

Primate copulation calls and postcopulatory female choice

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Females in some species of Old World monkeys and apes vocalize after copulation, but the function of these vocalizations is not clear. In this article, we examine the hypothesis that copulation calls are a form of postcopulatory female choice. According to this hypothesis, copulation calls are honest signals of fertility (i.e., ovulation) that are used by females to encourage mate guarding by their preferred mating partners and reduce the likelihood of sperm competition. Evidence in favor of this hypothesis is reviewed and discussed in relation to other hypotheses. We suggest that the evolution of female copulation calls in primates is linked to the evolution of other female mating signals such as exaggerated sexual swellings, the potential for sperm competition, and the opportunity for precopulatory female mate choice. *Key words*: copulation calls, female choice, mating, primates, sexual selection, sperm competition. [*Behav Ecol*]

In this article we examine the hypothesis that female copulation calls in Old World monkeys and apes are a form of postcopulatory female choice, the function of which is to encourage postcopulatory mate guarding by preferred males and minimize the probability of sperm competition by nonpreferred males.

We introduce the article by describing the two main forms of postcopulatory sexual selection, sperm competition and postcopulatory female choice, and discussing primate sexual swellings and female copulation calls as possible examples of sexually selected signals. In the following section, we review previous hypotheses advanced to explain the function of female copulation calls and briefly discuss the evidence in favor of and against these hypotheses. We then articulate the hypothesis that copulation calls reflect postcopulatory female choice, highlight the differences between this and the other hypotheses, review the evidence consistent with this hypothesis, and develop testable predictions. In the last section of the article, we discuss the distribution of female copulation calls across different primate species in relation to their mating system, the co-occurrence of sexual swellings, and the potential for sperm competition and postcopulatory female choice. The hypothesis that female copulation calls reflect postcopulatory female choice can be further tested with empirical data concerning the behavioral responses that these vocalizations elicit in other individuals as well as with the comparative method.

Mating signals and postcopulatory sexual selection

Mating is accompanied by signals in many animal species, and such signals are probably under strong pressure by sexual selection (Andersson, 1994). Many of these signals occur before copulation and serve to advertise individual characteristics that play an important role in mate competition, mate attraction and mate selection. It is now well known that sexual selection operates not only at the precopulatory level but also

at the postcopulatory level (Birkhead and Pizzari, 2002). Postcopulatory signals, however, are quite rare relative to precopulatory signals, and their role in sexual selection is poorly understood.

Postcopulatory sexual selection operates through two main mechanisms: sperm competition and postcopulatory (or cryptic) female choice (Birkhead and Pizzari, 2002). In sperm competition, the sperm of different males compete to fertilize the ova of a female. Females can play an active role in sperm competition by actively seeking insemination from several males, but the outcome of sperm competition is generally determined by the relative quantity and quality of the different sperm in the female reproductive tract, or by the order in which sperm is deposited (Birkhead and Møller, 1998). Postcopulatory female choice is the ability of a female to bias the fertilization success of the males that copulate with her (Eberhardt, 1996). Postcopulatory female choice is expected to evolve when females have little or no opportunity for mate choice, or when female mate choice is costly (Birkhead and Pizzari, 2002; Eberhardt, 1996; Jones, 2002). Under such circumstances, theoretical models have shown that postcopulatory female choice can provide an avenue by which females can circumvent male control of reproduction (Jones, 2002). Postcopulatory female choice can also evolve when female choice is based not only on male phenotype but also on compatibility between male and female genotypes (Birkhead and Pizzari, 2002). Two forms of postcopulatory female choice are recognized: in directional postcopulatory female choice there is consistency between female mating preferences for particular male phenotypes and female tendencies to bias sperm use after copulation. In other words, the criteria for female precopulatory and postcopulatory choice are the same. In nondirectional postcopulatory female choice, females favor the sperm of males with compatible genotypes regardless of their phenotype.

