Chemical cues of identity and reproductive status in Japanese macaques

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Short title: Chemical signaling in Japanese macaques

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Abstract

Olfactory communication plays an important role in the regulation of socio-sexual interactions in mammals. There is growing evidence that both human and non-human primates rely on odors to inform their mating decisions. Nevertheless, studies of primate chemical ecology remain scarce due to the difficulty of obtaining and analyzing samples. We analyzed 67 urine samples from 5 captive female Japanese macaques (*Macaca fuscata*) and 30 vaginal swabs from 3 of these females using gas chromatography–mass spectrometry and examined the relationship between odor (compounds identified, richness, intensity, and diversity) and female identity as well as cycle phase. We found a total of 36 urine compounds of which we identified 31, and 68 vaginal compounds of which we identified 37. Our results suggest that urine and vaginal odor varied more between individuals than within cycle phases. However, we found that within a female cycle, urine samples from similar phases may cluster more than samples from different phases. Our results suggest that female odor may encode information about identity (vaginal and urine odor) and reproductive status (urine odor). The question of how conspecifics use female urine and vaginal odor remains open and could be tested using bioassays. Our results and their interpretation are constrained by our limited sample size and our study design. Nonetheless, our study provides insight into the potential signaling role of female odor in sexual communication in Japanese macaques and contributes to our understanding of how odors may influence mating strategies in primates.

Keywords: olfactory communication, gas chromatography–mass spectrometry, sexual signaling, urine and vaginal odor, *Macaca fuscata*

Introduction

Communication plays a crucial role in mating decisions. Individuals are expected to choose or avoid potential mates based on the costs (e.g., disease transmission, energy investment, sexual competition, parental investment) and benefits (e.g., good genes, social support, increased fitness) associated with mating (Beltran-Bech & Richard, 2014; Møller et al., 1999; Thrall et al., 2000; Trivers, 1972). As a result, individuals exchange information about their attributes, including social rank, genotype, health, and fertility (e.g., sexual maturity, reproductive status) (Candolin, 2003; Snowdon, 2004), directly and indirectly benefitting both emitters and receivers. Emitters may attract potential mates and enhance intra-sexual competition, thus simultaneously increasing their mating opportunities and chances of producing attractive and strong offspring (*sexy-sons/daughters* and *good genes* hypotheses R. A. Fisher, 1915; Hamilton & Zuk, 1982). Meanwhile, receivers may balance the cost of mating by focusing their mating effort on mates that are fertile and capable of dealing with the costs of reproduction and by using information about their rivals' state to adjust their mating strategies to the level of competition.

Like many other animals, primates communicate through multiple sensory channels. Females display multiple traits that are attractive to males and correlate with their fixed (e.g., social rank, age) or variable (e.g., reproductive status) attributes (Tables 1-2). Most studies of these traits have focused on female visual traits such as sexual swellings (enlargement of the anogenital area) and skin coloration in relation to fertility, probably because the sense of vision is particularly well developed in primates (Jacobs, 2008; Osorio & Vorobyev, 2005). Females can also inform conspecifics about their fertility through auditory (vocalizations or voice), behavioral (proceptive behaviors), and olfactory (odors) traits (Table 1).

65 **Table 1.** Examples of the potential ovulatory signaling function of female behavioral, visual, auditory, and olfactory traits in primates.

Species	**Female trait**	**Reproductive status**	**Evidence**
common marmosets, *Callithrix jacchus*	Anogenital odor	Correlates with the fertile phase.	Encoded information and receivers' response (Kücklich et al., 2019)
pygmy marmosets, *Cebuella pygmaea*	Anogenital gland or secretion odor	Correlates with the fertile phase.	Receivers' response (Converse et al., 1995)
tufted capuchins, *Cebus apella*	Proceptive behaviors	Correlate with the fertile phase.	Encoded information (Carosi & Visalberghi, 2002)
crested macaques, *Macaca nigra*	Sexual swelling (size)	Correlates with the fertile phase and conception[1] and swellings are not expressed during pregnancy.	Encoded information (Higham et al., 2012)
	Proceptive behaviors	Correlate with the fertile phase and conception.	
	Copulation calls	Correlate with the fertile phase.	
Barbary macaques, *Macaca sylvanus*	Sexual swelling (size)	Correlates with the fertile phase and swellings are expressed during early pregnancy.	Encoded information (Brauch et al., 2007; Möhle et al., 2005; Young et al., 2013)
	Proceptive behaviors	Not clear.	Encoded information (Brauch et al., 2007; Young et al., 2013)
	Copulation calls	Do not correlate with the fertile phase.	Encoded information (Pfefferle et al., 2008, 2011; Semple & McComb, 2000) Receivers' response (Semple & McComb, 2000)
stumptailed macaques, *Macaca arctoides*	Vaginal secretions	May indicate the periovulatory period and stimulate male sexual arousal	Receivers' response (Cerda-Molina et al., 2006)
long-tailed macaques, *Macaca fascicularis*	Sexual swelling (size)	Does not correlate with the fertile phase and swellings are expressed during early pregnancy.	Encoded information (Engelhardt et al., 2005, 2007)

	Proceptive behaviors	Correlate with the fertile phase and are expressed during the early pregnancy.	
	Copulation calls	Do not correlate with the fertile phase.	Encoded information (Engelhardt et al., 2012)
Japanese macaques, *Macaca fuscata*	Red skin coloration (face and hindquarters)	Correlates with the pregnancy period (face coloration) but not with the fertile phase or conception.	Encoded information (Rigaill et al., 2015; Rigaill, MacIntosh, et al., 2017; Rigaill et al., 2019) Receivers' response (Rigaill & Garcia, 2021)
	Proceptive behaviors	Correlate with the pregnancy period but not with the fertile phase.	Encoded information (Garcia et al., 2009; O'Neill et al., 2004; Rigaill et al., 2015)
	Copulation and 'estrus' calls	Do not correlate with the fertile phase, and may correlate with pregnancy.	
	Urine odor	May not correlate with the fertile phase.	Receivers' response (Rigaill, Suda-Hashimoto, et al., 2017)
rhesus macaques, *Macaca mulatta*	Red skin coloration (face)	Correlates with the fertile phase.	Encoded information (Dubuc et al., 2009; Higham et al., 2010) Receivers' response (Higham et al., 2011)
olive baboons, *Papio anubis*	Sexual swelling (size or shape)	Correlates with the fertile phase and pregnancy.	Encoded information (Altmann, 1970; Higham, Heistermann, et al., 2008; Higham, MacLarnon, et al., 2008; Rigaill et al., 2013)
	Red skin coloration (sexual swelling)	Correlates with pregnancy status but not with the fertile phase.	Encoded information (Higham, MacLarnon, et al., 2008; Rigaill et al., 2013)
	Proceptive behaviors	May correlate with the fertile phase.	Encoded information (Higham et al., 2009; Rigaill et al., 2013)
	Vaginal secretions	Correlate with the fertile phase	Encoded information (Vaglio et al., 2021) Receivers' response (Rigaill et al., 2013)
yellow baboons, *Papio cynocephalus*	Copulation calls	Do not correlate with the fertile phase.	Encoded information and receivers' response (Semple, 2001; Semple et al., 2002)
chacma baboons, *Papio ursinus*	Vaginal odor	Correlates with the fertile phase	Receivers' response (P. M. R. Clarke et al., 2009)

mandrills, *Mandrillus sphinx*	Sexual swelling (size or shape)	May not correlate with conception.	Encoded information (Huchard et al., 2009; Setchell & Wickings, 2004a, 2004b)
	Red skin coloration (sexual swelling)	May not correlate with conception.	Encoded information (Setchell, Charpentier, et al., 2006; Setchell & Wickings, 2004a)
	Red skin coloration (face)	Correlates with the pregnancy status, but not with the fertile phase or conception.	Encoded information (Setchell et al., 2009; Setchell, Wickings, et al., 2006)
sooty mangbeys, *Cercocebus torquatus atys*	Sexual swelling (size)	Correlates with the fertile phase but not with pregnancy.	Encoded information (Gordon et al., 1991)
howler monkeys, *Alouatta pigra*	Proceptive behaviors	Correlate with the fertile phase.	Encoded information (Van Belle et al., 2009)
bonobos, *Pan paniscus*	Sexual swelling (size)	Does not correlate with the fertile phase or pregnancy.	Encoded information (Douglas et al., 2016; Furuichi, 1987)
chimpanzees, *Pan troglodytes*	Sexual swelling (size)	Correlates with the fertile phase but not with pregnancy.	Encoded information (Deschner et al., 2003, 2004; Emery & Whitten, 2003; Wallis & Lemmon, 1986)
	Copulation calls	Do not correlate of the fertile phase.	Encoded information (Townsend et al., 2011)
	Vaginal secretions	May correlate with the fertile phase	Encoded information (Matsumoto-Oda et al., 2003)
humans, *Homo sapiens*	Red skin coloration (cheeks and lips)	Does not correlate with the fertile phase.	Encoded information (Burriss et al., 2015; Rigaill, 2020)
	Proceptive behaviors	Not clear.	Encoded information (Gangestad et al., 2002; Haselton et al., 2007)
	Voice pitch	Correlates with the fertile phase.	Encoded information and receivers' response (Pipitone & Gallup, 2008, 2012; Pisanski et al., 2018; Shoup-Knox et al., 2019)

	Body odor	Pleasantness may correlate with the period of highest fertility.	Receivers' response (Gildersleeve et al., 2012; Haselton et al., 2007; Kuukasjärvi et al., 2004; Singh & Bronstad, 2001) but see (Mei et al., 2022)

[1] difference between conceptive and non-conceptive cycles.

In comparison to visual and auditory traits, little is known about the potential role of olfactory traits in primate sexual communication. This is probably because primates were long regarded as microsmatic (having a reduced sense of olfaction, Heymann, 2006; T. D. Smith & Bhatnagar, 2004). However, there is now good evidence that odors encode information about an individual's state and may regulate primate social interactions (Table 2). Therefore, there is ample reason to suspect that odors also influence mating decisions in both human and non-human primates. Indeed, males attend more to female odors during the period of highest fertility than at other times (Table 1).

