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

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Short title: Sexual signaling in olive baboons

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## Abstract

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

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

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

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

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

Similarly, whereas olfactory cues are associated with ovulation in a number of mammalian species, few attempts have been made to identify their use as a sexual signal in Catarrhines [Heymann 2006; Stevenson 2010]. Several studies have reported sniffing behaviors in a sexual context [Clarke et al. 2009; Engelhardt et al. 2004; 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).

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

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



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

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

## METHODS

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

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

### **Subjects and Housing**

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

### **Behavioral observations**

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

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

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

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

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

### **Reproductive parameters**

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

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

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

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

## Assessment of sexual skin size and color

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

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

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

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

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

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

### Statistical analysis

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



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

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

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

## RESULTS

### Menstrual cycle length

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

The number of ejaculatory mounts performed by adult males and received by a female per day during the fertile phase tended to be positively associated with her rank, with high-ranking females tending to receive more ejaculatory mounts (Fisher's 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 behaviors were related to female age or rank (fertile phase, all  $P>0.10$ ,  $N=9$ ).

The number of ejaculatory mounts received by females per day during the fertile phase was not correlated with the size or the color of the sexual swelling (A:  $r_s=-0.26$ ; 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 found a negative relationship between the number of male olfactory inspections, and swelling height ( $r_s=-0.76$ ,  $P=0.017$ ;  $N=9$ ).

## DISCUSSION

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

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

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

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

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

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

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



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

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

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

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

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

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

### **Multimodal signaling of fertility**

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

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

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

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

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

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

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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

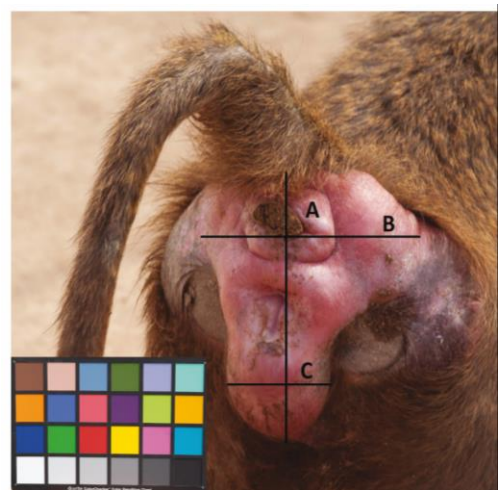


Figure 2

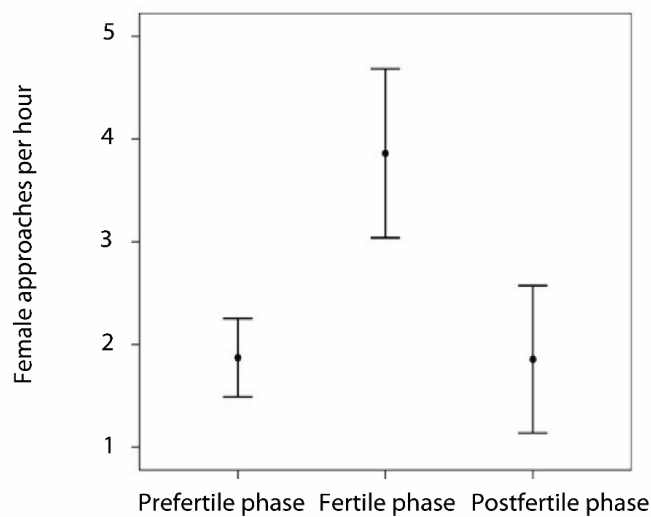


Figure 3

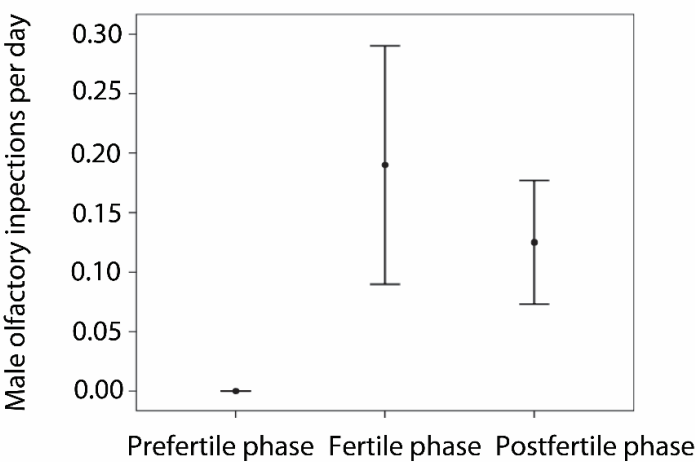
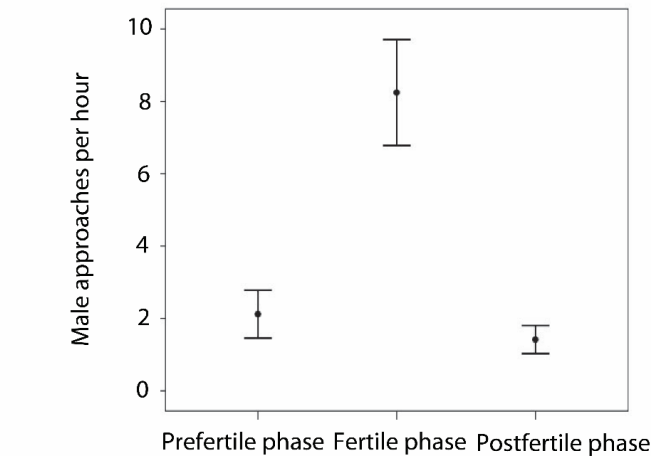


Figure 4



**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