Sperm competition has been demonstrated in a number of animal taxa, including nonhuman primates (Birkhead and Møller, 1998). Anatomical and physiological adaptations for post-copulatory female choice have been demonstrated, or postulated, in a number of insects, many other invertebrates, and in some vertebrates, including primates (Eberhardt, 1996). For example, Dixon (2002) has argued that large and deep sexual swellings allow primate females to increase

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the probability that they will be fertilized by males with longer penises, because these males can place their sperm deeper into their reproductive tract. Behavioral mechanisms for postcopulatory female choice are less well-documented. A good example has been reported in wild domestic fowl, *Gallus gallus domesticus*, in which females exhibit mating preferences for dominant males but cannot avoid some inseminations from subordinate males. Females, however, tend to expel the sperm of subordinate males immediately after insemination (Pizzari and Birkhead, 2000). Unfortunately, no similar examples are available for many other species of vertebrates and, in particular, for nonhuman primates. Although nonhuman primates often display signals both before and after mating interactions, the possibility that some of these signals may express postcopulatory female choice has not been taken into consideration.

Mating signals by female primates: sexual swellings and copulation calls

Two possible examples of nonhuman primate signals that may play an important role in postcopulatory sexual selection are exaggerated sexual swellings and female copulation calls. Moreover, female copulation calls may be one of the few well-known examples of signals in nonhuman primates or other vertebrates that specifically occur after mating instead of before it. Therefore, their possible role in sperm competition and/or postcopulatory female choice should be taken into serious consideration.

Females in some species of Old World monkeys and apes show exaggerated sexual swellings during the periovulatory period (Clutton-Brock and Harvey, 1976; Darwin, 1876; Dixson, 1983). Exaggerated sexual swellings are more common in species that live in multimale multifemale groups and have a promiscuous mating system than in monogamous or polygynous species, suggesting that sexual swellings are likely to be related to mating competition between males, between females, or both (Clutton-Brock and Harvey, 1976; Dixson, 1983; 1998; Nunn, 1999; Pagel, 1994; Sillén-Tullberg and Møller, 1993; Stallman and Froehlich, 2000). Many different hypotheses have been proposed to explain the specific function of sexual swellings, including that they serve to incite competition between males or between their sperm so that females can mate with the best male or be fertilized by the best sperm (Clutton-Brock and Harvey, 1976; Dixson, 1998); that they advertise the occurrence of ovulation, thereby increasing paternity certainty and encouraging paternal care (Hamilton, 1984); that they serve to promote mating with multiple males, thereby confusing paternity and reducing the risk of infanticide (see Hrdy, 1981); or that they are an honest indicator of female fitness (Domb and Pagel, 2001; Pagel, 1994; but see Nunn et al., 2001; Zinner et al., 2002).

In some species of Old World monkeys and apes, females are also likely to utter rhythmic vocalizations, referred to as “copulation calls” in conjunction with mating (Dixson, 1998). In macaques and baboons, these calls tend to be low-pitched (i.e., grunts), but in other species such as talapoin (*Miopithecus talapoin*) or chimpanzees (*Pan troglodytes*) they can be higher-pitched (i.e., screams). Typically, copulation calls begin during the final stage of the mount and continue after the copulation has ended and while the female is moving away from the male (see Aujard et al., 1998; Gouzoules et al., 1998; Hamilton and Arrowood, 1978; Hohmann and Herzog, 1985; Moos-Heilen and Sossinka, 1990; O’Connell and Cowlshaw, 1994; Saayman, 1970). The percentage of copulations that are followed by vocalizations is variable across different species and studies. The percentage of copulations followed by calls was 98.79% and 45% in two different studies of pigtail

macaques, *Macaca nemestrina* (Gouzoules et al., 1998; Oi, 1996); 93% and 74.3% in two studies of liontail macaques, *Macaca silenus* (Kumar and Kurup, 1985; Lindburg and Harvey, 1996); 96% in sooty mangabeys, *Cercocebus atys*, and chacma baboons, *Papio ursinus* (Gouzoules et al., 1998; Gust and Gordon, 1991; Hall and DeVore, 1965; O’Connell and Cowlshaw, 1994); 89% in Taiwan macaques, *Macaca cyclops* (Hsu et al., 2002); 80% in longtail macaques, *Macaca fascicularis* (Deputte and Goustard, 1980); 68.8% in chimpanzees (Hauser, 1990); 10% in olive baboons, *Papio anubis* (Hall and DeVore, 1965); 9% in Japanese macaques, *Macaca fuscata* (Oda and Masataka, 1992); and 6% in Tonkean macaques, *Macaca tonkeana* (Aujard et al., 1998).

