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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

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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) [Maestri 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 m² 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 α male, i.e. the dominant male, and the β 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 χ^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: $\chi^2=8.00$, $\text{df}=8$, $\text{P}=0.43$, $\text{N}=9$) or between successive cycles on the same
 362 females (exact Wilcoxon's test: $\text{Z}=0.00$, $\text{P}=1.00$, $\text{N}=4$). 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 α 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, $r_s=-0.08$, $\text{P}=0.080$). We found a negative relationship between female
 369 relative rank and cycle length, with low-ranking females having longer cycles than
 370 dominant ones ($r_s=-0.78$, $\text{P}=0.002$, $\text{N}=9$). These longer cycles were due to longer luteal
 371 phases ($r_s=-0.73$, $\text{P}=0.005$, $\text{N}=8$); 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: $|t|_{10000}=6.79$, $\text{P}=0.017$; fertile vs. postfertile: $|t|_{10000}=7.08$, $\text{P}=0.049$).
 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 $|t|_{10000}=6.67$, $\text{P}=0.022$; C: $|t|_{10000}=7.31$, $\text{P}=0.008$). 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 = $20.67 \pm SE 11.40$, 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

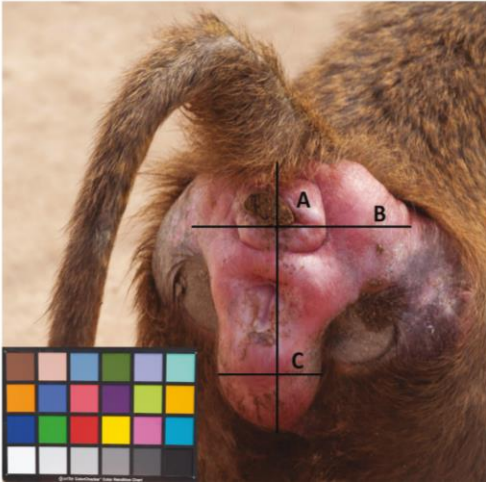


Figure 2

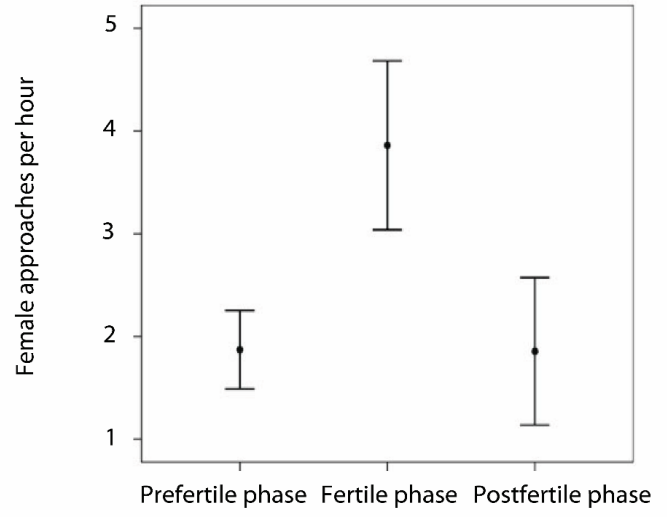


Figure 3

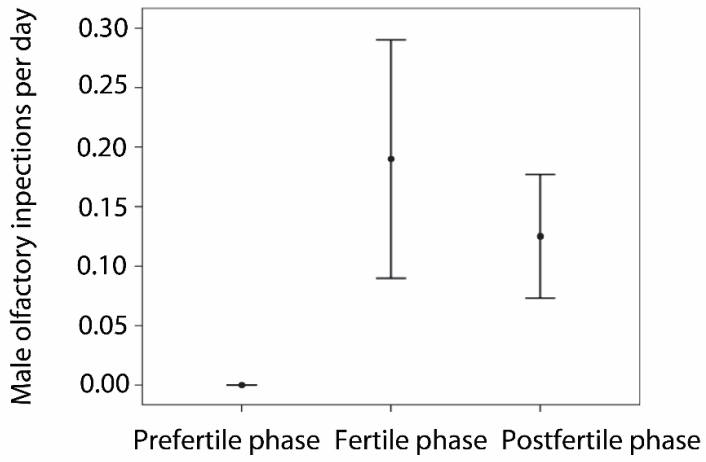


Figure 4

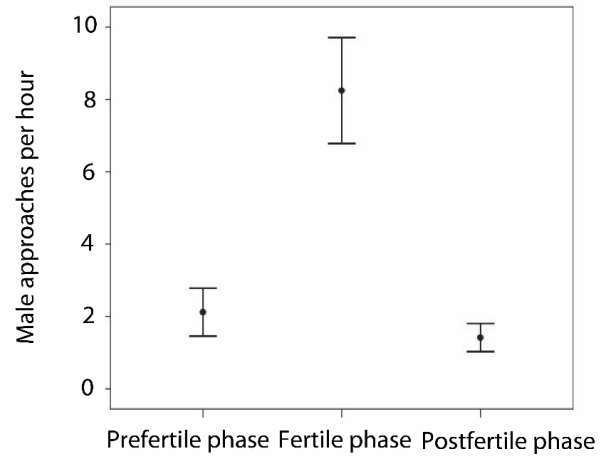


Table 1. Definitions of female and male sexual behaviors recorded.

	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