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

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7

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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

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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 unstability into male dominance hierarchies (see Fig. S1-S4 in Online ressource). 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 concomitently 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 ± 5.5 days (mean \pm sd) on
283 average (range: 13-43) and the number of consort males per swollen cycle was 1.1 ± 0.6
284 (mean \pm sd) (range: 0-2). Consortships lasted 8.8 ± 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 ± 0.6 (mean \pm sd)
287 (range: 0-2) and consortships during the fertile period lasted 3.9 ± 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 ± 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

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711

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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

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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

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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

Response variable	Fixed factors	Levels	Estimate ± se	95% confidence interval	LRT	df	P-value
(a) Probability of association with the most likely father	Reproductive state ^a	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 ^b	nulliparous	-1.916 ± 0.613	[-3.118 ; -0.715]	13.052	2	0.001
		primiparous	-2.135 ± 0.701	[-3.508 ; -0.762]			
	Troop ^c		0.574 ± 0.490	[-0.386 ; 1.534]	1.315	1	0.251
Year ^d		0.685 ± 0.594	[-0.479 ; 1.850]	1.270	1	0.260	
(b) Probability of association with the male	Reproductive state ^a	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 ^b	nulliparous		-0.042 ± 0.484	[-0.990 ; 0.906]	0.005	2	0.997
		primiparous		-0.002 ± 0.302	[-0.595 ; 0.591]			
	Troop ^c			0.267 ± 0.465	[-0.645 ; 1.179]	0.302	1	0.582
	Year ^d			1.072 ± 0.286	[0.512 ; 1.633]	13.669	1	<0.001

950

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^aReference category: L1 (six first months of lactation)

952

^bReference category: multiparous

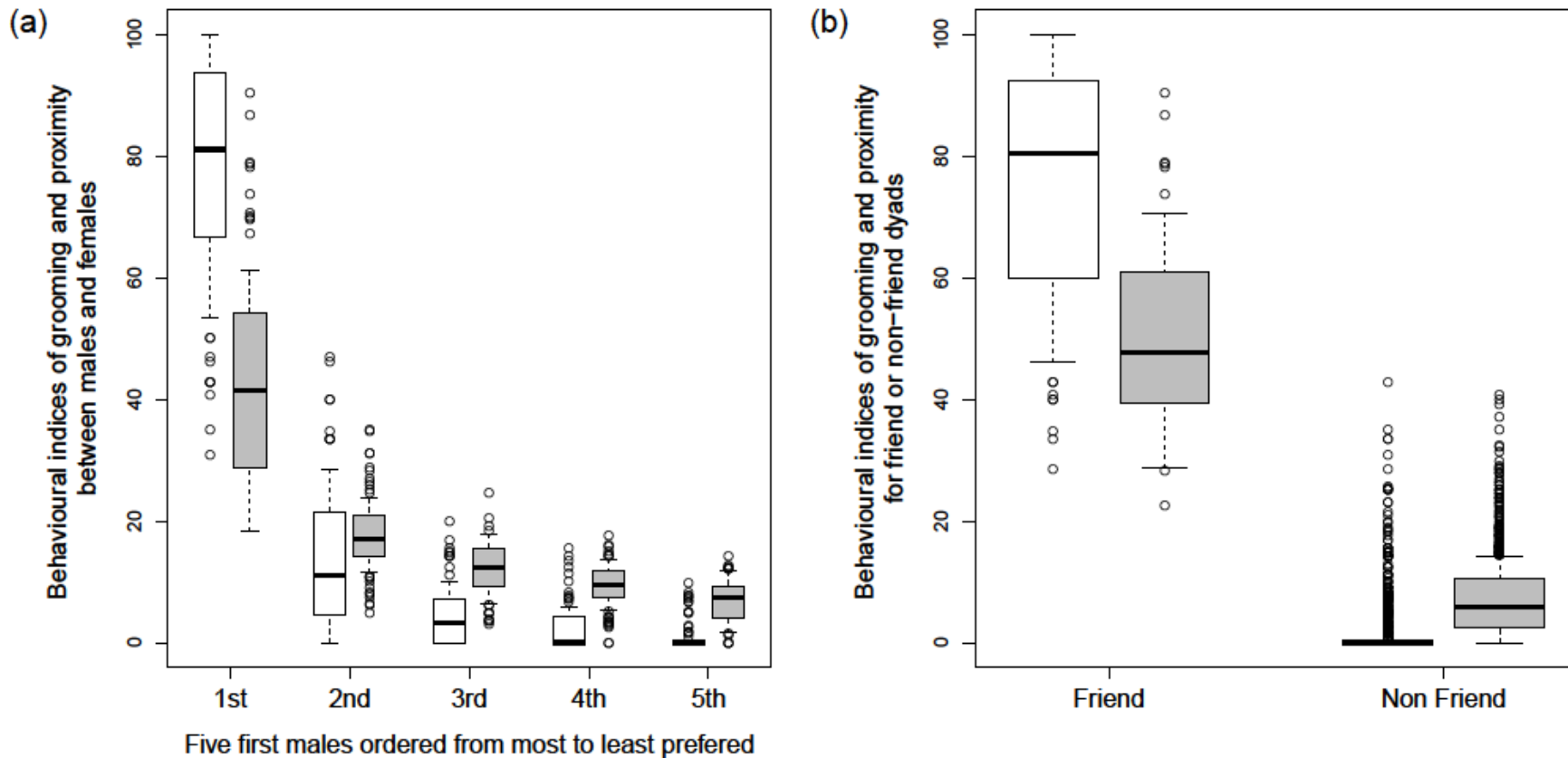
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^cReference category: J group

