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1 **Multimodal sexual signaling and mating behavior in olive baboons (*Papio anubis*)**

2

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12 Short title: Sexual signaling in olive baboons

13

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18

19

**20 Abstract**

21 In primate species, mating decisions seem to be based on multiple signal elements with  
22 different roles in the signaling of female reproductive status. Whereas some primate  
23 signals are relatively well described (e.g. sexual swellings and copulation calls), studies  
24 that simultaneously assess visual, auditory, behavioral and olfactory cues as signals of  
25 reproductive state are rarely undertaken. We used data on variation in sexual behaviors  
26 and sexual swellings in relation to the fertile period (estimated from the date of swelling  
27 detumescence) from a troop of semi-free ranging olive baboons (*Papio anubis*) to assess  
28 how different signals influence patterns of mate choice. Using an objective and  
29 quantitative measure of swelling size and color, along with detailed data on sexual  
30 behaviors from 13 cycles of 9 adult females, we found that fine-scale variation in sexual  
31 swelling size and female behavior could advertise the beginning of the fertile phase  
32 whereas swelling color and copulation call rates did not. Rates of olfactory inspections  
33 by males also tended to be higher during the fertile phase, suggesting that olfactory  
34 signals were of interest to males and may contain information about ovulation. There  
35 was no relationship between female characteristics (age and rank) and the expression of  
36 sexual signals, except for proceptive behaviors which increased with female rank. Males  
37 displayed more sexual behaviors such as approaches and holding and tended to direct  
38 more ejaculatory mounts during the fertile phase. All together, we suggest that whereas  
39 all males could have information concerning the timing of ovulation through female  
40 proceptive behaviors and swelling size, consorting males may have access to additional  
41 signals (olfactory cues). Sexual communication in olive baboons is consistent with a  
42 multimodal framework for fertility signaling, potentially allowing males and females to

43 establish different mating strategies. The possible selective pressures leading to multi-  
44 modal signaling are discussed.

45

46 Key words: sexual communication, multimodal signals, mating decisions, sexual  
47 swelling, ovulation.

48

49 Animals communication often depends on multiple signal elements expressed in  
50 multiple modalities [Candolin 2003; Hebets and Papaj 2005; Partan 2004; Partan and  
51 Marler 1999, 2005]. These signals may provide information on many different  
52 characteristics, including social and reproductive status with consequences for fitness  
53 and reproductive success; as such they are often under strong sexual selection. Primates  
54 are an excellent model for studies of multimodal communication and recent papers have  
55 urged more studies along these lines [Slocombe et al. 2011]. Old World monkeys have  
56 developed multiple signals with different hypothesized roles in the signaling of  
57 reproductive status, and several of these, such as sexual swellings and copulation calls,  
58 have a venerable place in the study of sexual selection. However, few attempts have  
59 been made to assess the extent to which primate females simultaneously signal fertility  
60 in multiple modalities, and how different signals may combine to influence patterns of  
61 male mate choice in group-living species.

62 In a number of primate species, males tend to mate during the period when  
63 ovulation is most likely [Daspre et al. 2009; Deschner et al. 2004; Emery Thompson  
64 and Wrangham 2008; Engelhardt et al. 2004; Garcia et al. 2009; Gesquiere et al. 2007;  
65 Higham et al. 2009] suggesting that they are able to make mating decisions based on the  
66 discrimination of fertility differences within female reproductive cycles. However, the  
67 signals and cues available to males for their mating decisions, and the relative reliability  
68 of these, are still poorly understood. There are several potential cues or signals involved  
69 in female primate ovulatory signaling: female behaviors [Bullivant et al. 2004;  
70 Engelhardt et al. 2005; Haselton et al. 2007; Higham et al. 2009; Miller et al. 2007; Van  
71 Belle et al. 2009], visual cues (e.g. sexual swelling and redness of face and sexual skin)  
72 [Bercovitch 1999; Dubuc et al. 2009; Gesquiere et al. 2007; Girolami and Bielert 1987;

73 Higham et al. 2008a, 2008b, 2010, 2011; Manning 1995; Nunn 1999; Roberts et al.  
74 2004; Waite et al. 2006], auditory signals (e.g. copulation calls) [Maestriperi et al.  
75 2005; Pfefferle et al. 2011; Pipitone and Gallup 2008; Pradhan et al. 2006; Semple et al.  
76 2002], and olfactory cues [Cerdeña Molina et al. 2006a, 2006b; Clarke et al. 2009;  
77 Havlicek et al. 2006; Keverne 1976; Matsumoto-Oda et al. 2007; Michael and Keverne  
78 1968, 1970; Michael and Zumpe 1982; Ober et al. 1997; Palagi et al. 2003].

79 In several primate species, the sexual swelling is one of the most conspicuous  
80 cues of fertility that could be used by males to allocate their mating activities [Dixon  
81 2012]. Besides swelling, several primate species exhibit color changes in the anogenital  
82 area and/or the face in relation to reproductive state [rhesus macaques: Dubuc et al.  
83 2009, Higham et al. 2010, 2011; mandrills: Setchell et al. 2006], but few studies have  
84 investigated the potential simultaneous links between female fertility, mating decisions,  
85 and red skin coloration in Catarrhine species. Changes in face coloration, but not in  
86 hindquarters, were related to the timing of ovulation in rhesus macaques [Dubuc et al.  
87 2009; Higham et al. 2010] and the closely related Japanese macaques [Fujita 2010],  
88 whereas a study of baboons found no relationship between sexual skin coloration and  
89 ovulation [Higham et al. 2008b]. The role of sexual skin coloration in mate preferences  
90 and mating decisions remains unclear for most species [Gauthier 1999; Hausfater 1975;  
91 Strum and Western 1982].

92 Similarly, whereas olfactory cues are associated with ovulation in a number of  
93 mammalian species, few attempts have been made to identify their use as a sexual  
94 signal in Catarrhines [Heymann 2006; Stevenson 2010]. Several studies have reported  
95 sniffing behaviors in a sexual context [Clarke et al. 2009; Engelhardt et al. 2004;  
96 Higham et al. 2009; Matsumoto-Oda et al. 2003, 2007; Van Belle et al. 2009] and

97 olfactory cues are known to advertise reproductive state, dominance rank, and  
98 individual identity in species such as lemurs and mandrills [Palagi et al. 2003; Setchell  
99 et al. 2010]. Female odors are also suggested to elicit both behavioral and  
100 endocrinological responses in male primates [Cerdeña-Molina et al. 2006a, 2006b;  
101 Keverne and Michael 1971; Michael and Zumpe 1982], and studies of macaques  
102 [Engelhardt et al. 2004] and baboons [Clarke et al. 2009; Higham et al. 2009] have  
103 suggested that olfactory cues may be critical elements in primate fertility signaling  
104 systems.