76 **Table 2.** Examples of individual characteristics encoded by odors in primates.

Species	**Olfactory traits**	**Individual characteristics**	**Evidence**
crowned lemurs, *Eulemur coronatus*	Anogenital odor (males: scent marks, females: secretion)	Correlates with sex.	Encoded information (Elwell et al., 2021)
ring-tailed lemurs, *Lemur catta*	Labial and scrotal secretions	Correlate with kinship, genetic compatibility and genetic quality. Are affected by health status.	Encoded information (Boulet et al., 2009, 2010; Charpentier et al., 2008; Grogan et al., 2019) Receivers' response (Charpentier et al., 2010; Grogan et al., 2019; Harris et al., 2018)
emperor tamarins, *Saguinus imperator*	Anogenital scent marks, scent gland secretions, and skin odor	Correlate with sex and differ between reproductive and non-reproductive individuals.	Encoded information (Poirier, Waterhouse, Dunn, et al., 2021; Poirier, Waterhouse, Watsa, et al., 2021)
Weddell's saddleback tamarins, *Leontocebus weddelli*	Anogenital scent marks, scent gland secretions, and skin odor	Correlate with sex and differ between reproductive and non-reproductive individuals.	Encoded information (Poirier, Waterhouse, Dunn, et al., 2021; Poirier, Waterhouse, Watsa, et al., 2021)
common marmosets, *Callithrix jacchus*	Circumgenital scent marks	Correlate with female familiarity, identity, age, and parity.	Encoded information (T. E. Smith et al., 1997; T. E. Smith, 2006; Kücklich et al., 2019) Receivers' response (Kücklich et al., 2019)
owl monkeys, *Aotus nancymaae*	Perianal gland secretions	Correlate with sex, age, and kinship.	Encoded information (Macdonald et al., 2008; Spence-Aizenberg et al., 2018)
rhesus macaques, *Macaca mulatta*	Body odor (genital area)	Correlates with familiarity or group membership.	Receivers' response (Henkel et al., 2015)
mandrills, *Mandrillus sphinx*	Sternal gland secretions and hairs	Correlate with sex, age, social rank in males, group identity, individual genetic quality, genetic compatibility, and health	Encoded information (Poirotte et al., 2017; Setchell et al., 2010, 2011; Vaglio et al., 2016) Receivers' response (Poirotte et al., 2017)

chimpanzees, *Pan troglodytes*	Urine odor	Correlates with group membership and kinship.	Receivers' response (Henkel & Setchell, 2018) 77
humans, *Homo sapiens*	Axillary or body odor	Is affected by health but does not correlate with human leucocyte antigen genotype.	Receivers' response (Olsson et al., 2014; Probst et al., 2017)

Variation in the chemical composition of female odor, such as the presence or absence of compounds and their relative abundance, across and within individuals may inform conspecifics about a female's fertility. For example, sex hormones can influence the composition of female odor (humans: Michael et al., 1974; rhesus macaques: Michael & Keverne, 1970). Across primate species, the chemical composition of female odor varies between mating and non-mating seasons (ring-tailed lemurs: Scordato & Drea, 2007; Greene & Drea, 2014; and potentially Milne-Edwards' sifakas, *Propithecus edwardsi*: Morelli et al., 2013), across cycle phases (common marmosets: Kücklich et al., 2019; olive baboons: Vaglio et al., 2021; but see for chimpanzees: Fox, 1982), and between reproductive and non-reproductive individuals (tamarins: Poirier, Waterhouse, Dunn, et al., 2021; Poirier, Waterhouse, Watsa, et al., 2021; owl monkeys: Spence-Aizenberg et al., 2018). However, only one study of naturally cycling female catarrhines (Afroeurasian monkeys and apes, including humans) has yet found evidence that fine-scale intra-cycle variation in vaginal odor intensity correlates with ovulation (Vaglio et al., 2021). This limits our understanding of whether and how female odors modulate male and female mating strategies across primates.

Here, we aimed to determine the potential signaling function (i.e., encoded information) of female odor in relation to sexual communication in Japanese macaques (*Macaca fuscata*). In this seasonal species, female behaviors, vocalizations, and skin coloration vary with female reproductive status, both between cycle phases (Garcia et al., 2009; O'Neill et al., 2004; Rigaill et al., 2019), and from pre- to post-conception periods (Rigaill et al., 2015), but do not accurately signal ovulation (Rigaill & Garcia, 2021). It is not clear yet if males have access to other information about ovulation. Males biased their mating effort to the fertile phase in one study (Garcia et al., 2009) but not in others (O'Neill et al., 2004; Rigaill & Garcia, 2021). However, females exhibit a strong vaginal or urinary odor during the mating season and males frequently inspect females' genital areas by sniffing or touching them (Garcia & Rigaill,

unpublished observations of Wakasa captive group housed at Kyoto University Primate Research Institute during the mating seasons in 2011-12 and 2015-16, and of Main Group of Kojima Island, Wildlife Research Center, Kyoto University during the mating season in 2013-14). Female odor may thus vary between individuals and cycle phases, as shown in other primates (Table 1), and guide male mating behaviors.

We aimed to determine if female odor contains information about a female's timing of ovulation. Here, we describe female urine and vaginal odor in Japanese macaques, focusing on their chemical composition, complexity, intensity, and diversity, and examine how odor varies between individuals and cycles (i.e., with a female's cycle) and within cycles (i.e., between pre-fertile, fertile, and post-fertile phases). Our sample size is small (67 samples from 5 females for urine, 30 samples from 3 females for vaginal odor), due to the difficulty inherent in obtaining samples, but our study informs two hypotheses:

1. Female vaginal or urine odor conveys information about individual characteristics. If so, we predict that the chemical composition, complexity, intensity, or diversity of female urine or vaginal odor will vary across individuals. We also predict greater variation across than within individuals.
2. Female odor conveys information about the timing of ovulation. If so, we predict that the chemical composition, complexity, intensity, or diversity of vaginal and urine odor will vary between a given cycle's cycle phases, particularly between the fertile phase and the pre- and post-fertile phases.

Methods

Study subjects

We sampled 5 adult and naturally cycling female Japanese macaques (12.2 ± SD 3.0 years old, range = 8–16 years) housed at the Kyoto University Center for the Evolutionary Origins of

Human Behavior (EHUB, Inuyama, Japan; previously the Primate Research Institute). During the training period, females were housed in individual cages (W90 cm, D76 cm, H85 cm) in the same room (size: W4.0 m, D6.0 m, temperature: 27°C). Females were moved to a different room (individual cage size: W78 cm, D65 cm, H80 cm, temperature: 20°C, window to the external environment) for the data collection period. In both periods, females were housed with 3 adult males with whom they had visual, auditory, and olfactory communication but no physical contact. Animals were fed twice daily (monkey pellets and sweet potatoes). Water was supplied *ad libitum*.

Our research protocol was reviewed and approved by the EHUB Center for Human Evolution Modeling Research (research protocol 2014-082-10). Our methods comply with the Guidelines for the Care and Use of Nonhuman Primates of Kyoto University EHUB and with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Animal training

We used positive reinforcement (Fernström et al., 2009) to train female macaques to present their anogenital area and allow us to collect vaginal swabs for odor sampling (methods developed by NSH for EHUB). We trained females for 26 weeks from May to October 2014. Each female was trained during a 2-min session between 10.30 and 11.30 AM, 3 to 5 times a week. One trainer (NSH or LR) conducted the training session with one observer (LR, NSH, or LD). We used 1 cm^3 diced apples and peanuts as the primary reinforcer, and a clicker as a secondary reinforcer. We carried out training step by step following a predetermined order of defined behaviors (see supplementary material, Table S1 adapted from Fernström et al., 2009). One female failed to reach cooperation level 2 after 60 training sessions. We thus excluded her from our training protocol and replaced her with another cycling adult female. We conducted

429 training sessions in total (mean per female = 86.8 sessions, range = 28–103 sessions). Success rates varied across individuals. All females achieved anogenital presentation training level 1 but only 2 allowed vaginal sampling. These 2 females already had experience with positive reinforcement training for similar or other purposes at EHUB. For vaginal sampling, we sampled these 2 females along with a third female, who did not complete training, but spontaneously presented her hindquarters to the experimenter and accepted odor sampling during the data collection period.

Collection of vaginal and urine samples

We collected data during the 2014–2015 mating season, from early November to late January (85 days in total). One experimenter (LR) collected vaginal and urine samples between 08.30 AM and 11.00 AM. We aimed to collect samples every 2 days starting from the end of the first observed menstruation, which we determined as the day when no fresh blood was observed on the female anogenital area. Mean menstrual cycle length is 27.3 ± SD 5.1 days in both wild and captive populations (Enomoto et al., 1979; Fooden & Aimi, 2005; Garcia et al., 2009; Nigi, 1975; O'Neill et al., 2004). If the experimenter failed to collect a vaginal or urine sample on a designated day, they tried again the following day. The experimenter collected vaginal samples by gently rubbing a sterile cotton swab (Rikaken, Japan) 5 times on the vaginal walls (N = 3 females). The experimenter started vaginal sample collection at least 10 min after entering the experimental room and after any observed micturition. The experimenter collected environmental controls by exposing sterile swabs to the air in the room to later identify volatiles that did not derive from the sampled females. To sample urine, the experimenter placed a plastic container, covered with mesh to prevent contamination from feces, under each female's individual cage to collect urine samples (approximately 2 ml) directly after micturition (N = 5 females). Our use of plastic containers to collect urine and the lack of matching controls such

as water collected from the same plastic containers to test for any effects of using plastic containers or vials on our urine results may affect subsequent chemical analyses (Drea et al., 2013).

