1 **TITLE**

2 Stability and strength of male-female associations in a polygynous primate society

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ABSTRACT

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

SIGNIFICANCE STATEMENT

45 Stable male-female bonds are rare in promiscuous mammals. Baboons are unusual in this

46 respect: tight friendships have been described between adult males and lactating females and

47 may protect infants against infanticide, but few studies have investigated whether these

48 associations may start before an infant's birth, or extend after its nutritional independence. We

49 explored the stability and strength of heterosexual relationships in the chacma baboon, and

50 found that friendships start before infant's conception, are maintained throughout pregnancy,

51 strengthen during lactation and disappear before mothers resume cycling. Such pattern of

52 association suggests that male-female bonds represent paternal effort, and may arise from

53 sexual activity before and during the conceptive cycle. Most females appear permanently

54 associated with one male regardless of their reproductive state, suggesting that heterosexual

55 bonds play an important, and under-appreciated, role in structuring the social organization of

56 baboon societies.

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INTRODUCTION

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

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

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

101 Smuts 1985; Lemasson et al. 2008; yellow baboons: Altmann 1980; Nguyen et al. 2009;

102 chacma baboons: Palombit et al. 1997; Huchard et al. 2010; Moscovice et al. 2010; rhesus

103 macaques: Manson 1994; Barbary macaques, *Macaca sylvanus*: Paul et al. 1996; Ménard et

104 al. 2001). These relationships are characterized by a high level of spatial proximity and

105 grooming interactions between partners and are actively maintained by females (Palombit et

106 al. 1997; Huchard et al. 2010). Their benefits to females are thought to be mainly related to

107 infanticide avoidance, where males protect vulnerable offspring (Palombit et al. 1997;

108 Palombit 1999; Palombit 2000; Weingrill 2000), although further benefits may include

109 protection from non-lethal conspecific aggression (Smuts 1985; Manson 1994; Lemasson et

110 al. 2008; Nguyen et al. 2009; Kulik et al. 2012), reduced predation risk (van Schaik and van

111 Noordwijk 1989), stress alleviation during social instability (Beehner et al. 2005; Engh et al.

112 2006) and promotion of male-infant associations after weaning, which can provide juveniles

113 with support in agonistic interactions with conspecifics (Buchan et al. 2003) and foraging

114 benefits (Charpentier et al. 2008; Huchard et al. 2013).

115   The benefits gained by males from such associations are less clear (Palombit 2000).

116 There are two alternative, non-exclusive hypotheses. First, the "care-then-mate" hypothesis

117 posits that males may trade protection services for reproductive opportunities (Seyfarth

118 1978a; Smuts 1985; review in van Schaik and Paul 1996), such that friendships increase a

119 male's future chances of mating with his female friend. This hypothesis has received some

120 support in olive baboons (Smuts 1985; Smuts and Gubernick 1992) and in Barbary macaques

121 (Ménard et al. 2001), where friendships predicted mating frequency during following cycles.

122 However, a relationship between male care-giving and subsequent mating activity has not

123 been observed in other species (yellow baboons: Nguyen et al. 2009; chacma baboons:

124 Weingrill 2000). Second, the "mate-then-care" hypothesis (Bales 1980; Smuts 1985;

125 Moscovice et al. 2010) proposes that males form friendships based on their likelihood of

126   paternity, in order to protect their own reproductive investment, i.e. to protect their offspring

127   from infanticide. This hypothesis has received greater support. Several studies found that

128   most males had mated with their female friend during her conceptive cycle (olive baboons:

129   Smuts 1985; yellow baboons: Nguyen et al. 2009; chacma baboons: Palombit et al. 1997;

130   Moscovice et al. 2010) and genetic studies confirmed that males are often - but not always -

131   the sire of the infant of their female friend (Moscovice et al. 2009; Nguyen et al. 2009;

132   Huchard et al. 2010; Ostner et al. 2013).

133   These observations raise an important question, namely how males may assess their

134   paternity in a promiscuous mating system. First, males might compare the phenotype of the

135   infant to their own using facial, vocal or olfactory cues (phenotype matching, review in

136   Widdig 2007). Alternatively, males might rely on their past mating history with the mother of

137   the infant (Palombit et al. 1997; Moscovice et al. 2010). As male-female friendships are

138   described to start with the birth of an infant (Palombit et al. 1997; Palombit 1999), such

139   assessment of paternity may require complex cognitive abilities: males may have to identify

140   which oestrus cycle corresponded to the conceptive cycle for a given infant, as well as to

141   evaluate and remember his mating activity with the mother during that cycle, including the

142   length of his monopolization (or the number of matings) in relation to the proximity of

143   ovulation and the mating activity of rivals. A more parsimonious scenario is that male-female

144   associations may not start with an infant birth but with its conception, and be subsequently

145   maintained throughout pregnancy, though perhaps at lower intensity than following the birth

146   because pregnant females do not face any risk of infanticide (but may still face a risk of

147   socially-induced abortion, Alberts et al. 1992; Roberts et al. 2012). Male-female associations

148   during pregnancy have been documented in Assamese macaques (Ostner et al. 2013) and in

149   some baboon populations (olive baboons: Smuts 1985; chacma baboons: Weingrill 2000), but

150   not in others (Palombit et al. 1997). It may therefore be necessary to assess the stability of

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

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

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

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

Materials & Methods

Field site and study subjects

We studied a population of wild chacma baboons living at Tsaobis Nature Park, on the edge of the Namib desert, Namibia (22º22'S 15º44'E) (for detailed information on the field site and population, see Cowlishaw 1997). Data were collected in June-October 2013 and May-November 2014 on two large groups of baboons: J group (2013: 7-10 males, 17 females, 29-32 juveniles; 2014: 7-8 males, 18 females, 35 juveniles) and L group (2013: 9-11 males, 18-19 females, 31-33 juveniles; 2014: 9 males, 17-19 females, 29 juveniles). All adults were individually recognizable and fully habituated to observation at close range. Age (in years) was estimated from a combination of known birth dates and dental patterns of tooth eruption

201 and wear, examined during prior captures (Huchard et al. 2009). Only adults were included in

202 the study. Males were considered adult when they reached eight years of age (Alberts and

203 Altmann 1995) and females when they reached menarche (Altmann and Alberts 2003).

204 Female parity (nulliparous, primiparous, multiparous) was taken from life-history data.

205 The reproductive state of each female was monitored on a daily basis and categorized

206 according to a chronology followed from the last cycle before birth (the conceptive cycle) to

207 the first cycle after birth. First, we considered the "swollen" period of the conceptive cycle

208 during which females were sexually receptive with a perineal swelling ("SWc"). Conceptive

209 cycles were distinguished from non-conceptive cycles *a posteriori*, identified as the last cycle

210 preceding pregnancy. To test the care-then-mate hypothesis, we further included all

211 documented swollen periods of a particular interbirth interval. Pregnancy ("P") was

212 determined *a posteriori* and encompassed the six months separating the conceptive cycle from

213 an infant birth. Lactation referred to the entire period during which females had a dependent

214 infant and were not cycling and was split between the first six months of lactation ("L1") and

215 the rest of lactation ("L2"). Finally, "SW1" refers to the first swollen period after lactational

216 amenorrhea when females resume cycling.