105       Earlier studies investigating primate sexual behavior have also yielded a  
106 contrasting picture of the extent to which female proceptive behavior may indicate the  
107 timing of ovulation to males. Female behavior has been related to the timing of  
108 ovulation in some species [e.g. humans: Bullivant et al. 2004; capuchins: Carosi and  
109 Visalberghi 2002; long-tailed macaques: Engelhardt et al. 2005], although such  
110 relationships may not be universal [e.g. Barbary macaques: Brauch et al. 2007; Japanese  
111 macaques: Garcia et al. 2009; olive baboons: Higham et al. 2009]. In primate species  
112 with a conspicuous sexual swelling whose size is correlated with the underlying  
113 probability of ovulation, such as baboons [Daspre et al. 2009; Gesquiere et al. 2007;  
114 Higham et al. 2008a], female proceptive behavior can be predicted to be more weakly  
115 linked to ovarian cycle stage. However, the importance of this signal in baboon  
116 ovulatory signaling has been relatively poorly investigated. In the only relevant study  
117 using hormonal profiles and female behaviors, Higham et al. [2009] showed that  
118 proceptive behaviors were unrelated to the timing of ovulation in baboons, although a  
119 number of potential indicators of female proceptivity were not measured and analyzed  
120 (i.e. female initiations and approaches).

121           Auditory cues in the context of sexual behavior, such as copulation calls, are  
122 relatively well described in some species of Old World monkeys and apes [long-tailed  
123 macaques: Engelhardt et al. 2012; Guinea baboons: Maestriperi et al. 2005; Barbary  
124 macaques: Pfefferle et al. 2011; yellow baboons: Semple et al. 2002; chimpanzees:  
125 Townsend et al. 2011]. These signals seem to be related to sexual hormones such as  
126 estrogen and progesterone levels though studies of almost all species have found that  
127 they do not accurately indicate the timing of ovulation [e.g. long-tailed macaques:  
128 Engelhardt et al. 2004; Barbary macaques: Pfefferle et al. 2008; but see crested  
129 macaques, Higham et al. 2012, which may be an exception]. Copulation calls provide  
130 information on female identities [Semple 2001; Townsend et al. 2011] which could  
131 influence female mating success [Maestriperi et al. 2005; Pfefferle et al. 2008] or  
132 decrease the capacity for male monopolization [Engelhardt et al. 2012; Townsend et al.  
133 2011]. Maestriperi and Roney [2005] suggested that copulation calls in baboons may  
134 aid postcopulatory female choice by enhancing sperm competition or promoting mate  
135 guarding, but as with olfactory cues and sex skin signals, their role in multimodal sexual  
136 signaling remains unclear for most species.

137           Among many primates with hierarchically-structured matrilineal social systems,  
138 males are also expected to use social parameters as further predictors of female fertility.  
139 They are predicted to discriminate in mating decisions based on fertility differences  
140 between females (if fertility changes with reproductive history or social parameters such  
141 as age and social rank, for instance), with males biasing their sexual behaviors  
142 particularly towards high-ranking and older females [Garcia et al. 2009; Muller et al.  
143 2006; Proctor et al. 2011]. Discriminating between high/low rank females or  
144 aged/young females may however only be relevant when both such females are



145 simultaneously available. Therefore, information from all other signal modalities should  
146 be salient in male mating behavior.

147 Baboons (*Papio anubis*) are an excellent species for exploring multimodal  
148 ovulatory signaling, since females exhibit a prominent sexual swelling, utter copulation  
149 calls during mating and produce vaginal secretions that could potentially offer  
150 information concerning the timing of ovulation. However, the simultaneous study of  
151 behavioral, visual (i.e. sexual skin size and color), auditory, and olfactory cues as  
152 signals of reproductive state in baboons has not been undertaken. This study was  
153 structured around four linked aims: 1) To determine the role of each female sexual  
154 signal (behavior, swelling, vocalization) in indicating the likely fertile phase; 2) To  
155 assess the inter-individual information content of signals by looking for correlates of  
156 female attributes such as social rank and age; 3) To relate male response to those signals  
157 by investigating changes in male sexual behavior (sexual mounts and olfactory  
158 inspections) with respect to the timing of ovulation and to the female characteristics. We  
159 seek to clarify whether males are discriminating in mating choices, e.g. whether they are  
160 most likely to mate with a given female at a given time (based on the likely fertile  
161 phase) and whether they are able to discriminate between females and to choose among  
162 several potential mates; 4) Ultimately, to examine whether females signal fertility in  
163 multiple modalities, and the extent to which males may utilize these different modalities  
164 in their decision-making.

165

## 166 **METHODS**

167 This research protocol was reviewed and approved by the appropriate institutional  
168 animal care and use committee (Comité Régional d’Ethique sur l’Expérimentation

169 Animale, Marseille, France). All research adhered to the legal requirements of the USA,  
170 and the specific principles of the American Society of Primatologists for the ethical  
171 treatment of animals.

172

### 173 **Subjects and Housing**

174 The subjects were 9 adult female olive baboons ranging in age from 5 to 19 years and  
175 housed in semi-free ranging conditions at the CNRS Primatology Station (Rousset-sur-  
176 Arc, France). We sampled 3 cycling and multiparous females (mean age =  $16.0 \pm SD$   
177  $6.6$  years) and 6 cycling and nulliparous females (mean age =  $6.2 \pm SD$   $0.8$  years).  
178 These females were part of a social group housed in Park 2 (220 m<sup>2</sup> enclosure with  
179 climbing apparatus), consisting of 57 individuals (2 adult males, 11 adult females, 7  
180 adolescent females, 8 subadult males, 21 juveniles and 8 infants). This study was  
181 conducted from February 2011 to the end of April 2011. Group composition remained  
182 unchanged during the study period and no major changes in the dominance hierarchy  
183 were observed. Animals had free access to water and they were fed three times per day  
184 with fruits and monkey pellets. Baboons at this study site breed throughout the year  
185 [Garcia et al. 2008].