A number of different studies have reported that copulation calls are most likely to occur (or they are most likely to be long or intense) in conjunction with maximum sexual swelling (Aujard et al., 1998; Gouzoules et al., 1998; Hamilton and Arrowood, 1978; Lindburg, 1990; Masataka and Thierry, 1993; O’Connell and Cowlshaw, 1994; Saayman, 1970; Todt et al., 1995), during mating with adult dominant males instead of subadult or subordinate males (Green, 1981; Hauser, 1990; O’Connell and Cowlshaw, 1994; Oda and Masataka, 1992; Saayman, 1970), and in conjunction with male ejaculation (Deputte and Goustard, 1980; Moos-Heilen and Sossinka, 1990; O’Connell and Cowlshaw, 1994; Saayman, 1970; Todt et al., 1995). In one study, however, the association between male ejaculation and copulation calls disappeared when other variables such as male rank and female swelling were statistically controlled for (Semple et al., 2002).

In some studies but not in others, female dominance rank or age affected the probability of occurrence of copulation calls or their acoustic characteristics. For example, in a study of sooty mangabeys and pigtail macaques, high-ranking females showed a higher range of delivery rates of copulation calls than did low-ranking females, and peak frequency of calls was higher in younger females than in older females in both species (Gouzoules et al., 1998). Call bout length was longer in younger females than in older females among the mangabeys but not among the pigtail macaques (Gouzoules et al., 1998). In Japanese macaques, younger females copulated more, with more males, and were more likely to call after copulation than older females (Oda and Masataka, 1995). In chacma baboons, however, adult females called more frequently than did younger females in conjunction with ovulation (Hamilton and Arrowood, 1978), and in the same species, female dominance rank did not affect the probability of calling during copulation (O’Connell and Cowlshaw, 1994). In some species, including baboons and talapoins, females with large sexual swellings sometimes give copulation calls while defecating (Dixson, 1988). Treating ovariectomized female talapoins with estrogen increases the rate of these “spontaneous” copulation calls, suggesting that the physical or physiological responses (e.g., sensory feedback) associated with defecation may trigger these vocalizations out of context through the edema associated with swelling or some other estrogen-sensitive mechanism (Dixson, 1998). This may suggest that particular males, or particular male copulatory patterns, might elicit especially strong vocal responses from their female mating partners.

Hypotheses concerning the functions of copulation calls

At least 15 different hypotheses have been proposed to explain the functional significance of female copulation calls in primates (Table 1), some of which are similar to those proposed for sexual swellings. The hypothesis that copulation calls simply reflect an orgasm-like reaction (hypothesis 1) is consistent with the observation that, in some cases, copulation

calls begin during the final phase of the copulatory sequence. This hypothesis, however, is inconsistent with the observation that the emission of copulation calls does not coincide with other behavioral expressions of female orgasm (e.g., the “clutching reaction”; Deputte and Goustard, 1980; Zumpe and Michael 1968) and that, in some cases, copulation calls clearly begin after the copulation has ended and the female is already physically separated from the male (see Deputte and Goustard, 1980; Gouzoules et al., 1998). Therefore, hypothesis 1 does not appear to have general validity. The observation that copulation calls sometimes begin after copulation has ended is also inconsistent with the hypothesis that these vocalizations serve to facilitate orgasm synchronization between males and females (hypothesis 4). This hypothesis would predict that copulation calls occur immediately before male ejaculation, whereas data from baboons indicate that these calls tend to follow, rather than precede, ejaculation (O’Connell and Cowlshaw, 1994). The hypotheses that copulation calls serve to advertise female sexual motivation (hypothesis 7) or to encourage mating interference by dominant males and the displacement of subordinate males who attempt to mate with them (hypothesis 11) would also predict that copulation calls should occur either before mounting or very early in the copulatory sequence. These hypotheses are also inconsistent with the timing of the vocalizations relative to the copulation, namely, the fact that they occur late in the sequence or after the copulation has ended. They may have some validity, however, in species in which males need multiple mounts to achieve ejaculation (Semple S, personal communication) or in situations in which females are highly motivated to mate again, and with different males (for some evidence in favor of hypothesis 11, see Oda and Masataka, 1992; 1995).