217

218 *Behavioural observations*

219 Observers on foot followed both groups daily from dawn to dusk, conducting focal animal

220 sampling (Altmann 1974) on all adult males and females. All observers (except AB) were

221 blind with respect to the research questions. Focal follows lasted 60 minutes on average

222 (mean focal length±sd: 58.6±7.2min, range: 23-97min) and were spread equally across the

223 day (split into four three-hour time blocks) for each individual. The focal individual was

224 chosen in a semi-random manner, in order to balance observation time equally across

225 individuals, and, for females, across reproductive states, and was only sampled once per day.

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

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

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

251   scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the

252   minimal score and thus the lowest ranking individual) and 1 (corresponding to the maximal

253   score and the highest ranking individual).

254   During the study period, the rate of alpha male takeover and male immigration were

255   high in both groups (1 and 4 immigration events in J group in 2013 and 2014 respectively; 6

256   and 1 immigration events in L group in 2013 and 2014 respectively), leading to some

257   unstability into male dominance hierarchies (see Fig. S1-S4 in Online ressource). Concerning

258   J group, dominance hierarchy was stable in 2013 with the same alpha male for the entire study

259   period (Fig. S1), while 2014 was very unstable with five males competing constantly for

260   dominance and alternating in reaching the alpha male status (Fig. S2). Concerning L group, in

261   2013 the alphamale lost his dominance in July 2013, then another resident male reached alpha

262   status but concomitently two new males immigrated and rised in rank, causing high instability

263   in the hierarchy (Fig. S3). In 2014, the dominance was contested among three males who

264   alternated as alpha males, then one new male immigrated toward the end of the study period

265   and reached dominance (Fig. S4).

266

267   *Data analysis*

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

269   We assessed the stability of male-female preferential associations across the consecutive

270   reproductive states of each female, in order to test (1) whether females remain associated to

271   the most likely father of their offspring from its conception to its independence (as predicted

272   by the mate-then-care hypothesis), or alternatively, (2) whether male-female relationships

273   predict the male's chances of subsequently consorting with her and/or increase his likelihood

274   of siring her next offspring (as predicted by the care-then-mate hypothesis).

275

<u>Identification of the most likely father</u>

277 Following previous studies (Smuts 1985; Nguyen et al. 2009; Moscovice et al. 2010), we

278 defined the most likely father of an infant as the male who mate-guarded the female during

279 the fertile period of her conceptive cycle, defined as the five days preceding the day of

280 detumescence when the probability of ovulation is maximal (Higham et al. 2008; Daspre et al.

281 2009). On 56 fully observed cycles, sexual receptivity lasted 22.1±5.5 days (mean±sd) on

282 average (range: 13-43) and the number of consort males per swollen cycle was 1.1±0.6

283 (mean±sd) (range: 0-2). Consortships lasted 8.8±6.0 days (mean±sd) on average (range: 0.5-

284 32, N=48 cycles). On 74 cycles observed during the fertile period (i.e. 5 days before

285 detumescence), the number of consort males during the fertile period was 0.99±0.6 (mean±sd)

286 (range: 0-2) and consortships during the fertile period lasted 3.9±1.5 days (mean±sd) (range:

287 0.5-5, N=60 cycles). As a result, only one male monopolized the female during the fertile

288 cycle in most cycles and assignments of most likely father were straightforward. On 3/26

289 conceptive cycles, two males consorted with a female consecutively during the fertile period.

290 However, the time spent in consortship was always very biased toward one male (mean

291 percentage of monopolization by the main male±sd: 83%±11%) so we selected that male as

292 the most likely father.

293

294 <u>Identification of the male friend</u>

295 During pregnancy, early lactation and late lactation, we identified the male friend of each

296 female from the dyadic proximity and grooming scores with all males in the group, as

297 follows.

298   *Grooming.* A grooming allocation index quantified grooming given by females to

299 males and relied on a combination of *ad lib* and male and female focal observations (see

300 Table S1 in the Online Resource for sample sizes). Grooming bouts involving the same dyad

301 were discarded if they occurred within 30 minutes of a previous bout, in order to ensure

302 independency among bouts. The strength of connection of a male-female dyad was estimated

303 as the share of grooming that a female allocated to a particular male, calculated as the number

304 of grooming bouts that a female gives to a male divided by the total number of grooming

305 bouts given by that female to any male during the period when this male was resident in the

306 group. This index controls for variation across females in the total time spent socializing with

307 males, as well as for variation across males in the time spent in the group.

308   *Spatial proximity.* A spatial proximity index was calculated using female focal

309 observations only (see Table S1 in the Online Resource for sample sizes). Every five minutes,

310 scans recorded the identity and distance of the nearest adult male. The strength of connection

311 of a male-female dyad was calculated as the number of scans where the male was the female's

312 nearest neighbour divided by the total number of informative scans (i.e., for which the nearest

313 neighbour is identified) collected for that female over the time period during which the male

314 was resident in the group. In a few scans (0.3 %), two adult males were equally distant. These

315 scans were counted in the dyadic index of both males. At Tsaobis, visibility is most of the

316 time excellent, and facilitates the collection of accurate proximity data. Male nearest

317 neighbours were on average at 14.0 ± 13.9 meters (mean$\pm$sd, range: 0-150m) from females.

318 The mean percentage ($\pm$sd) of informative scans per focal observation was 71.8% ($\pm$8.7%).

319 Other, non-informative scans were omitted by observers, or impossible to collect because of

320 poor visibility conditions, or because the focal individual was isolated from the rest of the

321 group.

322   For both indices, we favoured the use of relative over absolute measures of

323 heterosexual associations (i.e., we calculated female allocation of grooming and proximity

324 toward each male, rather than absolute frequency of grooming or time spent in proximity of

325 each male) in order to identify the favourite male(s) social partner of females while

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

For each behavioural index, we investigated if one or two males had an outstandingly high score compared to other males, hereafter referred as the "preferred male(s)". 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 had 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. Then, we compared the preferred male(s) designated by each behavioural index and considered as "male friend" the male that was preferred according to both grooming and proximity indices (see Supplementary text in the Online Resource for more details regarding male friend attribution, including cases of discrepancy between the preferred male(s) assigned by each index). Several females had more than one offspring during the study period and observations of the same female in a different interbirth interval were considered separately, as the male associate may likely change in different interbirth intervals.