186

### 187 **Behavioral observations**

188 Data were collected by a single observer (LR) via thirty-minute continuous focal animal  
189 sampling [Altmann 1974], yielding a total of 156 hours of observation (17.3 hours per  
190 female on average) over the 3-month study period. Focal samples were evenly  
191 distributed across days and weeks for all females, and were distributed between 9:00  
192 A.M. and 5:00 P.M. Focal subjects were rotated throughout the week, although this

193 depended somewhat on the schedule of image collection. Every effort was made to  
194 standardize the amount of time each female was sampled monthly by tabulating the  
195 number of samples for each female and making a special effort to sample any female for  
196 which data were lacking. During the 30-min samples, all social and sexual behaviors  
197 were recorded, along with the direction of behavior between the focal female and any  
198 adult male, and the identity of the other individual involved. *Ad libitum* data were also  
199 recorded for dominance hierarchy and mating activity. The total daily observation time  
200 was identical between days, and therefore there was no bias related to observation time  
201 on a given day in the estimation of the number of mounts and olfactory inspections  
202 observed per day.

203         Female and male dominance ranks were monitored using *ad libitum* data and  
204 were assessed by transcribing submissive (avoidances, retreats) and aggressive  
205 behaviors (initiation of attacks, threats, chases) as well as the outcome of dyadic  
206 interactions into an agonistic interaction matrix [see methods in Garcia et al. 2006].  
207 Female dominance rank order was deduced from the matrix of interactions among all  
208 females in the group and female ranks were expressed as a percentage of females  
209 dominated, with relative ranks ranging from 0 (low rank) to 1 (high rank). For the two  
210 adult males, we distinguished the  $\alpha$  male, i.e. the dominant male, and the  $\beta$  male.

211         During focal animal sampling, we recorded social behaviors between focal  
212 females and males, e.g. when a female was grooming or being groomed. Concerning  
213 sexual behaviors, we recorded behavioral indicators of proceptivity [Beach 1976;  
214 Campbell 2007]. Proceptivity refers to sexual behaviors displayed by females toward  
215 males to indicate their motivation to copulate [Van Belle et al. 2009]: these were  
216 approaches to males, sexual presentations to males, and copulation calls uttered during

217 copulation (see Table 1 for definitions and distribution). Male sexual behaviors directed  
218 toward females were used to assess male responses to females' signals; we recorded  
219 approaches by males, holding, ejaculatory and non-ejaculatory mounts, and olfactory  
220 (nasal) inspections of the anogenital area (Table 1). Changes in the rates of olfactory  
221 inspections by males were also used as a proxy for changes in the intensity of female  
222 olfactory signals. We also recorded proximity between males and the focal female at 1-  
223 min intervals; distances were classified in four categories (contact, less than 1 m, 1 to 2  
224 m and more than 2 m). Olfactory inspections and mounts (ejaculatory and non-  
225 ejaculatory) were also recorded by *ad libitum* observations.

226

### 227 **Reproductive parameters**

228 During the follicular phase of the menstrual cycle, the olive baboon anogenital area  
229 (AGA) increases in turgescence due to estrogenic stimulation [Dixson 1998]. Ovulation  
230 most commonly occurs during the last few days of maximal tumescence [Hendrickx and  
231 Kraemer 1969; Koyama et al. 1977], typically two days before the swelling subsides  
232 [Bercovitch 1987; Daspre et al. 2009; Higham et al. 2008a; Shaikh et al. 1982]. After  
233 ovulation, this decrease in swelling size coincides with a postovulatory rise in  
234 progesterone and a decrease in estrogen concentrations [Stevens 1997]. Daily records of  
235 morphological changes in the AGA and menstruation were made over 3 months. In  
236 addition, each female's reproductive history (parity and mean interbirth interval  
237 following surviving offspring) was known from colony records. It was not possible to  
238 investigate sexual signals with respect to infant survival because mortality rates are very  
239 low in this semi-free ranging population (Garcia, unpubl. data).

240 AGA characteristics analyzed here were: post-menstrual flat (immediately  
241 following menstruation, AGA is flat and uncolored), moderate genital swelling  
242 (reddening or partial tumescence of the AGA), large genital swelling (the volume of the  
243 swelling is maximal and bright pink), deflating swelling (the onset of detumescence was  
244 recognized from the appearance of wrinkles, reduction of visible tumescence and loss of  
245 coloration), full detumescence (no tumescence and pale colored).

246 Cycle length was calculated from the first day of menstruation to the subsequent  
247 first day of menstruation. The follicular phase was defined as the interval between the  
248 first day of menstruation and the estimated day of ovulation (2 days before  
249 detumescence), whereas the luteal phase comprised the period between the day of  
250 ovulation and the day before the next menstruation [see also Garcia et al. 2008]. A  
251 conceptive cycle was defined as the cycle prior to the onset of red coloration of the  
252 paracallosal skin of females, indicating pregnancy [Altmann 1970]. We analyzed a total  
253 of 13 menstrual cycles from the nine females, with all but one cycles non-conceptive.

254 We determined three distinct phases during the menstrual cycle. The  
255 periovulatory period, or fertile window, was then considered to be the time block  
256 covering the 2 days before detumescence (D0) plus the three preceding days in order to  
257 account for the life span of sperm in the female tract [humans, Wilcox et al. 1995]. The  
258 fertile phase was then defined as a period of 5 days (D-1 to D-5) [e.g. Barelli et al.  
259 2007; Brauch et al. 2007; Engelhardt et al. 2004; Heistermann et al. 2008], the period  
260 preceding this phase (D-6 to D-10) was taken to represent the prefertile phase (5 days)  
261 while the 5 days following the fertile phase were defined as postfertile phase (D0 to  
262 D+4). We only used data collected during this 15-day period in analyses.

263

**264 Assessment of sexual skin size and color**

265 Objective analysis of size and color of the sexual swelling followed Higham et al.  
266 [2008b]. We used a Canon EOS 350D camera with a 8 megapixel CMOS sensor and an  
267 EF 28-135mm f/3.5-5.6 IS USM lens. White balance was set manually with a X-Rite  
268 White Balance Card (GretagMacbeth ColorChecker) before every daily data collection.  
269 We collected images in RAW format with the flash disabled and with the shutter speed  
270 and aperture size determined automatically by the camera. We conducted image  
271 collection between 11:30 AM and 12:30 PM, a period preceding food distribution and  
272 characterized by locomotor activities.

273 To standardize images of size and color of the sexual swelling, we used a 30 x  
274 30 cm grid (with vertical and horizontal lines marked at 1 cm intervals) and a Gretag X-  
275 Rite Color Checker (24 colored squares of known and varying reflectance) placed on an  
276 easel 5 cm off the ground. Images of these two charts were taken immediately after the  
277 sexual swelling image. We placed the charts at the same distance from the camera as the  
278 subjects with camera settings being standardized such that the image of the swelling and  
279 the corresponding images of the charts were captured on all the same camera settings  
280 (same shutter speed and aperture size) [Bergman and Beehner 2008; Dubuc et al. 2009;  
281 Higham et al. 2008b]. This technique allowed images to be standardized such that size  
282 and color measurements were comparable across all images. A total of 95 images  
283 (mean=10; range=4-12 images) were used for color and size analysis. Females were  
284 photographed every day during their fully tumescent phase, and every other day during  
285 other phases.

