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Coevolution of female ovulatory signals and male–male competition in primates



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HIGHLIGHTS

- I develop an evolutionary model of ovulatory signals and male–male competition.
- I show that various types of ovulatory signals may evolve and can be multistable.
- Male–male competition becomes intense when the signal honestly indicates ovulation.
- Less exaggerated ovulatory signals may evolve in unimale groups.
- Monogamy is more likely to evolve when ovulation is concealed.

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ABSTRACT

Visual signals of ovulation vary among primate species. Although slight ovulatory signals are considered primate ancestral traits of which some species still exhibit, some show prominent swelling of their perineal skin (exaggerated sexual swellings) and others do not exhibit any signals of ovulation (concealed ovulation). These signals strongly affect male mating behaviors. I develop an evolutionary model of female ovulatory signals and male–male competition. I assume that each male allocates his effort between attraction of females and male–male competition for dominance. Each female gains a benefit if she is fertile and free from the alpha male who always guards one of the most fertile females in the group, but suffers a cost if she expresses a different ovulatory signal from an ancestral trait. I show that various types of ovulatory signals may evolve and can be multistable. Male–male competition becomes intense when the signal honestly indicates ovulation. Ovulatory signals may evolve to be less exaggerated in unimale groups than in multimale groups and monogamy is more likely to evolve when ovulation is concealed. These results may partly explain why various types of primate ovulatory signals evolved and how they have affected primate societies.

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1. Introduction

Primate social structures are strongly affected by mating strategies of males and females. Males generally compete with each other to fertilize more females than other males. In multimale groups, dominance hierarchies among males are universally observed and males make a large effort to raise their rank because dominant males have a larger chance to copulate with females than subordinate males (Constable et al., 2001; Vigilant et al., 2001; Inoue et al., 2008). Males also sometimes form a coalition to facilitate cooperative attacks against other males (Hill, 1997; Horiuchi, 2005, 2007; Singh et al., 2011). In unimale groups, males

guard their female partner(s) from outgroup males (Tilson, 1981; Watts, 1996). Primate males often have larger bodies and canines than females, suggesting that strong intrasexual selection acted on these traits.

Males also make an effort to attract females. Primate males (and females) often show costly courtship behaviors to increase the chance of copulation (Manson, 1997), for example, male bonobos (*Pan paniscus*) sometimes provide food to females to mate with them (de Waal, 1997). Moreover, female preferences for male behaviors and physical traits are sometimes observed in primates, which may affect male mating strategies. Although a dominant rank is attractive for females, females also prefer familiar (friendly) males (reviewed in Small, 1989) and males often groom females to form good friendships with them. For physical traits, adult male rhesus macaques (*Macaca mulatta*) increase

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reddening of facial skin during their mating season and females prefer red male faces (Waitt et al., 2003). Similarly, male mandrills (*Mandrillus sphinx*) have brighter and more extensive red coloration on the faces than females and female mandrills prefer brightly colored males (Setchell, 2005). These male behaviors and physical traits may be favored by intersexual selection.

Here, male traits for mating success are classified into two types, those associated with male–male competition and those with attraction of females, because intrasexual selection and intersexual selection are two major forms of sexual selection (Darwin, 1871). Although many theoretical studies of sexual selection assume a tradeoff between viability and attractiveness on male traits (Lande, 1981; Kirkpatrick, 1982), there may also be a tradeoff between male effort against intrasexual selection and that against intersexual selection because these two selection pressures may act differently on male behaviors and physical traits. Therefore, an allocation of effort between them is an important male mating strategy.

Not only male mating strategies but also female mating strategies are important for the evolution of primate social structures. One of the most prominent physical traits related to female mating strategy is visual signals of ovulation, which can be categorized into three types: absent, slight, and exaggerated. The relationship between visual signals of ovulation and mating systems is well investigated in primatology, and it is often considered that the absence of signals relates to monogamy and exaggerated signals relate to a multimale social system (Sillén-Tullberg and Møller, 1993; Nunn, 1999; Pagel and Meade, 2006). However, functional significance and evolutionary causes of these signals remain unknown.