351 <u>Test of the stability of male-female association between consecutive reproductive states</u>

352   *Test of the mate-then-care hypothesis*. We assessed whether females remain associated

353 with the most likely father of their offspring from conception to pregnancy (SWc-P) and with

354 the same male friend from pregnancy to lactation (P-L) of the same interbirth interval. For the

355 latter, we pooled females in both early and late lactation due to sample size limitation. We

356 tested whether the identity of the most likely father/male friend remained consistent in the

357 second state relative to the first state using two-tailed permutation tests. We only included

358 cases where the most likely father/male friend of the first reproductive state was still in the

359 group during the second reproductive state of the female. For each female, we created a pool

360 of males that were present in the two reproductive states of interest and assigned 1 to the most

361 likely father/male friend of each state. We randomized 50,000 times the identities of the most

362 likely father/male friend in one state, computed the random distribution of the proportion of

363 females associated with the same male across both reproductive states, and compared it to the

364 observed proportion (i.e. based on the original data). The exact two-tailed p-value was

365 computed as the proportion of cases displaying a higher or lower value than the observed

366 correlation on the upper or lower tail of the simulated distribution, respectively.

367   *Test of the care-then-mate hypothesis*. We used two complementary approaches. First,

368 we tested whether friendships predict male consortships during any future cycle of the next

369 interbirth interval. We used all cycles for which the identity of the previous male friend was

370 known, and for which he was still present in the group. For each cycle of each female and for

371 each male, we recorded whether he mate-guarded the female or not (regardless of whether it

372 was during the fertile period), and analysed variation in this variable using a generalized

373 linear mixed-effect model with a binomial error structure and logit link function. Fixed effects

374 included a categorical variable "Previous friend? (yes/no)", male rank (averaged across the

375   period considered) and group membership. Random factors included the identity of the cycle,

376   female and male.

377   For all mixed models in our study, the statistical significance of the full model was

378   assessed by comparing its fit with the respective null model (containing only the random

379   factors) using a log-likelihood ratio test (LRT). Given the significance of the full model, the

380   significance of the fixed factors was tested using a LRT test (assuming an asymptotic chi-

381   square distribution of the test statistic), and using the full model (to avoid problems arising

382   from stepwise model selection procedures: Whittingham et al. 2006; Mundry and Nunn

383   2009). We further computed the 95% confidence intervals (using the confint.merMod

384   function) of fixed factors (for multilevel categorical variables, confidence intervals were used

385   to test the significance of each level of the variable by checking that they did not cross zero).

386   To test for all differences between levels of a multilevel categorical variable, we changed the

387   reference category sequentially (Pinheiro and Bates 2000). Model stability was assessed by

388   randomly splitting the dataset in two and running the same GLMMs on the two subsets in

389   order to check the robustness of estimates and significance of fixed effects (results not

390   shown). All GLMMs were run using the lme4 package (Bates et al. 2014) in R version 1.1-7

391   (R Core development Team 2015).

392   Second, we restricted the previous dataset to conceptive cycles only, to test whether

393   male friends were the most likely fathers of their next offspring. We only included cases

394   where the previous friend was still in the group after the female had resumed cycling. Here,

395   there was only one cycle per female and a limited sample size, so that the significance of the

396   stability of male-female associations across reproductive states (Previous friend-SWc) was

397   assessed using two-tailed permutation tests as detailed above, rather than GLMMs.

398

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

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

3. Strength of heterosexual associations depending on female reproductive state

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

reproductive state, female dominance rank, female parity, male dominance rank, group

identity and year. Random effects included female identity, male identity and focal follow. In

the first model, we were interested in measuring variation in the strength of male-female

associations from conception, so the different levels of our variable "reproductive state"

included the swollen period of the conceptive cycle (including periods outside consortship),

pregnancy, early and late lactation. In contrast, in the second model, the male friend of a

female was not always the same across her successive reproductive state but we measured

variation in association with the male designated as her friend for any particular reproductive

state. These models were run as described above.

RESULTS

1. Stability of male-female associations across reproductive state

<u>Identification of the behavioural male friend</u>

The distribution of grooming and proximity indices among males, when ranked from the

highest to the fifth highest score, revealed that the strongest gap lies between the first and

second male within each index, while differences among subsequent males are considerably

weaker (Fig. 1a). This indicates that most pregnant and lactating females have a particularly

strong relationship with one male. One or two preferred male(s) were assigned to 96% of

females with the grooming index, and one or two male(s) were assigned to 61% of females

with the proximity index (see Table S2 in the Online Resource); other females did not have

any preferred male. Grooming and proximity indices were highly positively correlated across

dyads (Mantel test with Pearson correlation: r=0.83, N=67 females, p=0.001). As a result,

both indices were very congruent and assigned the same male in 97% of cases (see Online

Resources for more details). After the consensus between the two indices, all females had

only one male friend (i.e. there was no case where the same two males were considered as

450 preferred by both indices). Overall, we defined one male friend for 83% of females (N=67 out

451 of 81), including 83% of pregnant females, 95% of females in early lactation and 68% of

452 females in late lactation. Male friends obtain a much higher share of grooming and proximity

453 than non-friend males (Fig. 1b). In total, 70% of females and 55% of males were involved in

454 at least one friendship during the study period.

455

456 <u>Test of the mate-then-care hypothesis</u>

457 In support of the mate-then-care hypothesis, females remained associated with the same male

458 from offspring conception to independence (Table 1). The highest stability in association

459 patterns occurred between the swollen period of the conceptive cycle and pregnancy (SWc-P),

460 as 21 out of 25 females kept the same male associate. Ten of 19 females were also associated

461 with the same male from pregnancy to lactation (P-L). Notably, of the nine cases where

462 females were not associated with the same male in pregnancy and lactation, six had no male

463 friend during pregnancy and only started to associate with a male during lactation. Six

464 females out of 44 properly switched their male associate from conception to pregnancy (SWc-

465 P) or from pregnancy to lactation (P-L). For five out of those six females, the male associate

466 of the first reproductive state was always in the top two highest scores of grooming and/or

467 proximity index during the second state, suggesting that females may still maintain a bond

468 with the likely father of their offspring, even when they mainly associate with another male.

469 Overall, those results suggest that most male-female associations are stable from infant

470 conception to weaning.

471

472 <u>Test of the care-then-mate hypothesis</u>

473 When integrating information on all cycles for which the identity of the female's friend

474 during her previous interbirth interval was known, females were seen in consortship with their

475 previous male friend in six out of 20 cycles. The GLMM predicting the probability of

476 consorting between a male and a female as a function of their previous friendship (yes/no) and

477 of male rank was not significant (log-likelihood ratio test comparing the fit of the full model

478 with a null model containing only the random effects; χ^2=4.4, df=3, N=20 cycles, p=0.222),

479 suggesting that prior friendship does not predict a male's likelihood of mate-guarding a

480 female when she resumes cycling. When restricting the analysis to conceptive cycles, we

481 similarly found that friendship during pregnancy and lactation did not increase male chance of

482 consorting with a female during the fertile period of her next conceptive cycle (Table 1). Out

483 of 10 females for which information on the identity of her previous friend and next consort

484 was available, only one consorted with her previous friend.

