant females, 95% of females in early lactation and 68% of  
453 females in late lactation. Male friends obtain a much higher share of grooming and proximity  
454 than non-friend males (Fig. 1b). In total, 70% of females and 55% of males were involved in  
455 at least one friendship during the study period.

456

#### 457 Test of the mate-then-care hypothesis

458 In support of the mate-then-care hypothesis, females remained associated with the same male  
459 from offspring conception to independence (Table 1). The highest stability in association  
460 patterns occurred between the swollen period of the conceptive cycle and pregnancy (SWc-P),  
461 as 21 out of 25 females kept the same male associate. Ten of 19 females were also associated  
462 with the same male from pregnancy to lactation (P-L). Notably, of the nine cases where  
463 females were not associated with the same male in pregnancy and lactation, six had no male  
464 friend during pregnancy and only started to associate with a male during lactation. Six  
465 females out of 44 properly switched their male associate from conception to pregnancy (SWc-  
466 P) or from pregnancy to lactation (P-L). For five out of those six females, the male associate  
467 of the first reproductive state was always in the top two highest scores of grooming and/or  
468 proximity index during the second state, suggesting that females may still maintain a bond  
469 with the likely father of their offspring, even when they mainly associate with another male.  
470 Overall, those results suggest that most male-female associations are stable from infant  
471 conception to weaning.

472

#### 473 Test of the care-then-mate hypothesis

474 When integrating information on all cycles for which the identity of the female's friend  
475 during her previous interbirth interval was known, females were seen in consortship with their

476 previous male friend in six out of 20 cycles. The GLMM predicting the probability of  
477 consorting between a male and a female as a function of their previous friendship (yes/no) and  
478 of male rank was not significant (log-likelihood ratio test comparing the fit of the full model  
479 with a null model containing only the random effects;  $\chi^2=4.4$ ,  $df=3$ ,  $N=20$  cycles,  $p=0.222$ ),  
480 suggesting that prior friendship does not predict a male's likelihood of mate-guarding a  
481 female when she resumes cycling. When restricting the analysis to conceptive cycles, we  
482 similarly found that friendship during pregnancy and lactation did not increase male chance of  
483 consorting with a female during the fertile period of her next conceptive cycle (Table 1). Out  
484 of 10 females for which information on the identity of her previous friend and next consort  
485 was available, only one consorted with her previous friend.

486

## 487 *2. Sex roles in the maintenance of proximity across female reproductive states*

488 Average Hinde's indices were negatively and significantly different from zero for the  
489 swollen period of the conceptive cycle (one sample t-test,  $N=19$ ,  $t=-6.7$ ,  $p<0.001$ ) and for  
490 pregnancy (one sample t-test,  $N=20$ ,  $t=-5.7$ ,  $p<0.001$ ) (Fig. 2), meaning that males were  
491 primarily responsible for maintaining close proximity with their female associate during these  
492 periods. Pregnancy becomes conspicuous approximately 3-4 weeks after conception in  
493 baboons, when females exhibit a reddening of the paracallosal skin, called 'pregnancy sign'  
494 (Gilbert and Gillman 1952; Altmann 1973). In an attempt to understand whether males may  
495 keep maintaining proximity during pregnancy simply because they fail to detect early  
496 pregnancies, we calculated Hinde's indices between females and their consort partner when  
497 they are cycling but not swollen (i.e. when the previous oestrus cycle did not lead to  
498 conception), during their first month of pregnancy (when pregnancy is inconspicuous) and  
499 during the rest of their pregnancy (when pregnancy become obvious). We found that males  
500 maintained close proximity to cycling females (one sample t-test,  $n=16$ ,  $t=-5.1$ ,  $p<0.001$ ),

501 females in early pregnancy (one sample t-test,  $n=8$ ,  $t=-6.7$ ,  $p<0.001$ ), and also to a lesser  
502 extent to females that were at a later stage of pregnancy (one sample t-test,  $n=8$ ,  $t=-2.6$ ,  
503  $p=0.033$ ). Thus, males remained primarily responsible for maintaining proximity throughout  
504 pregnancy (Fig. S5). By contrast, the average Hinde's indices were positive and significantly  
505 different from zero during early lactation (one sample t-test,  $N=17$ ,  $t=2.8$ ,  $p=0.014$ ), indicating  
506 that females were responsible for close proximity maintenance, while both males and females  
507 were equally responsible for maintaining contact during late lactation (one sample t-test,  
508  $N=4$ ,  $t=-1.4$ ,  $p=0.266$ ) (Fig. 2).

509

### 510 ***3. Strength of heterosexual associations depending on female reproductive state***

#### 511 Variation in the strength of association between females and the most likely father

512 The strength of association between females and their male friend was estimated by the  
513 probability of spatial proximity between partners in any given scan. The set of predictor  
514 variables used had a clear influence on the probability of association between females and the  
515 likely father of their current offspring (log-likelihood ratio test comparing the fit of the full  
516 model with a null model containing only random effects;  $\chi^2=64.2$ ,  $df=9$ ,  $p<0.001$ ). The  
517 probability of association between females and the most likely father of their offspring varies  
518 according to female reproductive state (Fig. 3a). Namely, the probability of association is  
519 highest during the swollen period of the conceptive cycle and early lactation, and lowest  
520 during pregnancy (Table 2a, Fig. 3a). In addition, high-ranking females had a higher  
521 probability of association with the likely father compared to low-ranking females. Similarly,  
522 higher-ranking males exhibited a higher probability of association with females. Finally,  
523 female parity was also important, with multiparous females being most often associated with  
524 the likely father.

525

## 526 Variation in the strength of associations between females and their male friend

527 The set of predictor variables used influenced the probability of association between females  
528 and their male friend (log-likelihood ratio test comparing the fit of the full model with a null  
529 model containing only random effects;  $\chi^2=54.8$ ,  $df=9$ ,  $p<0.001$ ). The probability of  
530 association between a female and her male friend varied according to female reproductive  
531 state (Fig. 3b). The probability of association increased from pregnancy to early lactation,  
532 decreased from early to late lactation and decreased again from late lactation to the first  
533 postpartum swelling, where association with the male friend of the previous interbirth interval  
534 was weakest (Table 2b, Fig. 3b). Beyond reproductive state, female rank also had an effect on  
535 the probability of association, with high ranking females being more likely to be associated  
536 with their male friend.

537

## 538 **DISCUSSION**

539 This study investigated the structure and stability of heterosexual bonds in chacma baboons.  
540 While previous studies have emphasized the occurrence of strong bonds between lactating  
541 females and an adult male shortly after the birth of an infant, our results suggest that males  
542 and females form stable and preferential relationships at least from conception until the end of  
543 lactation. Here we explore the implications of our findings for our understanding of the  
544 function of heterosexual associations in baboons.

545 We found that 70% (N=31/44) of females have the same male friend over time, either  
546 from conception to pregnancy or from pregnancy to lactation, while 14% (N=6/44) switch  
547 their male friend in one or the other transition. The remaining 16% (N=4/44) of females were  
548 not associated to any friend during one state (mainly during pregnancy). Thus, overall, most -  
549 but not all - male-female bonds last from offspring conception to lactation. By contrast,  
550 friendships did not significantly increase a male's chance of siring the next offspring of his



551 female friend, suggesting that in chacma baboons, heterosexual associations have not evolved  
552 in response to mating benefits. Overall, our results indicate that friendships tend to follow,  
553 rather than precede, sexual activity between friends which suggests that male involvement in  
554 heterosexual friendships represents paternal care rather than mating effort. Although our study  
555 assesses the correlation between friendships and the probability of paternity (inferred from  
556 consortship activity during the conceptive cycle), rather than actual paternity, our results are  
557 consistent with previous studies investigating the correlation between friendships and actual  
558 paternity data in savanna baboons, showing that most male friends of lactating females had  
559 sired their friend's infant (Nguyen et al. 2009; Huchard et al. 2010; Moscovice et al. 2010). In  
560 addition, it's important to note that we attributed as male friend to a female the male who was  
561 both her most frequent male nearest neighbour and her main male grooming partner. These  
562 criteria are meant to maximize our ability to detect and characterize differentiated male-  
563 female relationships, regardless of variation in the degree of sociality between females.  
564 However, they do not quantify the total amount of time that friends actually spend (or groom)  
565 together. This may represent another important axis of variation to consider when examining  
566 the functional consequences of heterosexual relationships, as it could be associated with  
567 differences in the expression of paternal behaviour.