A slight ovulatory signal may be the ancestral trait of primates and some species still exhibit slight signals (Sillén-Tullberg and Møller, 1993). However, females of some species show prominent swelling or conspicuous coloration of their perineal skin, which is usually termed “exaggerated sexual swellings.” These traits are generally exhibited during the part of their menstrual cycle when they are most likely to ovulate, implying that exaggerated sexual swellings indicate sexual receptivity (fertility) of females (Hasegawa and Hiraiwa-Hasegawa, 1983; Domb and Pagel, 2001; Deschner et al., 2004; Barelli et al., 2007). Although swelling size may be related to the probability of ovulation, large swellings are also exhibited during non-ovulation (infertile) period in many species, suggesting that the signal is not perfectly honest (Nunn, 1999). In other words, females are exaggerating not only the morphology of the trait but also their fertility. Exaggerated sexual swellings may be costly for females because of both the energy required for travel and the risk of increased infection, but they may also serve to confuse paternity certainty among males, because dominant males do not always guard females with sexual swellings so that females can mate with multiple males (reviewed in Nunn, 1999; Nunn et al., 2001). Since male primates sometimes kill infants they have not sired (Sugiyama, 1965; Hrdy, 1979; Hiraiwa-Hasegawa, 1988; Hiraiwa-Hasegawa and Hasegawa, 1994), it is important for females to mate with multiple males during the fertile period and confuse paternity.

Ovulatory signals sometimes affect the nature of primate societies. Chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) are closely related to each other and have a similar morphology, but their temperaments and behaviors are somewhat different (de Waal, 1997; Stanford, 1998). Bonobos exhibit less severe aggression (Goodall, 1986; Kano, 1992; Parish and de Waal, 2000), greater social tolerance (Hare et al., 2007; Hare and Kwetuenda, 2010), and greater empathy (de Waal, 1997; Kano et al., 2015) than chimpanzees, which may be caused by differences in neural systems supporting social cognition (Rilling et al., 2012). Interestingly, while female chimpanzees usually do not exhibit sexual swellings (estrus) during postpartum amenorrhea or pregnancy,

female bonobos exhibit a prolonged “pseudo-estrus” during such non-conceptive periods (Furuichi, 2011). Their long periods of pseudo-estrus may increase the number of estrus females in a group and raise the social status of females, which contributes to the peaceful nature of bonobo society (Furuichi, 2011).

In some other primate species, females do not exhibit any signals of ovulation, which is usually termed “concealed ovulation.” It is difficult for primate females to completely conceal hormonal metabolites associated with ovulatory events (van Schaik et al., 1999), suggesting that concealed ovulation is a costly signal for females. Since human females also conceal their ovulation, this trait is often argued to have affected human evolution (Alexander and Noonan, 1979; Burley, 1979; Lovejoy, 1981, 2009; Strassmann, 1981; Pawłowski, 1999). In these arguments, concealed ovulation is considered to force males into a pair bond because a male has to always guard a female to monopolize her fertility if he cannot recognize her ovulation. However, ovulatory signals are also absent in some species with a unimale or a multimale mating system (Sillén-Tullberg and Møller, 1993), so that it remains unclear why female ovulatory signals evolved to be absent in some primates.

Since mating strategies of males and females interact with each other and there is often a conflict of interest between both sexes, it is difficult to study the evolution of mating systems without using mathematical models. However, while many game-theoretic models have been applied to this problem (Maynard Smith, 1977; Harada and Iwasa, 1996; Iwasa and Harada, 1998; Kokko, 1999; Ihara, 2002), they do not apply to the evolution of primate mating systems because they did not consider two essential factors of primate society, group structures and dominance hierarchies. Nakahashi and Horiuchi (2012) investigated the evolution of primate mating systems using a mathematical model that included these two factors, but the evolution of female ovulatory signals was not considered. Pagel (1994) investigated the evolution of exaggerated sexual swellings by using a mathematical model and argued that the trait evolved because of competition among females to attract males with good genes, but this is not supported by the available primatological evidence (Nunn, 1999). Theoretical studies predict that female traits indicative of their fertility tend to coevolve with male preferences for such traits (Nakahashi, 2008), which may explain the evolution of primate male preference for females with larger sexual swellings, since larger swellings may indicate higher fertility (reviewed in Nunn, 1999). However, it is difficult to understand why various types of female ovulatory signals evolved in primates. Since exaggerated sexual swellings and concealed ovulation are a quantitative difference in ovulatory signal, we should investigate the evolution of these traits by using a single mathematical model. In this paper, I develop a mathematical model to consider the coevolution of female ovulatory signals and male mating strategies, and discuss why various types of female ovulatory signals evolved in primates and how these signals have affected primate societies.

2. Model

2.1. Multimale group

2.1.1. Male and female strategies

In this model, we consider the coevolution of the male effort allocation strategy and the female estrus (advertisement of fertility) strategy. Males allocate their effort between male–male competition for dominance (intrasexual selection) and attraction of females (intersexual selection). Females change the morphology (size, shape, color, etc.) of their perineal skin in a certain period to advertise their sexual receptivity (fertility). We consider not the morphology of the trait but rather the length of period the trait is changed.

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