

1 **Post-copulatory behavior of olive baboons (*Papio anubis*) infected by**  
2 ***Treponema pallidum***

3

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20 **Abstract**

21 In nonhuman primates pathogens are known to exert a profound and pervasive cost  
22 on various aspects of their sociality and reproduction. In olive baboons (*Papio*  
23 *anubis*) at Lake Manyara National Park, genital skin ulcers caused by *Treponema*  
24 *pallidum* subsp. *pertenue* lead to mating avoidance in females and altered mating  
25 patterns at a pre-copulatory and copulatory level. Beyond this level, sexual behavior  
26 comprises also post-copulatory interactions among the sexual partners. To

27 investigate whether the presence of genital skin ulcers has an impact at the post-  
28 copulatory level, we analyzed 517 copulation events of 32 cycling females and 29  
29 males. The occurrence of post-copulatory behaviors (i.e., copulation calls, darting  
30 [female rapid withdraw from the male] and post-copulatory grooming) was not altered  
31 by the presence of genital skin ulcerations. Similarly to other baboon populations,  
32 females of our group were more likely to utter copulation calls after ejaculatory  
33 copulation. The likelihood of darting was higher after ejaculatory copulations and with  
34 the presence of copulation calls. Post-copulatory grooming was rarely observed but  
35 when it occurred, males groomed females for longer periods when females uttered  
36 copulation calls during, or preceding mating. Our results indicate that despite the  
37 presence of conspicuous genital skin ulcers, the post-copulatory behavior was not  
38 affected by the genital health status of the dyad. This suggests that infection cues  
39 play a major role before and during mating but do not affect post-copulatory behavior.

40

41 Keywords: sexually-transmitted infection, genital skin ulcers, copulation call, darting,  
42 post-copulatory grooming, diseases

43

44

## 45 **1 INTRODUCTION**

46 Mating is intrinsically associated with sexual selection, which occurs through  
47 competition over mates or mate choice (Darwin, 1871; Anderson, 1994). Mate choice  
48 might confer both direct and indirect fitness benefits to the choosy individual. Such  
49 benefits might be a higher level of parental care or the accumulation of “good genes”  
50 in the offspring (Andersson, 1994, Kokko et al., 2003). One important fitness criterion  
51 in the mating context is the health status of the potential partner. Thus, individuals  
52 should choose healthy partners, since mating with a sick individual may not only have  
53 negative effects on the offspring (i.e. a poor health status can be an indication of a  
54 poor immune system which would then passed on to the offspring), but also on the  
55 health of the choosy individual itself, if the disease can be transmitted (Hillgarth,  
56 1996; Martinez-Padilla et al., 2012). The latter becomes particularly obvious if the  
57 disease is sexually transmitted. A poor health status can alter both the individual’s  
58 attractiveness as a sexual partner, and its competitive ability and performance in the  
59 mating context (Beltran-Bech et al., 2014). This is particularly true when courtship  
60 and mating are energetically demanding phases (Key & Ross 1999).

61 In some primate species, males follow females for hours and days, maintain  
62 close proximity, increase their grooming bouts and try to monopolize mating (e.g.,  
63 Smuts, 1987; Dixson, 2013). Such an investment comes along with time and energy  
64 costs, which diseased males might not be able to cover. Likewise, females might not  
65 engage with males during copulation, e.g., not showing proceptive and receptive  
66 behavior, not permit subsequent matings or not showing interest in post-copulatory  
67 grooming.

68 In baboons, copulations are usually defined by male mounting with intromission  
69 and pelvic thrusts upon the female, which can culminate with ejaculation (Saayman,  
70 1970, Ransom, 1981). Yet, the number of mounts and pelvic thrusts per mount may

71 vary. An ejaculatory mount is usually identified by an ejaculation pause, where the  
72 male remains rigid upon the female for a few seconds (Saayman, 1970). During or  
73 after copulation, females might utter copulation calls which are typically low-  
74 frequency rhythmic vocalizations (Bouquet et al., 2018). In addition, female baboons  
75 often exhibit a characteristic post-coital sprint over several meters away from the  
76 male, a post-copulatory withdraw-behavior that is known as ‘darting’ (Hall & DeVore  
77 1965; Saayman, 1970; Ransom, 1981; Smuts, 1985; Bercovitch, 1995; Collins, 1981;  
78 O’Connell & Cowlshaw 1995). Finally, pairs may engage in post-copulatory grooming  
79 (PCG), which can be initiated either by the male or the female (Saayman, 1970).