286 We measured AGA color by integrating the color chart and swelling images into  
287 a single image. This image was converted to PNG format using Photoshop CS 5

288 (version 8) and exported in ColourWorker software (version 1.1 Beta). This software  
289 allows reflectance spectra to be extracted from selected parts of images as if they had  
290 been measured with a spectrometer [Stevens et al. 2009]. For the required reference  
291 spectra, we used samples of red signals from the long-tailed macaque (*Macaca*  
292 *fascicularis*), red uakari (*Cacajao rubicundus*), and mandrill (*Mandrillus sphinx*) taken  
293 from <http://vision.psychol.cam.ac.uk/spectra/>, as well as the human skin spectra with  
294 which the program already contains [Higham et al. 2010]. We assessed color from the  
295 whole sexual swelling and excluded anatomical parts like tails and callosities (Figure 1),  
296 taking measurements 3 times for each swelling, and using an average. The software  
297 estimates reflectance spectra in 5 nm intervals between 380 and 700 nm. We used these  
298 reflectance spectra to calculate the quantal catch of each of the three olive baboon  
299 receptors in response to the color [e.g. Stevens et al. 2009]. As peak spectral  
300 sensitivities are conserved across Old World monkeys [Jacobs and Deegan 1999], we  
301 took *Papio papio* peak spectral sensitivities from Bowmaker et al. [1991; 2003] and  
302 used a rhodopsin template [Govardosvskii et al. 2000] to estimate full sensitivity curves  
303 for each receptor. We then integrated the spectra and sensitivity curves using across a  
304 D65 “daylight” illuminance spectra across the whole visible spectrum to obtain our  
305 quantal catches for each receptor [Stevens et al. 2009]. As measures for use in our  
306 analyses, we then calculated the red-green opponency channel as  $(LW-$   
307  $MW)/(MW+LW)$  (to assess how swellings varied chromatically at long-wavelengths),  
308 and  $(MW+LW)/2$  as a luminance measure of how light-dark the swelling appeared  
309 [Higham et al. 2010; Stevens et al. 2009].

310 We used a method adapted from Higham et al. [2008b] to measure different  
311 dimensions of swellings using Photoshop CS5: the maximal swelling height (A), the

312 maximal swelling width (B) and the maximal labial width (C) (Figure 1). Measures  
313 were marked on the swelling's photo and copied on to the grid's photo where they were  
314 measured.

315

### 316 **Statistical analysis**

317 Data are expressed as mean  $\pm$  standard error of the mean (SE). We analyzed data using  
318 all 13 cycles (one cycle for 5 females and two cycles for 4 females). We averaged data  
319 from any 2 cycles per female, so that N=9 for the final analyses. Our sample size is  
320 comparable with previous studies of sexual swellings and reproductive behavior [e.g.  
321 Emery and Whitten 2003; Engelhardt et al. 2005; Higham et al. 2008a, 2009].  
322 Behavioral and swelling data were averaged for each female's three phases of the cycle  
323 (prefertile, fertile and postfertile). A mean rate (frequency per hour) was calculated from  
324 behavioral data for the three cycle phases. We also calculated the number of non-  
325 ejaculatory and ejaculatory mounts per day (sum of mounts observed during focal  
326 samples and *ad libitum* sampling) as well as the number of olfactory inspections per  
327 day. We log-transformed data and attempted to perform generalized linear models  
328 (GLM), but post-hoc tests of the homogeneity of variance in each model showed that  
329 data violated model assumptions. We therefore analyzed data using non-parametric  
330 statistics and permutation tests. Cycle length was analyzed by Friedman and Wilcoxon  
331 exact tests. Because of the size of our sample and the occasional missing value, we  
332 conducted permutation tests [Mundry 1999; Mundry and Fisher 1998] that prevent for  
333 type I errors and incorrect P-values. We generated 10,000 permutations with two-tailed  
334 P-values. The permutation analysis tests for an effect of cycle phase on the swelling  
335 data (color and size) and other variables of interest (proceptive behaviors, copulation



336 calls, and male sexual behaviors i.e. mounts and olfactory inspections). The analysis  
337 allows comparison of behavioral frequencies and swelling data across the three different  
338 phases. If results showed significant variation across these phases, we undertook post-  
339 hoc tests to compare each set of two phases against each other.

340 To test for a relationship between female signaling or male response and social  
341 characteristics (age and social rank), we used Spearman's rank exact correlation test.  
342 Given that age and parity are not independent, we only used age in our analysis.  
343 Correlations were performed for the overall 15-day period covering the pre-fertile, fertile  
344 and post-fertile phases. We therefore combined the Spearman's P-values using Fisher's  
345 omnibus test to correct for multiple testing [Haccou and Meelis 1994; Hohmann et al.  
346 2009]. This procedure combines a number of P-values into a single  $\chi^2$ -distributed  
347 variable with its degree of freedom equaling twice the number of P-values.

348 It may appear slightly circular to use detumescence to delineate the cycle phases  
349 and then relating swelling size to these phases. However, we used very fine-scale  
350 measurements of swelling size, and there is no reason to assume that such  
351 measurements will always peak just before detumescence (during our assumed fertile  
352 period). As such the swelling size measurements and our fertile phase estimates are  
353 independent. All analyses were conducted using SPSS 18.0 for Windows and R  
354 statistical software v.2.14.2 (R Development Core Team 2012) and used two-tailed  
355 probabilities with a significance level of 0.05.

356

## 357 **RESULTS**

### 358 **Menstrual cycle length**

359 The mean duration of the menstrual cycle was  $37.77 \pm \text{SE } 3.33$  days (range: 21-65  
 360 days). Cycle length did not differ significantly among the nine females (exact  
 361 Friedman's test:  $\chi^2=8.00$ ,  $\text{df}=8$ ,  $P=0.43$ ,  $N=9$ ) or between successive cycles on the same  
 362 females (exact Wilcoxon's test:  $Z=0.00$ ,  $P=1.00$ ,  $N=4$ ). The follicular phase had an  
 363 overall mean duration of  $21.00 \pm \text{SE } 1.68$  days (range: 15-38 days) and the luteal phase  
 364 lasted  $16.77 \pm \text{SE } 2.80$  days (range: 4-44 days). Only one (the  $\alpha$  female) of the 9  
 365 females conceived during the study period (during the second cycle after resumption of  
 366 cycling following post-partum amenorrhea).

