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Gauri R. Pradhan, Antje Engelhardt, Carel P. van Schaik, Dario Maestripieri

The evolution of female copulation calls in primates: a review and a new model

Correspondence to:

Dario Maestripieri, The University of Chicago, 5730 S. Woodlawn Avenue, Chicago, IL 60637, USA. email: dario@uchicago.edu

Present address:

Gauri R. Pradhan, Dario Maestripieri, Animal Behavior Research Group, The University of Chicago, Chicago, IL 60637, USA

Antje Engelhardt, German Primate Center, Gottingen, 37077, Germany

Carel P. van Schaik, Anthropological Institute and Museum, University of Zurich, Zurich, CH-2057, Switzerland

Abstract Female copulation calls are mating-associated vocalizations that occur in some species of Old World monkeys and apes. We argue that copulation calls have two immediate functions: to encourage mating attempts by other males and to increase mate guarding by the consort male. We hypothesize that female copulation calls have evolved under the selective pressures of risk of infanticide and sperm competition. When male mate guarding is effective, copulation calls allow females to concentrate paternity in dominant males and benefit from their protection against the risk of infanticide. When mate guarding is ineffective, copulation calls may bring genetic benefits to females through facilitation of sperm competition. We present a quantitative model in which interspecific variation in females' promiscuity predicts their tendency to use copulation calls in conjunction with mating. The model predicts that in species with little female promiscuity copulation calls should be rare and exhibited only in association with mating with dominant males. In species in which females are highly promiscuous, copulation calls should be frequent and unrelated to male dominance rank. The limited data available to test the model support its main predictions as well as the predicted relation between copulation calls and male dominance rank.

Introduction

In a number of different animal taxa, mating interactions are often preceded by an exchange of signals. These signals play an important role in the processes of mate attraction and mate choice and are probably under strong pressure by sexual selection (Andersson 1994). Signals that follow, rather than precede mating, are relatively rare and their functional significance is poorly understood. Although post-copulatory signals could play an important role in sperm competition and post-copulatory female choice (Birkhead and Pizzari 2002), the role of sexual selection in the evolution of post-copulatory signals is only beginning to be investigated (e.g. Dixson 1998; Maestripieri and Roney 2005).

Females of many primate species utter vocalizations in association with mating, which are referred to as copulation calls. Copulation calls typically occur in conjunction with the last stage of the mount or after copulation (Hamilton and Arrowood 1978; Hohmann and Herzog 1985; O'Connell and Cowlishaw 1994; Gouzoules et al. 1998). In macaques (*Macaca* spp.) and baboons (*Papio* spp.), female copulation calls take the form of grunts while in other species (e.g. talapoins, *Miopithecus talapoin*, and chimpanzees, *Pan troglodytes*) they resemble screams (e.g. Dixson 1998). Copulation calls are distinct from the estrous calls uttered by females in some primate species during periods of sexual receptivity but not necessarily during or after mating (woolly spider monkeys, *Brachyteles arachnoides,* Milton, 1985; aye-ayes, *Daubentonia madagascariensi*s, Sterling and Richard 1995; lion-tailed macaques, *Macaca silenus*, Lindburg 1990; gelada baboons, *Theropithecus gelada*, Moos-Heilen and Sossinka 1990; see Blake 1992, and Montgomerie and Thornhill 1989, for examples in other mammals and birds). Female

copulation calls should also not be confused with male copulation calls, i.e., squeak-like vocalizations that the males of some macaque species utter while ejaculating (Hauser 1993; Manson 1996; Hsu et al. 2002). Female copulation calls have mostly been reported in Old World monkeys and apes and especially in species that live in multi-male multi-female social groups in which females advertise sexual receptivity with exaggerated sexual swellings (Dixson 1998; van Schaik et al. 1999; Maestripieri and Roney 2005). In species where copulation calls occur, however, not all copulations are followed by copulation calls. In fact, the percentage of copulations followed by these calls varies widely within and across different species. The causes or correlates of this intra- and inter-specific variability in the occurrence of female copulation calls are poorly understood.

The aim of this article is to examine the functional significance of copulation calls and develop a model for their evolution. To this end, we first discuss some variables that may affect the occurrence of copulation calls and the responses they elicit in other individuals. Then we review the numerous hypotheses that have been proposed to explain their function and evaluate them in light of the available empirical evidence. We then develop a model for the evolution of female copulation calls that accounts for the inter- and intraspecific variability in their occurrence in the Primate order. Finally, we use data that are already available in the literature to test some of the predictions of the model.