568 Our finding that most male-female associations exist just after conception, and are  
569 maintained throughout pregnancy, suggests that males may assess their paternity using simple  
570 rules, such as protecting offspring born to the female(s) with whom they have become  
571 associated after consorting with them during the conceptive cycle. In previous studies, the  
572 observation that tight male-female associations only started during lactation (Palombit et al.  
573 1997; Palombit 1999), six months after conception, raised the question of how males might  
574 assess their paternity. Several studies suggested that males may rely on their past mating  
575 history, as they were found to form friendships based on mating effort and particularly on the

576 frequency and timing of copulations during the fertile period of a female's conceptive cycle  
577 (Palombit et al. 2000; Weingrill 2000; Moscovice et al. 2010). In Moscovice et al.'s study,  
578 females associated mainly with their main consort partner of the conceptive cycle and, when  
579 he was not present in the group around infant birth, they formed a friendship with their second  
580 former consort partner. This hypothesis suggests that males track and memorize their mating  
581 activity, and possibly that of their rivals, and eventually link the birth of the offspring to the  
582 conceptive cycle. Our results suggest an additional potential rule-of-thumb for male paternity  
583 assessment that relies on past mating history without requiring males to remember all their  
584 mates over the past 6-months period: male-female bonds may start during consortships and be  
585 subsequently maintained throughout pregnancy and lactation. It is important to note that  
586 males need to tolerate female friends selectively (and thus keep track of their previous mating  
587 activity) only if being involved in a friendship with a female is costly. If friendships are not  
588 costly to males, males may tolerate any female willing to associate with them and the  
589 observed pattern of male-female associations could be driven by a combination of female  
590 choice to associate with a male that does not represent a threat of infanticide given their  
591 mating history, and of male tolerance for any female.

592         At the proximate level, the formation and maintenance of affiliative pair-bonds and  
593 social relationships between mates have been show to be facilitated by physiological changes  
594 in oxytocin levels of females in monogamous rodents (Witt et al. 1990; Williams et al. 1994;  
595 Cushing and Carter 2000), non-human primates (Smith et al. 2010; Snowdon et al. 2010) and  
596 humans (Grewen et al. 2005; Feldman et al. 2012). Interestingly, in chacma baboons, females  
597 experience a surge of oxytocin during the period of most likely ovulation, and mate-guarded  
598 females displaying higher levels of oxytocin were found to maintain closer proximity to their  
599 consort partner (Moscovice and Ziegler 2012). Together with the present result that male-  
600 female associations exist from the conceptive cycle, this suggests that the formation of

601 heterosexual bonds in baboons might be hormonally mediated during consortships and  
602 subsequently maintained until infant's independence.

603         Preferential male-female bonds during pregnancy have already been documented in  
604 some baboon populations (Smuts 1985; Weingrill 2000, this study, but see Palombit et al.  
605 1997) but have rarely been investigated otherwise. In our population, 83% of pregnant  
606 females had a male friend. It is possible that looser bonds during pregnancy and late lactation  
607 may have led observers to focus on the stronger associations observed during early lactation  
608 (Palombit et al. 1997; Lemasson et al. 2008; Huchard et al. 2010; Moscovice et al. 2010).  
609 Male-female associations during pregnancy could have several benefits to both partners. In  
610 group-living species, foetus survival depends on a range of social and ecological variables and  
611 may impact the fitness of partners of both sexes (Kerhoas et al. 2014). Friendships with males  
612 during pregnancy could decrease risks of miscarriage if males support their female friend in  
613 conflicts with conspecifics (Seyfarth 1978; Smuts 1985), improve her feeding success by  
614 sharing foraging patches (King et al. 2008; Kaplan et al. 2011), or more generally contribute  
615 to decrease her physiological stress level (Smuts 1985; Weingrill 2000). In the latter case,  
616 several studies have reported an increase in abortion rates following male immigration into  
617 social groups ("Bruce effect", e.g. geladas, *Theropithecus gelada*: Roberts et al. 2012; yellow  
618 baboons: Pereira 1983; Alberts et al. 1992; hamadryas baboons, *P. hamadryas*: Colmenares  
619 and Gomendio 1988; Hanuman langurs, *Presbytis entellus*: Agoramorthy et al. 1988). Other  
620 studies have shown that lactating females with male friends experienced smaller increases in  
621 stress levels (than those without friends) when a new male immigrated (Beehner et al. 2005;  
622 Engh et al. 2006), and it is possible that pregnant females would experience the same benefits.  
623 From a male perspective, associating to the pregnant female who carries his foetus may  
624 contribute to protect his reproductive investment and prevent foetal losses due to "Bruce  
625 effect".

626           Responsibility for the maintenance of spatial proximity varies across the successive  
627 reproductive states of a female. Females are responsible for maintaining proximity during  
628 early lactation, as found in other studies (Palombit et al. 1997, 2001; Huchard et al. 2010).  
629 However, the fact that males are primarily responsible for maintaining close proximity during  
630 pregnancy was unexpected, and may suggest that males benefit from these associations as  
631 much as, or more than, females. In addition to the reproductive benefits mentioned above,  
632 males associated with a familiar female may gain social benefits, by receiving more grooming  
633 and affiliation, which may alleviate stress levels (Aureli and Yates 2009; Ellis et al. 2011) or  
634 facilitate their social integration in a group (Smuts 1985). Alternatively, a cause for those  
635 results may be methodological. In this study, we assessed the maintenance of proximity  
636 within 1m. In contrast, previous studies used a composite proximity measure, called ‘C-  
637 score’, which takes into account both close (0-1m) and intermediate (1-5m) proximity.  
638 Responsibility for the maintenance of close proximity (within 1m) mostly reflects the  
639 initiation of physical contacts between partners. As the direction of grooming is highly  
640 asymmetrical in heterosexual dyads (Palombit et al. 1997; Huchard et al. 2010), males may  
641 often approach females in a request to be groomed, and this may explain their responsibility  
642 in maintaining close proximity during pregnancy and the mixed maintenance during late  
643 lactation. A previous study assessing maintenance of close proximity (i.e. within 1m) between  
644 pregnant and lactating females and their male friend also found that males were responsible  
645 for proximity maintenance in over half of the dyads, while females were mostly responsible  
646 for maintaining proximity when using 0-5m proximity data (Smuts 1985). Analysing  
647 proximity data across the 0-5m range is likely to provide a more accurate reflect of the overall  
648 maintenance of proximity among heterosexual partners.

649           Finally, we found important variation in the strength of friendships across female  
650 reproductive states. Friendships were most prevalent (involving 95% of females) and most

651 intense during early lactation, encompassing the first 6 months of an infant life, when the risk  
652 of infanticide is highest (Palombit et al. 2001; Palombit 2003). By contrast, only 68% of  
653 females in late lactation were associated to a male friend and the strength of these associations  
654 decreased during this state compared to early lactation, suggesting that friendships might  
655 dissolve progressively, as infanticide risk decreases throughout infant development. The  
656 strength of friendships during pregnancy was lowest than during early lactation and  
657 comparable to late lactation. Evidence suggests that lactating females compete over male  
658 friends (Seyfarth 1978; Palombit et al. 2001). Pregnant females may renounce to stay around  
659 their friend at a time where the benefits of the association may not compensate the costs of  
660 competition.

661 In line with this, the strength of association with males was found to be influenced by  
662 female dominance rank, confirming that females were competing over access to male friends  
663 and their potential paternal services. In particular, high-ranking females, regardless of their  
664 reproductive state, associated more frequently to their male partner (friend and/or likely father  
665 of their offspring) than lower-ranking females. Female-female competition over males in  
666 chacma baboons was first reported in a two-male group where the dominant female seemed to  
667 prevent the formation of close bonds between the dominant male and other females (Seyfarth  
668 1978). A subsequent study showed that high-ranking mothers maintained closer associations  
669 to their male friends and actively excluded lower-ranking mothers from male proximity where  
670 friendships overlapped (Palombit et al. 2001). A male's ability to protect infants might be  
671 limited by the number of females and/or infants associated with him at a given time (Palombit  
672 et al. 2001). For instance, high-ranking males *Macaca nigra* who are frequently mate-  
673 guarding receptive females spend less time in proximity to their genetic offspring probably  
674 because they are seeking further mating opportunities instead of providing infant care (D.  
675 Kerhoas et al., unpubl. data). Similarly, subordinate male chacma baboons have fewer bonds

676 with juveniles than dominant males, but maintain stronger bonds with their associated  
677 juveniles (Huchard et al. 2013).

678         A range of social and demographical parameters may influence the temporal stability  
679 of male-female bonds in chacma baboons. First, infanticide risk is known to vary both within  
680 and among populations (Palombit 2003) and is likely to affect the benefits of male-female  
681 bonds (Palombit 1999, 2012). In our case, several immigration events induced social  
682 instability in both groups during the course of this study, which may have raised female  
683 perception of infanticide risk, and their incentive to form friendships. Second, male breeding  
684 tenure may also be an important determinant of the stability of male-female bonds in large  
685 multimale groups. When male dominance hierarchy is stable over long periods of time, the  
686 same male-female bonds might continue after offspring independence and cover more than  
687 one interbirth interval. By contrast, if male dominance changes while a female is pregnant or  
688 in lactation, she might stop her association to conceive her next offspring with the new alpha  
689 male. In this study, male dominance changed in both groups between the two study periods,  
690 which may explain why most male-female bonds vanish after one interbirth interval.