367 Female age was not associated with menstrual cycle length (exact Spearman's  
 368 correlation test,  $r_s=-0.08$ ,  $P=0.080$ ). We found a negative relationship between female  
 369 relative rank and cycle length, with low-ranking females having longer cycles than  
 370 dominant ones ( $r_s=-0.78$ ,  $P=0.002$ ,  $N=9$ ). These longer cycles were due to longer luteal  
 371 phases ( $r_s=-0.73$ ,  $P=0.005$ ,  $N=8$ ); there were no changes in the duration of follicular  
 372 phase with respect to rank.

373

#### 374 **Relation between female sexual signals and the cycle phase**

375 Fine-scale measurements of maximal swelling height (A) varied significantly according  
 376 to cycle phase, with maximal size during the fertile phase (Permutation test, prefertile  
 377 vs. fertile:  $|t|_{10000}=6.79$ ,  $P=0.017$ ; fertile vs. postfertile:  $|t|_{10000}=7.08$ ,  $P=0.049$ ).  
 378 Concerning maximal swelling width (B) and maximal labial width (C), the difference  
 379 was only significant for the comparison between the prefertile and the fertile phases (B:  
 380  $|t|_{10000}=6.67$ ,  $P=0.022$ ; C:  $|t|_{10000}=7.31$ ,  $P=0.008$ ). Swelling height was strongly  
 381 correlated with labial and swelling widths during the fertile phase (A-C:  $r_s=0.68$ ,

382  $P < 0.001$ ; A-B:  $r_s = 0.69$ ,  $P < 0.001$ ;  $N = 9$ ); whereas labial and swelling widths did not  
 383 covary ( $r_s = 0.26$ ,  $P = 0.18$ ,  $N = 9$ ).

384 Concerning color, neither swelling luminance nor the red-green opponency  
 385 channel varied with respect to cycle phase (luminance:  $|t|_{10000} = 10.54$ ,  $P = 0.26$ ; red-  
 386 green:  $|t|_{10000} = 0.62$ ,  $P = 0.91$ ).

387 We recorded 186 events of proceptive behavior (see table 1 for distribution;  
 388 mean per female =  $20.67 \pm \text{SE } 11.40$ , range = 6-41), and 46 events of social grooming  
 389 during the study period. Females approached more males during the fertile phase  
 390 ( $|t|_{10000} = 39.24$ ,  $P = 0.040$ ; prefertile vs. fertile:  $|t|_{10000} = 7.00$ ,  $P = 0.044$ ; fertile vs.  
 391 postfertile  $|t|_{10000} = 8.19$ ,  $P = 0.020$ ; Figure 2) and spent more time in contact with males  
 392 during the fertile phase ( $|t|_{10000} = 62.38$ ,  $P = 0.013$ ; fertile vs. postfertile:  
 393  $|t|_{10000} = 10.72$ ,  $P = 0.002$ ). The rates of female presentations did not vary according to  
 394 cycle phase ( $|t|_{10000} = 0.57$ ,  $P = 0.95$ ). Grooming performed by females towards males  
 395 did not vary according to cycle phase (grooming frequency:  $|t|_{10000} = 23.37$ ,  $P = 0.16$ ).  
 396 The number of copulation calls emitted by females per hour did not vary according to  
 397 cycle phase ( $|t|_{10000} = 4.53$ ,  $P = 0.16$ ).

398 Concerning the relationship between the different female signals, we found that  
 399 the frequency of female approaches during the fertile phase was strongly related to fine-  
 400 scale variation in swelling size, e.g. swelling width ( $r_s = 0.77$ ,  $P = 0.015$ ,  $N = 9$ ). None of  
 401 the other female signals were correlated to each other (all  $P > 0.10$ ,  $N = 9$ ). Moreover, size  
 402 (A, B and C) and color (luminance and red-green channel) of the swelling did not  
 403 covary (all  $P > 0.10$ ,  $N = 9$ ).

404

405 **Female sexual signals in relation to female characteristics**

406 Neither female age nor rank was correlated with swelling color (effect of age:  
 407 luminance:  $r_s=0.48$ ,  $P=0.19$ ; red-green:  $r_s=-0.28$ ,  $P=0.47$ ;  $N=9$ ; effect of rank:  
 408 luminance:  $r_s=0.28$ ,  $P=0.46$ ; red-green:  $r_s=0.28$ ,  $P=0.46$ ;  $N=9$ ) or swelling size during  
 409 the fertile phase (all  $P>0.10$ ,  $N=9$ ).

410 Rates of female approaches and presentations during the postfertile phase  
 411 differed according to female rank (Fisher's omnibus test: approaches:  $\chi^2=12.91$ ,  $df=6$ ,  
 412  $P=0.044$ ; presentations:  $\chi^2=13.65$ ,  $df=6$ ,  $P=0.034$ ), with high-ranking females  
 413 performing more approaches ( $r_s=0.78$ ,  $P=0.023$ ,  $N=8$ ) and more presentations ( $r_s=0.85$ ,  
 414  $P=0.005$ ,  $N=8$ ) toward males than subordinate females did. None of the female  
 415 proceptive behaviors during the fertile phase were correlated with female age (all  
 416  $P>0.10$ ,  $N=9$ ). Copulation calls and olfactory cues were not related to female age or  
 417 rank (fertile phase, all  $P>0.10$ ,  $N=9$ ).

418

419 **Male sexual behaviors with respect to the timing of ovulation and to the female**  
 420 **characteristics**

421 The analysis of male sexual responses to female signals was based on a total of 278  
 422 observed behavioral interactions (see table 1 for distribution; mean per individual= $30.89$   
 423  $\pm$  SE  $17.85$ , range= $11-68$ ). Rates of male approaches and holding behaviors varied  
 424 significantly according to cycle phase (approaches:  $|t|_{10000}=102.97$ ,  $P<0.001$ ; holding:  
 425  $|t|_{10000}=73.07$ ,  $P<0.001$ ), with higher rates during the fertile phase (approaches:  
 426 prefertile vs. fertile:  $|t|_{10000}=11.28$ ,  $P=0.002$ ; fertile vs. postfertile:  $|t|_{10000}=13.31$ ,  
 427  $P<0.001$ , Figure 3; holding: fertile vs. postfertile:  $|t|_{10000}=11.82$ ,  $P<0.001$ ). Male  
 428 olfactory inspections tended to be higher during the fertile and postfertile phases  
 429 (number of olfactory inspections received by females per day: prefertile vs. fertile:

430  $|t|_{10000}=6.00$ ,  $P=0.059$ ; prefertile vs. postfertile:  $|t|_{10000}=6.25$ ,  $P=0.063$ , Figure 4).  
 431 We also recorded 88 events of social grooming. We found that grooming frequency  
 432 varied according to cycle phase ( $|t|_{10000}=36.31$ ,  $P=0.034$ ) and was highest during the  
 433 fertile phase (fertile vs. postfertile:  $|t|_{10000}=8.31$ ,  $P=0.012$ ).