485

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

487   Average Hinde's indices were negatively and significantly different from zero for the

488 swollen period of the conceptive cycle (one sample t-test, N=19, t=-6.7, p<0.001) and for

489 pregnancy (one sample t-test, N=20, t=-5.7, p<0.001) (Fig. 2), meaning that males were

490 primarily responsible for maintaining close proximity with their female associate during these

491 periods. Pregnancy becomes conspicuous approximately 3-4 weeks after conception in

492 baboons, when females exhibit a reddening of the paracallosal skin, called 'pregnancy sign'

493 (Gilbert and Gillman 1952; Altmann 1973). In an attempt to understand whether males may

494 keep maintaining proximity during pregnancy simply because they fail to detect early

495 pregnancies, we calculated Hinde's indices between females and their consort partner when

496 they are cycling but not swollen (i.e. when the previous oestrus cycle did not lead to

497 conception), during their first month of pregnancy (when pregnancy is inconspicuous) and

498 during the rest of their pregnancy (when pregnancy become obvious). We found that males

499 maintained close proximity to cycling females (one sample t-test, n=16, t=-5.1, p<0.001),

500   females in early pregnancy (one sample t-test, n=8, t=-6.7, p<0.001), and also to a lesser

501   extent to females that were at a later stage of pregnancy (one sample t-test, n=8, t=-2.6,

502   p=0.033). Thus, males remained primarily responsible for maintaining proximity throughout

503   pregnancy (Fig. S5). By contrast, the average Hinde's indices were positive and significantly

504   different from zero during early lactation (one sample t-test, N=17, t=2.8, p=0.014), indicating

505   that females were responsible for close proximity maintenance, while both males and females

506   were equally responsible for maintaining contact during late lactation (one sample t-test,

507   N=4,t=-1.4, p=0.266) (Fig. 2).

508

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

510   <u>Variation in the strength of association between females and the most likely father</u>

511   The strength of association between females and their male friend was estimated by the

512   probability of spatial proximity between partners in any given scan. The set of predictor

513   variables used had a clear influence on the probability of association between females and the

514   likely father of their current offspring (log-likelihood ratio test comparing the fit of the full

515   model with a null model containing only random effects; χ^2=64.2, df=9, p<0.001). The

516   probability of association between females and the most likely father of their offspring varies

517   according to female reproductive state (Fig. 3a). Namely, the probability of association is

518   highest during the swollen period of the conceptive cycle and early lactation, and lowest

519   during pregnancy (Table 2a, Fig. 3a). In addition, high-ranking females had a higher

520   probability of association with the likely father compared to low-ranking females. Similarly,

521   higher-ranking males exhibited a higher probability of association with females. Finally,

522   female parity was also important, with multiparous females being most often associated with

523   the likely father.

524

525   <u>Variation in the strength of associations between females and their male friend</u>

526   The set of predictor variables used influenced the probability of association between females

527   and their male friend (log-likelihood ratio test comparing the fit of the full model with a null

528   model containing only random effects; χ^2=54.8, df=9, p<0.001). The probability of

529   association between a female and her male friend varied according to female reproductive

530   state (Fig. 3b). The probability of association increased from pregnancy to early lactation,

531   decreased from early to late lactation and decreased again from late lactation to the first

532   postpartum swelling, where association with the male friend of the previous interbirth interval

533   was weakest (Table 2b, Fig. 3b). Beyond reproductive state, female rank also had an effect on

534   the probability of association, with high ranking females being more likely to be associated

535   with their male friend.

536

537   **DISCUSSION**

538   This study investigated the structure and stability of heterosexual bonds in chacma baboons.

539   While previous studies have emphasized the occurrence of strong bonds between lactating

540   females and an adult male shortly after the birth of an infant, our results suggest that males

541   and females form stable and preferential relationships at least from conception until the end of

542   lactation. Here we explore the implications of our findings for our understanding of the

543   function of heterosexual associations in baboons.

544   We found that 70% (N=31/44) of females have the same male friend over time, either

545   from conception to pregnancy or from pregnancy to lactation, while 14% (N=6/44) switch

546   their male friend in one or the other transition. The remaining 16% (N=4/44) of females were

547   not associated to any friend during one state (mainly during pregnancy). Thus, overall, most -

548   but not all - male-female bonds last from offspring conception to lactation. By contrast,

549   friendships did not significantly increase a male's chance of siring the next offspring of his

550 female friend, suggesting that in chacma baboons, heterosexual associations have not evolved

551 in response to mating benefits. Overall, our results indicate that friendships tend to follow,

552 rather than precede, sexual activity between friends which suggests that male involvement in

553 heterosexual friendships represents paternal care rather than mating effort. Although our study

554 assesses the correlation between friendships and the probability of paternity (inferred from

555 consortship activity during the conceptive cycle), rather than actual paternity, our results are

556 consistent with previous studies investigating the correlation between friendships and actual

557 paternity data in savanna baboons, showing that most male friends of lactating females had

558 sired their friend's infant (Nguyen et al. 2009; Huchard et al. 2010; Moscovice et al. 2010). In

559 addition, it's important to note that we attributed as male friend to a female the male who was

560 both her most frequent male nearest neighbour and her main male grooming partner. These

561 criteria are meant to maximize our ability to detect and characterize differentiated male-

562 female relationships, regardless of variation in the degree of sociality between females.

563 However, they do not quantify the total amount of time that friends actually spend (or groom)

564 together. This may represent another important axis of variation to consider when examining

565 the functional consequences of heterosexual relationships, as it could be associated with

566 differences in the expression of paternal behaviour.

567   Our finding that most male-female associations exist just after conception, and are

568 maintained throughout pregnancy, suggests that males may assess their paternity using simple

569 rules, such as protecting offspring born to the female(s) with whom they have become

570 associated after consorting with them during the conceptive cycle. In previous studies, the

571 observation that tight male-female associations only started during lactation (Palombit et al.

572 1997; Palombit 1999), six months after conception, raised the question of how males might

573 assess their paternity. Several studies suggested that males may rely on their past mating

574 history, as they were found to form friendships based on mating effort and particularly on the

575   frequency and timing of copulations during the fertile period of a female's conceptive cycle

576   (Palombit et al. 2000; Weingrill 2000; Moscovice et al. 2010). In Moscovice et al.'s study,

577   females associated mainly with their main consort partner of the conceptive cycle and, when

578   he was not present in the group around infant birth, they formed a friendship with their second

579   former consort partner. This hypothesis suggests that males track and memorize their mating

580   activity, and possibly that of their rivals, and eventually link the birth of the offspring to the

581   conceptive cycle. Our results suggest an additional potential rule-of-thumb for male paternity

582   assessment that relies on past mating history without requiring males to remember all their

583   mates over the past 6-months period: male-female bonds may start during consortships and be

584   subsequently maintained throughout pregnancy and lactation. It is important to note that

585   males need to tolerate female friends selectively (and thus keep track of their previous mating

586   activity) only if being involved in a friendship with a female is costly. If friendships are not

587   costly to males, males may tolerate any female willing to associate with them and the

588   observed pattern of male-female associations could be driven by a combination of female

589   choice to associate with a male that does not represent a threat of infanticide given their

590   mating history, and of male tolerance for any female.