691         To conclude, our findings suggest that heterosexual associations represent paternal  
692 effort rather than mating effort in chacma baboons, show greater temporal stability than  
693 previously thought, and vary in strength according to female reproductive state and  
694 dominance rank. We found that heterosexual friendships exist since infant conception, are  
695 maintained throughout pregnancy and strengthen at birth. Such pattern of association may  
696 clarify how males and females use their mating history to make decisions about heterosexual  
697 bonds by suggesting that long-term memory of prior mating activity is not necessary to invest  
698 into friendships and offspring care. In addition, our results indicate that most females are  
699 permanently associated with one male regardless of their reproductive status, suggesting that

700 heterosexual bonds may play an important, and under-appreciated, role in the social  
701 organization and structure of baboon societies.

702

### 703 **COMPLIANCE WITH ETHICAL STANDARDS**

704 **Funding:** AB was supported by a studentship from the ‘Ministère de l’Education Nationale,  
705 de l’Enseignement Supérieur et de la Recherche’, France. Additional financial support was  
706 provided by a grant from the Primate Society of Great Britain.

707 **Conflict of Interest:** The authors declare that they have no conflict of interest.

708 **Ethical approval:** All applicable international, national, and/or institutional guidelines for the  
709 care and use of animals were followed. This article does not contain any studies with human  
710 participants performed by any of the authors.

711

### 712 **REFERENCES**

- 713 Agoramoorthy G, Mohnot SM, Sommer V, Srivastavz A (1988) Abortions in free ranging  
714 Hanuman langurs (*Presbytis entellus*) - a male induced strategy
- 715 Alberts SC, Altmann J (1995) Balancing costs and opportunities: dispersal in male baboons.  
716 *Am Nat* 145:279–306
- 717 Alberts SC, Altmann J, Wilson ML (1996) Mate guarding constrains foraging activity of male  
718 baboons. *Anim Behav* 51:1269–1277
- 719 Alberts SC, Sapolsky RM, Altmann J (1992) Behavioral, endocrine, and immunological  
720 correlates of immigration by an aggressive male into a natural primate group. *Horm*  
721 *Behav* 26:167–178
- 722 Albers PCH, de Vries H (2001) Elo-rating as a tool in the sequential estimation of dominance  
723 strengths. *Anim Behav* 61:489–495
- 724 Altmann J (1974) Observational study of behaviour: sampling methods. *Behaviour* 49:227–  
725 267
- 726 Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, MA
- 727 Altmann J, Alberts SC (2003) Variability in reproductive success viewed from a life-history  
728 perspective in baboons. *Am J Hum Biol* 15:401–409
- 729 Altmann SA (1973) The pregnancy sign in savannah baboons. *J Zoo Anim Med* 4:8–12
- 730 Archie EA, Tung J, Clark M, Altmann J, Alberts SC (2014) Social affiliation matters : both  
731 same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc R*  
732 *Soc B* 281:20141261

- 733 Aureli F, Yates K (2009) Distress prevention by grooming others in crested black macaques.  
734 Biol Lett 6:27–29
- 735 Bales KB (1980) Cumulative scaling of paternalistic behavior in primates. Am Nat 454–461
- 736 Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using  
737 Eigen and S4. R package version 1.1-7, [https://cran.rproject.org/web/packages/lme4/  
738 index.html](https://cran.rproject.org/web/packages/lme4/index.html)
- 739 Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL (2005) The effect of new  
740 alpha males on female stress in free-ranging baboons. Anim Behav 69:1211–1221
- 741 Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank  
742 and kinship in baboons. Science 302:1234–1236
- 743 Buchan JC, Alberts SC, Silk JB, Altmann J (2003) True paternal care in a multi-male primate  
744 society. Nature 425:179–181
- 745 Bulger JB (1993) Dominance rank and access to estrous females in male savanna baboons.  
746 Behaviour 127:67–103
- 747 Cacioppo JT, Hawkley LC (2003) Social isolation and health, with an emphasis on underlying  
748 mechanisms. Perspect Biol Med 46:S39–S52
- 749 Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females  
750 increase reproductive success in feral horses. Proc Natl Acad Sci USA 106:13850–13853
- 751 Charpentier MJE, Van Horn RC, Altmann J, Alberts SC (2008) Paternal effects on offspring  
752 fitness in a multimale primate society. Proc Natl Acad Sci USA 105:1988–1992
- 753 Cheney DL, Silk JB, Seyfarth RM (2012) Evidence for intrasexual selection in wild female  
754 baboons. Anim Behav 84:21–27
- 755 Colmenares F, Gomendio M (1988) Changes in female reproductive condition following male  
756 take-overs in a colony of hamadryas and hybrid baboons. Folia Primatol 50:157–174
- 757 Cowlshaw G (1997) Refuge use and predation risk in a desert baboon population. Anim  
758 Behav 54:241–53
- 759 Cushing BS, Carter CS (2000) Peripheral pulses of oxytocin increase partner preferences in  
760 female, but not male, prairie voles. Horm Behav 37:49–56
- 761 Daspre A, Heistermann M, Hodges JK, Lee PC, Rosetta L (2009) Signals of female  
762 reproductive quality and fertility in colony-living baboons (*Papio h. anubis*) in relation  
763 to ensuring paternal investment. Am J Primatol 71:529–538
- 764 DeVries AC, Glasper ER, Detillion CE (2003) Social modulation of stress responses. Physiol  
765 Behav 79:399–407
- 766 Ellis JJ, Maclarnon AM, Heistermann M, Semple S (2011) The social correlates of self-  
767 directed behaviour and faecal glucocorticoid levels among adult male olive baboons  
768 (*Papio hamadryas anubis*) in Gashaka-Gumti National Park, Nigeria. Afr Zool 46:302–  
769 308
- 770 Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL  
771 (2006) Female hierarchy instability, male immigration and infanticide increase  
772 glucocorticoid levels in female chacma baboons. Anim Behav 71:1227–1237
- 773 Feldman R, Zagoory-Sharon O, Weisman O, Schneiderman I, Gordon I, Maoz R, Shalev I,



- 774 Ebstein RP (2012) Sensitive parenting is associated with plasma oxytocin and  
775 polymorphisms in the OXTR and CD38 Genes. *Biol Psychiat* 72:175–181
- 776 Frere CH, Krutzen M, Mann J, Connor RC, Bejder L, Sherwin WB (2010) Social and genetic  
777 interactions drive fitness variation in a free-living dolphin population. *Proc Natl Acad*  
778 *Sci USA* 107:19949–19954
- 779 Gilbert C, Gillman J (1952) Pregnancy in the baboon (*Papio ursinus*). *S Afr J Med Sci*  
780 16:115–124.
- 781 Grewen KM, Girdler SS, Amico J, Light KC (2005) Effects of partner support on resting  
782 oxytocin, cortisol, norepinephrine, and blood pressure before and after warm partner  
783 contact. *Psychosom Med* 67:531–538
- 784 Handley LJJ, Perrin N (2007) Advances in our understanding of mammalian sex-biased  
785 dispersal. *Mol Ecol* 16:1559–1578
- 786 Higham JP, Heistermann M, Ross C, Semple S, MacLarnon A (2008) The timing of ovulation  
787 with respect to sexual swelling detumescence in wild olive baboons. *Primates* 49:295–  
788 299
- 789 Hinde RA, Atkinson S (1970) Assessing the role of social partners in maintaining mutual  
790 proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim Behav*  
791 18:169–176
- 792 Hinde RA, Proctor LP (1977) Changes in the relationships of captive rhesus monkeys on  
793 giving birth. *Behaviour* 61:304–321
- 794 Holt-Lunstad J, Smith TB, Bradley Layton J (2010) Social relationships and mortality risk: a  
795 meta-analytic review. *PLoS Med* 7:859
- 796 Huchard E, Alvergne A, Fejan D, Knapp LA, Cowlshaw G, Raymond M (2010) More than  
797 friends? Behavioural and genetic aspects of heterosexual associations in wild chacma  
798 baboons. *Behav Ecol Sociobiol* 64:769–781
- 799 Huchard E, Charpentier MJ, Marshall H, King AJ, Knapp LA., Cowlshaw G (2013) Paternal  
800 effects on access to resources in a promiscuous primate society. *Behav Ecol* 24:229–236
- 801 Huchard E, Courtiol A, Benavides JA, Knapp LA, Raymond M, Cowlshaw G (2009) Can  
802 fertility signals lead to quality signals? Insights from the evolution of primate sexual  
803 swellings. *Proc R Soc Lond B* 276:1889–1897
- 804 Huchard E, Cowlshaw G (2011) Female-female aggression around mating: an extra cost of  
805 sociality in a multimale primate society. *Behav Ecol* 22:1003–1011
- 806 Kaplan BS, O’Riain MJ, van Eeden R, King AJ (2011) A low-cost manipulation of food  
807 resources reduces spatial overlap between baboons (*Papio ursinus*) and humans in  
808 conflict. *Int J Primatol* 32:1397–1412
- 809 Kerhoas D, Perwitasari-Farajallah D, Agil M, Widdig A, Engelhardt A (2014) Social and  
810 ecological factors influencing offspring survival in wild macaques. *Behav Ecol* 25:1164–  
811 1172
- 812 King AJ, Douglas CMS, Huchard E, Isaac NJB, Cowlshaw G (2008) Dominance and  
813 affiliation mediate despotism in a social primate. *Curr Biol* 18:1833–1838
- 814 Kulik L, Muniz L, Mundry R, Widdig A (2012) Patterns of interventions and the effect of  
815 coalitions and sociality on male fitness. *Mol Ecol* 21:699–714