80 At Lake Manyara National Park (LMNP), olive baboons (*Papio anubis*) are  
81 infected with a putative sexually transmitted infection caused by the bacterium  
82 *Treponema pallidum* subsp. *pertenue* (*TPE*, Knauf et al., 2012, 2018; Harper et al.,  
83 2012; Chuma et al., 2016). Clinical symptoms are characterized by genital skin ulcers  
84 (in the following referred to as genital ulcers), a moderate to severe ulceration of the  
85 anogenital skin in both males and females (Figure 1). Progressive scarification of the  
86 tissue can lead to a permanently open state of the vagina and anus in females; while  
87 in males it cause phimosis or loss of the corpus penis (Knauf et al., 2012). At LMNP,  
88 genital ulcers in baboons have been linked with mating avoidance by females and  
89 altered copulatory patterns by males, i.e., ulcerated individuals exhibit fewer pelvic  
90 thrusts (Paciência et al., 2019). Since *TPE* infection has been associated with pre-  
91 copulatory mate choice, we aimed to investigate whether the post-copulatory  
92 behavior is altered by the genital health status (i.e. presence of genital ulcers) of the  
93 mating pairs.

94



95  
96 **FIGURE 1** Genital skin ulcerations caused by *Treponema pallidum* subsp. *pertenue* in an  
97 adult female (top) and a subadult male (bottom) olive baboon at Lake Manyara National  
98 Park, Tanzania.

99

## 100 **2 MATERIALS AND METHODS**

101 This research adhered to the rules and regulations of the Tanzanian and German  
102 laws. The Animal Welfare and Ethics Committee of the German Primate Center  
103 approved the entire study.

104

105

## 106 2.1 Study site and subjects

107 Fieldwork was conducted at LMNP, Northern Tanzania, during two field seasons  
108 (April to December) in 2015 and 2016. Our baboon group was habituated during four  
109 months before the data collection phase of the study to facilitate behavioral  
110 observations from a distance of fewer than five meters.

111 The group consisted of approximately 170 individuals, of which 53 were adult  
112 and subadult females, 35 adult and subadult males and more than 70 immature  
113 individuals. In our analyses, we included 32 cycling females and their 29 male  
114 partners which could all be individually identified. The genital health status (GHS)  
115 was visually assessed and all adult and subadult individuals were classified as either  
116 genitally “ulcerated” or “non-ulcerated” using macroscopic visual cues (Knauf et al.,  
117 2012). Genital ulcerations could range from small-medium ulcers to a severe  
118 mutilation of the outer genitalia (Figure 1).

119

## 120 2.2 Behavioral data

121 We conducted full-day focal follows (Altmann, 1974) from dawn to dusk on 32 cycling  
122 females. To maximize the number of observed mating events, we focused on  
123 females in their peak estrus, denoted by maximal tumescence and bright pink color of  
124 their anogenital skin (Zinner et al., 2004). We collected 597 hours of observation  
125 data, with an average of  $16.40 \pm 10.02$  hours (mean  $\pm$  SD, range 1.50 – 39.00 hours)  
126 per focal female. We collected data on the number of mating events, type of  
127 copulation, and the presence of copulation calls, darting behavior and PCG (Table 1).  
128 Behavioral data were recorded in the field on a hand-held Samsung Galaxy using  
129 Pendragon 5.1.2 software (Pendragon Software Corporation, USA).

130

131

132 **TABLE 1** Definition of variables

133

	<b>Definition</b>
<b>Copulation/mating event</b>	male mounting an estrous female and performing pelvic thrusts (with intromission*) and with or without ejaculation
<b>Type of copulation</b>	ejaculatory or non-ejaculatory: indicated by visible fresh sperm on the male's penis or by the sperm plug on the female's genitalia after copulation
<b>Pelvic thrusts</b>	number of male pelvic thrusts during copulation
<b>Copulation call</b>	context-specific calls female utter during, or at the end of a copulation
<b>Darting</b>	rapid withdraw in which a female can run away several meters from the male after copulation
<b>Post-copulatory grooming (PCG)</b>	male/female grooms the mating partner 15 seconds after copulation occurred

134 \*Except for severely ulcerated males that lack the corpus penis as intromission cannot occur

135

### 136 2.3 Statistical analysis

137 We run generalized linear mixed models (GLMM, Baayen, 2008) to examine the  
138 post-copulatory behavior of our baboon population. All models were performed in R  
139 v3.4.4 (R Core Team 2018) with the lme4 package v 1.1-15 (Bates et al., 2015) and  
140 collinearity of the variables was checked using the package car (Fox & Weisberg  
141 2011). Maximum likelihood ratio tests were used to test the full model with fixed  
142 factors against the null model (Faraway, 2006). Since interactions between the fixed  
143 predictors did not significantly improve any model fit, we excluded them from all  
144 models for parsimony and a more reliable interpretation of the main effects. In all  
145 models, female, male and pair identities were included as random factors.