We stored all samples in sterile sealed glass vials at -80 °C at EHUB to prevent chemical degradation of the volatile compounds (Drea et al., 2013). We used screw-capped clear glass vials of different diameters (D) and heights (H) (19x 10 ml vials of D 18 mm X H 50 mm, 94x 20 ml vials D 25 mm X H 50 mm, 8x 50ml vials of D 30 mm X H 80 mm). We used different sizes of vial to store different types of sample. This may have affected our results because evaporation of samples depends on the available air space, and may be confounded with our predictor variables. In parallel, we kept a fraction of each urine sample at -20 °C for hormonal analyses to determine the female's reproductive status. In total, we collected 35 vaginal samples (mean per female = 11.7 ± SD 4.5, N = 3 females), 169 urine samples (mean per female = 33.8 ± SD 6.7, N = 5 females), and 45 environmental control samples over two consecutive menstrual cycles for each female.

Determination of ovulation periods

We determined sex hormone concentrations in a subset of 157 urine samples selected to determine ovulation dates (2 consecutive menstrual cycles per female, 10 menstrual cycles in total, mean per female = 31.4 ± SD 5.9 samples). This sample is slightly smaller than the total because we excluded samples collected on consecutive days, and those collected just before or after menstruation. We analyzed urine samples for estrone conjugates (E1C) and pregnanediol-3-glucuronide (PdG) using previously described and validated enzyme immunoassays (EIA) (Rigaill, Suda-Hashimoto, et al., 2017). We estimated that ovulation (day 0) occurred the day following a urinary E1C peak associated with a continuous raise in PdG concentrations (Fujita et al., 2001). We labelled the day directly preceding the estimated ovulation day as day -1, the

day directly following it as day +1, and so on. We defined the fertile phase as the 5-day period covering day -2 to day +2 to account for the life span of sperm in the female tract (macaques: Behboodi et al., 1991). The pre-fertile and post-fertile phases covered the 5 days preceding (day -7 to day -3) and following (day +3 to day +7) the fertile phase. Hormonal profiles showed that one of the 5 females (female 1) had abnormal hormonal patterns after her first cycle, so we excluded her second cycle from the analyses. The cycle length of the 8 cycles for which we observed menstrual bleeding was 29.4 ± SD 6.9 days.

Chemical analyses

We used 67 urine samples (mean per female = 7.4 ± SD 0.7 samples, 2 consecutive cycles per female except for one female, Table 3) and 30 vaginal samples (mean per female = 7.5 ± SD 0.6 samples, one menstrual cycle for two females and two consecutive menstrual cycles for the remaining female, Table 4) collected during the pre-fertile, fertile, and post-fertile phases for odor analyses, along with 24 corresponding environmental control samples collected on the same day as the test samples. We did not analyze the remaining 102 urine samples (mean per female = 21.4 ± SD 8.0 samples) and 5 vaginal samples (5 samples from female 1, second abnormal cycle) collected outside the 15-day period of interest.

We carried out laboratory analyses of odor at the Laboratory for Analysis and Research in Environmental Chemistry - Italian National Research Council, Florence, Italy. We shipped samples via airmail, using dry ice to keep them cold (-30°C). We investigated the volatile compounds found in the Japanese macaque odor using solid-phase microextraction and gas chromatography-mass spectrometry, applying the same methods used in other work on primate odor signals (reviewed in Walker & Vaglio, 2021).

We introduced a 65 μm polydimethylsiloxane/divinylbenzene solid-phase microextraction syringe needle through the vial septum and exposed the fiber to the headspace

above the sample in the vial for 15 minutes at 40°C. We analyzed the adsorbed volatile analytes using a 597 5C mass spectrometer (Agilent Technologies, Santa Clara, CA) EI, 70 eV, coupled directly to a 7890B gas chromatograph (Agilent Technologies) equipped with a fused silica HP5-MS UI capillary column (Agilent Technologies) 30 m x 0.25 mm crossbonded 5%-phenyl-95%-dimethylpolysiloxane, film thickness 0.25µm. We maintained the injector temperature at 270°C and transfer line temperature at 280°C. We made injections in spitless mode (purge valve opened after 1 minute) with a constant flow of helium carrier gas of 1 ml per minute. We started the oven temperature program at 45°C for 2 minutes, then raised it by 4°C per minute to 170 °C and then by 20°C per minute to 300°C.

We assessed potential contamination from the laboratory environment using blank analyses of an empty 10 ml vial (Supelco) following the same procedure used for the samples (laboratory controls). We conditioned the fiber at 260°C for 5 minutes pre-injection and 20 minutes post-injection to avoid any possible carry-over effects. We conducted these conditioning steps every day before analyzing samples.

Identification of compounds

From visual inspection of chromatograms (see examples of typical chromatograms in the supplementary material, Figure S1), we detected 36 peaks from urine samples and 68 peaks from vaginal samples that were absent in both environmental and laboratory controls. We found 25 compounds that did not derive from the animals and removed these from the swab results. We standardized peak retention times using an internal standard (alpha pinene). We integrated chromatograms to obtain retention time and peak area data using ChemStation software (Agilent Technologies). We tentatively identified the eluted compounds by comparing the experimental spectra with the spectra provided by the National Institute of Standards and Technology (NIST) mass spectral database, version MSDF.01.01.2317 (Agilent Technologies).

We considered the identification valid when the minimum matching factor exceeded 80%. If more than one compound was a good match for the same chromatographic peak, we compared Kovats' retention index with values reported in the literature for the same chromatographic column type to minimize the chances of misidentification. We also checked whether more than one compound co-eluted below the same detected peak by checking the mass fragments using ChemStation software.

We determined the relative amounts of compounds by integrating the areas of the corresponding peaks in the total ion current profile and calculated percentages with respect to the total area. We retained peaks that comprised at least 0.05% of the total area of the chromatogram to avoid problems associated with unreliable quantification at very low relative amounts (i.e., to exclude the background noise), although this may mean that we missed trace chemicals (T. E. Smith et al., 2001). We analyzed all samples over a few days to minimize interassay variability.

We describe the chemical composition of the 67 urine and 30 vaginal samples according to female identity as well as cycle phases, including the percentage of samples in each category that included each compound detected for urine (N = 36 compounds) and vaginal (N = 68 compounds) samples (Tables 3-4). For the following analyses, we excluded all compounds that co-eluted as we cannot be sure about the measure of their contribution to the total ion current (Drea et al., 2013). Two urine samples only contained co-eluted compounds, this may be due to a mistake occurring at any step between data collection and chemical evaluation. We thus removed these samples from the data set. Overall, we excluded 1 of 36 (3%) urine compounds (Table 3) and 10 of 68 (15%) vaginal compounds (Table 4).

Data analyses

We carried out analyses using R software (version 4.0.3). We conducted our analyses on 35 compounds detected across 65 urine and 58 compounds detected across 30 vaginal samples.

We investigated the relationship between female odor and identity as well as cycle phase. Several quantitative or qualitative analytic tools can be used to investigate chemical data. The choice of one approach over another largely depends on the nature of the data (and the methods used for chemical analyses), the species (e.g., whether chemical profiles are composed of single or multiple compounds), the number of samples, and the research question (Drea et al., 2013). Some studies assess the presence/absence of one or few compounds or categories of compounds of interest (e.g., fatty acids or alcohols), while others reduce the dimensionality of the data set (Drea et al., 2013). However, these methods may underestimate or overestimate variance in chemical composition between samples by analyzing only a subset of the data (Drea et al., 2013).

We opted for a conservative approach, keeping all compounds of the animal swab results in the analyses and avoiding subjective thresholds such as retaining compounds or variables based on *a priori* assumptions about these compounds' roles or on mathematical rather than biological reasons. We used Nonmetric Multidimensional Scaling (NMDS), a rank-based approach relying on distance or dissimilarity matrix, to represent pairwise dissimilarity between samples in a dimensional space.

We tested for differences in both urine and vaginal samples according to female identity and cycle phases. We computed a distance matrix for the data with the Bray-Curtis dissimilarity index using the vegdist function in the *vegan* package (Oksanen et al., 2020). We then calculated the 2-dimentional NMDS coordinates from these Bray-Curtis indices using the metaMDS function in the *vegan* package and plotted the outcomes (Wickham, 2016). The stress factors, which roughly represent the goodness of fit, associated with the coordinates were 0.19 for urine and 0.18 for vaginal data, and are thus considered fair (K. R. Clarke, 1993). We then

performed a permutational multivariate analysis of variance (PERMANOVA) using distance matrices by using the *Adonis* function in (*vegan* package). This analysis tests whether the centroids and dispersion of the groups tested as defined by measure space are equivalent for all groups (Anderson, 2017). Because females contributed the data for one or two consecutives menstrual cycles, we used "a female's cycle" in our analyses as a proxy for both "menstrual cycle" and "female identity". Here we thus tested the effect of the interaction between a female's cycle and cycle phase (i.e., *Are samples from the same cycle phase more or less similar than samples from another cycle phase within a female given cycle?*).

To facilitate comparison with other studies of similar research questions and substrates (e.g., vaginal secretions, Vaglio et al., 2021), we also calculated three diversity indexes to graphically investigate variation in sample richness (total number of detected peaks per sample), Shannon's H (which accounts for the relative abundance of each compound within a sample) and odor intensity (total area of detected peaks per sample). Richness and Shannon H of both urine and vaginal samples followed a normal distribution while urine and vaginal intensity followed a lognormal distribution. We explored variation across females and cycle phases graphically by plotting urine and vaginal richness, Shannon H, and intensity against either female identity (categorical variable) or cycle phase (categorical variable).

Data availability statement

The data that support the findings of this study are openly available in figshare, doi:10.6084/m9.figshare.19649766.