- 816 Lemasson A, Palombit RA, Jubin R (2008) Friendships between males and lactating females  
817 in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from  
818 playback experiments. *Behav Ecol Sociobiol* 62:1027–1035
- 819 Machanda ZP, Gilby IC, Wrangham RW (2013) Male-female association patterns among  
820 free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Int J Primatol* 34:917–938
- 821 Manson JH (1994) Mating patterns, mate choice, and birth season heterosexual relationships  
822 in free-ranging rhesus macaques. *Primates* 35:417–433
- 823 Massen JJM, Overduin-de Vries AM, de Vos-Rouweler AJM, Spruijt BM, Doxiadis GGM,  
824 Sterck EHM (2012) Male mating tactics in captive rhesus macaques (*Macaca mulatta*):  
825 the influence of dominance, markets, and relationship quality. *Int J Primatol* 33:73–92
- 826 Ménard N, von Segesser F, Scheffrahn W, Pastorini J, Vallet D, Gaci B, Martin RD, Gautier-  
827 Hion A (2001) Is male-infant caretaking related to paternity and/or mating activities in  
828 wild Barbary macaques (*Macaca sylvanus*). *CR Acad Sci III-Vie* 324:601–610
- 829 Moscovice LR, Di Fiore A, Crockford C, Kitchen DM, Wittig R, Seyfarth RM, Cheney DL  
830 (2010) Hedging their bets? Male and female chacma baboons form friendships based on  
831 likelihood of paternity. *Anim Behav* 79:1007–1015
- 832 Moscovice LR, Heesen M, Di Fiore A, Seyfarth RM, Cheney DL (2009) Paternity alone does  
833 not predict long-term investment in juveniles by male baboons. *Behav Ecol Sociobiol*  
834 63:1471–1482
- 835 Moscovice LR, Ziegler TE (2012) Peripheral oxytocin in female baboons relates to estrous  
836 state and maintenance of sexual consortships. *Horm Behav* 62:592–597
- 837 Mundry R, Nunn CL (2009) Stepwise model fitting and statistical inference: turning noise  
838 into signal pollution. *Am Nat* 173:119–123
- 839 Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A  
840 (2011) Assessing dominance hierarchies: validation and advantages of progressive  
841 evaluation with Elo-rating. *Anim Behav* 82:911–921
- 842 Nguyen N, Van Horn RC, Alberts SC, Altmann J (2009) “Friendships” between new mothers  
843 and adult males: adaptive benefits and determinants in wild baboons (*Papio*  
844 *cynocephalus*). *Behav Ecol Sociobiol* 63:1331–1344
- 845 Ostner J, Vigilant L, Bhagavatula J, Franz M, Schülke O (2013) Stable heterosexual  
846 associations in a promiscuous primate. *Anim Behav* 86:623–631
- 847 Palombit RA (1999) Infanticide and the evolution of pair bonds in nonhuman primates. *Evol*  
848 *Anthropol* 7:117–129
- 849 Palombit RA (2000) Infanticide and the evolution of male-female bonds in animals. In: van  
850 Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge  
851 University Press, Cambridge, pp 239–268
- 852 Palombit RA (2003) Male infanticide in wild savanna baboons: adaptive significance and  
853 intraspecific variation. In: Jones CB (ed) *Sexual selection and reproductive competition*  
854 *in primates: new perspectives and directions*. American Society of Primatologists, pp  
855 367–412
- 856 Palombit RA (2012) Infanticide: male strategies and female counterstrategies. In: Mitani JC,  
857 Call J, Kappeler PM, Palombit RA, Silk JA (eds) *The evolution of primate societies*.  
858 University of Chicago Press, Chicago, pp 432–468

- 859 Palombit RA, Cheney DL, Fisher J, Johnson S, Rendall D, Seyfarth RM, Silk JB (2000) Male  
860 infanticide and defense of infants in chacma baboons. In: van Schaik C, Janson C (eds)  
861 Infanticide by males and its implications, Cambridge. Cambridge, pp 123–152
- 862 Palombit RA, Cheney DL, Seyfarth RM (2001) Female-female competition for male “friends”  
863 in wild chacma baboons, *Papio cynocephalus ursinus*. Anim Behav 61:1159–1171
- 864 Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of “friendships” to female  
865 baboons: experimental and observational evidence. Anim Behav 54:599–614
- 866 Paul A, Kuester J, Arnemann J (1996) The sociobiology of male-infant interactions in  
867 Barbary macaques, *Macaca sylvanus*. Anim Behav 51:155–170
- 868 Pereira ME (1983) Abortion following the immigration of an adult male baboon (*Papio*  
869 *cynocephalus*). Am J Primatol 4:93–98
- 870 Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-plus. Springer, New York
- 871 R Core Development Team (2015) R: A language and environment for statistical computing.  
872 Vienna, Austria, <http://www.r-project.org/>
- 873 Roberts EK, Lu A, Bergman TJ, Beehner JC (2012) A Bruce effect in wild geladas. Science  
874 335:1222–1225
- 875 Rosal MC, King J, Ma Y, Reed GW (2004) Stress, social support, and cortisol: inverse  
876 associations? Behav Med 30:11–21
- 877 Seyfarth RM (1976) Social relationships among adult female baboons. Anim Behav 24:917–  
878 938
- 879 Seyfarth RM (1978) Social relationships among adult male and female baboons. II. Behaviour  
880 throughout the female reproductive cycle. Behaviour 64:227–247
- 881 Silk JB (2007a) The adaptive value of sociality in mammalian groups. Philos T Roy Soc B  
882 362:539–559
- 883 Silk JB (2007b) Social components of fitness in primate groups. Science 317:1347–1351
- 884 Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant  
885 survival. Science 302:1231–1232
- 886 Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM,  
887 Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds  
888 among female baboons enhance offspring survival. Proc R Soc Lond B 276:3099–3104
- 889 Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM,  
890 Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the  
891 longevity of female baboons. Curr Biol 20:1359–1361
- 892 Smith AS, Ågmo A, Birnie AK, French JA (2010) Manipulation of the oxytocin system alters  
893 social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. Horm  
894 Behav 57:255–262
- 895 Smuts BB (1985) Sex and friendship in baboons. Aldine, New York
- 896 Smuts BB, Gubernick DJ (1992) Male-infant relationships in nonhuman primates: paternal  
897 investment or mating effort? In: Hewlett BS (ed) Father-child relations: cultural and  
898 biosocial contexts. Adline, New York, pp 1–30
- 899 Snowdon CT, Pieper BA, Boe CY, Cronin KA, Kurian A V, Ziegler TE (2010) Variation in

- 900 oxytocin is related to variation in affiliative behavior in monogamous, pairbonded  
901 tamarins. *Horm Behav* 58:614–618
- 902 Stanton MA, Mann J (2012) Early social networks predict survival in wild bottlenose  
903 dolphins. *PLoS ONE* 7:e47508
- 904 Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in  
905 nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- 906 Uchino BN (2006) Social support and health: a review of physiological processes potentially  
907 underlying links to disease outcomes. *J Behav Med* 29:377–387
- 908 van Schaik CP (1989) The ecology of social relationships amongst female primates. In:  
909 Standen V, Foley RA (eds) *Comparative socioecology: the behavioral ecology of*  
910 *humans and other mammals*. Blackwell Scientific, Oxford, GB, pp 195–218
- 911 van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female  
912 association in primates. *Proc R Soc Lond B* 264:1687–1694
- 913 van Schaik CP, Paul A (1996) Male care in primates: does it ever reflect paternity? *Evol*  
914 *Anthropol* 5:152–156
- 915 van Schaik CP, van Noordwijk MA (1989) The special role of male *Cebus monkeys* in  
916 predation avoidance and its effect on group composition. *Behav Ecol Sociobiol* 24:265–  
917 276
- 918 Weingrill T (2000) Infanticide and the value of male-female relationships in mountain  
919 chacma baboons. *Behaviour* 137:337–359
- 920 Weingrill T, Lycett JE, Barrett L, Hill RA, Henzi SP (2003) Male consortship behaviour in  
921 chacma baboons: the role of demographic factors and female conceptive probabilities.  
922 *Behaviour* 140:405–427
- 923 Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use  
924 stepwise modelling in ecology and behaviour? *J Anim Ecol* 75:1182–1189
- 925 Widdig A (2007) Paternal kin discrimination: the evidence and likely mechanisms. *Biol Rev*  
926 82:319–334
- 927 Williams JR, Insel TR, Harbaugh CR, Carter CS (1994) Oxytocin administered centrally  
928 facilitates formation of a partner preference in female prairie voles (*Microtus*  
929 *ochrogaster*). *J Neuroendocrinol* 6:247–250
- 930 Witt DM, Carter CS, Walton DM (1990) Central and peripheral effects of oxytocin  
931 administration in prairie voles (*Microtus ochrogaster*). *Pharmacol Biochem Behav*  
932 37:63–69