146

### 147 2.5 Model description

#### 148 *Model 1: Copulation calls*

149 The first model analyzed whether the occurrence of copulation calls was affected by  
150 the male or female GHS, the type of copulation, or the number of pelvic thrusts. The

151 response variable was the presence or absence of copulation calls per mating event  
152 (1/0) with a binomial error structure and a logit link function.

153

154 *Model 2: Darting behavior*

155 With the second model, we examined whether post-copulatory darting was affected  
156 by the male or female GHS, type of copulation and the occurrence of copulation calls.  
157 The response variable was the presence or absence of darting per mating event (1/0)  
158 with a binomial error structure and a logit link function.

159

160 *Model 3: Occurrence of post-copulatory grooming (PCG)*

161 With the third model we investigated whether the occurrence of PCG is affected by  
162 the GHS of the male and female, respectively, presence of copulation calls and the  
163 type of copulation. Here the response variable was the presence or absence of PCG  
164 per mating event (1/0) with a binomial error structure and a logit link function.

165

166 *Model 4: Duration post-copulatory grooming (PCG)*

167 With this model, we examined whether the duration of PCG (in seconds) was  
168 affected by the presence of copulation calls and the type of copulation. Here we  
169 generated two GLMMs; one model for PCG performed by males (PCG-M) and  
170 another for PCG performed by females (PCG-F). Each model assumed that the  
171 duration of PCG depended on the presence of copulation calls and type of  
172 copulation. Both models were fitted using the glmmADMB package (Fournier et al.,  
173 2012) with a negative binomial error structure and a logit link function.