434 We recorded a total of 76 mounts performed by adult males during the study  
 435 period (i.e. during focal observations and *ad libitum* sampling); 90.79% were  
 436 ejaculatory mounts. The number of ejaculatory mounts performed by males per day  
 437 tended to vary between the fertile and postfertile phases ( $|t|_{10000}=3.30$ ,  $P=0.061$ ),  
 438 whereas the number of non-ejaculatory mounts per day did not vary according to cycle  
 439 phase ( $|t|_{10000}=5.68$ ,  $P=0.28$ ).

440 The number of ejaculatory mounts performed by adult males and received by a  
 441 female per day during the fertile phase tended to be positively associated with her rank,  
 442 with high-ranking females tending to receive more ejaculatory mounts (Fisher's  
 443 omnibus test:  $\chi^2=16.77$ ,  $df=6$ ,  $P=0.01$ ;  $r_s=0.63$ ,  $P=0.067$ ,  $N=9$ ). None of the other male  
 444 behaviors were related to female age or rank (fertile phase, all  $P>0.10$ ,  $N=9$ ).

445 The number of ejaculatory mounts received by females per day during the fertile  
 446 phase was not correlated with the size or the color of the sexual swelling (A:  $r_s=-0.26$ ;  
 447 B:  $r_s=0.07$ ; C:  $r_s=0.47$ ; luminance:  $r_s=0.58$ ; red-green:  $r_s=-0.60$ ; all  $P>0.10$ ,  $N=9$ ). We  
 448 found a negative relationship between the number of male olfactory inspections, and  
 449 swelling height ( $r_s=-0.76$ ,  $P=0.017$ ;  $N=9$ ).

450

## 451 **DISCUSSION**

452 Male baboons in our study can reliably discriminate intra-cycle differences in fertility  
 453 but do not accurately discriminate inter-individual differences. Males may be more

454 stimulated to mate with females at the appropriate time due to behavioral and visual  
455 cues (e.g. female behavior and sexual swelling size), while sexual skin color and  
456 auditory cues (i.e. copulation calls) seem to be uninformative concerning the intra-cycle  
457 probability of fertility. Males already in consort with a fully swollen female may have  
458 access to additional olfactory cues, which could allow them to time their mating to  
459 ovulation more accurately. These results are consistent with a multimodal framework  
460 for ovulatory signaling in olive baboons.

461

#### 462 **The role of female sexual signals in indicating the fertile phase**

463 Females displayed several informative clues of ovulatory state. Sexual swelling size  
464 acted as a visual signal that correlated with the fertile phase [see also Brauch et al. 2007;  
465 Daspre et al. 2009; Deschner et al. 2004; Gesquiere et al. 2007; Higham et al. 2008a;  
466 Möhle et al. 2005]. Females also exhibited more approaches and spent more time close  
467 to males during their fertile phase, suggesting that proceptive behaviors were potentially  
468 informative to males about female fertility as seen in a number of other species [e.g.  
469 long-tailed macaques: Engelhardt et al. 2005; humans: Gangestad et al. 2002, Miller et  
470 al. 2007; howler monkeys: Van Belle et al. 2009]. These results contrast with those  
471 from other studies of some species of non-human primates, in which such behaviors  
472 have not been found to increase around the fertile phase [Barbary macaques: Brauch et  
473 al. 2007; chimpanzees: Emery Thompson and Wrangham 2008; Japanese macaques:  
474 Garcia et al. 2009; olive baboons: Higham et al. 2009]. In Higham et al.'s [2009]  
475 baboon study, some proceptive behaviors, such as presentations, were related to sex  
476 hormones but there was no relationship between these behaviors and the timing of  
477 ovulation specifically. However, Higham et al. [2009] did not have data on female

478 initiations and approaches as in the present study. Besides visual and behavioral signals,  
479 we also found that olfactory cues, as indexed by male olfactory inspections, tended to  
480 be higher during the fertile and postfertile phases [Cerdeña-Molina et al. 2006b; Clarke et  
481 al. 2009; Van Belle et al. 2009], i.e. when consortship is already established. Olfactory  
482 signals may allow consorting males to detect subtle changes in vaginal secretions which  
483 may encode information concerning the timing of ovulation. These olfactory signals  
484 could have proximate effects on mating: they could stimulate male sexual interest and  
485 behaviors, especially ejaculatory mounts, by promoting sperm production [Keverne  
486 1976; Matsumoto-Oda et al. 2003; Wallen 2001] and mate guarding [Smith 2006].  
487 These cues could also facilitate penis intromission and ejaculation by lubricating the  
488 vagina during the most fertile phase. The role of olfactory cues in ovulatory  
489 communication still remains unclear but they could be crucial to influencing mating  
490 choices.

491 Females also displayed other clues which may be uninformative concerning the  
492 timing of the fertile phase. As with previous studies [long-tailed macaques: Engelhardt  
493 et al. 2004, 2012; Barbary macaques: Pfefferle et al. 2011], auditory signals, i.e.  
494 copulation calls, did not indicate the likely fertile phase. The most commonly cited and  
495 best-supported hypotheses for the function of copulation calls focus on their role in  
496 inducing male-male competition, and potentially sperm competition, but also in  
497 increasing mate guarding by the copulating male, by informing other males that  
498 copulation has occurred [Maestriperi and Roney 2005; Maestriperi et al. 2005;  
499 Pfefferle et al. 2008]. However, in our captive context, male competition was low (i.e.  
500 only two adult males with preferred mating females) and the distances between males  
501 and females were relatively small, such that females may not need to advertise their

502 ovulatory status by long-distance clues. Therefore, these auditory signals may be of  
503 lesser important to indicating ovulation. We also found no sexual swelling color  
504 variation specifically associated with the differences in cycle phases, consistent with  
505 previous findings of olive baboons [Higham et al. 2008b]. Baboons differ from species  
506 with reproductive state changes in facial skin color, such as macaques, where facial  
507 signal variation is suggested to contain reliable information about the timing of  
508 ovulation [e.g. rhesus macaques: Dubuc et al. 2009, Higham et al. 2010]. In species  
509 where sexual swellings are small or lacking [e.g. rhesus macaques: Dubuc et al. 2009;  
510 Japanese macaques: Garcia et al. 2009], face coloration could be a highly visible cue  
511 available to males at a considerable distance to gauge the timing of the fertile phase. In  
512 baboons, on the other hand, with large advertisements of fertility, e.g. exaggerated  
513 sexual swelling, sexual skin color variation may be of lesser important to indicating the  
514 likely fertile phase.