933 **Table 1** Results of the permutation tests investigating whether females remain associated with the same male across reproductive states (likely  
 934 father: most likely father of their offspring, identified as the main consort during the swollen period of the conceptive cycle, friend P: male friend  
 935 during pregnancy, friend L: male friend during lactation, previous friend: male friend during pregnancy or lactation of the previous interbirth  
 936 interval). The observed proportion of females associated with the same male is calculated as the number of females associated with the same  
 937 male across both reproductive states divided by the total number of females

938

Transition	Observed proportion of females associated with the same male	Proportion of females associated with the same male between randomized matrices [95% CI]	P-value	Number of females	Number of females associated with the same male across both reproductive states	Number of females switching males across both reproductive states	Number of females without associate in one state
Likely father - friend P	0.840	0.118 [0.000 ; 0.240]	<0.001	25	21	3	1
Friend P - friend L	0.526	0.114 [0.000 ; 0.263]	<0.001	19	10	3	6
Previous friend - likely father	0.100	0.093 [0.000 ; 0.300]	0.579	10	1	9	0

939

940

941

942 **Table 2** Results of the mixed models analysing the frequency of association (a) between a female and her consort partner and (b) between a  
943 female and her male friend, during the conceptive cycle (SWc), pregnancy (P), early lactation (L1), late lactation (L2) and the first postpartum  
944 cycle (SW1). The parameters are based on observations including 52 females in a particular reproductive state (26 individual females), 11 males  
945 and 5085 and 2407 proximity scans for the first model and on 71 females in a particular reproductive state (33 individual females), 18 males and  
946 7584 proximity scans for the second models. Parameter estimates were computed using mixed models controlling for the non-independence of  
947 scans within focal observations, and for the repeated appearance of females and males (fitted as random factors). se: standard error. Significant  
948 effects (for which confidence interval does not cross zero) are indicated in bold

949

<b>Response variable</b>	<b>Fixed factors</b>	<b>Levels</b>	<b>Estimate ± se</b>	<b>95% confidence interval</b>	<b>LRT</b>	<b>df</b>	<b>P-value</b>
(a) Probability of association with the most likely father	Reproductive state <sup>a</sup>	SWc	0.812 ± 0.833	[-0.820 ; 2.444]	31.276	3	<0.001
		P	-1.572 ± 0.772	[-3.086 ; -0.058]			
		L2	-0.121 ± 1.023	[-2.126 ; 1.883]			
	Female rank		2.801 ± 0.741	[1.349 ; 4.253]	12.130	1	<0.001
	Male rank		2.848 ± 1.041	[0.808 ; 4.889]	7.402	1	0.007
	Parity <sup>b</sup>	nulliparous	-1.916 ± 0.613	[-3.118 ; -0.715]	13.052	2	0.001
		primiparous	-2.135 ± 0.701	[-3.508 ; -0.762]			
	Troop <sup>c</sup>		0.574 ± 0.490	[-0.386 ; 1.534]	1.315	1	0.251
Year <sup>d</sup>		0.685 ± 0.594	[-0.479 ; 1.850]	1.270	1	0.260	
(b) Probability of association with the male	Reproductive state <sup>a</sup>	P	-1.380 ± 0.283	[-1.934 ; -0.825]	33.144	3	<0.001
		L2	-0.861 ± 0.379	[-1.603 ; -0.118]			
		SW1	-2.359 ± 0.486	[-3.312 ; -1.407]			

friend	Female rank		1.318 ± 0.492	[0.354 ; 2.281]	6.167	1	0.013	
	Male rank		-0.961 ± 0.532	[-2.003 ; 0.081]	3.275	1	0.070	
	Parity <sup>b</sup>	nulliparous		-0.042 ± 0.484	[-0.990 ; 0.906]	0.005	2	0.997
		primiparous		-0.002 ± 0.302	[-0.595 ; 0.591]			
	Troop <sup>c</sup>			0.267 ± 0.465	[-0.645 ; 1.179]	0.302	1	0.582
	Year <sup>d</sup>			1.072 ± 0.286	[0.512 ; 1.633]	13.669	1	<0.001

950

951

<sup>a</sup>Reference category: L1 (six first months of lactation)