Results

Identity of volatile compounds

We detected 36 volatile compounds from the analysis of 67 urine samples. We proposed a tentative identification for 31 of these compounds, including one that may result from chromatic co-elution (Table 3). We detected 68 volatile compounds from the analysis of 30 vaginal samples. We proposed a tentative identification for 37 of these vaginal compounds, with nine compounds that may result from chromatic co-elution (Table 4). Only five volatile compounds were found in both urine and vaginal samples (2-pentanone, 2-hexanone, dimethyl disulfide, toluene, 2-heptanone, Tables 3-4). This represents 5% (5/104) of all the compounds detected in urine and vaginal samples.

Inter-individual variation in female odor

Nineteen of 36 urine compounds (53%) were unique to one of the five females (Table 3). Although the two dimensions extracted from the NMDS did not clearly cluster samples per female identity (Fig. 1), the results of the PERMANOVA suggest that a female's cycle explains 25% of the variance in the data (Table 5). Urine richness, and odor intensity varied across females (Fig. 2), with lower richness values in female 2 (Fig. 2A) and higher odor intensity in female 1 (Fig. 2C). Shannon H index showed lower inter-individual variation (Fig. 2).

Twenty-eight of 68 vaginal compounds (41%) appeared to be unique to one of the three females (Table 4). The two dimensions extracted from NMDS and the results of the PERMANOVA suggest that a female's cycle explains 29% of the variance in the data and the grouping patterns of samples (Fig. 3, Table 5). Vaginal richness, Shannon's H index, and odor intensity varied across females (Fig. 2). One female (female 1) showed lower vaginal richness, Shannon H, and intensity values than the two other females sampled (Fig. 2D, E, F).

Intra-cycle variation in female odor

Ten urine compounds (28%) were only found during the fertile phase (Table 3). The cycle phase explained only 3% of the variance in urine data (Table 5). However, the interaction between a female's cycle and cycle phase explained most of the variance in the data (27%, Table 5). Thus, within a given female cycle, samples from same phases may cluster more than samples from different phases. There was little intra-cycle variation in urine richness, Shannon H, or intensity (Fig. 4). Urine richness, but not Shannon H (Fig. 4B), values tended to decrease from pre- to post-fertile phase (Fig. 4A), while urine intensity increased slightly during the fertile phase compared to pre- and post-fertile phases (Fig. 4C).

Six vaginal compounds (9%) were only found during the fertile phase (Table 4). The cycle phase or the interaction between a female's cycle and cycle phase explained respectively 6% and 17% of the variance in vaginal data (Table 5). Vaginal richness, Shannon H, or intensity did not appear to vary across the menstrual cycle (Fig. 4).

Individual trajectories are presented in the supplementary materiel (Fig. S2-3).

Table 3. The 36 chemical compounds retrieved from 65 urine samples, their tentative identification, their mean peak area, and their presence in all samples and in samples from the fertile phase. Data are presented for all females and for each female's menstrual cycle. Compounds marked * co-eluted and are not included in graphical exploration of the data. [1] Compounds often used as lab solvents (Drea et al., 2013) but kept in the analyses for comparison with previously published data set (Delbarco-Trillo et al., 2013; Vaglio et al., 2021).

(Table 4 is provided as a separate file as it didn't fit in the manuscript)

Table 4. The 68 chemical compounds retrieved from 30 vaginal samples, their tentative identification, their mean peak area, and their presence in all samples and in samples from the

fertile phase. Data are presented for all females and for each female's menstrual cycle. Compounds marked * co-eluted and are not included in graphical exploration of the data. [1] Compounds often used as lab solvents (Drea et al., 2013) but kept in the analyses for comparison with previously published data set (Vaglio et al., 2021).

(Table 4 is provided as a separate file as it didn't fit in the manuscript)

Table 5. PERMANOVA results based on Bray-Curtis dissimilarities using abundance data for female odors from urine and vaginal samples

	df	Sum of Squares	Mean of Squares	F	R^2
Urine samples					
Female's cycle	8	4.88	0.61	2.62	0.25
Cycle phase	2	0.63	0.31	1.35	0.03
Interaction	16	5.39	0.34	1.45	0.27
Residuals	38	8.84	0.23		0.45
Total	64	19.74			1.00
Vaginal samples					
Female's cycle	3	3.15	1.05	3.59	0.29
Cycle phase	2	0.62	0.31	1.06	0.06
Interaction	6	1.90	0.32	1.08	0.17
Residuals	18	5.27	0.29		0.48
Total	29	10.94			1.00

Discussion

We analyzed inter-individual and intra-cycle variation in urine and vaginal samples in female Japanese macaques based on identified compounds, odor richness, diversity and intensity. We identified 31 urine and 37 vaginal compounds of potential semiochemical importance in this species that may be of interest for future work. Although our limited sample size restricts the interpretation of our results, our analyses suggest that urine and vaginal odors varied more between females than between cycle phases. However, we also found that, within a female's cycle, urine samples from the same cycle phase may cluster more than samples from different phases.

393 We tentatively identified 31 (86%) of 36 volatile compounds found in urine samples
394 and 37 (54%) of 68 volatile compounds detected in female vaginal secretions. Some of the
395 volatile compounds we identified are known to play a role in plant or insect communication or
396 metabolism (source: https://pubchem.ncbi.nlm.nih.gov). Some of the compounds we detected
397 may be from the diced apples we used as a food reward during data collection (e.g., aldehydes:
398 hexanal, nonanal, decanal, benzaldehyde; alcohols: ethanol, 1-butanol, 3-methyl-; esters: ethyl
399 acetate, (Espino-Díaz et al., 2016)). However, it is also possible that these compounds are
400 widespread across plant and animal species due to their role in both intra- and inter-species
401 communication (e.g., pollination, alarm signals, mate attraction: (Das et al., 2013; Kelliher,
402 2007; Leonhardt et al., 2016). Indeed, 16 (51%) and 13 (35%) of the volatile compounds we
403 identified in urine and vaginal samples are found in female odor profiles (urine, vaginal
404 secretions, glands, hairs) of other primate species, from strepsirrhines to hominins (Tables 3-
405 4). Despite these general similarities across species, vaginal secretions have very dissimilar
406 odor profiles in Japanese macaques (Table 4) and olive baboons (Vaglio et al., 2021). This is
407 consistent with the hypothesis that (dis)similarities in odor profiles across primates relate to
408 socio-ecological and phylogenetic factors (Delbarco-Trillo et al., 2011; delBarco-Trillo &
409 Drea, 2014; Heymann, 2006; Jänig et al., 2019; Ueno, 1994).

410 We found that the relative abundance of compounds across urine and vaginal samples
411 varied across individuals in female Japanese macaques. Urine is known to play a role in the
412 individual recognition mechanisms of several species of mammals, including some platyrrhines
413 (mice, *Mus domesticus*: J. L. Hurst et al., 2001; common marmosets: T. E. Smith, 2006). To
414 our knowledge, our study is the first to show that urine odor, along with vaginal odor, may
415 convey information about identity in a catarrhine species.

416 Exchanging information about identity through odors may benefit Japanese macaques,
417 a species that lives in large cohesive groups (Fooden & Aimi, 2005). As proposed by Henkel

418 and colleagues for rhesus macaques (Henkel et al., 2015), the ability to identify individuals –
419 and thus potentially kin, familiar, or higher-ranking conspecifics – may be crucial to coordinate
420 movement and regulate social interactions. Males may pay particular attention to female odor
421 during the mating season. Dominant or central males, which have a closer access to females,
422 could use female anogenital (vaginal and urine) odor to follow and mate-guard fertile females
423 during group movement and to frustrate females' attempts to escape male monopolization.
424 Subordinate or peripheral males may also use female odor to find mating opportunities. Urine
425 odor may be of particular interest in this latter case: since the information can be decoupled
426 from the emitters, receivers may follow such fingerprints in the environment to find receptive
427 and fertile females.

428 Our study provides some evidence that urine, but not vaginal, odor can be informative
429 about a female's reproductive status in Japanese macaques. This may explain why in a previous
430 study, male Japanese macaques did not investigate (i.e., smell or taste) urine samples from the
431 fertile phase more than samples from other phases, as they were exposed to unknown rather
432 than familiar females' odors (Rigaill, Suda-Hashimoto, et al., 2017). Across animals, urine is
433 known to play a role in sexual signaling (Rothschild's giraffes, *Giraffa camelopardalis*
434 *rothschildi*: Bercovitch et al., 2006; common squirrel monkeys, *Saimiri sciureus*: Candland et
435 al., 1980; woolly spider monkeys, *Brachyteles arachnoides*: Milton, 1985; capuchin monkeys,
436 *Cebus apella*: Phillips et al., 2011; Asian elephants, *Elephas maximus*: Rasmussen et al., 1982;
437 giant pandas, *Ailuropoda melanoleuca*: Swaisgood et al., 2002). Our results suggest that this
438 communicative process through urine may also be present in catarrhines. To investigate this
439 hypothesis further, studies should assess male response to familiar female urine odor across
440 different cycle phases using bioassays.

441 The fact that vaginal odor does not appear to encode information about the fertile period
442 is surprising considering previous results in other primate species (Table 1 and Introduction).

443 It is possible that our small sample size prevented us from detecting any intra-cycle variation.
444 Moreover, variation may occur within a few days of ovulation rather than across the broader
445 cycle phases we studied. More and finer-scaled data are needed to better understand the
446 relationship between vaginal odor and ovulatory signaling in Japanese macaques and other
447 primate species.

448 Exciting research questions remain to be tested. If female odor varies in relation to sex
449 hormone concentrations, then does odor vary with reproductive status in the same individual:
450 e.g., between mating and non-mating periods, from prepubescent to sexually mature, between
451 cycling and non-cycling phases, and from pre- to post-conception phases? Do female age,
452 genetic profile, and health status influence this relationship and how might this affect female
453 reproductive capacity and success? And, finally, does female odor modulate socio-sexual
454 interactions, especially in relation to the level of female-female competition, and if so, how?
455 This last question is particularly interesting as, besides advertising their fertility, females would
456 also benefit from receiving information about their rivals' fertility status to increase their own
457 mating success. They may intensify competition with other fertile females through agonistic
458 interactions (Baniel et al., 2018; A. C. Hurst et al., 2017) or by exaggerating their own
459 attractivity (e.g., behavioral or vocal solicitations (Fallon et al., 2016)). However, whether and
460 how female odor modulates the level of intra-sexual competition is little studied in mammals,
461 including primates (M. L. Fisher & Burch, 2021; Stockley et al., 2013). Investigating these
462 research questions will provide valuable information about primate olfactory communication.
463 However, doing so will be challenging in both captive and wild populations as such studies
464 require longitudinal observations and data collection, a considerable budget for data storage
465 and analyses, and may conflict with population management plans (e.g., use of contraceptives
466 in breeding programs preclude analyses of female cycles).