174

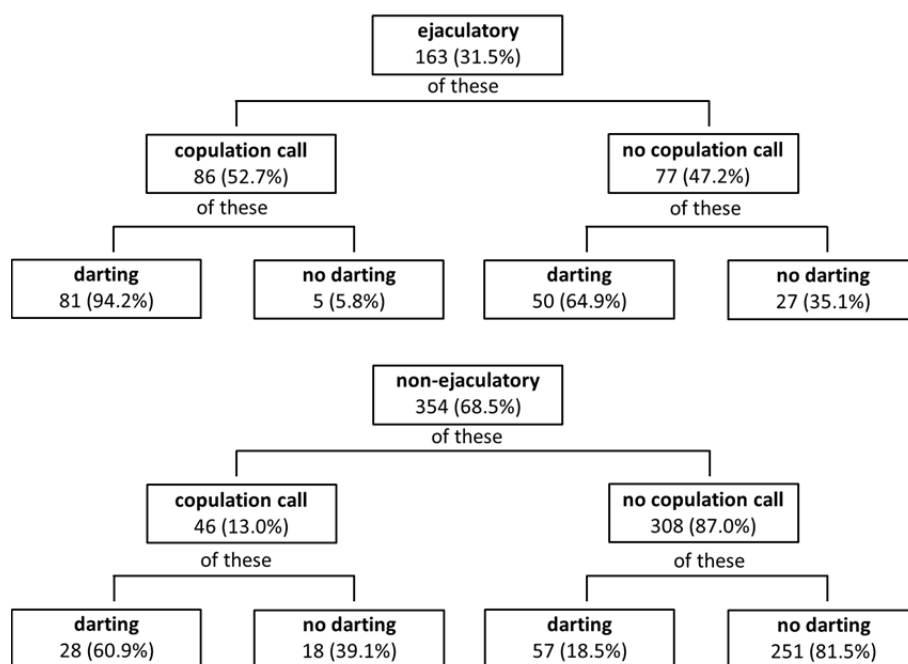
175



176 **3 RESULTS**

177 The prevalence of 'genital ulcerated' individuals in our study group (determined  
178 visually) remained relatively stable throughout the 18-months study period. Only  
179 three adult females and three adult males switched from 'non-ulcerated' to 'ulcerated'  
180 between field seasons. Therefore, at the end of the study, 44% (N=23) of the 53 adult  
181 and subadult females and 47% (N=17) of the 35 adult and subadult males displayed  
182 genital ulcers (Figure 1). Genital ulcers were observed in 40% (N=32) of the females  
183 participating in sexual interactions and in 53% (N=35) of the males. In total, we have  
184 observed 517 copulations among 32 females and 29 males. Evidence for ejaculation  
185 was found in 31.5% (N=163) of the copulations. Females uttered copulation calls in  
186 25.5% (N=132), darting occurred in 41.7% (N=216) and PCG in 27.2% (N=141). The  
187 frequency of copulations calls and darting differed slightly between ejaculatory to  
188 non-ejaculatory copulations (Figure 2). But the likelihood of uttering copulation calls  
189 increased with ejaculatory mating ( $p < 0.001$ , Table 2). Males who lacked the corpus  
190 penis were observed ejaculating towards the ground or against their legs as there  
191 was no way to direct the sperm into the female's genital tract. Nevertheless, two  
192 females in our study group uttered copulation calls even when mating with males  
193 lacking the corpus penis, where intromission was not observed (i.e., males solely  
194 performed pelvic thrusts).

195



196  
 197 **FIGURE 2** Frequency of copulation calls and darting after ejaculatory copulations (top; n =  
 198 163) and non-ejaculatory copulations (bottom; n = 354). Total number of copulations = 517.  
 199

200 **TABLE 2** Copulation call model. Binary GLMM evaluating if the likelihood of uttering a  
 201 copulation call is affected by the male and female genital health status (GHS), the number of  
 202 pelvic thrusts and the type of copulation. Estimates, standard errors (SE), z-values, and 2.5%  
 203 and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept with a reference  
 204 category for non-ulcerated individuals and non-ejaculatory events.  
 205

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-3.725	0.830	-5.639	-2.245	-4.490	-
Male GHS	0.057	0.803	-1.518	1.758	0.071	0.944
Female GHS	1.482	0.945	-0.347	3.553	1.569	0.117
Type of copulation	2.800	0.430	2.005	3.706	5.759	<0.001

206  
 207 Darting was observed in 80% (N=131) of the copulations with ejaculation, in contrast  
 208 to only 24% (N=85) of the non-ejaculatory copulations. Darting was also more  
 209 frequent when females uttered copulation calls (94%, N= 81). These observations  
 210 were corroborated by our second model. The likelihood of darting was higher when  
 211 females gave copulation calls and when the male ejaculated (p<0.001, Table 3).  
 212 Darting never led to the termination of a consortship as males kept track of the  
 213 females, even if the female covered distances of more than 10 meters. Moreover,

214 consort take-overs were rarely observed in our group (n=7 over the 18-months study  
215 period).

216

217 **TABLE 3** Post-copulatory darting model. Binomial GLMM evaluating if the likelihood of  
218 darting is influenced by the male and female genital health status (GHS), presence of  
219 copulation calls and type of copulation. Estimates, standard errors (SE), z-values, and 2.5%  
220 and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept with reference  
221 category for non-ulcerated individuals, absence of copulation calls and non-ejaculatory  
222 events.

223

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-1.468	0.503	-2.537	-0.497	-2.919	-
Male GHS	-0.525	0.621	-1.714	0.770	-0.844	0.118
Female GHS	0.883	0.565	-0.242	2.092	1.563	0.398
Copulation call	2.408	0.480	1.502	3.402	5.017	<0.001
Type of copulation	2.500	0.380	1.781	3.277	6.586	<0.001

224

225 In most cases (72.8%, N= 376), no PCG occurred. When it occurred, males initiated  
226 PCG more often than females regardless of the type of copulation (Table 4). The  
227 occurrence of PCG was neither affected by the occurrence of copulation calls nor by  
228 the type of copulation (Table 5). However, the duration of PCG performed by males  
229 was longer when females uttered copulation calls (p=0.019). No effect was found for  
230 PCG initiated by females (Table 6).

231

232 **TABLE 4** Frequency of post-copulatory grooming (PCG) initiation in relation to copulation  
233 type (number of cases in parentheses).