952

<sup>b</sup>Reference category: multiparous

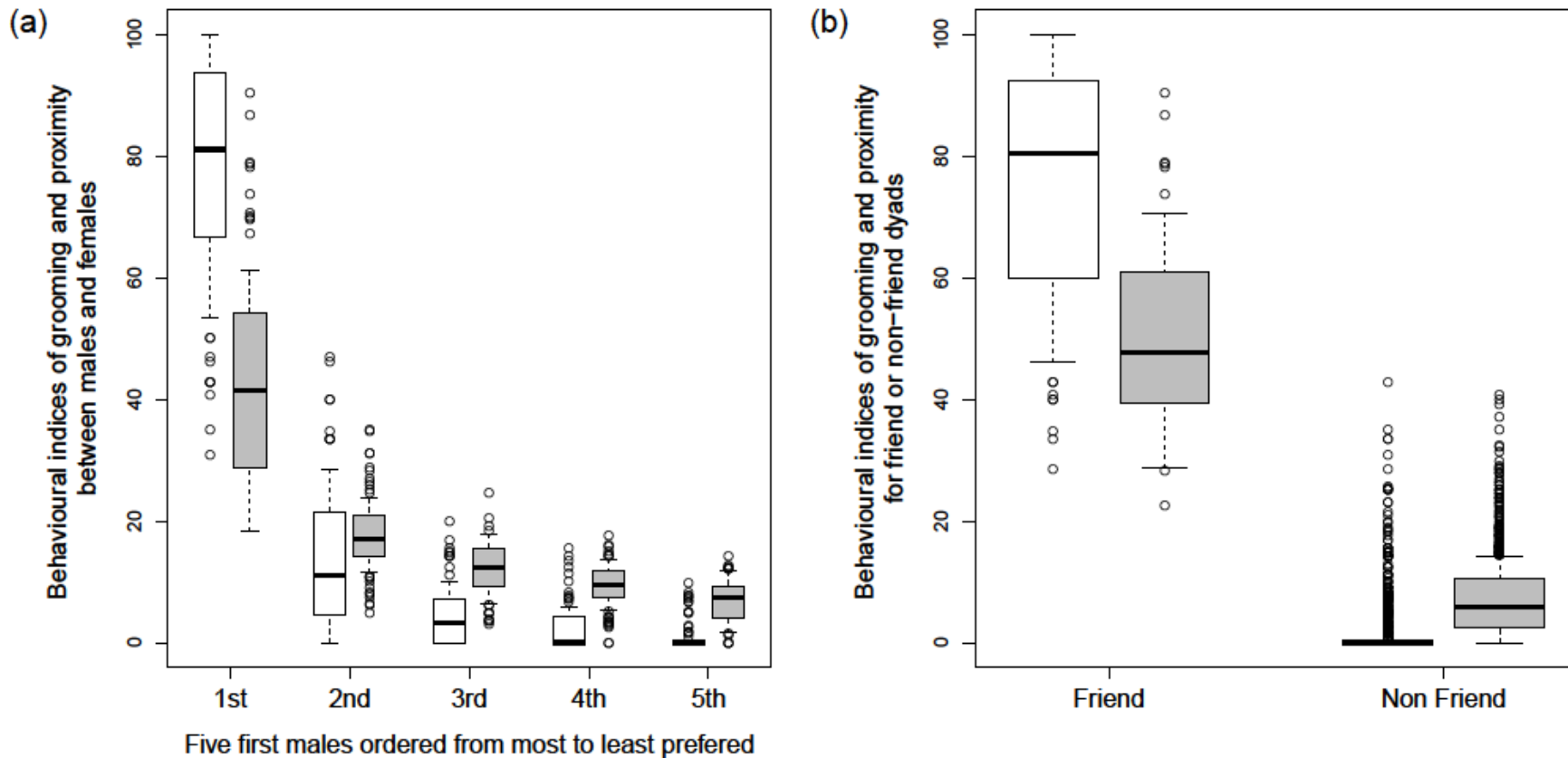
953

<sup>c</sup>Reference category: J group

954

<sup>d</sup>Reference category: 2013

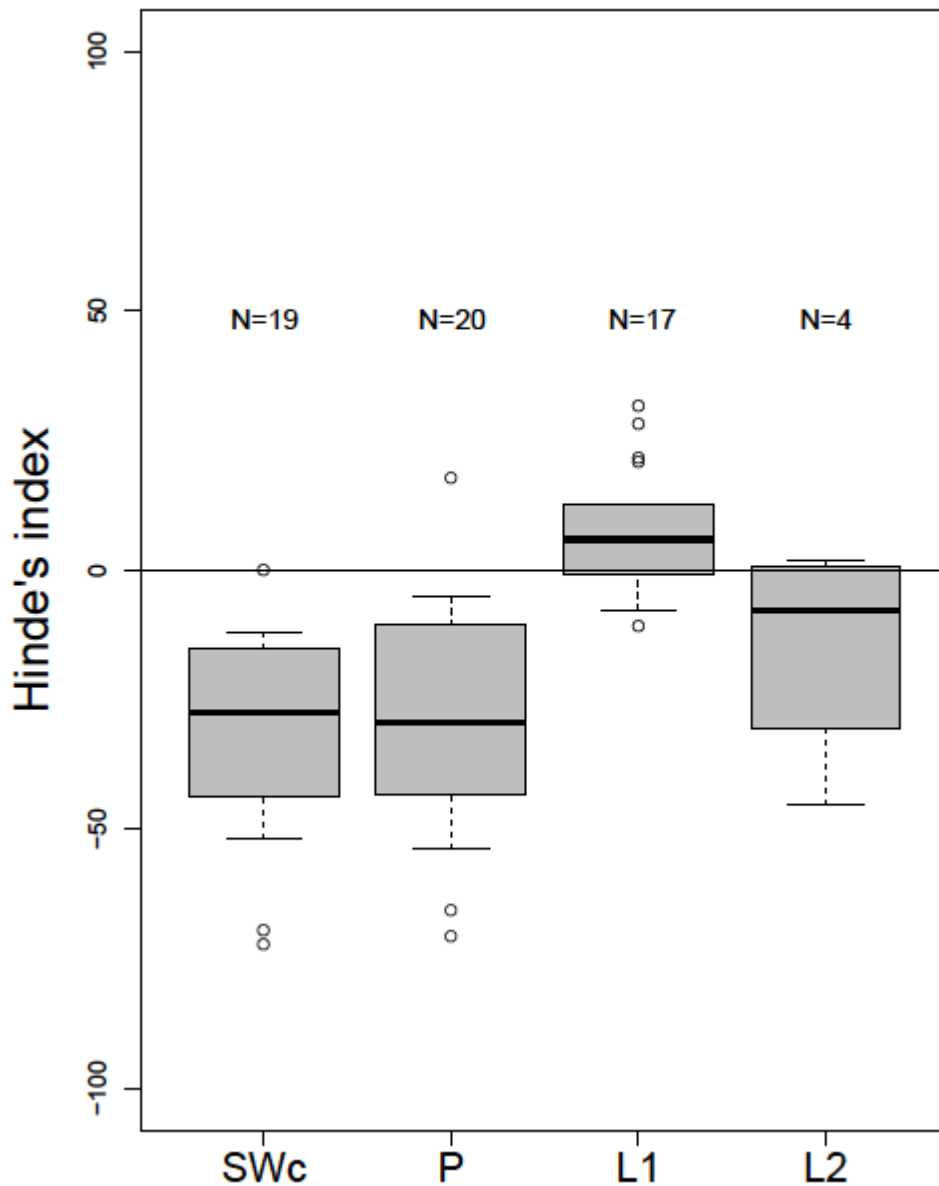
955 **Fig. 1** Distribution of grooming (white bars) and spatial proximity (grey bars) indices (a) between each female and five male residents in her  
 956 group that ranked from the highest to the fifth highest score, and (b) for friend dyads (N=77 for grooming index, N=55 for proximity index)  
 957 versus non-friend dyads (N=902 for grooming index, N=812 for proximity index). On each box, the black horizontal line represents the median  
 958 of the distribution, while the bottom and top of the box represent respectively the 25th and 75th quartiles. Whiskers include a maximum of half of  
 959 the interquartile range. Open dots represent outliers. Note that the boxes representing the grooming index distribution for the fifth male and for  
 960 non-friend dyads is not visible because the median, the 25<sup>th</sup> and 75<sup>th</sup> quartiles are equal to zero  
 961



962



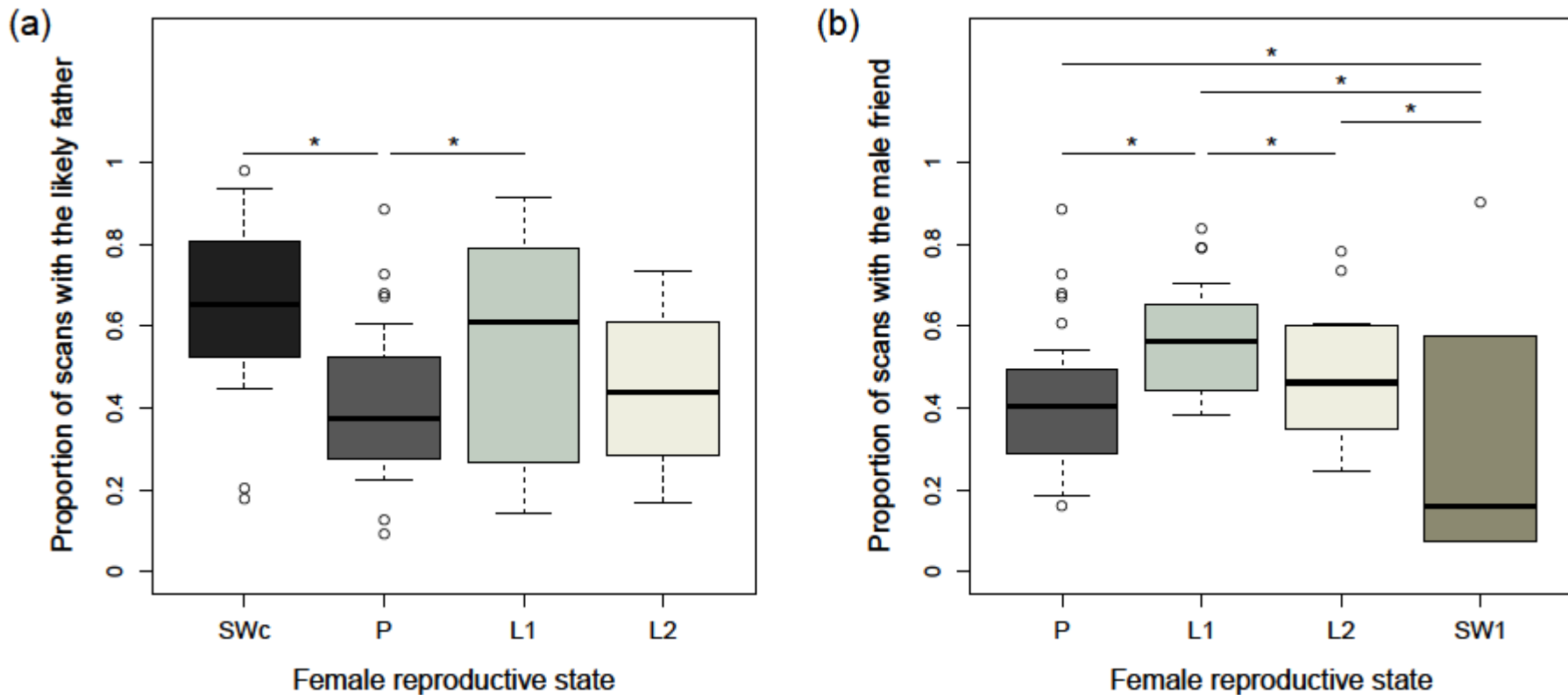
963 **Fig. 2** Responsibility for the maintenance of close spatial proximity (within 1m) between  
 964 females and their male associates. The male associate is the male consort during the swollen  
 965 period of the conceptive cycle (SWC) and the male friend during pregnancy (P), early  
 966 lactation (L1) and late lactation (L2). Responsibility is measured by Hinde's index: positive  
 967 (vs negative) values indicate that the female (vs male) is primarily responsible for maintaining  
 968 proximity. The number of females in each reproductive state is indicated above the boxplot.  
 969 On each box, the black horizontal line represents the median of the distribution, while bottom  
 970 and top of the box represent respectively the 25th and 75th quartiles. Whiskers include a  
 971 maximum of half of the interquartile range. Open dots represent outliers