In conclusion, our study identifies 31 volatile urine compounds and 37 volatile vaginal compounds of possible importance in olfactory communication in Japanese macaques. We found evidence for inter-individual (urine and vaginal samples) and intra-cycle (urine samples) differences in female odors. While we cannot draw clear conclusions about the role of female odors in Japanese macaque sexual communication, our results contribute to studies investigating how olfaction mediates socio-sexual interactions in human and non-human primates. To assess whether female odor has an adaptive sexual signaling function, further work is needed to increase sampling effort and determine if males and females can perceive inter-individual and intra-cycle differences in female odors, and whether female odors modify the receiver's behavior.

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Figures

Fig 1. Nonmetric multidimensional scaling plots of similarity in urine sample chemical composition across cycles in relation to female identity and menstrual cycle phases.

Fig 2. Variation in urine (A, B, C) and vaginal (D, E, F) richness (A, D), Shannon H (B, E), and intensity (C, F) across females. Plots show the median (black horizontal line), first and third quartiles (top and bottom of the box), and the range (upper and lower whiskers) values.

Fig 3. Nonmetric multidimensional scaling plots of similarity in vaginal sample chemical composition in relation to female identity and menstrual cycle phases.

Fig 4. Variation in urine (A, B, C) and vaginal (D, E, F) richness (A, D), Shannon H (B, E), and intensity (C, F) across cycle phases. Plots show the median (black horizontal line), the first and third quartiles (top and bottom of the box), and the range (upper and lower whiskers) values.

Fig S1. Example of typical chromatographs from urine (A) and vaginal (B) samples during the fertile phase.

Fig S2. Individual variation in urine richness (A), Shannon H (B), and intensity (C) across cycle phases. Plots show the median (black horizontal line), first and third quartiles (top and bottom of the box), and the range (upper and lower whiskers).

Fig S3. Individual variation in vaginal richness (A), Shannon H (B), and intensity (C) across cycle phase. Plots show the median (black horizontal line), first and third quartiles (top and bottom of the box), and the range (upper and lower whiskers).

References

Altmann, S. A. (1970). The pregnancy sign in savannah baboons. *The Journal of Zoo Animal Medicine*, *4*(2), 8-12. https://doi.org/10.2307/20094180

515 Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). In
516 *Wiley StatsRef : Statistics Reference Online* (p. 1-15). John Wiley & Sons, Ltd.
517 https://doi.org/10.1002/9781118445112.stat07841
518 Baniel, A., Cowlishaw, G., & Huchard, E. (2018). Jealous females? Female competition and
519 reproductive suppression in a wild promiscuous primate. *Proc. R. Soc. B*, *285*(1886),
520 20181332. https://doi.org/10.1098/rspb.2018.1332
521 Behboodi, E., Katz, D., Samuels, S., Tell, L., Hendrickx, A., & Lasley, B. (1991). The use of a
522 urinary estrone conjugates assay for detection of optimal mating time in the
523 cynomolgus macaque (*Macaca fascicularis*). *Journal of Medical Primatology*, *20*(5),
524 229-234.
525 Beltran-Bech, S., & Richard, F.-J. (2014). Impact of infection on mate choice. *Animal*
526 *Behaviour*, *90*, 159-170. https://doi.org/10.1016/j.anbehav.2014.01.026
527 Bercovitch, F. B., Bashaw, M. J., & del Castillo, S. M. (2006). Sociosexual behavior, male
528 mating tactics, and the reproductive cycle of giraffe *Giraffa camelopardalis*.
529 *Hormones and Behavior*, *50*(2), 314-321.
530 https://doi.org/10.1016/j.yhbeh.2006.04.004
531 Boulet, M., Charpentier, M. J., & Drea, C. M. (2009). Decoding an olfactory mechanism of kin
532 recognition and inbreeding avoidance in a primate. *BMC Evolutionary Biology*, *9*, 281.
533 https://doi.org/10.1186/1471-2148-9-281
534 Boulet, M., Crawford, J. C., Charpentier, M. J. E., & Drea, C. M. (2010). Honest olfactory
535 ornamentation in a female-dominant primate. *Journal of Evolutionary Biology*, *23*(7),
536 1558-1563. https://doi.org/10.1111/j.1420-9101.2010.02007.x
537 Brauch, K., Pfefferle, D., Hodges, K., Möhle, U., Fischer, J., & Heistermann, M. (2007). Female
538 sexual behavior and sexual swelling size as potential cues for males to discern the

female fertile phase in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Hormones and Behavior*, *52*(3), 375-383. https://doi.org/10.1016/j.yhbeh.2007.06.001

Burriss, R. P., Troscianko, J., Lovell, P. G., Fulford, A. J. C., Stevens, M., Quigley, R., Payne, J., Saxton, T. K., & Rowland, H. M. (2015). Changes in women's facial skin color over the ovulatory cycle are not detectable by the human visual system. *PLoS ONE*, *10*(7), e0130093. https://doi.org/10.1371/journal.pone.0130093

Candland, D. K., Blumer, E. S., & Mumford, M. D. (1980). Urine as a communicator in a New World primate, *Saimiri sciureus*. *Animal Learning & Behavior*, *8*(3), 468-480. https://doi.org/10.3758/BF03199636

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, *78*(4), 575-595. https://doi.org/10.1017/S1464793103006158

Carosi, M., & Visalberghi, E. (2002). Analysis of tufted capuchin (*Cebus apella*) courtship and sexual behavior repertoire : Changes throughout the female cycle and female interindividual differences. *American Journal of Physical Anthropology*, *118*(1), 11-24. https://doi.org/10.1002/ajpa.10083

Cerda-Molina, A. L., Hernández-López, L., Rojas-Maya, S., Murcia-Mejía, C., & Mondragón-Ceballos, R. (2006). Male-induced sociosexual behavior by vaginal secretions in *Macaca arctoides*. *International Journal of Primatology*, *27*(3), 791-807. https://doi.org/10.1007/s10764-006-9045-0

Charpentier, M. J. E., Boulet, M., & Drea, C. M. (2008). Smelling right : The scent of male lemurs advertises genetic quality and relatedness. *Molecular Ecology*, *17*(14), 3225-3233. https://doi.org/10.1111/j.1365-294X.2008.03831.x

562 Charpentier, M. J. E., Crawford, J. C., Boulet, M., & Drea, C. M. (2010). Message 'scent' :
563 Lemurs detect the genetic relatedness and quality of conspecifics via olfactory cues.
564 *Animal Behaviour*, *80*(1), 101-108. https://doi.org/10.1016/j.anbehav.2010.04.005
565 Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community
566 structure. *Australian Journal of Ecology*, *18*(1), 117-143.
567 https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
568 Clarke, P. M. R., Barrett, L., & Henzi, S. P. (2009). What role do olfactory cues play in chacma
569 baboon mating? *American Journal of Primatology*, *71*(6), 493-502.
570 https://doi.org/10.1002/ajp.20678
571 Converse, L. J., Carlson, A. A., Ziegler, T. E., & Snowdon, C. T. (1995). Communication of
572 ovulatory state to mates by female pygmy marmosets, *Cebuella pygmaea*. *Animal*
573 *Behaviour*, *49*(3), 615-621. https://doi.org/10.1016/0003-3472(95)80194-4
574 Das, A., Lee, S.-H., Hyun, T. K., Kim, S.-W., & Kim, J.-Y. (2013). Plant volatiles as method of
575 communication. *Plant Biotechnology Reports*, *7*(1), 9-26.
576 https://doi.org/10.1007/s11816-012-0236-1
577 Delbarco-Trillo, J., Burkert, B. A., Goodwin, T. E., & Drea, C. M. (2011). Night and day : The
578 comparative study of strepsirrhine primates reveals socioecological and phylogenetic
579 patterns in olfactory signals. *Journal of Evolutionary Biology*, *24*(1), 82-98.
580 https://doi.org/10.1111/j.1420-9101.2010.02145.x
581 delBarco-Trillo, J., & Drea, C. M. (2014). Socioecological and phylogenetic patterns in the
582 chemical signals of strepsirrhine primates. *Animal Behaviour*, *97*, 249-253.
583 https://doi.org/10.1016/j.anbehav.2014.07.009
584 Delbarco-Trillo, J., Harelimana, I. H., Goodwin, T. E., & Drea, C. M. (2013). Chemical
585 differences between voided and bladder urine in the aye-aye (*Daubentonia*

madagascariensis) : Implications for olfactory communication studies. *American Journal of Primatology*, *75*(7), 695-702. https://doi.org/10.1002/ajp.22083

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, *66*(3), 551-560. https://doi.org/10.1006/anbe.2003.2210

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*, *46*(2), 204-215. https://doi.org/10.1016/j.yhbeh.2004.03.013

Douglas, P. H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., & Deschner, T. (2016). Mixed messages : Wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evolutionary Biology*, *16*, 140. https://doi.org/10.1186/s12862-016-0691-3

Drea, C. M., Boulet, M., Delbarco-Trillo, J., Greene, L. K., Sacha, C. R., Goodwin, T. E., & Dubay, G. R. (2013). The « secret » in secretions : Methodological considerations in deciphering primate olfactory communication. *American Journal of Primatology*, *75*(7), 621-642. https://doi.org/10.1002/ajp.22143