234

	Copulations (512)*	Ejaculatory 30.6 % (159)	Non-ejaculatory 68.2 (353)
<b>No PCG</b>	72.7% (376)	77.3 % (123)	71.46% (253)
<b>Male initiated</b>	17.7% (92)	15 % (24)	19.2 % (68)
<b>Female initiated</b>	8.5% (44)	4.5 % (12)	9 % (32)

235 \*Five copulations excluded from the total (n= 517) as PCG could not be assessed properly

236

237

238 **TABLE 5** Post-copulatory grooming (PCG)-presence model. Binomial GLMM evaluating if  
 239 the likelihood of PCG is affected by the male and female genital health status (GHS),  
 240 presence of copulation calls and type of copulation. Estimates, standard errors (SE), z-  
 241 values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept  
 242 with reference category for non-ulcerated individuals, absence of copulation calls and non-  
 243 ejaculatory events.

244

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-1.278	0.257	-1.819	-0.770	-4.978	-
Male GHS	0.520	0.307	-0.125	1.130	1.695	0.090
Female GHS	0.017	0.377	-0.828	0.681	-0.045	0.964
Copulation call	-0.070	0.319	-0.707	0.561	-0.220	0.826
Type of copulation	-0.178	0.278	-0.739	0.362	-0.641	0.521

245

246 **TABLE 6** PCG duration model. GLMMs evaluating if the duration of PCG is affected by the  
 247 presence of copulation calls and type of copulation. Estimates, standard errors (SE), z-  
 248 values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. PCG  
 249 performed by males and females is shown in PCG-M and PCG-F respectively. Intercept with  
 250 reference category for non-ulcerated individuals, absence of copulation calls and non-  
 251 ejaculatory events (GHS = genital health status).

252

Term	Estimate	SE	CI lower	CI upper	z value	P
<b>PCG-M</b>						
Intercept	5.213	0.185	4.851	5.575	28.24	-
Male GHS	0.106	0.191	-0.268	0.480	0.555	0.579
Female GHS	-0.197	0.180	-0.550	0.156	-1.091	0.275
Copulation call	0.472	0.201	0.078	0.864	2.352	<b>0.019</b>
Type of copulation	0.029	0.198	-0.359	0.417	0.147	0.883
<b>PCG-F</b>						
Intercept	5.229	0.229	4.780	5.677	22.84	-
Male GHS	0.337	0.327	-0.304	0.978	1.029	0.304
Female GHS	-0.124	0.331	-0.773	0.525	-0.375	0.708
Copulation call	-0.147	0.456	-0.485	0.780	0.456	0.648
Type of copulation	0.164	0.588	-0.381	0.709	0.588	0.556

253

## 254 **4 DISCUSSION**

255 The impact of sexually transmitted infections on the mating behavior of nonhuman  
 256 primates is still poorly understood. Our data from the LMNP baboons suggest that  
 257 genital ulcers have an impact on female mate choice and male mating performance

258 (Paciência et al., 2019), whereas the post-copulatory behavior seems to remain  
259 unaffected by the presence of genital ulcers.

260 Female olive baboons at LMNP produce copulation calls less often than other  
261 baboon species (yellow baboons: 80%, Collins, 1981; 96.9%, Semple, 1998; chacma  
262 baboons: 83%, Saayman, 1970; O'Connell & Cowlshaw 1994; Guinea baboons:  
263 39%, Boese, 1973; olive baboons: 19%, Ransom, 1981; 62%, Bercovitch. 1985, 25%  
264 this study; but not hamadryas baboons: 18%, Swedell & Saunders 2006; 26.1%  
265 Nitsch et al., 2011). Moreover, female olive baboons at LMNP uttered copulation calls  
266 more likely when mating was followed by ejaculation. Similar findings were observed  
267 in previous studies, where copulation calls occurred more frequently, or had a longer  
268 duration after ejaculatory copulations (Saayman, 1970; Deputte & Goustard 1980;  
269 Collins, 1981; Todt et al., 1995; O'Connell & Cowlshaw 1994; Walz, 2016, but see  
270 Semple et al., 2002). Copulation calls have been suggested to constitute a  
271 mechanism to incite male-male competition in chacma baboons (O'Connell &  
272 Cowlshaw 1994; Crockford et al., 2007). In olive baboons, however, due to the long-  
273 term consortships (i.e. during the estrous periods) and even "friendships" (i.e.,  
274 outside the estrus period (Smuts, 1985)), it was proposed that copulation calls  
275 function to reassure consortship formation and/or continuation with mating partners  
276 (Walz, 2016). According to the female choice hypothesis, calls can be directed to the  
277 current partner to encourage mate-guarding or to continue copulating (Todt et al.,  
278 1995). This can lead to a reduction of the likelihood of copulating with other partners  
279 and an increase in paternity certainty in males preferred by the female (Maestriperi &  
280 Roney 2005).