972

973

974 **Fig. 3** Distribution of the proportion of proximity scans for which (a) the likely father and (b) the male friend is the nearest neighbour (calculated  
 975 as the number of scans with the male partner as the nearest neighbour divided by the total number of scans available for the female), according to  
 976 female reproductive state: cycling swollen during the conceptive cycle (SWc), pregnant (P), early lactation (L1), late lactation (L2) and first  
 977 postpartum cycle (SW1). On each box, the black horizontal line represents the median of the distribution, while bottom and top of the box  
 978 represent respectively the 25th and 75th quartiles. Whiskers include a maximum of half of the interquartile range. Open dots represent outliers.  
 979 The significance of the comparisons between reproductive states is evaluated by changing contrasts in the GLMM. Significant comparisons are  
 980 denoted by "\*"



981

## Supplementary Text

### **Identification of male friend**

We identified the male friend of each female observed in pregnancy, early lactation and late lactation using dyadic indices of spatial proximity and grooming between each female and all males in the group – see main text for the description of these indices. For each behavioural index, we ranked males from the highest to the lowest score, then calculated the ratio of the highest index divided by the second highest index and the ratio of the second highest index divided by the third highest index. If the first ratio was higher than two (i.e. the male with the highest index has twice as many interactions with the female than the second male), we assigned only one preferred male - the one with the highest score - to the female. If the second ratio was also higher than two, we assigned two preferred males - the ones with first and second highest indices - to the female. Otherwise, we considered that the female had no preferred male for this reproductive state. Thus, females could have one, two or no preferred male(s) if no male had a highly differentiated score compared to the others. When the first highest male had a score of 100 and the second highest male had a score of 0, the ratio was infinite (100/0). In those cases, the first highest male was assigned as male friend. Similarly, if the ratio between the first and second highest ranking males was inferior to 2 and the ratio between the second and third highest ranking male was infinite, the two first males were assigned as male friends. Females in a given reproductive state were included in the analysis if they had at least 5 grooming bouts recorded with adult males (for the grooming index) and only if they had been the subject of at least 4 focal observations (representing a minimum of 28 informative scans) (see Table S1 for sample size of each index).

Then, we compared the preferred male(s) assigned by each behavioural index and considered as "male friend" the male(s) that was preferred according to both grooming and

proximity indices. There were more preferred males assigned by the grooming indices than by the proximity indices, because grooming relationships are more differentiated. When a male was assigned as preferred by one index but not by the other (N=23 out of 81 cases), we checked whether he was also ranking first or second with the other index. In such cases (N=17 out of 23), we assigned this male as male friend. Otherwise, we did not assign any male friend (N=6 out of 23). Both indices were very congruent: except for cases where one index did not assign a preferred male while the other did, females had one (and only one) preferred male in common using grooming and proximity indices in 41 out of 42 cases. In the one case when grooming and proximity indices assigned different preferred males (N=1 out of 81), we considered that the female had no male friend. In a few cases, sample sizes were insufficient to calculate indices using both grooming and proximity (N=6 cases for proximity, where less than four focal follows were available for a female in a given reproductive state and N=8 cases for grooming, where less than five grooming bouts were available for a female in a given reproductive state). We assigned as male friend the male that was assigned as preferred according to the index available. There was no single case where the two same males were assigned by both indices, thus all females had only one male friend. After taking the consensus between both indices, we defined one male friend for 83% of females (N=67 out of 81), namely 83% of pregnant females, 95% of females in early lactation and 68% for females in late lactation had one male friend.

### Supplementary Tables

**Table S1** Sample size available to calculate the behavioural indices of heterosexual associations: grooming allocation and spatial proximity allocation (P: pregnant, L1: six first months of lactation, L2: rest of lactation)

Measure	Reproductive State	Number of females*	Sample size per female (mean±sd ; [min-max])
Grooming bouts (N=73 females)	P	35	35.2±33.0 ; [6-142]
	L1	20	43.9±48.8 ; [6-188]
	L2	18	16.1±9.8 ; [5-38]
Proximity scans (N=75 females)	P	37	114.6±44.0 ; [37-198]
	L1	20	115.3±39.4 ; [43-182]
	L2	18	80.7±30.2 ; [28-151]

\* Several females were observed in different reproductive states (pregnant, early lactation, late lactation) or in different interbirth intervals. They are considered as different statistical units because friendships were established for each reproductive state and interbirth interval.

**Table S2** Sample size and results of the process of friendship assignment for each female in each reproductive state (P: pregnant, L1: six first months of lactation, L2: rest of lactation)

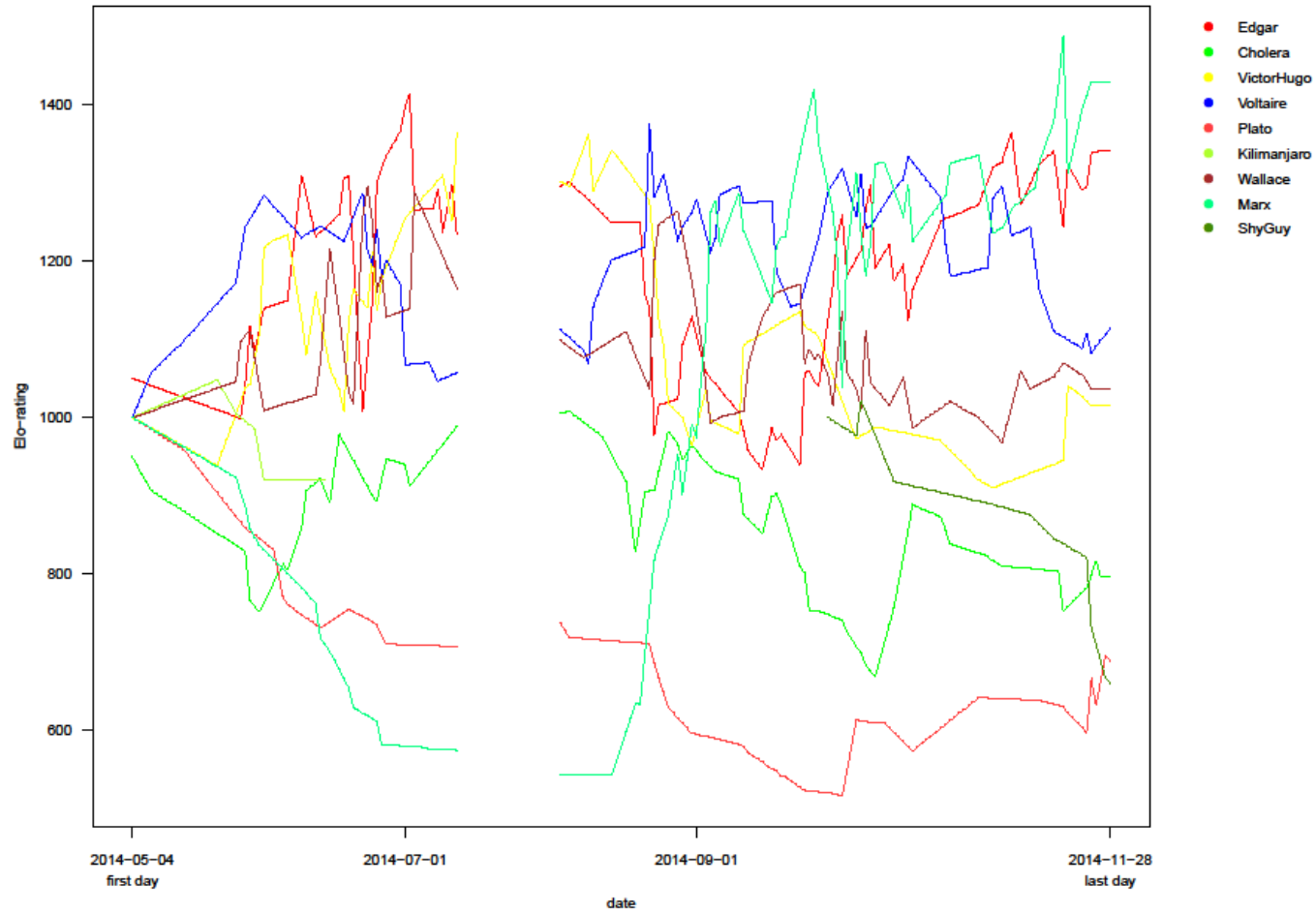
Measure	Reproductive State	Number of females with one or two preferred male(s)	Number of females with no preferred male identified
Grooming (N=73 females)	P	33	2
	L1	20	0
	L2	17	1
Proximity (N=75 females)	P	18	19
	L1	17	3
	L2	11	7
Consensus (N=81 females)	P	33	7
	L1	21	1
	L2	13	6

## Supplementary Figures

**Fig. S1** Variation in the Elo-rating dominance rank of males during the study period in J group in 2013. The gap is due to a 15 days interruption in data collection