591   At the proximate level, the formation and maintenance of affiliative pair-bonds and

592   social relationships between mates have been show to be facilitated by physiological changes

593   in oxytocin levels of females in monogamous rodents (Witt et al. 1990; Williams et al. 1994;

594   Cushing and Carter 2000), non-human primates (Smith et al. 2010; Snowdon et al. 2010) and

595   humans (Grewen et al. 2005; Feldman et al. 2012). Interestingly, in chacma baboons, females

596   experience a surge of oxytocin during the period of most likely ovulation, and mate-guarded

597   females displaying higher levels of oxytocin were found to maintain closer proximity to their

598   consort partner (Moscovice and Ziegler 2012). Together with the present result that male-

599   female associations exist from the conceptive cycle, this suggests that the formation of

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

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

625   Responsibility for the maintenance of spatial proximity varies across the successive

626   reproductive states of a female. Females are responsible for maintaining proximity during

627   early lactation, as found in other studies (Palombit et al. 1997, 2001; Huchard et al. 2010).

628   However, the fact that males are primarily responsible for maintaining close proximity during

629   pregnancy was unexpected, and may suggest that males benefit from these associations as

630   much as, or more than, females. In addition to the reproductive benefits mentioned above,

631   males associated with a familiar female may gain social benefits, by receiving more grooming

632   and affiliation, which may alleviate stress levels (Aureli and Yates 2009; Ellis et al. 2011) or

633   facilitate their social integration in a group (Smuts 1985). Alternatively, a cause for those

634   results may be methodological. In this study, we assessed the maintenance of proximity

635   within 1m. In contrast, previous studies used a composite proximity measure, called 'C-

636   score', which takes into account both close (0-1m) and intermediate (1-5m) proximity.

637   Responsibility for the maintenance of close proximity (within 1m) mostly reflects the

638   initiation of physical contacts between partners. As the direction of grooming is highly

639   asymmetrical in heterosexual dyads (Palombit et al. 1997; Huchard et al. 2010), males may

640   often approach females in a request to be groomed, and this may explain their responsibility

641   in maintaining close proximity during pregnancy and the mixed maintenance during late

642   lactation. A previous study assessing maintenance of close proximity (i.e. within 1m) between

643   pregnant and lactating females and their male friend also found that males were responsible

644   for proximity maintenance in over half of the dyads, while females where mostly responsible

645   for maintaining proximity when using 0-5m proximity data (Smuts 1985). Analysing

646   proximity data across the 0-5m range is likely to provide a more accurate reflect of the overall

647   maintenance of proximity among heterosexual partners.

648   Finally, we found important variation in the strength of friendships across female

649   reproductive states. Friendships were most prevalent (involving 95% of females) and most

650   intense during early lactation, encompassing the first 6 months of an infant life, when the risk

651   of infanticide is highest (Palombit et al. 2001; Palombit 2003). By contrast, only 68% of

652   females in late lactation were associated to a male friend and the strength of these associations

653   decreased during this state compared to early lactation, suggesting that friendships might

654   dissolve progressively, as infanticide risk decreases throughout infant development. The

655   strength of friendships during pregnancy was lowest than during early lactation and

656   comparable to late lactation. Evidence suggests that lactating females compete over male

657   friends (Seyfarth 1978; Palombit et al. 2001). Pregnant females may renounce to stay around

658   their friend at a time where the benefits of the association may not compensate the costs of

659   competition.

660   In line with this, the strength of association with males was found to be influenced by

661   female dominance rank, confirming that females were competing over access to male friends

662   and their potential paternal services. In particular, high-ranking females, regardless of their

663   reproductive state, associated more frequently to their male partner (friend and/or likely father

664   of their offspring) than lower-ranking females. Female-female competition over males in

665   chacma baboons was first reported in a two-male group where the dominant female seemed to

666   prevent the formation of close bonds between the dominant male and other females (Seyfarth

667   1978). A subsequent study showed that high-ranking mothers maintained closer associations

668   to their male friends and actively excluded lower-ranking mothers from male proximity where

669   friendships overlapped (Palombit et al. 2001). A male's ability to protect infants might be

670   limited by the number of females and/or infants associated with him at a given time (Palombit

671   et al. 2001). For instance, high-ranking males *Macaca nigra* who are frequently mate-

672   guarding receptive females spend less time in proximity to their genetic offspring probably

673   because they are seeking further mating opportunities instead of providing infant care (D.

674   Kerhoas et al., unpubl. data). Similarly, subordinate male chacma baboons have fewer bonds

675   with juveniles than dominant males, but maintain stronger bonds with their associated

676   juveniles (Huchard et al. 2013).

677   A range of social and demographical parameters may influence the temporal stability

678   of male-female bonds in chacma baboons. First, infanticide risk is known to vary both within

679   and among populations (Palombit 2003) and is likely to affect the benefits of male-female

680   bonds (Palombit 1999, 2012). In our case, several immigration events induced social

681   instability in both groups during the course of this study, which may have raised female

682   perception of infanticide risk, and their incentive to form friendships. Second, male breeding

683   tenure may also be an important determinant of the stability of male-female bonds in large

684   multimale groups. When male dominance hierarchy is stable over long periods of time, the

685   same male-female bonds might continue after offspring independence and cover more than

686   one interbirth interval. By contrast, if male dominance changes while a female is pregnant or

687   in lactation, she might stop her association to conceive her next offspring with the new alpha

688   male. In this study, male dominance changed in both groups between the two study periods,

689   which may explain why most male-female bonds vanish after one interbirth interval.

690   To conclude, our findings suggest that heterosexual associations represent paternal

691   effort rather than mating effort in chacma baboons, show greater temporal stability than

692   previously thought, and vary in strength according to female reproductive state and

693   dominance rank. We found that heterosexual friendships exist since infant conception, are

694   maintained throughout pregnancy and strengthen at birth. Such pattern of association may

695   clarify how males and females use their mating history to make decisions about heterosexual

696   bonds by suggesting that long-term memory of prior mating activity is not necessary to invest

697   into friendships and offspring care. In addition, our results indicate that most females are

698   permanently associated with one male regardless of their reproductive status, suggesting that

699 heterosexual bonds may play an important, and under-appreciated, role in the social

700 organization and structure of baboon societies.

701

702 **COMPLIANCE WITH ETHICAL STANDARDS**

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

707 **Ethical approval:** All applicable international, national, and/or institutional guidelines for the

708 care and use of animals were followed. This article does not contain any studies with human

709 participants performed by any of the authors.

