Multimodal sexual signaling and mating strategies in olive baboons and Japanese macaques

Lucie Rigaill, Social Systems Evolution Section, Primate Research Institute, Kyoto University

Chapter 1. General introduction

Reproduction and mating activities can be costly to females (e.g. sexual coercion and maternal investment) and males (e.g. mate guarding and intra-sexual competition). Therefore there should have been selection for the ability to signal (for females) and discriminate (for males) reproductive state and individual qualities in order to not waste energy on non-reproductive mating and mating with low-quality mates. Multimodal sexual communication might have evolved as a trade-off between the costs and benefits from signaling and mating. However, only few studies have investigating how multiple sensory channels play a role in advertizing female reproductive status (ovulation and pregnancy) and individual characteristics, and thus their influence on male and female mating strategies in primates. Olive baboons and Japanese macaques are good primate models to understand how different systems of sexual signaling can modulate male and female mating strategies. Female olive baboons and Japanese macaques display behavioral (proceptive behaviors), auditory (copulation and estrous calls), and visual (swelling size & color, face color) signals, and potential olfactory cues (vaginal odor) of their reproductive status. However, whereas olive baboons seem to have evolved a system of "obvious" advertisements of the ovulation timing and pregnancy period, reproductive status seems to be more "concealed" in Japanese macaques. Lastly, whereas Japanese macaques are characterized by a strict mating season, olive baboons mate throughout the year. Investigating the differences in sexual signaling expression (and their implication in mating strategies) between olive baboons and Japanese macaques might help to understand how environmental and social constrains have modulated the evolution of sexual signals among primate species.

Chapter 2. Multimodal sexual signaling and mating behavior in olive baboon (*Papio anubis*)

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 the role of visual, auditory, behavioral, and olfactory channels are rarely undertaken. I 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 sensory channels 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 nine adult females, I found that fine-scale variation in sexual swelling size, female behavior and copulation call rates could advertise the beginning of the fertile phase whereas swelling color did not. Rates of olfactory inspections by males also increased during the fertile phase, suggesting that female odors were of interest to males and may contain information about ovulation. There was no relationship between female characteristics (age and rank), swelling size/color, and copulation calls, but proceptive behaviors 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, this suggests 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 information (female odors). Sexual communication in olive baboons is consistent with a multimodal framework for fertility signaling, potentially allowing males and females to establish different mating strategies.

Chapter 3. Multimodal advertisement of pregnancy in free-ranging female Japanese macaques (*Macaca fuscata*)

The role of multiple sexual signals in indicating the timing of female ovulation, and discrimination of this timing by males, has been particularly well studied among primates. However the exhibition of pregnancy signals, and how such signals might modulate male post-conception mating decisions, is still poorly understood. I aimed to determine if Japanese macaque males use changes in female sexual signals (behavioral, visual and auditory) to discriminate pregnancy and adjust their socio-sexual behaviors. I combined behavioral observations, digital photography and endocrinological (progestogen and estrogen) data, collected systematically during three one-month periods: the pre-conceptive period, the 1st month of pregnancy and the 2nd month of pregnancy. I analyzed variation in the probability of detecting male and female socio-sexual behaviors and oestrus calls, as well as changes in female face color parameters, in relation to female reproductive state. Based on my focal observations, I found that males did not copulate during the pregnancy period, and that female socio-sexual behaviors generally decreased from the pre-conceptive to post-conceptive periods. Female face luminance decreased from the pre-conceptive month to the pregnancy period whereas face color only varied between the 1st and 2nd month of gestation. My results suggest that Japanese macaque females display sexual signals of pregnancy that males might use to reduce energy wasted on non-reproductive copulations with pregnant females. I hypothesize that females advertize their pregnancy through changes in behavioral, visual and potential auditory signals that males can use to adjust their mating behaviors. I finish by discussing implications for male and female post-conception strategies.