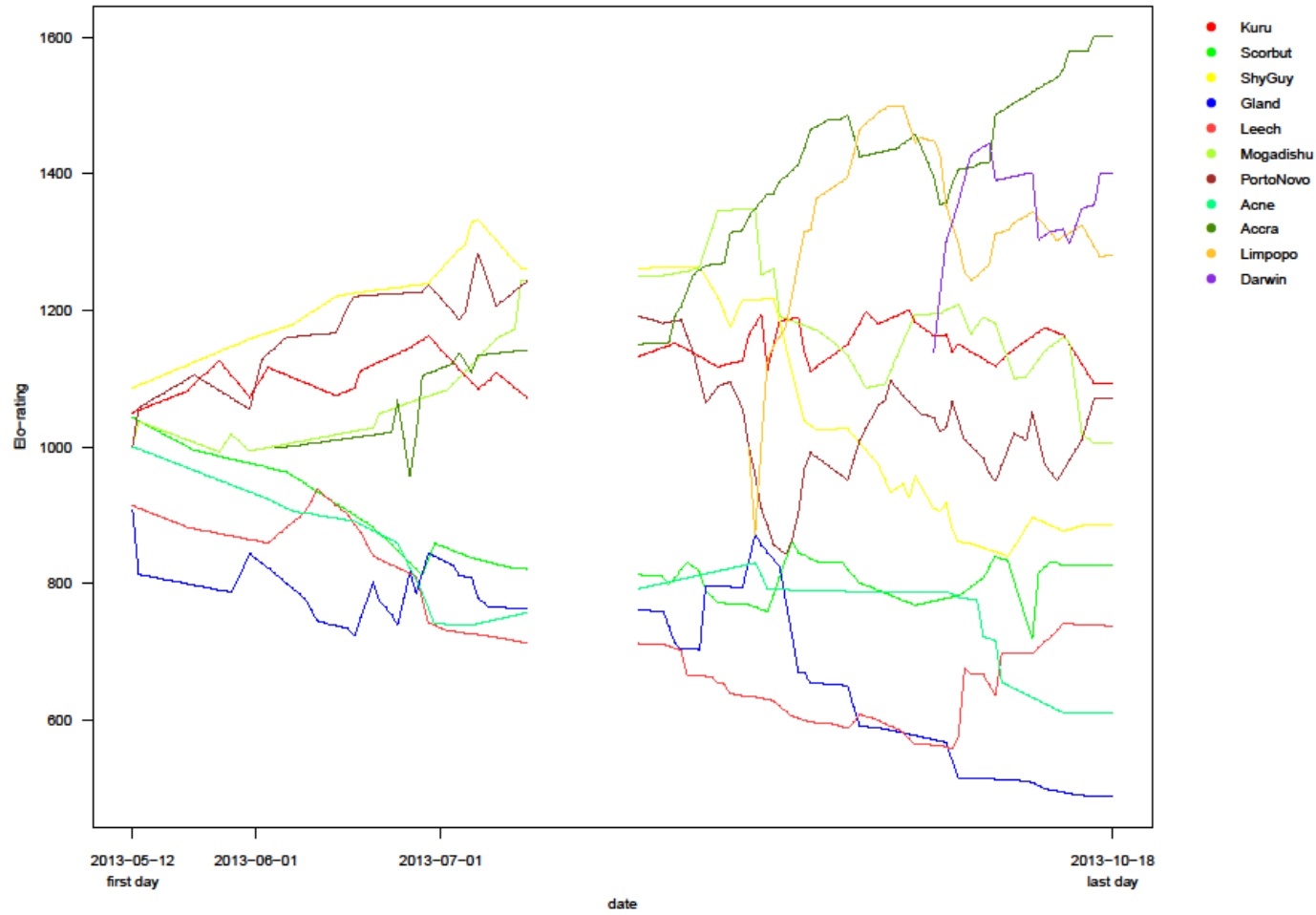


**Fig. S2** Variation in the Elo-rating dominance rank of males during the study period in J group in 2014. The gap is due to a 15 days interruption in data collection

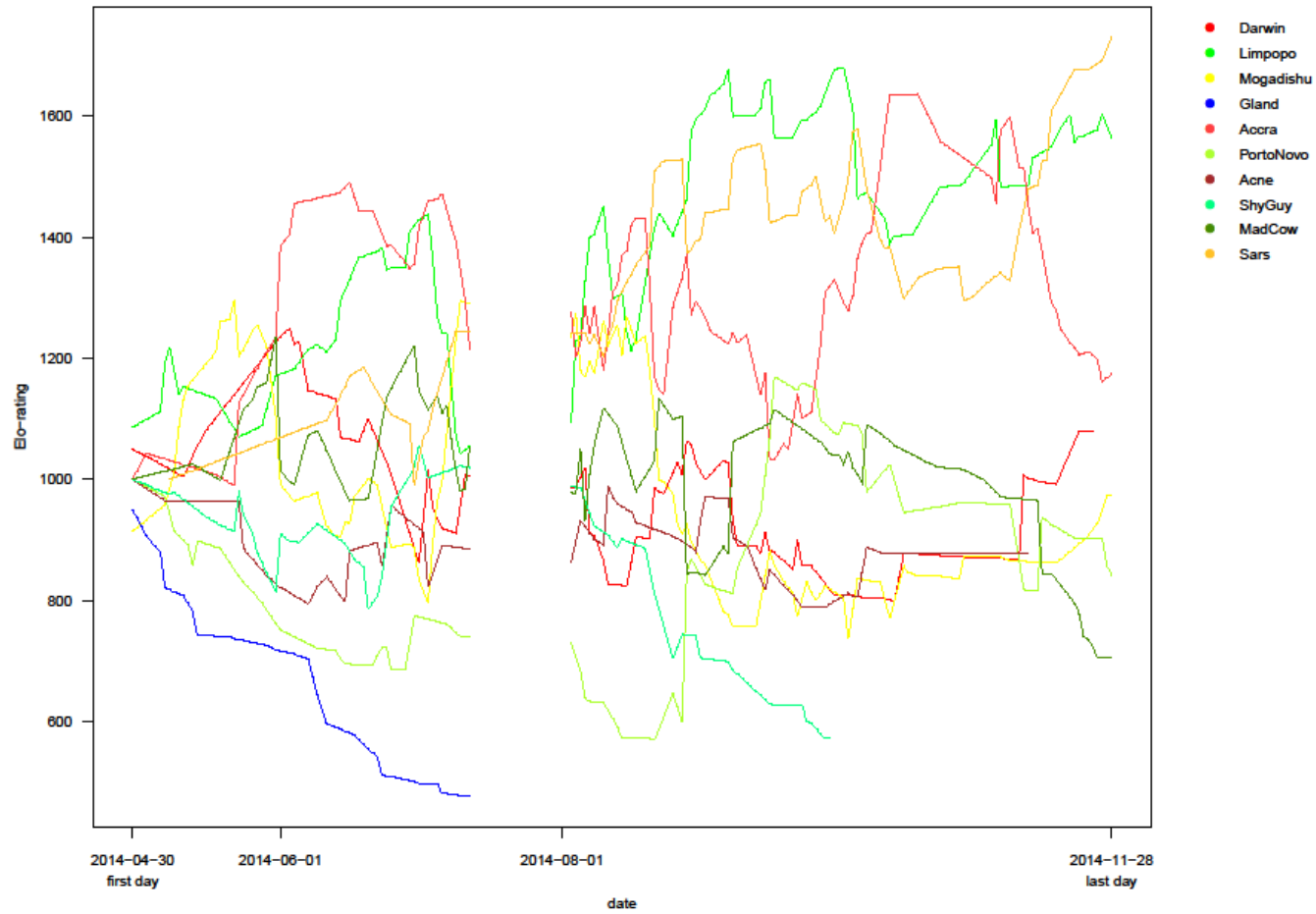




**Fig. S3** Variation in the Elo-rating dominance rank of males during the study period in L group in 2013. The gap is due to a 15 days interruption in data collection



**Fig. S4** Variation in the Elo-rating dominance rank of males during the study period in L group in 2014. The gap is due to a 15 days interruption in data collection



**Fig. S5** Responsibility for the maintenance of close spatial proximity (within 1m) (a) between cycling non-swollen females (NSW) and their previous male consort (i.e. their consort during the fertile period of their last oestrus cycle), (b) between early pregnant females (1<sup>st</sup> month of pregnancy, when it is inconspicuous) and the male consort of their conceptive cycle and (c) between late pregnant females (2<sup>nd</sup>-6<sup>th</sup> month of pregnancy, when it is conspicuous) and the most likely father of their conceptive cycle. Responsibility is measured by Hinde's index: positive (vs negative) values indicate that the female (vs male) is primarily responsible for maintaining proximity. The number of females in each reproductive state is indicated above the boxplot. On each box, the black horizontal line represents the median of the distribution, while bottom and top of the box represent respectively the 25th and 75th quartiles. Whiskers include a maximum of half of the interquartile range