The hypothesis that primate copulation calls may play a role in postcopulatory sexual selection has already received some attention. In particular, several recent studies have suggested that copulation calls function to incite mating with multiple males, thereby promoting sperm competition and increasing the probability that females are fertilized by the male with the best sperm (hypothesis 12) or confusing paternity certainty and reducing the risk of infanticide (hypothesis 13; Cowlshaw and O’Connell, 1996; O’Connell and Cowlshaw, 1994; Semple, 1998; 2001; Semple and McComb, 2000; Semple et al., 2002; but see Henzi, 1996). These two hypotheses are difficult to distinguish from each other and will therefore be referred to as the sperm competition/paternity confusion hypothesis.

Unlike the previously discussed hypotheses, the sperm competition/paternity confusion hypothesis is fully consistent with the timing of occurrence of copulation calls relative to copulation and male ejaculation. This hypothesis has also received some support from a recent study of Barbary macaques in which male responses to playbacks of female copulation calls were assessed (Semple, 1998). In this study, all males looked toward the loudspeaker on playback of the copulation calls, and when tested in pairs, only the dominant male in the pair approached the loudspeaker. Furthermore, estrous females were mated by males more quickly after the playback of their copulation call than after playback of a white noise control stimulus, a result that might suggest the effectiveness of copulation calls in eliciting sperm competition. Because copulation calls, however, contain cues of individual identity (see Semple, 2001) and control stimuli did not include female vocalizations other than copulation calls, it is possible that male interest and mating behavior might have been elicited also by other vocalizations from the same female, or any other signs of her presence.

The sperm competition/paternity confusion hypothesis predicts that copulation calls given by a female in consort with a particular male should stimulate interest in other

Table 1**Hypotheses about the function of female copulation calls in primates**

(1) nonadaptive by-product of sexual intercourse	Hamilton and Arrowood, 1978
(2) nonadaptive phenomenon maintained by phylogenetic inertia	Henzi, 1996
(3) self-stimulates the occurrence of ovulation	Semple, 1998 (after method of Cheng, 1992)
(4) promote synchronization of male and female orgasm	Hamilton and Arrowood, 1978
(5) strengthen the pair bond	Hamilton and Arrowood, 1978
(6) honest signals with which females advertise their reproductive status	Aich et al., 1990
(7) honest signals with which low-ranking females advertise their sexual motivation	Gouzoules et al., 1998
(8) advertise mating to other females and inhibit breeding synchrony	Hohmann and Herzog, 1985
(9) advertise mating to other females and promote breeding synchrony	Semple, 1998 (after method of Viljoen, 1977)
(10) advertise the presence of a male partner and reduce female harassment	O’Connell and Cowlshaw, 1994
(11) incite male competition and increase the probability of mating with dominant males	Hamilton and Arrowood, 1978
(12) incite male sperm competition to ensure that sons will inherit the best sperm (sexy son)	O’Connell and Cowlshaw, 1994
(13) incite multiple male matings to reduce paternity certainty and the risk of infanticide	O’Connell and Cowlshaw, 1994
(14) announce paternity certainty to promote paternal investment	Henzi, 1996 (after method of Hamilton, 1984)
(15) encourage mate guarding by the consort male	Todt et al., 1995

nonconsorting males and be effective in promoting promiscuous mating. A recent study investigating male yellow baboons’ (*Papio cynocephalus*) response to playbacks of female copulation calls, however, showed that male baboons looked toward the loudspeaker and approached it when the loudspeaker played the copulation calls of their consort partners but showed no such responses to the copulation calls of nonconsorting females (Semple, 2001). Although the interest shown by males in the calls of their consort partners is consistent with the sperm competition/paternity confusion hypothesis, the lack of response to the calls of nonconsorting females is difficult to reconcile with such a hypothesis.