Variation in copulation calls in relation to female and male characteristics

In species in which females advertise fertility with exaggerated sexual swellings, female copulation calls are most likely to occur in conjunction with maximum swellings, i.e. around the time of ovulation (Saayman 1970; Aich et al. 1990; O'Connell and Cowlishaw 1994; Todt et al. 1995; Gouzoules et al. 1998; Maestripieri et al. 2005). In chacma baboons (*Papio ursinus*), O'Connell and Cowlishaw (1994) reported that copulation calls were longer in conjunction with full sexual swellings. In yellow baboons (*Papio cynocephalus*), the size of the swelling did not account for a significant amount of variance in call length, mean peak fundamental frequency of tonal call units, or percentage of tonal call units per copulation call (Semple et al. 2002). Swelling size did affect, however, other acoustic parameters such as the number of call units in a call, rate of call unit delivery and mean call unit duration. Using a playback experiment, Semple (1998b) showed that Barbary macaque (*Macaca sylvanus*) males responded more strongly to the copulation calls given near ovulation than to the calls recorded in other stages of the cycle (see also Semple and McComb 2000). Taken together, these findings suggest that females may advertise their fertility through the rate or the acoustic structure of their copulation calls. It is worth noting, however, that in some primate species virtually all copulations are followed by copulation calls, (e.g. in pigtail macaques, *Macaca nemestrina*, Oi 1996), that even pregnant females have been reported to call after mating (e.g. in longtail macaques, *Macaca fascicularis*, van Noordwijk 1985; Nikitopoulos et al. 2004), and that in many of these cases systematic variation in the structure of these calls still remains to be demonstrated.

A few studies have suggested that the occurrence of copulation calls and/or their acoustic characteristics vary in relation to female dominance rank or age. Gouzoules et al.

(1998) reported that in sooty mangabeys (*Cercocebus torquatus atys*) low ranking females had a significantly higher mean rate of delivery of copulation calls than high ranking females. Furthermore, call length was greater in younger females than in older females. In Japanese macaques (*Macaca fuscata*), younger females copulated more, with more males, and were more likely to call after copulation than older females (Oda and Masataka 1995). In other studies, however, female dominance rank or age did not affect the occurrence of copulation calls (e.g., O'Connell and Cowlishaw 1994; Maestripieri et al. 2005).

An association between female copulation calls and male dominance rank has been reported by a large number of studies. Specifically, copulation calls are more likely to occur, or are longer, when females mate with dominant adult males than with subordinate or immature males, regardless of swelling size or other female characteristics (Saayman 1970; Hauser 1990; Oda and Masataka 1992; O'Connell and Cowlishaw 1994; Maestripieri et al. 2005; but see Nikitopoulos et al. 2004). Since primate females in many species are more likely to mate with dominant males in conjunction with ovulation than with subordinates, the association between copulation calls and male dominance rank may, at least in part, account for the observed association between copulation calls and maximum swelling size. Some studies have also reported that copulation calls occurred more frequently, or were longer, in conjunction with male ejaculation (Saayman 1970; Deputte and Goustard 1980; Todt et al. 1995; O'Connell and Cowlishaw 1994). Semple et al. (2002), however, showed that when other variables such as male rank and female swelling size were statistically controlled for, the correlation between copulation calls and male ejaculation was no longer significant.

Responses to copulation calls

Female copulation calls clearly elicit responses in other individuals. In macaques and baboons these vocalizations attract the attention of other males, who often approach and investigate the calling female (van Noordwijk 1985; Maestripieri et al. 2005). Playback experiments conducted by Semple (1998b; Semple and McComb 2000) with Barbary macaques showed that males respond to hearing copulation calls of estrous females by looking towards the loudspeaker and approaching. Moreover, Semple (1998b) showed that females were mated more quickly following the playback of their copulation call than following the playback of a control stimulus. These experiments indicate that copulation calls function to attract males to the calling female. Aside from these experimental data, however, no other evidence is available showing that copulation calls stimulate mating with multiple males. In fact, studies of Barbary macaques and Guinea baboons (*Papio papio*) have shown that female copulation calls were followed by an increase in mate guarding by the consort male, which included both a reduced tendency to leave the female and increased male following, proximity, and grooming (Todt et al. 1995; Maestripieri et al. 2005). Increased mate guarding by the consort male may also be accompanied by repeated mating with the calling female (in longtail macaques, Nikitopoulos et al. 2004). In Guinea baboons, copulation calls also elicited responses in other females, who approached the consort male at higher rates shortly after the vocalizations (Maestripieri et al. unpublished data). No other studies reported the responses of females to copulation calls.