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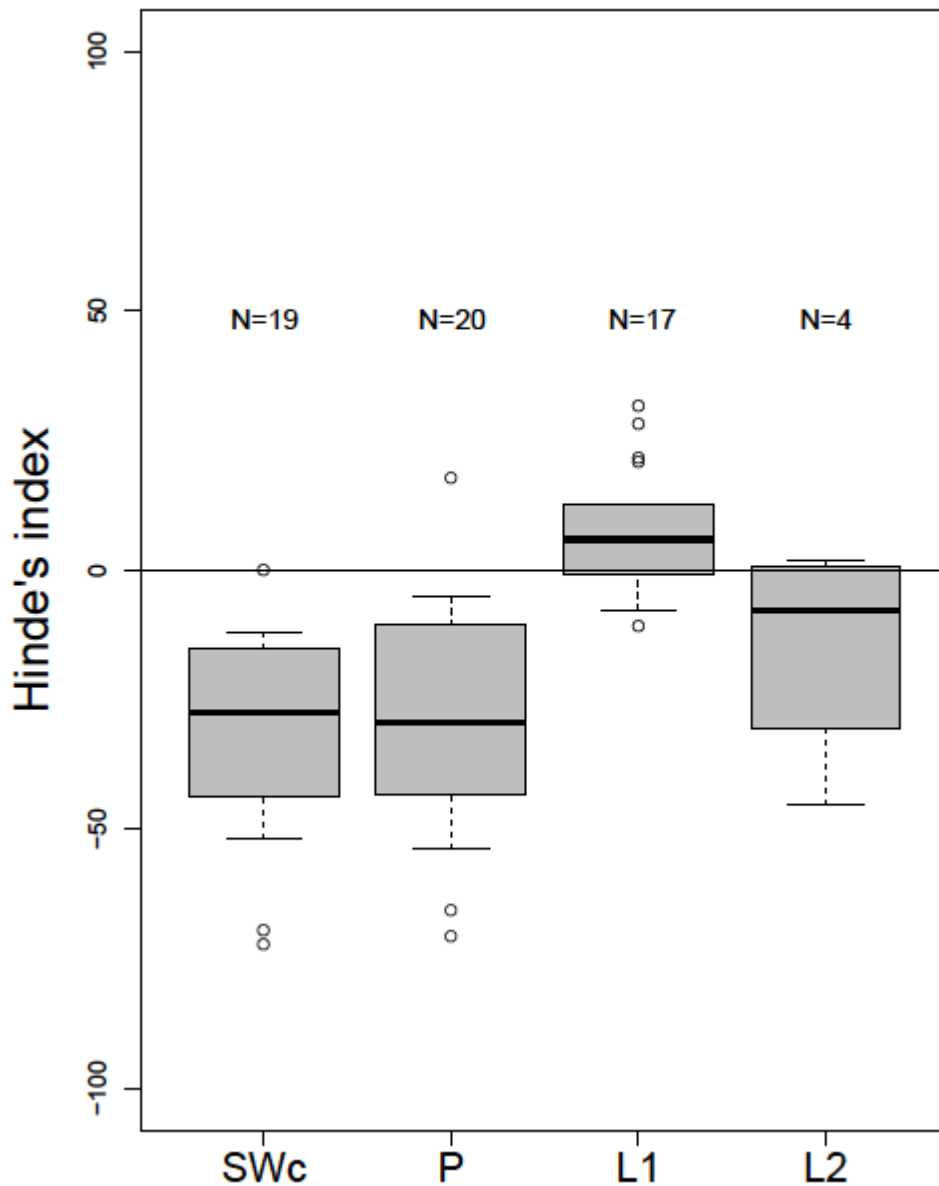
^dReference category: 2013