The strong responses of male baboons to the playback vocalizations of their consort partners are also consistent with a different hypothesis, the hypothesis that copulation calls function to encourage mate guarding by the consort male (hypothesis 15). In a study of Barbary macaques (*Macaca sylvanus*), Todt et al. (1995) reported that female copulation calls were associated with both peak sexual swellings and male ejaculation. In this study, however, there was no evidence that

females were approached by other males after giving their calls. Instead, after the call, the consort male remained in proximity to the female and engaged in grooming with her longer than was normal. Todt et al. (1995) concluded that the copulation calls were directed predominantly to the consort male, and their function was to encourage mate guarding.

Copulation calls and postcopulatory female choice

Building on the findings of Semple (2001) and Todt et al. (1995), we propose that female copulation calls in primates may indeed play an important role in postcopulatory sexual selection, but that they represent a form of postcopulatory female choice instead of a strategy to encourage sperm competition and/or paternity confusion. According to this “female choice” hypothesis, females use copulation calls to increase the probability of mate guarding by the consort partner, thereby increasing the chances of fertilization. This hypothesis argues that copulation calls function to minimize, rather than maximize, the likelihood of sperm competition. This hypothesis also argues that by calling after copulation with certain males, females express their preferences for these males and their sperm. In contrast, by not calling after copulation with other males, females do not encourage mate guarding by these males, thereby opening up the possibility that other males will mate with them and engage in sperm competition. Both the female choice hypothesis and the sperm competition/paternity confusion hypothesis are consistent with the findings that copulation calls are associated with peak sexual swellings and male ejaculation. These two hypotheses, however, can be conceptually and empirically distinguished in a number of ways.

The female choice hypothesis predicts that females should call after copulation with males that reliably and effectively guard them, whereas the sperm competition/paternity confusion hypothesis predicts that females should call after copulation with males that are unwilling or unable to effectively guard them. Second, the female choice hypothesis predicts that females should call preferentially after copulation with higher-quality males. In contrast, if the function is to solicit other sperm for competition, calls should either be emitted indiscriminately or preferentially after copulation with lower-quality mates. Thus, whereas the sperm competition/paternity confusion hypothesis may or may not involve direct female discrimination among males and their attributes, the female choice hypothesis implies a form of direct female choice with discrimination among males and their attributes (Wiley and Poston, 1996). The previously reported association between female copulation calls and mating with adult dominant males (see references above) is consistent with the female choice hypothesis and inconsistent with the sperm competition/paternity confusion hypothesis.

Consistent with hypotheses 6 and 14, the female choice hypothesis argues that female copulation calls are honest signals that advertise female reproductive status (i.e., ovulation) and announce a high probability of conception. However, the female choice hypothesis also argues that females choose to advertise their fertility and likely conception with some males but not with others. By assuming that the female calls are directed to the copulating male and that calls are more likely to be emitted after copulation with males who can effectively mate guard, the female choice hypothesis is consistent with the results of playback experiments showing that males respond to the calls of their consort partners but not to those of nonconsorting females (Semple, 2001). Furthermore, the female choice hypothesis explains why copulation calls often begin during the last phase of the copulation. In fact, it is crucial that the calls be heard by the

consort male, and that the calls be uttered quickly after male ejaculation, when the male is still in close proximity. By using vocalizations that can be heard also by other males, however, females can also effectively blackmail their consort partners and further encourage them to engage in mate guarding behavior. This “extortion” argument has already been applied to begging calls by bird chicks, whereby chicks may be successful in extracting additional parental effort from their parents by alerting predators of their presence and placing themselves in danger (see Godfray, 1995). The notion that the use of copulation calls may have an extortion component is not incompatible with the hypothesis that these vocalizations convey honest information about fertility and express choice for particular males.