281 The occurrence and frequency of darting behavior is highly variable among  
282 olive baboons (25%, Ransom, 1981; 92%, Bercovitch, 1985; 76%, Walz, 2016,  
283 41.7%, this study) as well as in chacma baboons (78%, Hall, 1962; 75%, Hall &

284 DeVore 1965; 86–89%, Saayman, 1970; 78%, O’Connell & Cowlshaw 1995). In our  
285 study group, females darted more often after an ejaculatory mating and when the  
286 female uttered copulation calls. Similar observations were reported in another  
287 population of olive baboons, where females darted longer distances after ejaculatory  
288 copulations (Walz, 2016). While darting distance in chacma baboons was not  
289 affected by the occurrence of ejaculation, it was positively correlated with the duration  
290 of copulation calls (O’Connell & Cowlshaw 1995). In olive baboons, females have  
291 been described to run immediately after the copulation from the mating male towards  
292 another male (Hall & DeVore 1965), leading to consort take-overs (Smuts, 1985).  
293 Such behavior was not observed at LMNP as the darting female was usually followed  
294 by the consorting male, and consort take-overs were seldom observed. This might be  
295 due to the long term bonds observed between males and females in estrus, as  
296 females would frequently mate with the same male during different cycling periods  
297 (Paciência et al., 2019).

298         The function of post-copulatory grooming (PCG) is still unclear. Males might use  
299 PCG to prevent females from mating with other males and reduce sperm competition  
300 (Berenstain & Wade 1983; Kuester & Paul 1992; Nurnberg et al., 1994; Sonnweber  
301 et al., 2015). On the other hand, females might employ PCG as a means to either  
302 stimulate or avoid mating with the same male (Slob et al., 1986; Bancroft, 2005;  
303 Gumert, 2007) or decrease the risk of harassment by males (Smuts, 1985).  
304 Quantitative studies on PCG in baboons are scarce. In olive baboons, PCG presence  
305 has been related to the quality of the social bonds between the mating partners  
306 (Smuts, 1985). Yet, in chacma baboons, it is more frequently performed by females  
307 than males, except for females in their “swollen phase”, (i.e. maximum turgescence  
308 phase), where the grooming frequency by the male partners is higher (Saayman,  
309 1970). In Barbary macaques, where PCG has been studied extensively, this behavior

310 is known to occur in half of the mating events (Taub, 1980; Small 1990; Kuester &  
311 Paul 1992; Sonnweber et al., 2015). In this species, males are more likely to groom  
312 females after ejaculatory copulations, while females groom more often males after  
313 non-ejaculatory events (Sonnweber et al., 2015). This stands in contrast to our data  
314 from olive baboons at LMNP, where PCG did not take place in the majority of the  
315 cases and was neither affected by the type of copulation nor the presence of  
316 copulation calls. However, PCG duration performed by males was affected by female  
317 copulation calls irrespective of the type of copulation. Because copulation calls give  
318 hints to all males in the group that copulation just occurred, it might lead to male-male  
319 competition, and thus, males might be willing to increase their grooming bouts to  
320 prevent females from searching subsequent copulations with other males, which  
321 could aid in reducing sperm competition.

322         The clear comprehension of the possible functions of post-copulatory behaviors  
323 in nonhuman primates is still missing. In order to fill this gap, it is essential to collect  
324 and share quantitative data on sexual behavior and mating patterns of nonhuman  
325 primates. This is particularly important when group living species are affected by a  
326 sexually transmitted infection that has an impact on both sociality and reproduction  
327 leading to altered group dynamics.

328

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338

### 339 **AUTHOR CONTRIBUTIONS**

340 F.M.D.P, S.K and D.Z designed the study. F.M.D.P, I.S.C, I.F.L and S.K performed  
341 field work. F.M.D.P collected the data in the field. Data analysis was done by  
342 F.M.D.P. The paper was written by F.M.D.P, S.K and D.Z.

343

### 344 **COMPETING INTERESTS**

345 The authors declare that they have no conflict of interest.

346

### 347 **DATA AVAILABILITY STATEMENT**

348 The data that support the findings of this study are available from the corresponding  
349 author upon reasonable request.

350

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