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 25th and 75th quartiles are equal to zero
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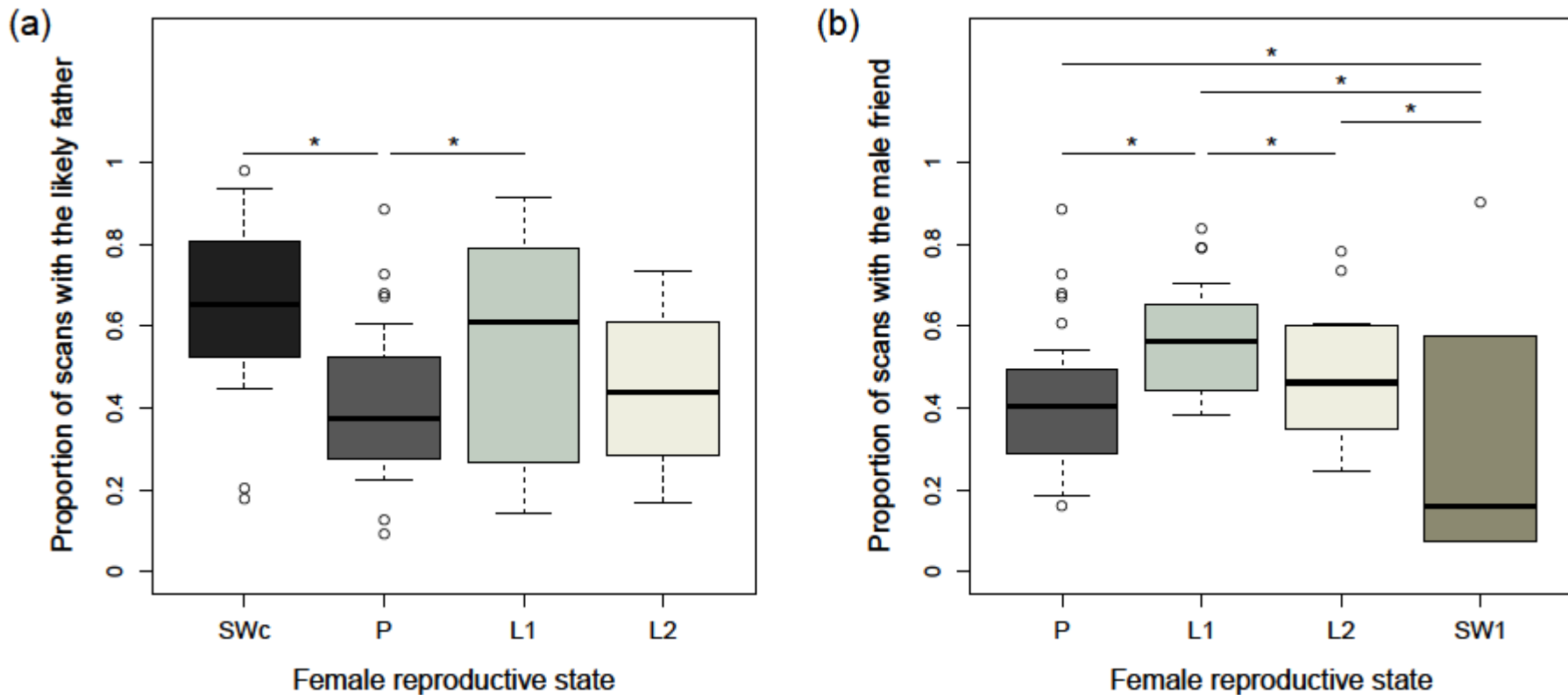
963 **Fig. 2** Responsibility for the maintenance of close spatial proximity (within 1m) between
 964 females and their male associates. The male associate is the male consort during the swollen
 965 period of the conceptive cycle (SWC) and the male friend during pregnancy (P), early
 966 lactation (L1) 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