The adaptive significance of female copulation calls

Previous hypotheses

The association between copulation calls, sexual swellings, and promiscuous mating systems suggests that these vocalizations may have evolved by sexual selection and are a component of female mating strategies. However, the specific adaptive function of copulation calls is widely debated. In some cases, the adaptive nature of copulation calls has also been directly questioned. The following are the main hypotheses that have been proposed to explain the function of copulation calls, if any (see also Nikitopoulos 2004; Maestripieri and Roney 2005). Our discussion assumes that the function is uniform across species; thus, if a study on a particular species convincingly refutes a hypothesis, we assume that it can be rejected in general. While some hypotheses are mutually incompatible, most are not; thus, more than one hypothesis may be supported by the data.

Hypothesis 1: Copulation calls reflect an orgasm-like reaction and are non-adaptive byproducts of sexual intercourse (Hamilton and Arrowood 1978). This hypothesis is not supported by the observation that the utterance of copulation calls does not coincide with other behavioral expressions of female orgasm (e.g. the "clutching reaction"; Deputte and Goustard 1980) and that in some cases copulation calls begin after the copulation has ended and the female is already physically separated from the male.

Hypothesis 2: Female copulation calls are a non-adaptive phenomenon maintained by phylogenetic inertia (Henzi 1996). This hypothesis is difficult to test but it

implies that copulation costs have no significant costs or benefits to the calling female or any other individuals. Given the responses these calls elicit in other individuals, this is unlikely to be the case.

Hypothesis 3: Copulation calls self stimulate the occurrence of ovulation (see Cheng 1992 for doves). This hypothesis might apply to female estrus calls but not to copulation calls because it would not explain why these calls occur after copulation. Moreover, in most primates, ovulation is largely independent of self- or social stimuli (e.g. Dixson 1998).

Hypothesis 4: Copulation calls promote synchronization of male and female orgasm (Hamilton and Arrowood, 1978). This hypothesis predicts that copulation calls should occur immediately before male ejaculation. However, the available data indicate that the calls tend to follow and not precede ejaculation (e.g. O'Connell and Cowlishaw 1994; Gouzoules et al. 1998; Nikitopoulos et al. 2004).

Hypothesis 5: Copulation calls strengthen the pair bond (Hamilton and Arrowood 1978). This hypothesis predicts that female copulation calls should be more common in pair-bonded primate species than in highly promiscuous primate species, but the opposite seems to be the case (see references above).

Hypothesis 6: Copulation calls are signals with which females advertise their fertility or sexual motivation (e.g. Aich et al. 1990; Gouzoules et al. 1998). This hypothesis is consistent with the observation that copulation calls are most likely to occur in conjunction with maximum sexual swelling but inconsistent with the observation that calls may occur in any stage of the menstrual cycle and even during pregnancy.

Furthermore, this hypothesis does not explain why females should advertise their fertility or sexual motivation shortly after copulation.

Hypothesis 7: *Copulation calls advertise mating to other females and inhibit breeding synchrony (Hohmann and Herzog 1985)*. This hypothesis is supported by a study of captive long-tailed macaques in which only one female came into estrus and copulated at any given time (Hohmann and Herzog 1985). Most other studies of macaques and baboons, however, have shown that multiple females can be receptive at the same time and emit copulation calls in conjunction with mating (e.g., O'Connell and Cowlishaw 1994; Nikitopoulos et al. 2004).

Hypothesis 8: *Copulation calls advertise mating to other females and promote breeding synchrony (see Viljoen 1977 for a nonprimate mammal)*. This hypothesis predicts that copulation calls should be more common in seasonally breeding species (in which females are more likely to be synchronous) than in nonseasonal species. However, nonseasonal (e.g. baboons) as well as seasonal primate species (e.g. Japanese macaques) exhibit female copulation calls. Furthermore, no study so far has reported a clear association between copulation calls and female breeding synchrony within a group.