Dubuc, C., Brent, L. J. N., Accamando, A. K., Gerald, M. S., MacLarnon, A., Semple, S., Heistermann, M., & Engelhardt, A. (2009). Sexual skin color contains information about the timing of the fertile phase in free-ranging *Macaca mulatta*. *International Journal of Primatology*, *30*(6), 777-789. https://doi.org/10.1007/s10764-009-9369-7

Elwell, E. J., Walker, D., & Vaglio, S. (2021). Sexual dimorphism in crowned lemur scent-marking. *Animals: An Open Access Journal from MDPI*, *11*(7), 2091. https://doi.org/10.3390/ani11072091

610 Emery, M. A., & Whitten, P. L. (2003). Size of sexual swellings reflects ovarian function in
611 chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*, *54*(4), 340-351.
612 https://doi.org/10.1007/s00265-003-0648-6
613 Engelhardt, A., Fischer, J., Neumann, C., Pfeifer, J.-B., & Heistermann, M. (2012). Information
614 content of female copulation calls in wild long-tailed macaques (*Macaca fascicularis*).
615 *Behavioral Ecology and Sociobiology*, *66*(1), 121-134.
616 https://doi.org/10.1007/s00265-011-1260-9
617 Engelhardt, A., Hodges, J. K., & Heistermann, M. (2007). Post-conception mating in wild long-
618 tailed macaques (*Macaca fascicularis*) : Characterization, endocrine correlates and
619 functional significance. *Hormones and Behavior*, *51*(1), 3-10.
620 https://doi.org/10.1016/j.yhbeh.2006.06.009
621 Engelhardt, A., Hodges, J. K., Niemitz, C., & Heistermann, M. (2005). Female sexual behavior,
622 but not sex skin swelling, reliably indicates the timing of the fertile phase in wild long-
623 tailed macaques (*Macaca fascicularis*). *Hormones and Behavior*, *47*(2), 195-204.
624 https://doi.org/10.1016/j.yhbeh.2004.09.007
625 Enomoto, T., Seiki, K., & Haruki, Y. (1979). On the correlation between sexual behavior and
626 ovarian hormone level during the menstrual cycle in captive Japanese monkeys.
627 *Primates*, *20*(4), 563-570. https://doi.org/10.1007/BF02373438
628 Espino-Díaz, M., Sepúlveda, D. R., González-Aguilar, G., & Olivas, G. I. (2016). Biochemistry of
629 apple aroma : A review. *Food Technology and Biotechnology*, *54*(4), 375-397.
630 https://doi.org/10.17113/ftb.54.04.16.4248
631 Fallon, B. L., Neumann, C., Byrne, R. W., & Zuberbühler, K. (2016). Female chimpanzees
632 adjust copulation calls according to reproductive status and level of female

633 competition. *Animal Behaviour*, *113*, 87-92.
634 https://doi.org/10.1016/j.anbehav.2015.12.028
635 Fernström, A.-L., Fredlund, H., Spångberg, M., & Westlund, K. (2009). Positive reinforcement
636 training in rhesus macaques—Training progress as a result of training frequency.
637 *American Journal of Primatology*, *71*(5), 373-379. https://doi.org/10.1002/ajp.20659
638 Fisher, M. L., & Burch, R. L. (2021). Female-Female Competition. In T. K. Shackelford & V. A.
639 Weekes-Shackelford (Éds.), *Encyclopedia of Evolutionary Psychological Science* (p.
640 3043-3046). Springer International Publishing. https://doi.org/10.1007/978-3-319-
641 19650-3_1408
642 Fisher, R. A. (1915). The evolution of sexual preference. *The Eugenics Review*, *7*(3), 184-192.
643 Fooden, J., & Aimi, M. (2005). Systematic review of Japanese macaques, *Macaca fuscata*
644 (Gray, 1870). *Fieldiana Zoology*, *104*, 1-198.
645 Fox, G. J. (1982). Potentials for pheromones in chimpanzee vaginal fatty acids. *Folia*
646 *Primatologica*, *37*(3-4), 255-266. https://doi.org/10.1159/000156036
647 Fujita, S., Mitsunaga, F., Sugiura, H., & Shimizu, K. (2001). Measurement of urinary and fecal
648 steroid metabolites during the ovarian cycle in captive and wild Japanese macaques,
649 *Macaca fuscata*. *American Journal of Primatology*, *53*(4), 167-176.
650 https://doi.org/10.1002/ajp.3
651 Furuichi, T. (1987). Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee
652 females at Wamba, Zaïre. *Primates*, *28*(3), 309-318.
653 https://doi.org/10.1007/BF02381014
654 Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests
655 and their partners' mate-retention tactics across the menstrual cycle : Evidence for

shifting conflicts of interest. *Proceedings. Biological Sciences / The Royal Society*, *269*(1494), 975-982. https://doi.org/10.1098/rspb.2001.1952

Garcia, C., Shimizu, K., & Huffman, M. (2009). Relationship between sexual interactions and the timing of the fertile phase in captive female Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, *71*(10), 868-879. https://doi.org/10.1002/ajp.20717

Gildersleeve, K. A., Haselton, M. G., Larson, C. M., & Pillsworth, E. G. (2012). Body odor attractiveness as a cue of impending ovulation in women : Evidence from a study using hormone-confirmed ovulation. *Hormones and Behavior*, *61*(2), 157-166. https://doi.org/10.1016/j.yhbeh.2011.11.005

Gordon, T. P., Gust, D. A., Busse, C. D., & Wilson, M. E. (1991). Hormones and sexual behavior associated with postconception perineal swelling in the sooty mangabey (*Cercocebus torquatus atys*). *International Journal of Primatology*, *12*(6), 585-597. https://doi.org/10.1007/BF02547671

Greene, L. K., & Drea, C. M. (2014). Love is in the air : Sociality and pair bondedness influence sifaka reproductive signalling. *Animal Behaviour*, *88*, 147-156. https://doi.org/10.1016/j.anbehav.2013.11.019

Grogan, K. E., Harris, R. L., Boulet, M., & Drea, C. M. (2019). Genetic variation at MHC class II loci influences both olfactory signals and scent discrimination in ring-tailed lemurs. *BMC Evolutionary Biology*, *19*(1), 171. https://doi.org/10.1186/s12862-019-1486-0

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds : A role for parasites? *Science (New York, N.Y.)*, *218*(4570), 384-387.

678 Harris, R. L., Boulet, M., Grogan, K. E., & Drea, C. M. (2018). Costs of injury for scent
679 signalling in a strepsirrhine primate. *Scientific Reports*, *8*(1), 9882.
680 https://doi.org/10.1038/s41598-018-27322-3
681 Haselton, M. G., Mortezaie, M., Pillsworth, E. G., Bleske-Rechek, A., & Frederick, D. A. (2007).
682 Ovulatory shifts in human female ornamentation : Near ovulation, women dress to
683 impress. *Hormones and Behavior*, *51*(1), 40-45.
684 https://doi.org/10.1016/j.yhbeh.2006.07.007
685 Henkel, S., Lambides, A. R., Berger, A., Thomsen, R., & Widdig, A. (2015). Rhesus macaques
686 (*Macaca mulatta*) recognize group membership via olfactory cues alone. *Behavioral*
687 *Ecology and Sociobiology*, *69*(12), 2019-2034. https://doi.org/10.1007/s00265-015-
688 2013-y
689 Henkel, S., & Setchell, J. M. (2018). Group and kin recognition via olfactory cues in
690 chimpanzees (*Pan troglodytes*). *Proceedings of the Royal Society B: Biological*
691 *Sciences*, *285*(1889), 20181527. https://doi.org/10.1098/rspb.2018.1527
692 Heymann, E. W. (2006). The neglected sense-olfaction in primate behavior, ecology, and
693 evolution. *American Journal of Primatology*, *68*(6), 519-524.
694 https://doi.org/10.1002/ajp.20249
695 Higham, J. P., Brent, L. J. N., Dubuc, C., Accamando, A. K., Engelhardt, A., Gerald, M. S.,
696 Heistermann, M., & Stevens, M. (2010). Color signal information content and the eye
697 of the beholder : A case study in the rhesus macaque. *Behavioral Ecology*, *21*(4),
698 739-746. https://doi.org/10.1093/beheco/arq047
699 Higham, J. P., Heistermann, M., Ross, C., Semple, S., & Maclarnon, A. (2008). The timing of
700 ovulation with respect to sexual swelling detumescence in wild olive baboons.
701 *Primates*, *49*(4), 295-299. https://doi.org/10.1007/s10329-008-0099-9

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, *12*, 89. https://doi.org/10.1186/1471-2148-12-89

Higham, J. P., Hughes, K. D., Brent, L. J. N., Dubuc, C., Engelhardt, A., Heistermann, M., Maestriperi, D., Santos, L. R., & Stevens, M. (2011). Familiarity affects the assessment of female facial signals of fertility by free-ranging male rhesus macaques. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1723), 3452-3458. https://doi.org/10.1098/rspb.2011.0052

Higham, J. P., MacLarnon, A. M., Ross, C., Heistermann, M., & Semple, S. (2008). Baboon sexual swellings : Information content of size and color. *Hormones and Behavior*, *53*(3), 452-462. https://doi.org/10.1016/j.yhbeh.2007.11.019

Higham, J. P., Semple, S., MacLarnon, A., Heistermann, M., & Ross, C. (2009). Female reproductive signaling, and male mating behavior, in the olive baboon. *Hormones and Behavior*, *55*(1), 60-67. https://doi.org/10.1016/j.yhbeh.2008.08.007

Huchard, E., Benavides, J. A., Setchell, J. M., Charpentier, M. J. E., Alvergne, A., King, A. J., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2009). Studying shape in sexual signals : The case of primate sexual swellings. *Behavioral Ecology and Sociobiology*, *63*(8), 1231-1242. https://doi.org/10.1007/s00265-009-0748-z