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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

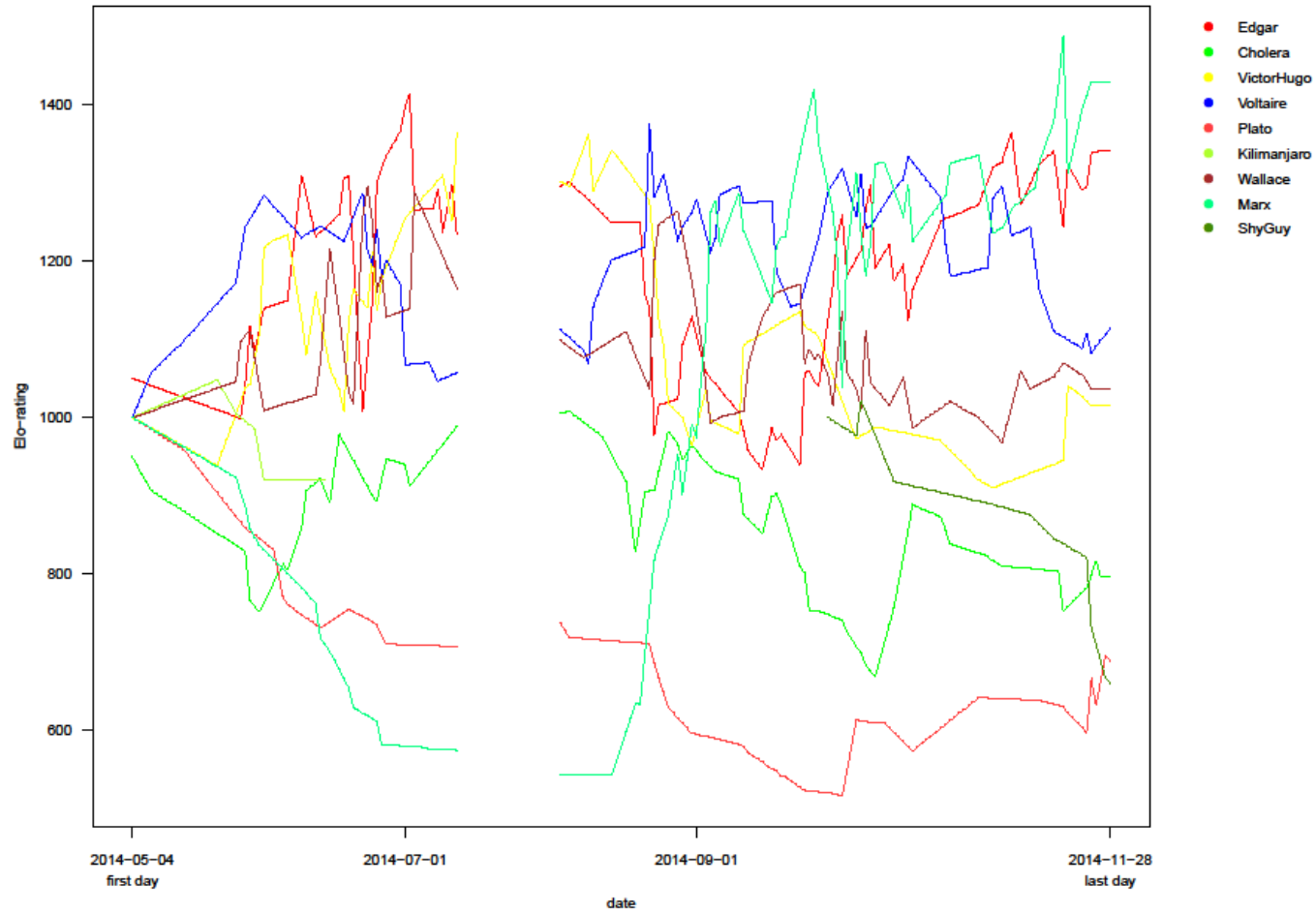


Fig. S3 Variation in the Elo-rating dominance rank of males during the study period in L group in 2013. The gap is due to a 15 days interruption in data collection