Hypothesis 9: *Copulation calls advertise the presence of a male partner and reduce the risk of female harassment (O'Connell and Cowlishaw 1994)*. This hypothesis predicts that harassment of the mating female by other females should be a prominent feature of species in which copulation calls occur and that low-ranking females should be most likely to call. Contrary to this hypothesis, however, female-female harassment during mating is rarely observed in primate species in which female copulation calls occur, there is no evidence that copulation calls are effective in reducing such

harassment, and low female dominance rank is generally not a good predictor of the occurrence of copulation calls.

Hypothesis 10: Female copulation calls incite male-male competition and increase the probability of mating with dominant male (see Cox and LeBoeuf 1977 *for elephant seals, Mirounga angustirostris).* This hypothesis predicts that females should call before, or immediately after the male begins to mount, and mostly when mounted by subordinate males. Contrary to this hypothesis, however, females call more often with dominant males and mostly at the end of the mount sequence or after copulation has ended. This hypothesis, however, might apply to species in which males need multiple mounts to achieve ejaculation or in situations in which females are highly motivated to mate again (S. Semple, personal communication).

Hypothesis 11: Copulation calls incite male sperm competition thereby increasing the probability that females are fertilized by the male with the best sperm or the most compatible genotype (O'Connell and Cowlishaw 1994). This hypothesis explains a crucial feature of female copulation calls, i.e. the fact that they occur at the end of the copulatory sequence. In fact, in order for sperm competition to be most effective, females need to have the sperm of as many as males as possible in a short period of time. The sperm competition hypothesis implies that there is a conflict of interest between the mating male and the female, and that mate guarding by the mating male is ineffective in preventing the female from mating with other males. Although there is at present no clear evidence for primates that females gain genetic benefits from sperm competition (but see Jennions and Petrie 2000 for other animals), this hypothesis is consistent with the results

of playback experiments in Barbary macaques showing that copulation calls elicit the mating interest of other males.

Hypothesis 12: *Copulation calls incite polyandrous mating thereby reducing paternity certainty and the risk of infanticide (O'Connell and Cowlishaw 1994).* Although confusion of paternity and reduced risk of male infanticide may be a by-product of polyandrous mating and sperm competition, this is unlikely to be the primary adaptive function of female copulation calls. In fact, risk of infanticide would be reduced most effectively if females mated surreptitiously with multiple males so that each male would have high confidence of paternity. In other words, female sexual promiscuity alone would guarantee confusion of paternity and such promiscuity should not be advertised with vocalizations. If anything, female promiscuity should be advertised with estrous calls and not with copulation calls. Advertising mating through copulation calls would not produce any additional benefits in terms of paternity confusion but would instead have the counterproductive effect of reducing the confidence of paternity of all the males with which the calling female mates.

Hypothesis 13: *Females give copulation calls to announce paternity certainty to promote paternal investment (Henzi 1996).* This hypothesis predicts that females should give copulation calls in species where males engage in paternal behaviors such as infant carrying, grooming, or protection. In most species of Old World monkeys and apes in which copulation calls are frequent, adult males rarely carry or groom their offspring but may protect them from other males. This hypothesis, however, does not explain the mechanism through which the occurrence of copulation calls would result in increased infant protection, or paternal investment in general.

Hypothesis 14: *Copulation calls are used by females to encourage mate guarding by their preferred mating partners (Maestripieri and Roney 2005).* This hypothesis assumes that females use copulation calls to incite mate guarding by preferred mating partners either by providing precise information about their fertility (and therefore increasing the benefits of guarding to the consort male) or by advertising mating to other males and therefore forcing the consort male into mate guarding. Increased mate guarding following copulation may also be accompanied by repeated mating with the consort male. Females may benefit from increased mate guarding by (and repeated mating with) particular males by increasing the probability that they will be fertilized by males with good genes, or by increasing the confidence of paternity of dominant males and therefore their investment in protection from infanticide. This version of the "female choice" hypothesis shares some features with hypothesis # 13 but is more specific in terms of the benefit to the female (reduced risk of infanticide vs generic paternal investment) as well as the mechanism (increased male mate guarding). This hypothesis is generally consistent with the findings that females are more likely to call with dominant or otherwise successful males, and that copulation calls result in increased mate guarding (see references above). Similar to the sperm competition hypothesis (#11), this hypothesis also explains a crucial feature of female copulation calls, i.e. the fact that they occur at the end of the copulatory sequence. This hypothesis, however, does not seem to apply to species in which almost 100% of copulations are accompanied by copulation calls.