Hurst, A. C., Alquist, J. L., & Puts, D. A. (2017). Women's fertility status alters other women's jealousy and mate guarding. *Personality and Social Psychology Bulletin*, *43*(2), 191-203. https://doi.org/10.1177/0146167216678859

Hurst, J. L., Payne, C. E., Nevison, C. M., Marie, A. D., Humphries, R. E., Robertson, D. H., Cavaggioni, A., & Beynon, R. J. (2001). Individual recognition in mice mediated by

major urinary proteins. *Nature*, *414*(6864), 631-634. https://doi.org/10.1038/414631a

Jacobs, G. H. (2008). Primate color vision : A comparative perspective. *Visual Neuroscience*, *25*(5-6), 619-633. https://doi.org/10.1017/S0952523808080760

Jänig, S., Weiß, B. M., Birkemeyer, C., & Widdig, A. (2019). Comparative chemical analysis of body odor in great apes. *American Journal of Primatology*, *81*(6), e22976. https://doi.org/10.1002/ajp.22976

Kelliher, K. R. (2007). The combined role of the main olfactory and vomeronasal systems in social communication in mammals. *Hormones and Behavior*, *52*(5), 561-570. https://doi.org/10.1016/j.yhbeh.2007.08.012

Kücklich, M., Weiß, B. M., Birkemeyer, C., Einspanier, A., & Widdig, A. (2019). Chemical cues of female fertility states in a non-human primate. *Scientific Reports*, *9*(1), 1-12. https://doi.org/10.1038/s41598-019-50063-w

Kuukasjärvi, S., Eriksson, C. J. P., Koskela, E., Mappes, T., Nissinen, K., & Rantala, M. J. (2004). Attractiveness of women's body odors over the menstrual cycle : The role of oral contraceptives and receiver sex. *Behavioral Ecology*, *15*(4), 579-584. https://doi.org/10.1093/beheco/arh050

Leonhardt, S. D., Menzel, F., Nehring, V., & Schmitt, T. (2016). Ecology and evolution of communication in social insects. *Cell*, *164*(6), 1277-1287. https://doi.org/10.1016/j.cell.2016.01.035

Macdonald, E. A., Fernandez-Duque, E., Evans, S., & Hagey, L. R. (2008). Sex, age, and family differences in the chemical composition of owl monkey (*Aotus nancymaae*) subcaudal scent secretions. *American Journal of Primatology*, *70*(1), 12-18. https://doi.org/10.1002/ajp.20450

Matsumoto-Oda, A., Oda, R., Hayashi, Y., Murakami, H., Maeda, N., Kumazaki, K., Shimizu, K., & Matsuzawa, T. (2003). Vaginal fatty acids produced by chimpanzees during menstrual cycles. *Folia Primatologica*, *74*(2), 75-79.

Mei, M., Grillot, R. L., Abbey, C. K., Emery Thompson, M., & Roney, J. R. (2022). Does scent attractiveness reveal women's ovulatory timing? Evidence from signal detection analyses and endocrine predictors of odour attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1970), 20220026. https://doi.org/10.1098/rspb.2022.0026

Michael, R. P., Bonsall, R. W., & Warner, P. (1974). Human vaginal secretions : Volatile fatty acid content. *Science (New York, N.Y.)*, *186*(4170), 1217-1219.

Michael, R. P., & Keverne, E. B. (1970). Primate sex pheromones of vaginal origin. *Nature*, *225*(5227), 84-85. https://doi.org/10.1038/225084a0

Milton, K. (1985). Urine washing behavior in the woolly spider monkey (*Brachyteles arachnoides*). *Zeitschrift Für Tierpsychologie*, *67*(1-4), 154-160. https://doi.org/10.1111/j.1439-0310.1985.tb01384.x

Möhle, U., Heistermann, M., Dittami, J., Reinberg, V., Wallner, B., & Hodges, J. K. (2005). Patterns of anogenital swelling size and their endocrine correlates during ovulatory cycles and early pregnancy in free-ranging barbary macaques (*Macaca sylvanus*) of Gibraltar. *American Journal of Primatology*, *66*(4), 351-368. https://doi.org/10.1002/ajp.20161

Møller, A. P., Christe, P., & Lux, E. (1999). Parasitism, host immune function, and sexual selection. *The Quarterly Review of Biology*, *74*(1), 3-20.

772 Morelli, T. L., Hayes, R. A., Nahrung, H. F., Goodwin, T. E., Harelimana, I. H., Macdonald, L. J.,
773 & Wright, P. C. (2013). Relatedness communicated in lemur scent. *Die*
774 *Naturwissenschaften*, *100*(8), 769-777. https://doi.org/10.1007/s00114-013-1074-x
775 Nigi, H. (1975). Menstrual cycle and some other related aspects of Japanese monkeys
776 (*Macaca fuscata*). *Primates*, *16*(2), 207-216. https://doi.org/10.1007/BF02381418
777 Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Lengendre, P., McGlinn, D., Minchin, P. R.,
778 O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H.
779 (2020). *vegan : Community ecology package*. https://CRAN.R-
780 project.org/package=vegan
781 Olsson, M. J., Lundström, J. N., Kimball, B. A., Gordon, A. R., Karshikoff, B., Hosseini, N.,
782 Sorjonen, K., Olgart Höglund, C., Solares, C., Soop, A., Axelsson, J., & Lekander, M.
783 (2014). The scent of disease : Human body odor contains an early chemosensory cue
784 of sickness. *Psychological Science*, *25*(3), 817-823.
785 https://doi.org/10.1177/0956797613515681
786 O'Neill, A. C., Fedigan, L. M., & Ziegler, T. E. (2004). Relationship between ovarian cycle
787 phase and sexual behavior in female Japanese macaques (*Macaca fuscata*). *American*
788 *Journal of Physical Anthropology*, *125*(4), 352-362.
789 https://doi.org/10.1002/ajpa.20024
790 Osorio, D., & Vorobyev, M. (2005). Photoreceptor sectral sensitivities in terrestrial animals :
791 Adaptations for luminance and colour vision. *Proceedings of the Royal Society of*
792 *London B: Biological Sciences*, *272*(1574), 1745-1752.
793 https://doi.org/10.1098/rspb.2005.3156
794 Pfefferle, D., Brauch, K., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Female Barbary
795 macaque (*Macaca sylvanus*) copulation calls do not reveal the fertile phase but

influence mating outcome. *Proceedings. Biological Sciences / The Royal Society*, *275*(1634), 571-578. https://doi.org/10.1098/rspb.2007.1499

Pfefferle, D., Heistermann, M., Pirow, R., Hodges, J. K., & Fischer, J. (2011). Estrogen and progestogen correlates of the structure of female copulation calls in semi-free-ranging Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, *32*(4), 992-1006. https://doi.org/10.1007/s10764-011-9517-8

Phillips, K. A., Buzzell, C. A., Holder, N., & Sherwood, C. C. (2011). Why do capuchin monkeys urine wash? An experimental test of the sexual communication hypothesis using fMRI. *American Journal of Primatology*, *73*(6), 578-584. https://doi.org/10.1002/ajp.20931

Pipitone, R. N., & Gallup, G. G. (2008). Women's voice attractiveness varies across the menstrual cycle. *Evolution and Human Behavior*, *29*(4), 268-274. https://doi.org/10.1016/j.evolhumbehav.2008.02.001

Pipitone, R. N., & Gallup, G. G. (2012). The unique impact of menstruation on the female voice : Implications for the evolution of menstrual cycle cues. *Ethology*, *118*(3), 281-291. https://doi.org/10.1111/j.1439-0310.2011.02010.x

Pisanski, K., Oleszkiewicz, A., Plachetka, J., Gmiterek, M., & Reby, D. (2018). Voice pitch modulation in human mate choice. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1893), 20181634. https://doi.org/10.1098/rspb.2018.1634

Poirier, A. C., Waterhouse, J. S., Dunn, J. C., & Smith, A. C. (2021). Scent marks signal species, sex and reproductive status in tamarins (*Saguinus spp.*, neotropical primates). *Chemical Senses*, *bjab008*. https://doi.org/10.1093/chemse/bjab008

Poirier, A. C., Waterhouse, J. S., Watsa, M., Erkenswick, G. A., Moreira, L. A. A., Tang, J., Dunn, J. C., Melin, A. D., & Smith, A. C. (2021). On the trail of primate scent signals : A

field analysis of callitrichid scent-gland secretions by portable gas chromatography-mass spectrometry. *American Journal of Primatology*, *83*(3), e23236. https://doi.org/10.1002/ajp.23236

Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P. M., Kappeler, P. M., & Charpentier, M. J. E. (2017). Mandrills use olfaction to socially avoid parasitized conspecifics. *Science Advances*, *3*(4), e1601721. https://doi.org/10.1126/sciadv.1601721

Probst, F., Fischbacher, U., Lobmaier, J. S., Wirthmüller, U., & Knoch, D. (2017). Men's preferences for women's body odours are not associated with human leucocyte antigen. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864), 20171830. https://doi.org/10.1098/rspb.2017.1830

Rasmussen, L. E., Schmidt, M. J., Henneous, R., Groves, D., & Daves, G. D. (1982). Asian bull elephants : Flehmen-like responses to extractable components in female elephant estrous urine. *Science*, *217*(4555), 159-162. https://doi.org/10.1126/science.7089549

Rigaill, L. (2020). Fine-scale variation in lip and cheek colour according to the timing of ovulation in women. *Behavioral Ecology and Sociobiology*, *74*(6), 71. https://doi.org/10.1007/s00265-020-02851-y

Rigaill, L., & Garcia, C. (2021). Does male mate choice select for female coloration in a promiscuous primate species? *Animal Behaviour*, *177*, 171-181. https://doi.org/10.1016/j.anbehav.2021.05.002

Rigaill, L., Higham, J. P., Lee, P. C., Blin, A., & Garcia, C. (2013). Multimodal sexual signaling and mating behavior in olive baboons (*Papio anubis*). *American Journal of Primatology*, *75*(7), 774-787. https://doi.org/10.1002/ajp.22154