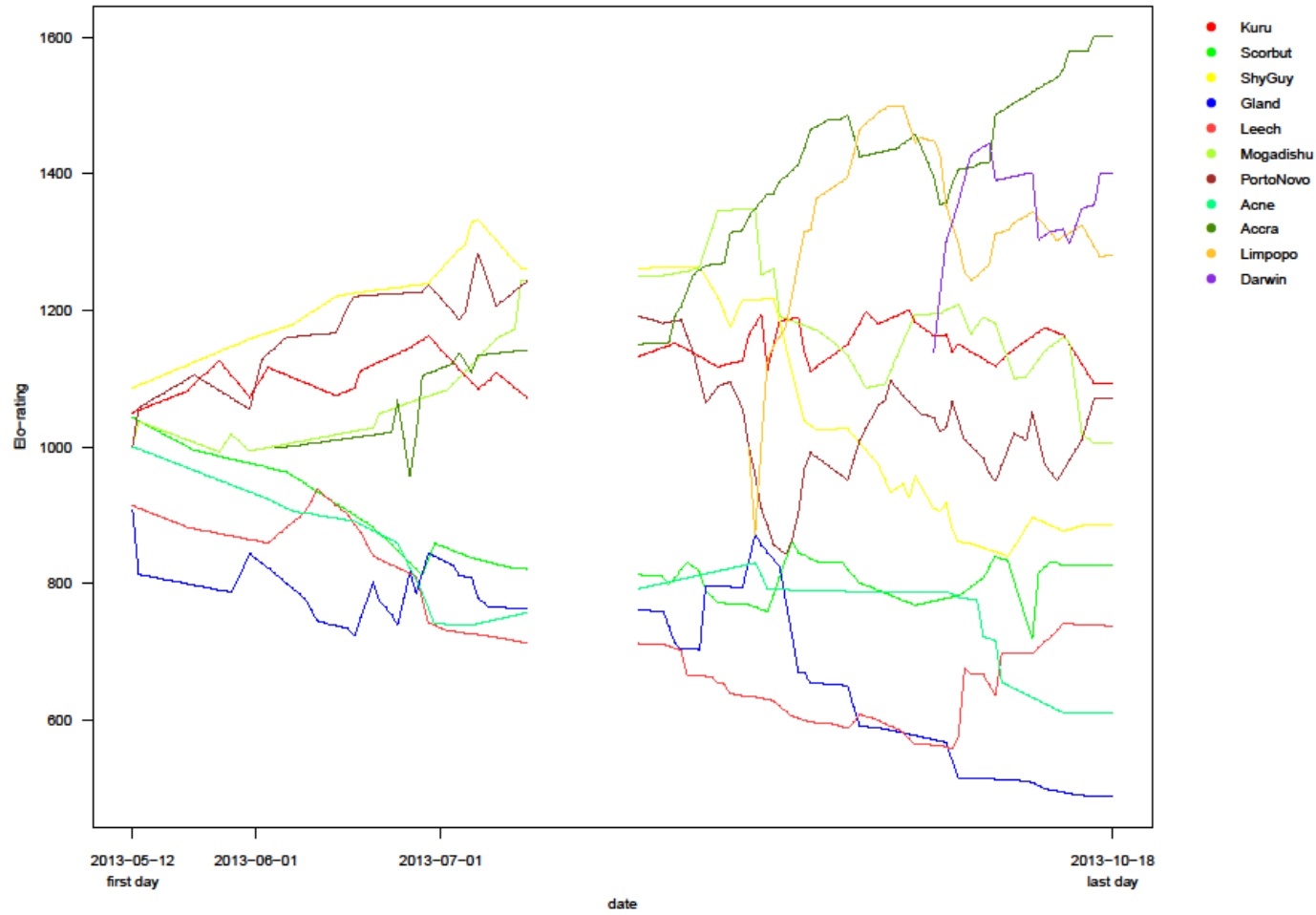


Fig. S4 Variation in the Elo-rating dominance rank of males during the study period in L group in 2014. The gap is due to a 15 days interruption in data collection