General discussion of functional hypotheses

The most parsimonious view of the immediate function of female copulation calls is that they simply advertise mating to other individuals, without necessarily conveying direct information about female fertility or sexual motivation. Since other females are rarely reported to respond to copulation calls, it is reasonable to hypothesize that the primary audiences for the copulation calls are the other males in the group ("non-mating males") and the mating (or consort) male. The immediate response elicited by copulation calls in the non-mating males is to attempt to mate with the calling female, while the immediate response of the mating male is to increase mate guarding. These two immediate consequences of female copulation calls may correspond to the following ultimate, or adaptive functions of these vocalizations: (1) inciting sperm competition, and thus acquiring genes with the highest viability in the present environment; and (2) concentrating paternity in dominant males, and especially the alpha male, thereby enjoying the benefit of his protection against other potentially infanticidal males.

Any viable hypothesis about the function of female copulation calls should effectively explain the most crucial feature of these calls, i.e. their timing of occurrence relative to copulation. Some of the hypotheses reviewed above predict that copulation calls should occur prior to mating, or to male ejaculation, or in conjunction with female orgasm. These predictions are not supported by the data. Other hypotheses do not provide compelling reasons as to why females should vocalize immediately after copulation. Two hypotheses that specifically address the timing of copulation calls in relation to copulation and are also supported by the data are the sperm competition hypothesis (#11) and the female choice hypothesis (# 14). Both hypotheses emphasize that copulation calls

have adaptive benefits to females through post-copulatory sexual selection processes (Birkhead and Pizzari 2002).

Although the sperm competition and the female choice hypotheses seemingly make opposite predictions about the immediate consequences of female copulation calls (Maestripieri and Roney 2005), they are in fact mutually compatible although they impose clear trade-offs on the females. Whenever the benefits of concentrating paternity in dominant males (and the consequent reduction in risk of infanticide) outweigh the benefits of sperm competition involving other males, females should always call when mating with dominants. Whenever the benefits of sperm competition outweigh the benefits of concentrating paternity in the dominant males, females should use copulation calls to advertise mating with all males, regardless of their dominance rank.

According to this framework, female copulation calls evolved in relation to the responses they elicit in both the mating male and the non-mating males and under the pressures of both natural selection (increased offspring survival in relation to reduced risk of infanticide) and sexual selection (sperm competition and post-copulatory female choice). In the next section we present a quantitative socio-ecological model to explain the evolution of female copulation calls in primates and to provide testable predictions about the proportion of copulations followed by copulation calls in different species. Because risk of infanticide, along with sperm competition, is thought to have played a major role in driving the evolution of copulation calls, we will begin to illustrate our model with a discussion of female counterstrategies to infanticide.

The evolution of female copulation calls: a new model

Protection from infanticide through paternity concentration

Females of many primate species and other mammals are vulnerable to infanticide by males (van Schaik 2000). Given the high investment primate females make in gestation and lactation, infanticide imposes high fitness costs to females and, therefore, they are expected to evolve counterstrategies to it (Hrdy 1974; 1979; van Schaik et al. 1999). Such counterstrategies may involve: 1) obtaining the protection of one or more adult males by concentrating paternity in them; 2) reducing the infanticidal tendencies of adult males present near the female by confusing paternity and increasing the probability that by committing infanticide they will kill their own offspring. These two strategies are not mutually exclusive and may be pursued by females at the same time, albeit with some trade-offs between them.

In order to reduce risk of infanticide through male protection, there must be fitness benefits to protection that outweigh the potential costs involved in fighting with other males, and this protection must be effective. Male motivation to protect infants can be enhanced by increasing their confidence of paternity. Females can increase the confidence of paternity of an adult male by mating exclusively with that male. Since male protection must be effective, females should always concentrate paternity in the most dominant male, the alpha male, or in the male that is expected to be alpha when the infant is born. Females, however, may gain various benefits from mating with multiple males (e.g., keeping the males within the group and benefiting from their protection from predators, or increasing the probability of being fertilized by a male with good genes) or

may be forced to do so (e.g. if individual males are larger than females and if females cannot be effectively guarded by the alpha male). Female promiscuity probably varies as a function of the species' social system; for example, there may be more opportunities (and more benefits) for female promiscuity in species that live in groups than in socially monogamous species, and in species that live in large groups with many males than in species that live in small one-male groups. As female promiscuity increases, the benefit derived from infanticide protection through paternity concentration in the alpha male will decrease rapidly. This is because with increasing female promiscuity the alpha male's confidence of paternity will decrease and so will his motivation to protect infants from infanticide.