710

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932 **Table 1** Results of the permutation tests investigating whether females remain associated with the same male across reproductive states (likely

933 father: most likely father of their offspring, identified as the main consort during the swollen period of the conceptive cycle, friend P: male friend

934 during pregnancy, friend L: male friend during lactation, previous friend: male friend during pregnancy or lactation of the previous interbirth

935 interval). The observed proportion of females associated with the same male is calculated as the number of females associated with the same

936 male across both reproductive states divided by the total number of females

937

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

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]			
		P	-1.572 ± 0.772	[-3.086 ; -0.058]	31.276	3	<0.001
		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]			
		L2	-0.861 ± 0.379	[-1.603 ; -0.118]	33.144	3	<0.001
		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

949

[a]Reference category: L1 (six first months of lactation)

[b]Reference category: multiparous

[c]Reference category: J group

[d]Reference category: 2013

Figure Legends:

Fig. 1 Distribution of grooming (white bars) and spatial proximity (grey bars) indices (a)

between each female and five male residents in her 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) versus non-friend dyads (N=902 for grooming index, N=812 for proximity index). On

each box, the black horizontal line represents the median 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 the interquartile range. Open dots represent outliers. Note that the boxes

representing the grooming index distribution for the fifth male and for non-friend dyads is not

visible because the median, the 25th and 75th quartiles are equal to zero

Fig. 2 Responsibility for the maintenance of close spatial proximity (within 1m) between

females and their male associates. The male associate is the male consort during the swollen

period of the conceptive cycle (SWC) and the male friend during pregnancy (P), early

lactation (L1) and late lactation (L2). 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. Open dots represent outliers

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 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 female reproductive state: cycling swollen during the conceptive cycle

979   (SWc), pregnant (P), early lactation (L1), late lactation (L2) and first postpartum cycle (SW1).

980   On each box, the black horizontal line represents the median of the distribution, while bottom

981   and top of the box represent respectively the 25th and 75th quartiles. Whiskers include a

982   maximum of half of the interquartile range. Open dots represent outliers. The significance of

983   the comparisons between reproductive states is evaluated by changing contrasts in the

984   GLMM. Significant comparisons are denoted by "*"

(a)

Behavioural indices of grooming and proximity between males and females
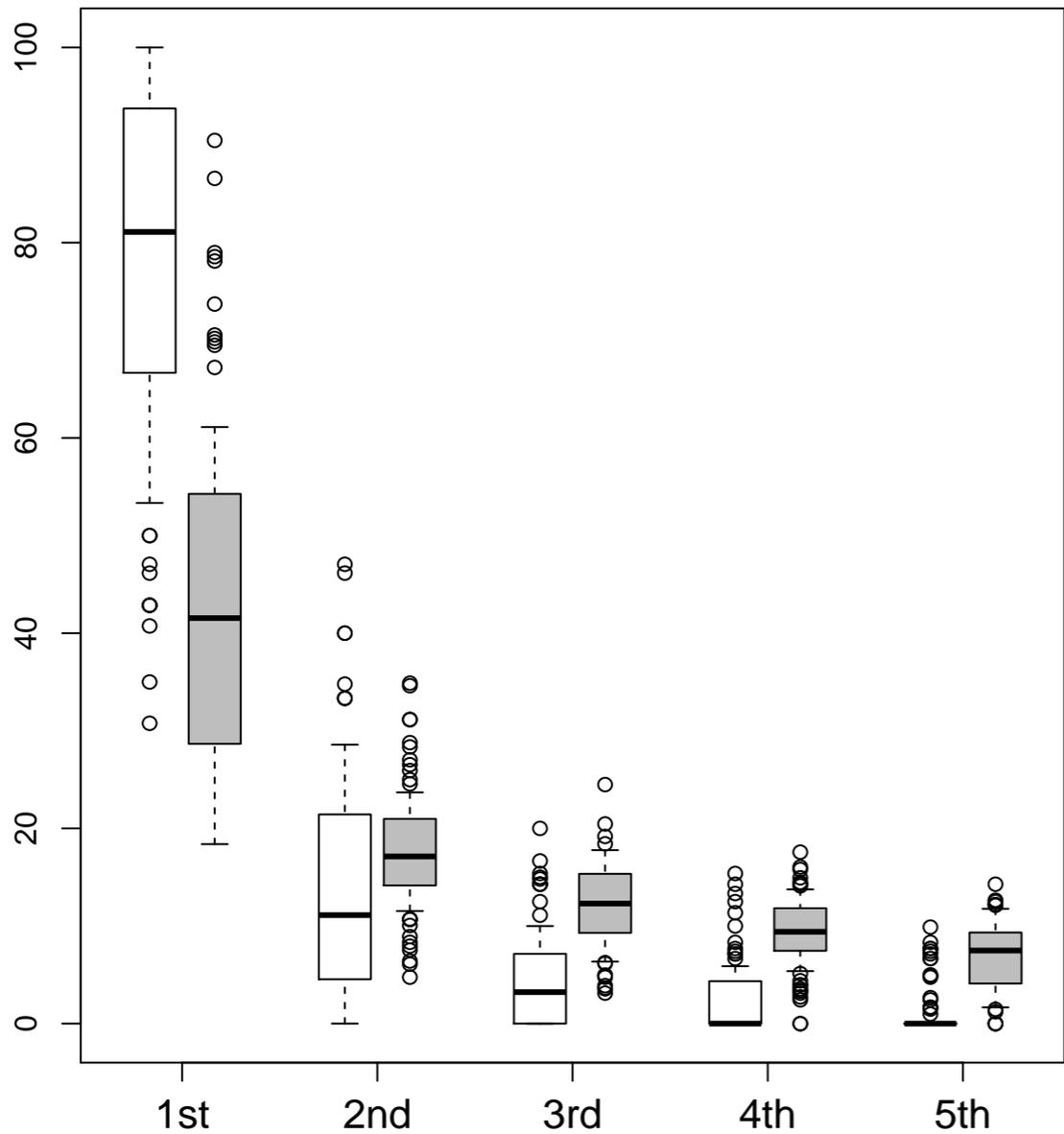
Five first males ordered from most to least prefered

(b)