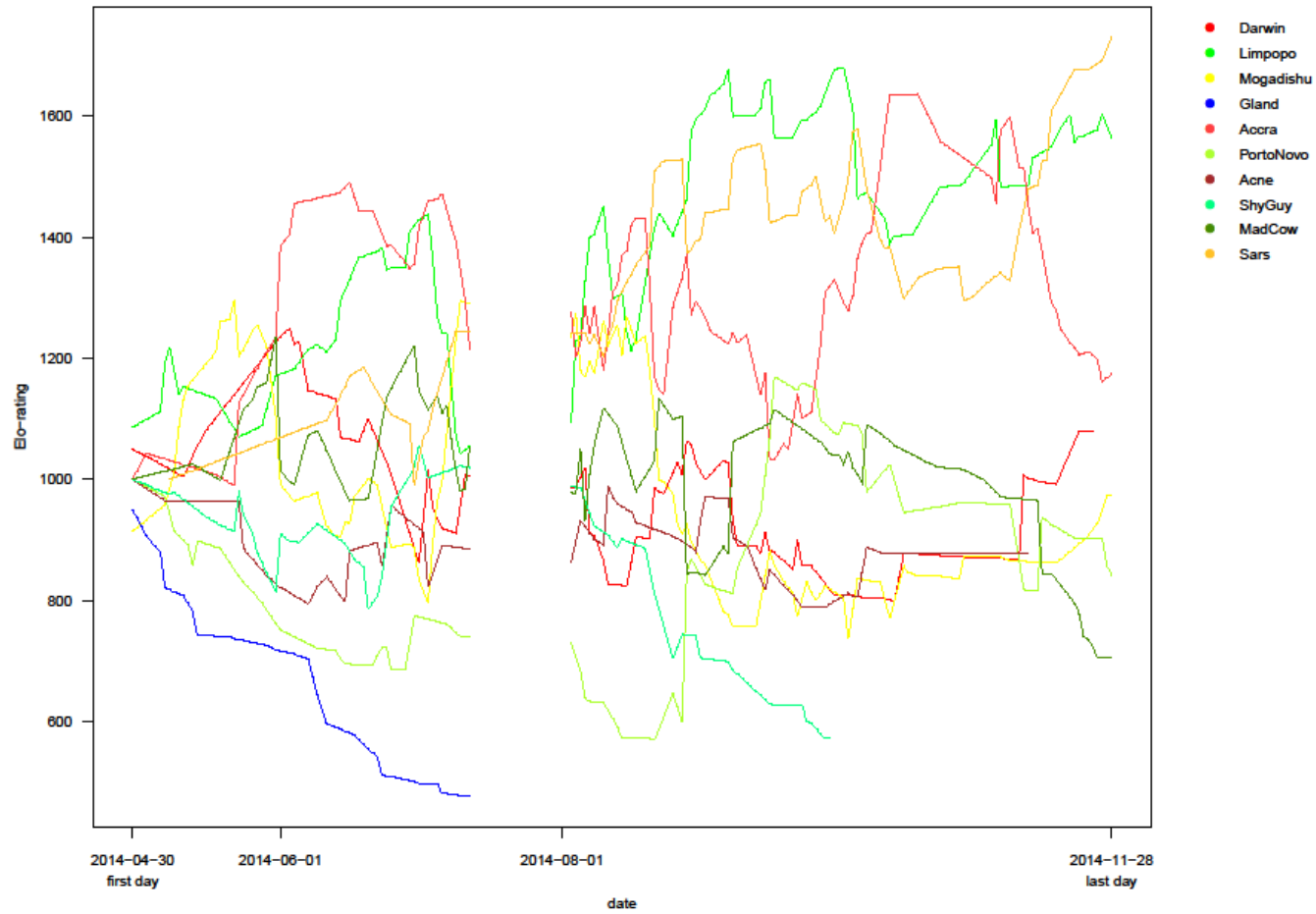


Fig. S5 Responsibility for the maintenance of close spatial proximity (within 1m) (a) between cycling non-swollen females (NSW) and their previous male consort (i.e. their consort during the fertile period of their last oestrus cycle), (b) between early pregnant females (1st month of pregnancy, when it is inconspicuous) and the male consort of their conceptive cycle and (c) between late pregnant females (2nd-6th 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