The hypothesized relation between female promiscuity and protection from infanticide through paternity concentration is conveniently represented by an inverse sigmoidal function and is depicted by curve (1) in Fig. 1a. Here we define promiscuity (p) as the proportion of males within the group with which the female mates, i.e., $p = (i-1)/N$ where i is the number of adult males the female mates with and N is the total number of adult males in the group. Thus when the female mates with all the males in the group, $p = (N-1)/N$, whereas $p = 0$ when the female is strictly monandrous. We prefer this definition of p over the alternative of $p = i/N$ because of the more intuitive minimum of zero, even though its maximum is not 1, but depends on the number of males.

Although female promiscuity probably has multiple ecological, social, and reproductive determinants, for the purposes of our model, we will simply assume that female promiscuity varies along a continuum, between the extremes of sexually

monogamous species and highly promiscuous species, without considering the causes of this variation.

If $f_\alpha(p)$ is the inverse sigmoidal function giving the probability of infant survival due to protection from the dominant male, then

$$f_\alpha(p) = 1 - \frac{1}{1 + \exp(-k(p - B))} \qquad (1)$$

where B and k are constants. B determines the value of promiscuity at which the probability of infant survival due to concentration of paternity in the dominant male reaches half its maximum attainable value whereas k determines how this probability of infant survival declines with increasing promiscuity. As high value of k, infant protection goes to zero at a faster rate[1].

When female promiscuity equals 0, protection from infanticide through paternity concentration in the alpha male is very high. When females mate with another male in addition to the alpha male, protection by the alpha male begins to decrease; as females mate with more males in the group protection from the alpha male will continue to decrease and will eventually reach the 0 value when $p = 1$ (assuming large N).

Protection from infanticide through paternity confusion

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[1] The values of B and k are set to 0.4 and 10, respectively. The setting of these parameters is somewhat intuitive and based on a previous model of male infanticide (van Schaik et al. 2004). The model predicts probabilities within acceptable limits for a wide range of

When females are sexually promiscuous, they benefit in terms of protection from infanticide through paternity confusion. In other words, since any male that mates with a female has a nonzero chance of being the father of her offspring, his infanticidal tendencies will be reduced by the risk of killing his own offspring. In species with limited female promiscuity, females will still benefit from mating mostly with the alpha male because the level of protection from infanticide provided by the alpha male is high. As female promiscuity increases, the benefits of infanticide protection through paternity confusion will increase accordingly. In a situation of very high promiscuity, females are expected to mate with all males within the group and produce a similar level of paternity confidence in all of them. At this point, the probability of infant survival due to confusion of paternity rises to a maximum value. The hypothesized relation between female promiscuity and protection from infanticide through paternity confusion is best represented by the sigmoidal function depicted by curve 2 in Fig. 1a.

If $f_\beta(p)$ is the sigmoidal function giving the probability of infant survival due to confusion of paternity, then

$$f_\beta(p) = \frac{1}{1 + \exp(-k'(p - B'))} \tag{2}$$

where B' and k' are constants. B' determines the value of female promiscuity at which the probability of infant survival due to paternity confusion in all males equals

these parameter values, therefore the exact values of these parameters should not affect the main outcome of the model.

0.5, while $k^{'}$ determines how quickly this probability of infant survival increases with increasing promiscuity[2].

When female promiscuity equals 0, protection from infanticide through paternity confusion is very low. As females mate with other males in addition to the alpha male, these males begin to risk killing their own offspring by committing infanticide. Infant protection through paternity confusion will reach its maximum value 1 when females mate with all the males in the group.

Protection from infanticide and female copulation calls

How can probabilities of infant survival (1) and (2) be combined? If there is a risk of infanticide and females need a protector, then there is a direct tradeoff between the two probabilities. In other words, we may assume that the probabilities are independent and thus simply add them to calculate the overall probability of infant survival. This results in the curve depicted in Fig. 1b, which suggests that for a range of species included between the extremes of sexual monandry and high female promiscuity, females are highly vulnerable to risk of infanticide due to the fact that the levels of protection from infanticide provided by paternity concentration in the alpha male and from paternity confusion in the subordinates are relatively low. There are therefore, strong selective pressures for females to evolve behavioral strategies to protect their infants from infanticide. We hypothesize that copulation calls are one of these strategies. Specifically,

by advertising mating with the alpha male through copulation calls, females in effect blackmail the male into increasing his mate guarding behavior. This will in turn increase his confidence of paternity and his potential to protect the female from risk of infanticide.