Behavioural indices of grooming and proximity for friend or non-friend dyads
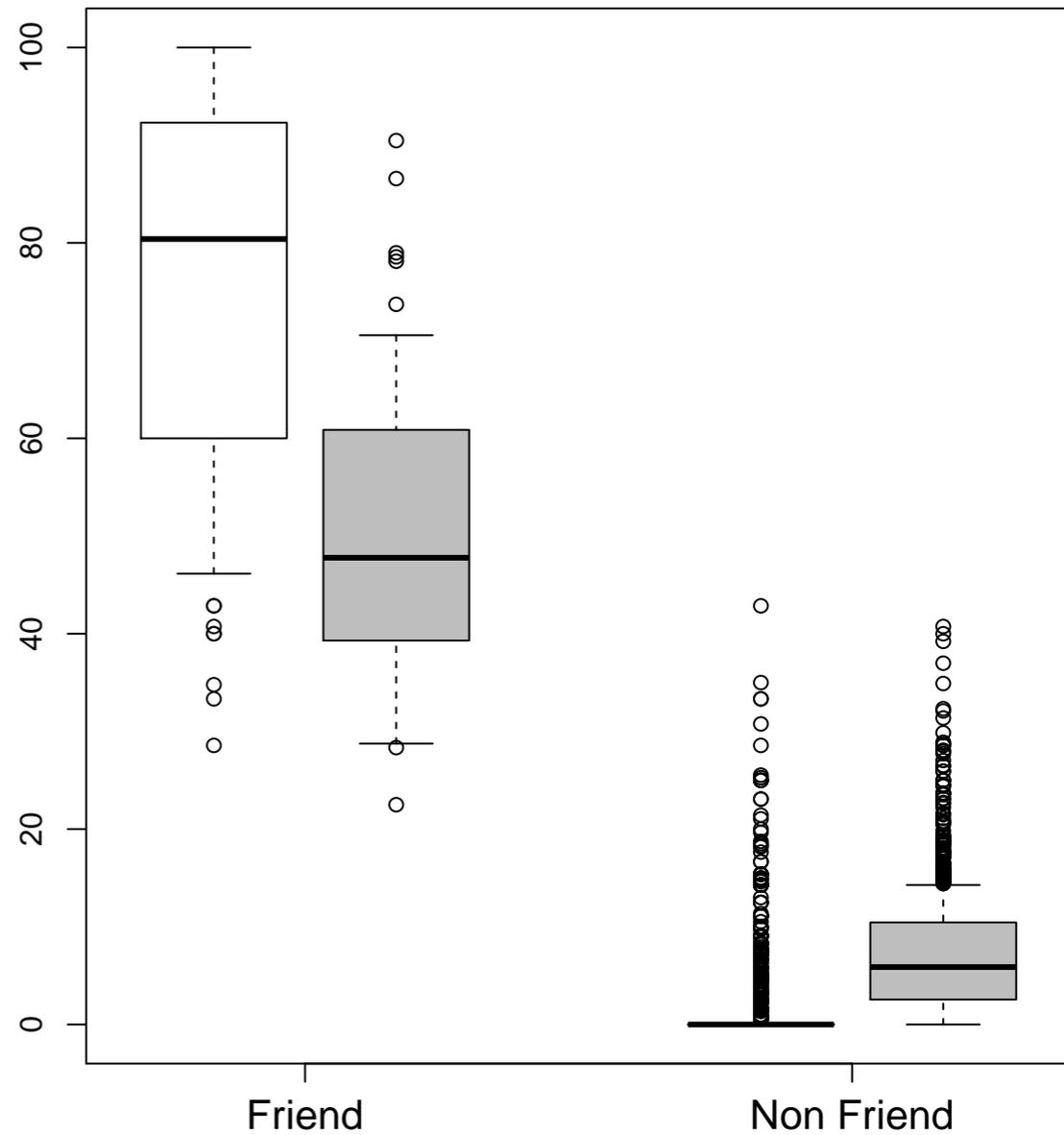
Friend   Non Friend