Chapter 4. Testing for links between face color and age, dominance status, parity, weight, and intestinal nematode infection in a sample of female Japanese macaques (*Macaca fuscata*)

Studies of the role of secondary sexual ornaments in mate choice tend to focus on colorful traits in males, but females of many animal species express colorful ornamentation too. Among non-human primates, investigations into the role of female secondary sexual traits as indicators of life history characteristics, reproductive success, and health status have mostly focused on sexual swellings, whereas only few studies have been conducted on the role of facial color. Recent studies on rhesus macaques and mandrills suggested that female ornamentation might provide information about female life history characteristics, but not on disease resistance factors and parasite infection, which have been shown to affect male ornamentation in other studies. In Japanese macaques (*Macaca fuscata*), females have brightly colored faces that are indicative of their reproductive status. I aimed to determine whether female facial color might also convey information about age, dominance rank, parity, weight, and intestinal nematode infection in free-ranging individuals. I analyzed whether female facial parameters (luminance and redness) were linked to these individual characteristics, using digital photography and data on intestinal parasite infection collected systematically during one month for each of 7 free-ranging females. I found no evidence to suggest that female facial color is an indicator of any of these measures in Japanese macaques. Considering my small data set, it is still preliminary to draft any clear conclusions. Future studies combining digital, hormonal, parasitological and behavioral data are needed to assess the possible role of female face color on male preferences and mating choice in Japanese macaques.

Chapter 5. Testing for links between female urine odor and male sexual behaviors in Japanese macaques (*Macaca fuscata*)

Previous studies in primates underline that female odors may play a greater role in fertility signaling and mate attraction than previously suggested. Urine is already known to be involved in New World monkey and lemur sexual communication, but most of the Old World

monkey studies have rather focused on the role of vaginal secretions. I investigated whether female urine might promote male sexual behaviors (approaches and inspections of female genital area) in Japanese macaques (*Macaca fuscata*). I used a non-invasive protocol for urine sample collection and a sequential presentation paradigm for the behavioral experiments presenting female urine vs. control cotton swabs to males living in a social group with cycling females. I first tested whether males showed an increase in processing behaviors (e.g. licking, sniffing, tasting) toward unfamiliar female urine stimuli (from pre-fertile, fertile, and post-fertile phases) vs. neutral stimuli (saline solution). I then analyzed variation in male investigatory behaviors toward resident females in relation to their reproductive status (i.e. peri-ovulatory, non-fertile, and pregnancy periods) between pre- and post-exposure to female urine and neutral stimuli. Male processing behaviors increased significantly toward urine swabs compared to control stimuli but did not vary between the 3 different cycling phases. Males performed significantly fewer approaches toward pregnant females, but approaches did not vary between peri-ovulatory and non-fertile females or after exposure to female urine stimuli. Male inspections of the female genital area were not related to female reproductive status and/or exposure to urine. These results suggest that although female urine contains some olfactory and/or gustatory compounds that males might detect; female urine might not trigger male sexual behaviors in this species. I then discuss the alternative hypothesis that males might be inspecting for other visual and/or olfactory information that derive from females (i.e. vaginal secretions), or from males (sperm).

Chapter 6. General discussion

This research is the first to investigate multimodal sexual communication in olive baboons and Japanese macaques. Although most of the previous studies of sexual selection and mating behaviors have been focused on the male perspective (sexual signaling and mating decisions), my research has shown that in two Cercopithecine species, sexual selection seems to operate by broadcasting female reproductive state (ovulation and pregnancy) through multiple sensory channels, i.e. behavioral, visual, auditory, and olfactory communication. I suggest that such framework of multimodal sexual signaling might have evolved from sexual selection favoring ‘mutual mate choice” and from socio-environmental constraints. To conclude, I suggest that investigating different frameworks of sexual signaling and the role of multiple signals, rather than focusing on “obvious signals”, could provide critical information about male and female mating strategies in primates. More holistic studies investigating the link between sexual signaling, female reproductive periods (menstrual cycle and pregnancy), male responses to signaling, and socio-ecological constraints (e.g. infanticide risks and environmental factors) are needed to better understand the costs and benefits from multimodal sexual signaling. Such future research would greatly contribute to our understanding of the underlying mechanisms modulating primate sexual signaling andmating strategies, and therefore the evolution of primate sexuality.