From the discussion in the previous section we know that $f_\alpha(p) + f_\beta(p)$ denotes the probability of infant survival and that $1 - (f_\alpha(p) + f_\beta(p))$ denotes the probability that the infant is at risk from infanticide. Therefore, the probability of occurrence of copulation calls in a given species (i.e. the percentage of copulations that are followed by copulation calls) is expected to follow the pattern provided by $1 - (f_\alpha(p) + f_\beta(p))$ and result in a curve inverse to that shown in Fig. 1b. This new curve, depicted in Fig. 2a, shows that copulation calls will increase with increasing female promiscuity up to a peak and then decrease again. Specifically, in species in which females are sexually monandrous or have very little promiscuity, female copulation calls may not occur at all or occur at low rates. This is because in these species females are adequately protected by virtue of their mating pattern, and copulation calls do not provide any additional benefits in terms of infant protection from infanticide. As female vulnerability to risk of infanticide increases, so do the benefits provided by copulation calls through concentration of paternity in the mating male, and consequently the copulation call curve rises to a peak. The decrease in copulation calls following the peak at increasing values of *p* reflects the increasing costs of copulation calls derived from reduction of paternity confidence in all the males.

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[2]The values of B' and k' are here set to 0.6 and 10, respectively (see previous footnote

Sperm competition and female copulation calls

Females may benefit considerably from sperm competition and post-copulatory female choice (Birkhead and Pizzari 2002). These benefits may include fertilization insurance, genetic compatibility with specific male genotypes, and being fertilized by genotypes containing highly viable genes. Sperm competition and post-copulatory female choice are expected especially where females have limited opportunities to choose their mates.

The curve in Fig. 2a describes the occurrence of copulation calls in relation to variation in female promiscuity if paternity concentration in the mating male is the only benefit accrued to females through copulation calls. When female promiscuity becomes > 0, however, the opportunity arises for females to gain additional genetic benefits from inciting sperm competition and such benefits will increase with increasing promiscuity. If copulation calls are only used to incite sperm competition, their relation with female promiscuity is conveniently described by a polynomial function as illustrated by the curve depicted in Fig. 2b. Note that we assume here that copulation calls affect the timing of promiscuous mating (i.e. they incite males to mate in close temporal succession) but not how promiscuous females are (i.e. the proportion of males within a group with which females mate).

Since females are expected to pursue both the sperm competition benefits and the infanticide protection benefits, the probability of occurrence of copulation calls (q) in relation to promiscuity is obtained through a convex combination of the sperm competition and the infanticide protection functions:

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and van Schaik et a. 2004).

$$q(p,\varepsilon) = (1-\varepsilon)(1-(f_\alpha(p)+f_\beta(p))) + \varepsilon(1-(p-1)^2) \qquad (3)$$

where ε is the effect of the number of males, conveniently represented as a function of N

(the number of adult males in the group), such that $\varepsilon = 1 - \dfrac{1}{N}$. The function shows that as

the number of males in a group increases, sperm competition becomes more important.

Thus ε reflects the relative contribution made by sperm competition while $1-\varepsilon$ reflects

the relative contribution made by infanticide protection. We assume that as the

contribution to the probability of calling from sperm competition increases, the

contribution from infanticide avoidance decreases, thus allowing us to represent their

combination as an exclusive one. Clearly, when $0 < \varepsilon < 1$ the probability of calling is the

result of both sperm competition and infanticide avoidance through paternity

concentration. Thus, in this model, the probability that a female gives copulation calls (q)

is a function of two variables, p (promiscuity) and ε (effect of number of males). The

surface plot shown in Fig. 3 illustrates that if information is available on the average

female promiscuity for a species or group, one can predict the probability of occurrence

of female copulation calls for that species or group.