The female choice hypothesis is consistent with the hypothesis that copulation calls “strengthen the bond” between the mating partners (hypothesis 5; Table 1) but also clarifies that bond strengthening is actually mate guarding and that its function is to minimize the chances of sperm competition and maximize the chances of fertilization by preferred males. The female choice hypothesis is also consistent with the hypothesis that copulation calls announce a high probability of paternity (hypothesis 14). Unlike hypothesis 14, however, the main function of copulation calls according to the female choice hypothesis would not be to encourage paternal investment when offspring are born but to encourage mate guarding following copulation. For example, the female choice hypothesis predicts that males should respond to the playbacks of copulation calls of their partners but not to those of nonconsort females, whereas hypothesis 14 predicts differences in male behavior after infants are born but not necessarily in response to copulation calls.

In summary, the female choice hypothesis makes a number of predictions that can be empirically tested. Specifically, the female choice hypothesis predicts that female copulation calls should be most likely to occur in association with (1) peak female fertility as expressed by maximal sexual swellings, (2) high-quality males (e.g. dominant and/or with best genotype), (3) male ejaculation, and (4) high potential for insemination by other males and subsequent sperm competition. As a result of copulation calls, (5) the consort males should be less likely to leave the females and more likely to spend time in proximity to them, (6) the calling females should show no active interest in (or active avoidance of) mating with other males, and (7) the calling females should be less likely to mate with other males than non-calling females. Predictions 1 through 4 are also consistent with a number of other hypotheses and are already supported by existing evidence (see above). Prediction 5 could also be consistent with the sperm competition/paternity confusion hypothesis, whereas predictions 6 and 7 are opposite to those made by the sperm competition/paternity confusion hypothesis. These predictions have recently been supported by data from Guinea baboons (*Papio papio*; Maestriperieri et al., in press).

In addition to providing an explanation for the variation in the occurrence of copulation calls across individuals (e. g. in relation to male identity or quality), the female choice hypothesis can also account for variation in the occurrence of copulation calls across primate species. Before this argument can be made, however, it may be useful to examine the taxonomic distribution of female copulation calls, and discuss a possible scenario for the evolution of primate copulation calls in relation to mating systems and other mating signals such as exaggerated sexual swellings.

Table 2
Occurrence of exaggerated sexual swellings and copulation calls in papionin monkeys

Species	Swellings	Cop. calls	References
<i>Papio anubis</i>	yes	yes	Hall and DeVore, 1965
<i>Papio cynocephalus</i>	yes	yes	Semple, 2001
<i>Papio ursinus</i>	yes	yes	Saayman, 1970
<i>Papio hamadryas</i>	yes	yes	Dixson, 1983; Swedell and Saunders, 2003
<i>Papio papio</i>	yes	yes	Byrne, 1981
<i>Theropithecus gelada</i>	yes	yes	Moos-Heilen and Sossinka, 1990
<i>Cercocebus albigena</i>	yes	yes	Chalmers, 1968
<i>Cercocebus aterrimus</i>	yes	?	Dixson, 1983
<i>Cercocebus atys</i>	yes	yes	Gouzoules et al., 1998
<i>Cercocebus galeritus</i>	yes	yes	Dixson, 1983; van Schaik et al., 1999
<i>Cercocebus torquatus</i>	yes	yes	Dixson, 1983; van Schaik et al., 1999
<i>Mandrillus sphinx</i>	yes	no	Dixson, 1983, Dixson AF, personal communication
<i>Mandrillus leucophaeus</i>	yes	?	Dixson, 1983
Macaca			
Sylvanus-silenus group			
<i>Macaca sylvanus</i>	yes	yes	Semple, 1998
<i>Macaca silenus</i>	yes	yes	Kumar and Kurup, 1985
<i>Macaca nemestrina</i>	yes	yes	Gouzoules et al., 1998
<i>Macaca brunnescens</i>	yes	?	Fooden, 1969
<i>Macaca hecki</i>	yes	?	Fooden, 1969
<i>Macaca maurus</i>	yes	?	Fooden, 1969
<i>Macaca nigra</i>	yes	?	Fooden, 1969
<i>Macaca nigrescens</i>	yes	?	Fooden, 1969
<i>Macaca ochreata</i>	yes	?	Fooden, 1969
<i>Macaca tonkeana</i>	yes	yes	Masataka and Thierry, 1993
Sinica group			
<i>Macaca sinica</i>	no	no	Hrdy and Whitten, 1987
<i>Macaca arctoides</i>	no	no	Bertrand, 1969
<i>Macaca assamensis</i>	no	?	Hrdy and Whitten, 1987
<i>Macaca radiata</i>	no	no	Glick, 1980
<i>Macaca thibetana</i>	little	?	Zhao, 1993
Fascicularis group			
<i>Macaca fascicularis</i>	little	yes	Dixson, 1983; Deputte and Goustard, 1980
<i>Macaca cyclopis</i>	little	yes	Peng et al., 1973; Hsu et al., 2002
<i>Macaca fuscata</i>	little	yes	Dixson, 1983; Oda and Masataka, 1992
<i>Macaca mulatta</i>	little	no	Dixson, 1983; Rowell and Hinde, 1962