Figure
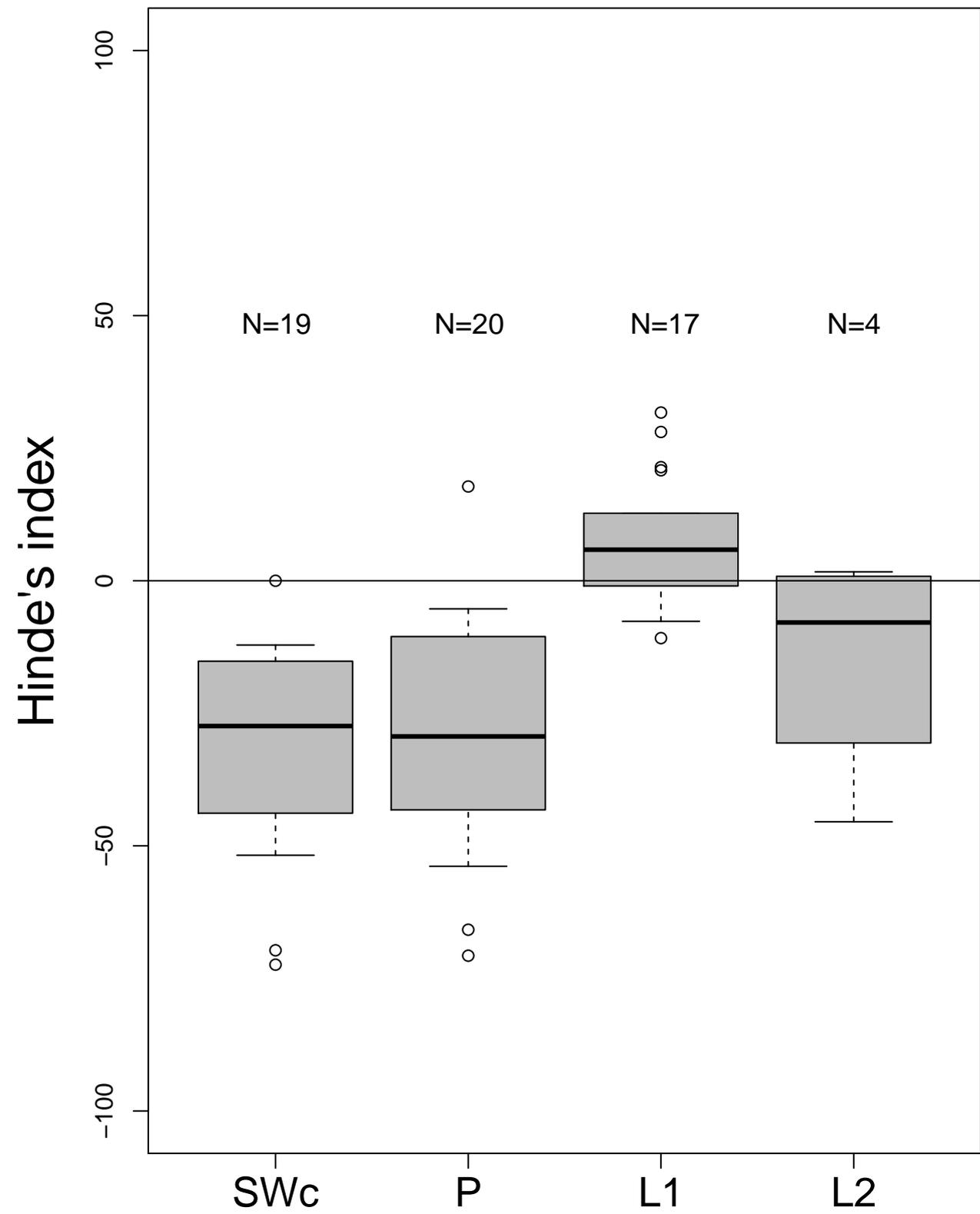
Figure

(a)
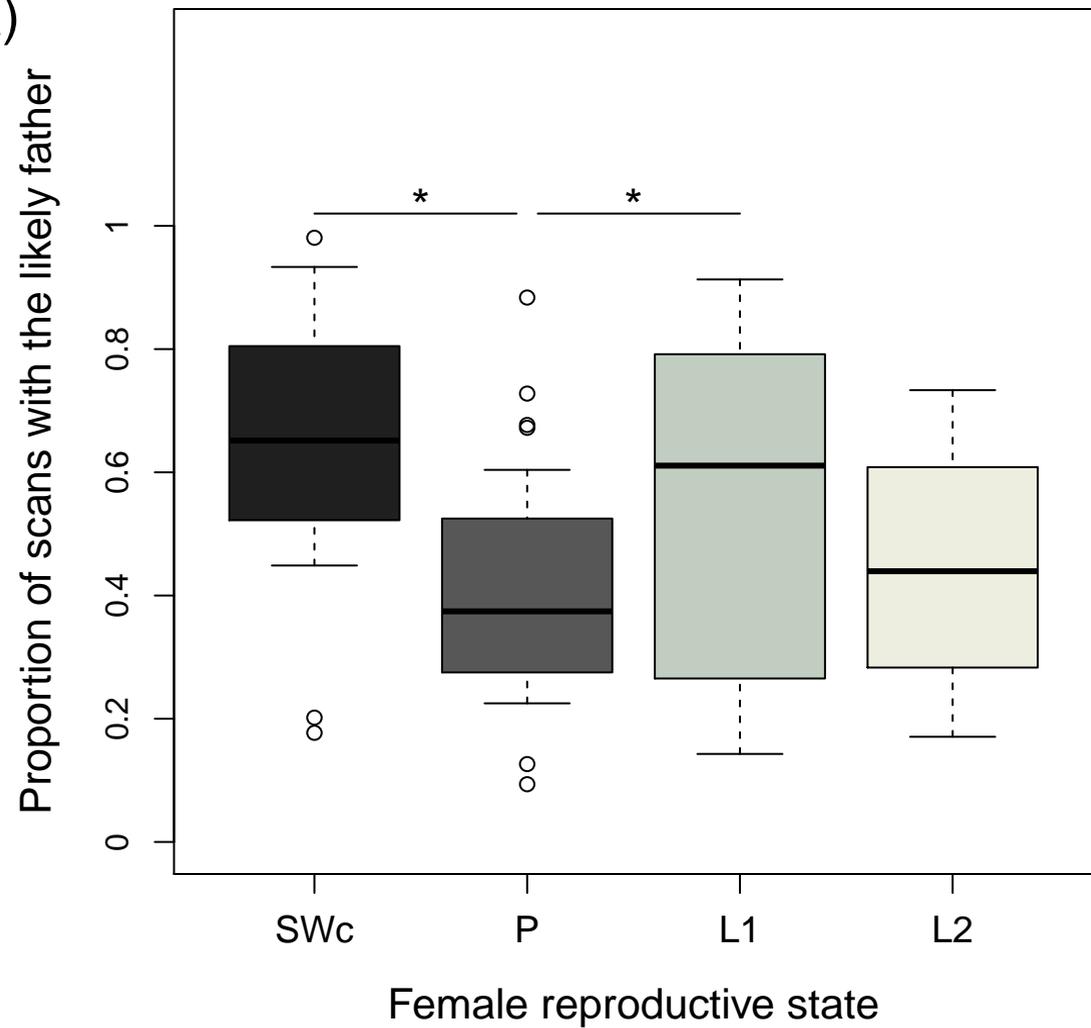
(b)
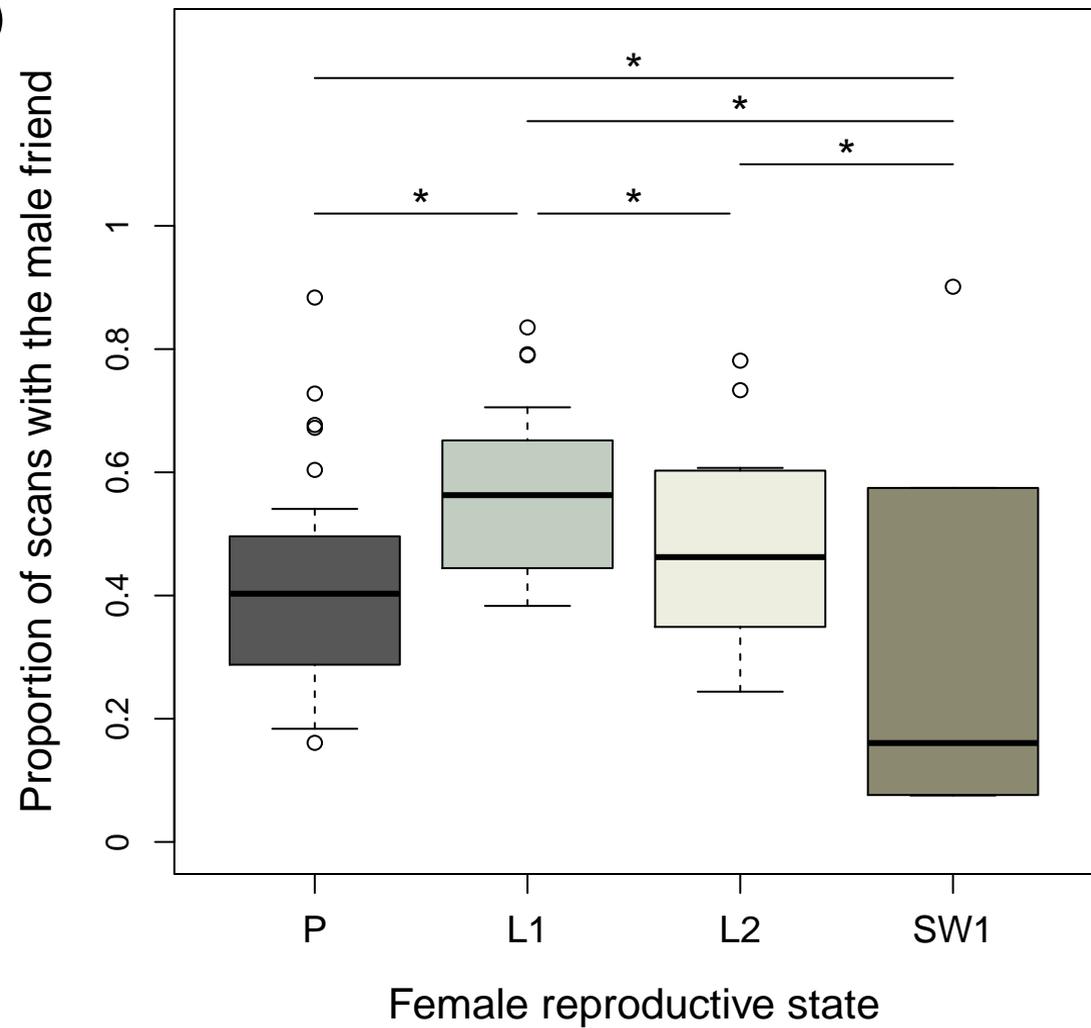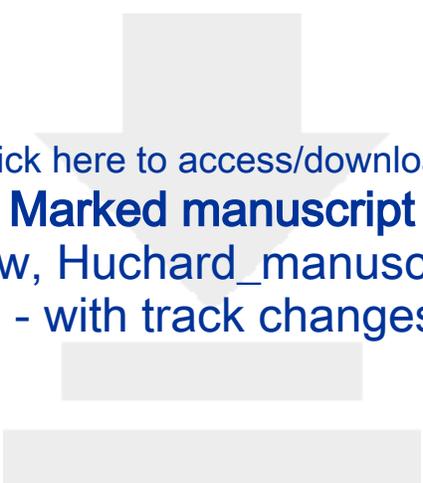
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