Copulation calls in relation to male dominance rank

In addition to predicting the percentage of copulations followed by copulation calls in

relation to female promiscuity, the model also predicts a relationship between female

copulation calls and the dominance rank of the males with which they mate. For low

values of female promiscuity, females should advertise mating with dominant males and

avoid calling following mating with subordinates. As promiscuity increases, females

should continue to advertise mating with dominants while their tendency to call following mating with subordinates will increase up the point where, in association with very high levels of promiscuity, females are expected to advertise mating with all males with which they mate, regardless of their dominance rank. Therefore, in this model, the probability of calling following mating with dominants is always at ceiling level for any value of female promiscuity, and variation in the proportion of copulations followed by copulation calls is regulated by the relative tendency of females to call or not to call with subordinates. Since many studies have reported that copulation calls are more likely to occur when females mate with dominant adult males than with subordinates (see above for references), we already know that this prediction of the model is supported by the data.

Testing the model

To test the predictions of the model, we gathered information on the average number of adult males present in a group, the average percentage of adult males with which a female mates during one cycle, and the average % of copulations followed by copulation calls in primate species for which this information is available. This information is presented in Table 1. We then used the equation (3) to calculate the expected % of copulations followed by copulation calls in a given species.

Table 1 shows that, with two exceptions, the observed percentage of copulations followed by copulation calls falls within 20% of the values predicted by the model. Thus the model is reasonably accurate in predicting variation in the occurrence of copulation

calls among different primate species. The exceptions involve two species, *Macaca fuscata* and *Macaca nemestrina*, for which the difference between the expected and observed values exceeds 20%. Data on the number of males in the group and female promiscuity for these species, however, were obtained from a single study and might have been somewhat inaccurate (e.g. observations of *M. nemestrina* were only made at a food provisioning site and without accurate individual recognition; Oi 1996). Therefore, more data for the species in Table 1 as well as for others not included here are needed for a comprehensive test of our model.

Table 1 only reports data on species in which copulation calls occur. Since we hypothesized that female copulation calls evolved as a result of joint selective pressures from risk of infanticide and opportunities for sperm competition, one corollary of our model is that copulation calls should be absent or rare in species in which both risk of male infanticide and sperm competition are absent or negligible, despite the fact that these species live in multi-male multi-female social groups and females mate with multiple males. Although it may be argued that opportunities for sperm competition are always present, it is worth emphasizing that selective pressures for sperm competition are only significant when females cannot discriminate among males on the basis of their quality or genotype compatibility, or they can discriminate but cannot choose their mates. If females can discriminate among males and are free to mate with their preferred males, sperm competition would not be selected for. Possible examples of species in which female copulation calls are not expected to occur would be species in which males advertise their quality with sexual adornments, or species with little or no sexual dimorphism in body size. In such species, there would be greater opportunities for female

mate choice, thus rendering post-copulatory mechanisms unnecessary. A more comprehensive test of our model would therefore include predicting not only the % copulation calls based on female promiscuity, but also in which species copulation calls would be present or absent based on the occurrence of male infanticide and the intensity of sperm competition. At present, we believe that the data on infanticide and sperm competition in primates are too sketchy for such a test.

Because in our model the evolution of female copulation calls is intrinsically related to both female and male mating strategies, a full understanding of these strategies is required to account for the distribution of copulation calls within the Primate order and the extent to which their occurrence varies both between and within species. Further research is therefore needed not only to assess the occurrence of male infanticide, sperm competition, and female copulation calls in a larger number of primate species, but also to better understand male and female reproductive strategies in these species. We hope that our model and its preliminary test presented here will stimulate more empirical work on sexual selection processes in primates and enable the development of more comprehensive models of female copulation calls.

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Figure captions

Fig. 1. (a). Estimated probability of infant survival from infanticide in relation to female promiscuity as a result of concentration of paternity in the dominant male and his protection (1) or as a result of paternity confusion among all males (2). (b). Estimated probability of infant survival from infanticide in relation to female promiscuity when protection obtained from paternity concentration in the dominant male and paternity confusion in all males are combined.

Fig. 2. (a). Expected probability of occurrence of female copulation calls in relation to female promiscuity, if reduced risk of infanticide is the only fitness benefit gained from copulation calls. (b). Expected probability of occurrence of female copulation calls in relation to female promiscuity, if genetic benefits from sperm competition are the only fitness benefits gained from copulation calls.

Fig. 3. Surface plot of probability of occurrence of female copulation calls as a function of female promiscuity (p) and ε (= 1-1/N, where N is the number of adult males in the group). The color code for the plot is such that black corresponds to probability 0 whereas white corresponds to probability 1.