515

#### 516 **Female sexual signals of inter-individual differences**

517 Swelling size was not correlated with female rank or age and thus sexual swellings did  
518 not seem to advertise a female's reproductive value as predicted by the reliable-  
519 indicator hypothesis [Domb and Pagel 2001; Pagel 1994], but rather were in line with  
520 the graded-signal hypothesis [Nunn 1999; Nunn et al. 2001], representing probabilistic  
521 intra-cycle signals of the likelihood of ovulation. Our results contrast with another study  
522 in baboons showing that sexual swelling size was a reliable indicator of maturation  
523 stage fertility differences [Gesquiere et al. 2007]; and the question of whether sexual  
524 swellings represent a sexually selected signal of enduring individual-level differences  
525 remains unanswered.



526 That sexual skin color did not indicate female age or rank again contrasts with  
527 studies of mandrills [Setchell and Wickings 2004; Setchell et al. 2006], and the  
528 signaling functions of baboon sexual swellings are still far from being fully understood.  
529 Intra-specific variability is extraordinarily important in papionins, raising the possibility  
530 that swellings may have different functions in different species and even populations  
531 [Higham et al. 2009]. Further comparative studies in this taxon are required.

532 Neither copulation calls nor olfactory signals were found to be informative of  
533 female characteristics, again in contrast to previous studies [copulation calls: Guinea  
534 baboons: Maestriperi et al. 2005; Chacma baboons: O'Connell and Cowlishaw 1994;  
535 olfactory cues: mandrills: Setchell et al. 2010]. The only phenotypic trait conveying  
536 information about female characteristics, e.g. dominance status, was female behavior.

537

#### 538 **Male response to female signals: are males discriminating in mating choices?**

539 Adult males were able to discriminate intra-cycle differences in fertility. They displayed  
540 more sexual behaviors and tended to direct more ejaculatory mounts toward females  
541 during the expected time of ovulation [as in Daspre et al. 2009; Higham et al. 2009],  
542 which suggests that male olive baboons can use female sexual signals to discriminate  
543 intra-cycle differences in fertility. Two mechanisms could explain the relationship  
544 between male sexual behaviors and cycle phase: a passive response to changes in  
545 female sexual signals and an active concentration of male mating effort. Since  
546 proceptive behaviors varied in relation to the timing of ovulation, we suggest that these  
547 female behaviors may mediate the temporal links between male mating activities and  
548 period of the cycle. Moreover, the fact that we only found an increase in the number of  
549 ejaculatory mounts during the fertile period and not in the number of non-ejaculatory

550 mounts suggests that males may actively concentrate their reproductive effort during the  
551 period of highest probability of conception. It could also be argued that different female  
552 signals (e.g. female behaviors and olfactory cues) may stimulate male responses.

553 Males tended to bias their sexual behaviors toward high-ranking females [Garcia  
554 et al. 2009; Muller et al. 2006; Proctor et al. 2011; Zumpe and Michael 1996],  
555 suggesting that female mating success was dominance-rank related. As visual, auditory  
556 and olfactory cues were not found to convey information about female characteristics,  
557 we suggest that males could use behavioral cues to discriminate among females based  
558 on rank differences. Contrary to previous studies [yellow baboons: Gesquiere et al.  
559 2007; chimpanzees: Muller et al. 2006, Proctor et al. 2011], we found that males did not  
560 preferentially mate with older females.

561

### 562 **Multimodal signaling of fertility**

563 A variety of elements acted in concert to provide information to males about the timing  
564 of the fertile phase. A multimodal framework of signals provides clues as to female  
565 reproductive status in olive baboons, with signals being displayed in several sensory  
566 modalities [Candolin 2003]. The use of multiple cues (swelling size, behavioral traits  
567 and olfactory cues) is consistent with the back-up hypothesis [Johnstone 1997; Møller  
568 and Pomiankowski 1993] which proposes that multiple signals allow a more accurate  
569 assessment of mate quality and a decrease in mate choice errors.

570 Our results are also consistent with previous suggestions that all males present  
571 could have information about the fertile window, through female behavioral signaling  
572 and sexual swelling size, but that only consorting males could accurately determine the  
573 timing of highest ovulation probability through precise olfactory signals that are only

574 accessible from close range [baboons: Clarke et al. 2009, Higham et al. 2009; long-  
575 tailed macaques: Engelhardt et al. 2004]. They are also in agreement with previous  
576 suggestions that differential distribution and access to ovulatory clues, due to the  
577 different “active spaces” of different signals [Candolin and Reynolds 2001; Lopez and  
578 Martin 2001], may allow females and males to establish different mating strategies.

579         The use of multiple sexual signals by females may consist of a tradeoff between  
580 costs of sexual signaling and benefits from mating. As previously suggested [Higham et  
581 al. 2009], by combining long-distance signals such as swelling size, and short-distance  
582 cues such as olfactory components, for which different males (i.e. consorting and non-  
583 consorting males) have differential access, females may assure (by promoting mate  
584 guarding) and confuse (by increasing male and sperm competition) paternity  
585 simultaneously [Nunn 1999; van Schaik 2000]. Moreover, females may decouple these  
586 two signals (e.g. swelling size and olfactory cues) and provide slightly misleading  
587 information about their reproductive status to non-consorting males through slight  
588 changes in swelling size while they are more fertile, whereas the consorting male could  
589 still use olfactory cues to detect ovulation. If only a subset of males is able to get close  
590 enough to key in on cues available only at close-range (such as olfactory or tactile  
591 signals), indirect female choice may be operating.