Rigaill, L., Higham, J. P., Winters, S., & Garcia, C. (2019). The redder the better? Information content of red skin coloration in female Japanese macaques. *Behavioral Ecology and Sociobiology*, *73*(8), 103. https://doi.org/10.1007/s00265-019-2712-x

Rigaill, L., MacIntosh, A. J. J., Higham, J. P., Winters, S., Shimizu, K., Mouri, K., Furuichi, T., & Garcia, C. (2015). Multimodal advertisement of pregnancy in free-ranging female Japanese macaques (*Macaca fuscata*). *PLoS ONE*, *10*(8), e0135127. https://doi.org/10.1371/journal.pone.0135127

Rigaill, L., MacIntosh, A. J. J., Higham, J. P., Winters, S., Shimizu, K., Mouri, K., Suzumura, T., Furuichi, T., & Garcia, C. (2017). Testing for links between face color and age, dominance status, parity, weight, and intestinal nematode infection in a sample of female Japanese macaques. *Primates*, *58*(1), 83-91. https://doi.org/10.1007/s10329-016-0575-6

Rigaill, L., Suda-Hashimoto, N., Ducroix, L., Mouri, K., Furuichi, T., & Garcia, C. (2017). Testing for links between female urine odor and male sexual behaviors in Japanese macaques (*Macaca fuscata*). *International Journal of Primatology*, *38*(5), 823-837. https://doi.org/10.1007/s10764-017-9980-y

Scordato, E. S., & Drea, C. M. (2007). Scents and sensibility : Information content of olfactory signals in the ringtailed lemur, *Lemur catta*. *Animal Behaviour*, *73*(2), 301-314. https://doi.org/10.1016/j.anbehav.2006.08.006

Semple, S. (2001). Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour*, *61*(5), 1023-1028. https://doi.org/10.1006/anbe.2001.1692

Semple, S., & McComb, K. (2000). Perception of female reproductive state from vocal cues in a mammal species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1444), 707-712. https://doi.org/10.1098/rspb.2000.1060

Semple, S., McComb, K., Alberts, S., & Altmann, J. (2002). Information content of female copulation calls in yellow baboons. *American Journal of Primatology*, *56*(1), 43-56. https://doi.org/10.1002/ajp.1062

Setchell, J. M., Charpentier, M. J. E., Abbott, K. M., Wickings, E. J., & Knapp, L. A. (2009). Is brightest best? Testing the Hamilton-Zuk hypothesis in mandrills. *International Journal of Primatology*, *30*(6), 825-844. https://doi.org/10.1007/s10764-009-9371-0

Setchell, J. M., Charpentier, M. J. E., Bedjabaga, I.-B., Reed, P., Wickings, E. J., & Knapp, L. A. (2006). Secondary sexual characters and female quality in primates. *Behavioral Ecology and Sociobiology*, *61*(2), 305-315. https://doi.org/10.1007/s00265-006-0260-7

Setchell, J. M., Vaglio, S., Abbott, K. M., Moggi-Cecchi, J., Boscaro, F., Pieraccini, G., & Knapp, L. A. (2011). Odour signals major histocompatibility complex genotype in an Old World monkey. *Proceedings. Biological Sciences / The Royal Society*, *278*(1703), 274-280. https://doi.org/10.1098/rspb.2010.0571

Setchell, J. M., Vaglio, S., Moggi-Cecchi, J., Boscaro, F., Calamai, L., & Knapp, L. A. (2010). Chemical composition of scent-gland secretions in an old world monkey (*Mandrillus sphinx*) : Influence of sex, male status, and individual identity. *Chemical Senses*, *35*(3), 205-220. https://doi.org/10.1093/chemse/bjp105

Setchell, J. M., Wickings, E. J., & Knapp, L. A. (2006). Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2395-2400. https://doi.org/10.1098/rspb.2006.3573

889 Setchell, J. M., & Wickings, J. E. (2004a). Sexual swelling in mandrills (*Mandrillus sphinx*) : A
890 test of the reliable indicator hypothesis. *Behavioral Ecology*, *15*(3), 438-445.
891 https://doi.org/10.1093/beheco/arh027
892 Setchell, J. M., & Wickings, J. E. (2004b). Social and seasonal influences on the reproductive
893 cycle in female mandrills (*Mandrillus sphinx*). *American Journal of Physical*
894 *Anthropology*, *125*(1), 73-84. https://doi.org/10.1002/ajpa.10375
895 Shoup-Knox, M. L., Ostrander, G. M., Reimann, G. E., & Pipitone, R. N. (2019). Fertility-
896 dependent acoustic variation in women's voices previously shown to affect listener
897 physiology and perception. *Evolutionary Psychology*, *17*(2), 1474704919843103.
898 https://doi.org/10.1177/1474704919843103
899 Singh, D., & Bronstad, P. M. (2001). Female body odour is a potential cue to ovulation.
900 *Proceedings of the Royal Society B: Biological Sciences*, *268*(1469), 797-801.
901 https://doi.org/10.1098/rspb.2001.1589
902 Smith, T. D., & Bhatnagar, K. P. (2004). Microsmatic primates : Reconsidering how and when
903 size matters. *The Anatomical Record Part B: The New Anatomist*, *279B*(1), 24-31.
904 https://doi.org/10.1002/ar.b.20026
905 Smith, T. E. (2006). Individual olfactory signatures in common marmosets (*Callithrix jacchus*).
906 *American Journal of Primatology*, *68*(6), 585-604. https://doi.org/10.1002/ajp.20254
907 Smith, T. E., Abbott, D. H., Tomlinson, A. J., & Mlotkiewicz, J. A. (1997). Differential display of
908 investigative behavior permits discrimination of scent signatures from familiar and
909 unfamiliar socially dominant female marmoset monkeys (*Callithrix jacchus*). *Journal*
910 *of Chemical Ecology*, *23*(11), 2523-2546.
911 https://doi.org/10.1023/B:JOEC.0000006664.38169.e5

912 Smith, T. E., Tomlinson, A. J., Mlotkiewicz, J. A., & Abbott, D. H. (2001). Female marmoset
913 monkeys (*Callithrix jacchus*) can be identified from the chemical composition of their
914 scent marks. *Chemical Senses*, *26*(5), 449-458.
915 https://doi.org/10.1093/chemse/26.5.449
916 Snowdon, C. T. (2004). Sexual selection and communication. In C. P. van Schaik & P. M.
917 Kappeler (Éds.), *Sexual Selection in Primates : New and Comparative Perspectives* (p.
918 57-70). Cambridge University Press.
919 https://doi.org/10.1017/CBO9780511542459.006
920 Spence-Aizenberg, A., Kimball, B. A., Williams, L. E., & Fernandez-Duque, E. (2018). Chemical
921 composition of glandular secretions from a pair-living monogamous primate : Sex,
922 age, and gland differences in captive and wild owl monkeys (*Aotus spp.*). *American*
923 *Journal of Primatology*, *80*(2), e22730. https://doi.org/10.1002/ajp.22730
924 Stockley, P., Bottell, L., & Hurst, J. L. (2013). Wake up and smell the conflict : Odour signals in
925 female competition. *Philosophical Transactions of the Royal Society B: Biological*
926 *Sciences*, *368*(1631), 20130082. https://doi.org/10.1098/rstb.2013.0082
927 Swaisgood, R. R., Lindburg, D. G., & Zhang, H. (2002). Discrimination of oestrous status in
928 giant pandas (*Ailuropoda melanoleuca*) via chemical cues in urine. *Journal of Zoology*,
929 *257*(3), 381-386. https://doi.org/10.1017/S0952836902000985
930 Thrall, P. H., Antonovics, J., & Dobson, A. P. (2000). Sexually transmitted diseases in
931 polygynous mating systems : Prevalence and impact on reproductive success.
932 *Proceedings of the Royal Society B: Biological Sciences*, *267*(1452), 1555-1563.
933 Townsend, S. W., Deschner, T., & Zuberbühler, K. (2011). Copulation calls in female
934 chimpanzees (*Pan troglodytes schweinfurthii*) convey identity but do not accurately

reflect fertility. *International Journal of Primatology*, *32*(4), 914-923. https://doi.org/10.1007/s10764-011-9510-2

Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871–1971*. B. Campbell.

Ueno, Y. (1994). Olfactory discrimination of urine odors from five species by tufted capuchin (*Cebus apella*). *Primates*, *35*(3), 311-323. https://doi.org/10.1007/BF02382728

Vaglio, S., Minicozzi, P., Kessler, S. E., Walker, D., & Setchell, J. M. (2021). Olfactory signals and fertility in olive baboons. *Scientific Reports*, *11*(1), 8506. https://doi.org/10.1038/s41598-021-87893-6

Vaglio, S., Minicozzi, P., Romoli, R., Boscaro, F., Pieraccini, G., Moneti, G., & Moggi-Cecchi, J. (2016). Sternal gland scent-marking signals sex, age, rank, and group identity in captive mandrills. *Chemical Senses*, *41*(2), 177-186. https://doi.org/10.1093/chemse/bjv077

Van Belle, S., Estrada, A., Ziegler, T. E., & Strier, K. B. (2009). Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*) : Male mate guarding and female mate choice. *American Journal of Primatology*, *71*(2), 153-164. https://doi.org/10.1002/ajp.20635

Walker, D., & Vaglio, S. (2021). Sampling and analysis of animal scent signals. *Journal of Visualized Experiments: JoVE*, *168*. https://doi.org/10.3791/60902

Wallis, J., & Lemmon, W. B. (1986). Social behavior and genital swelling in pregnant chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *10*(2), 171-183. https://doi.org/10.1002/ajp.1350100207

Wickham, H. (2016). *ggplot2 : Elegant graphics for data analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2013). Male mating behaviour in relation to female sexual swellings, socio-sexual behaviour and hormonal changes in wild Barbary macaques. *Hormones and Behavior*, *63*(1), 32-39. https://doi.org/10.1016/j.yhbeh.2012.11.004