592         On the other hand, males may combine information from multiple cues and  
593 signals of the probability of ovulation in order to discriminate in mating choices and to  
594 reduce the cost of mating (sperm production and active mate guarding). By increasing  
595 the number of sensory modalities, males may obtain more information. Moreover, a  
596 sequential use of multiple female signals may allow males to reduce mate choice costs.  
597 When multiple cues are used sequentially, a first cue (e.g. morphological traits of the

598 sexual swelling) may indicate which females are worth inspecting for a second cue that  
599 is more costly to evaluate than the first but that gives more precise information about  
600 mate quality (olfactory and tactile cues). This strategy could reduce the number of  
601 females that are inspected more closely and, thus, mate-choice costs. That olfactory  
602 inspections were reduced, rather than increased, when swelling height was maximal,  
603 does not invalidate this suggestion, but rather may imply that the strength of the  
604 olfactory cues is higher during this phase of the cycle, such that males need not directly  
605 inspect females to detect them.

606

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618

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920

921 **Table 1.** Definitions of female and male sexual behaviors recorded.

922 **Figure 1:** Picture of a sexual swelling with Gretag color standard, showing measures of  
923 the maximal height (A), the maximal swelling width (B) and the maximal labial width  
924 (C).

925 **Figure 2:** Comparison between the prefertile, fertile, and postfertile phases concerning  
926 the frequency of approaches directed by females toward adult males. The figure shows  
927 mean  $\pm$  SEM.

928 **Figure 3:** Comparison between the prefertile, fertile, and postfertile phases concerning  
929 the frequency of approaches directed by adult males toward females. The figure shows  
930 mean  $\pm$  SEM.

931 **Figure 4:** Comparison between the prefertile, fertile, and postfertile phases concerning  
932 the frequency of olfactory inspections performed by adult males. The figure shows  
933 mean  $\pm$  SEM.

Figure 1

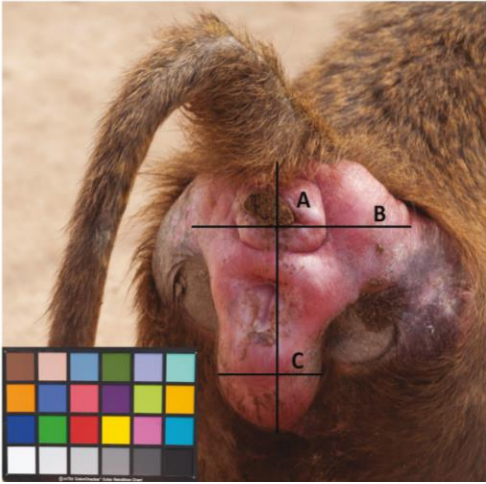


Figure 2

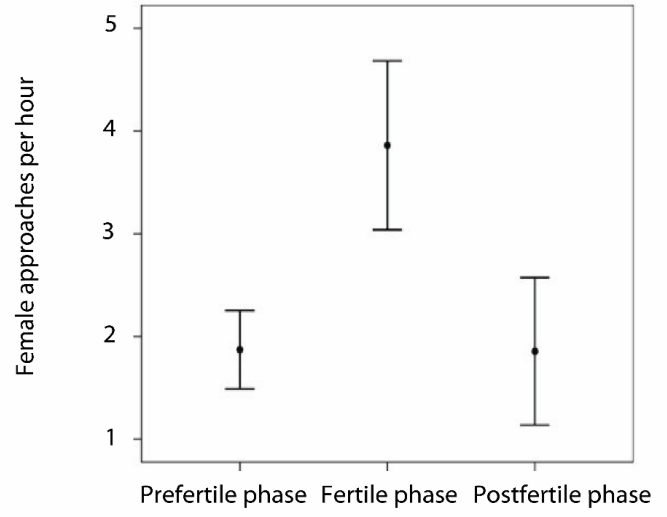


Figure 3

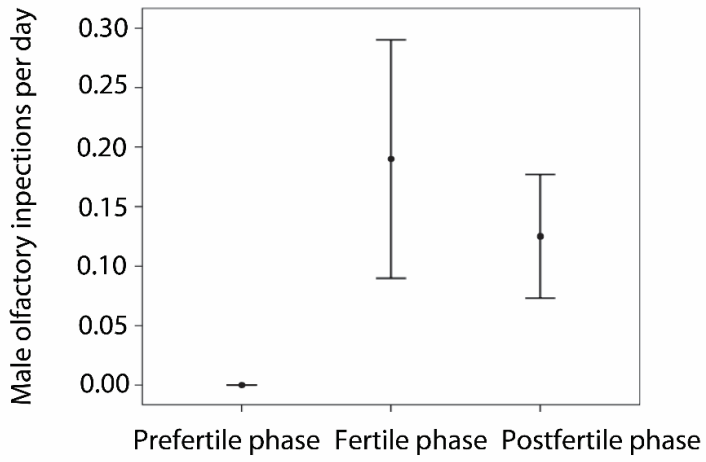
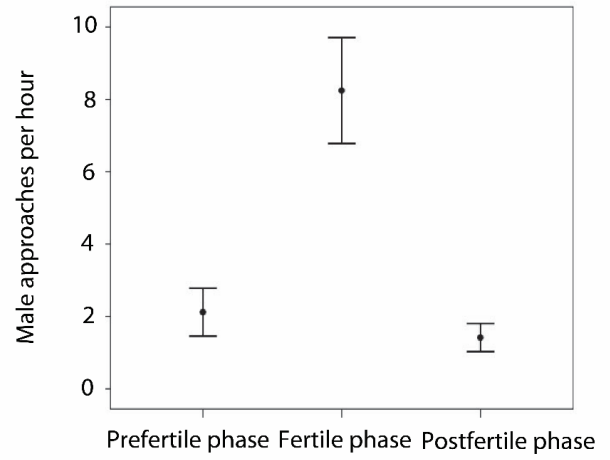


Figure 4



**Table 1.** Definitions of female and male sexual behaviors recorded.

	Female behaviors	Number of events recorded during focal sampling
Approaches	Female comes close (less than 1m) or in contact with a male	120
Sexual presentations	Female directs her anogenital area toward a male, the tail is generally raised to expose sexual swelling	45
Copulation calls	Female utters special vocalizations during the last stage of the mount	21
	Male behaviors	Number of events recorded during focal sampling
Approaches	Male comes close (less than 1m) or in contact with a female	212
Holding behaviors	Male grabs female hips, generally observed just before mating	52
Mounts	- Ejaculatory mounts: male mounts a female, with intromission and ejaculation (i.e. successful)	34
	- Non-ejaculatory mounts: male mounts a female, with intromission but without ejaculation (i.e. unsuccessful)	4
Olfactory inspections	Deliberate placing of the nostrils to within 5 cm of a female's anogenital area [cf. Clarke et al. 2009]. Male sniffs female's anogenital area or licks his finger after a tactile inspection.	14