The evolution of female copulation calls in primates

Postcopulatory sexual selection, either in the form of sperm competition or postcopulatory female choice, is expected to be intense in species living in multimale multifemale groups in which mating is promiscuous or polyandrous (Birkhead and Pizzari, 2002). Many species of Old World monkeys and apes, including baboons, macaques, and chimpanzees, fit this pattern. However, even in species in which females live in small harems with only two males, the harem leader and the follower (e.g., gelada baboons, *Theropithecus gelada*, and hamadryas baboons, *Papio hamadryas*; Stammbach, 1987), there is opportunity for females to mate with both males, and therefore, there is the potential for sperm competition and postcopulatory female choice. Moreover, extragroup copulations have been observed or are possible in these species (see Nunn, 1999).

Evidence of intense sperm competition in some of the primate species mentioned above is provided by comparative data on testis size, ejaculation rates, and sperm morphology (Anderson and Dixson, 2002; Bercovitch, 1989; Dixson, 1998; Harcourt et al., 1981; 1995; Short, 1979) and by the occurrence of postcopulatory mate guarding (Manson, 1997). The exact mechanisms of sperm competition in primates (e.g., whether they involve first-male or last-male sperm precedence or some type of lottery mechanism) are not

known (see Bercovitch, 1989). In other species of mammals, there are no consistent order effects, the outcome of sperm competition being determined by an interaction between timing of ovulation, timing of insemination, and the time necessary for sperm capacitation in the female reproductive tract (Birkhead and Pizzari, 2002).

As noted earlier, exaggerated female sexual swellings tend to occur in primate species with promiscuous or polyandrous mating (Clutton-Brock and Harvey, 1976; Dixson, 1983; Nunn, 1999; Sillén-Tullberg and Møller, 1993). Exaggerated sexual swellings are absent in the prosimians and New World monkeys, and among the Old World monkeys, they are absent in the Asian colobines, present in some species of African colobines (e.g., red colobus, *Colobus badius*), and prominent in the cercopithecines (Dixson, 1983; Sillén-Tullberg and Møller, 1993). Among the cercopithecines, swellings are especially developed in papionin monkeys: all species of *Cercocebus*, *Mandrillus*, *Theropithecus*, and *Papio* have exaggerated female swellings (Table 2); in the genus *Macaca*, in which three or four distinct phyletic groups are recognized (Delson, 1980; Fooden, 1980), exaggerated sexual swellings are found in the *sylvanus-silenus* phyletic group; bright red sexual skin but little swelling is found in the *fascicularis* group, and no sexual skin or swelling is found in the *sinica* group, including *Macaca arctoides*, which is sometimes classified within this

group and sometimes in a group by itself (Table 2) (Delson, 1980; Dixon, 1983; 1998; Fooden, 1980; Nunn, 1999). Sexual swellings are generally absent in gibbons and siamangs (but see Dahl and Nadler, 1992), and among the great apes, they are prominent in chimpanzees and bonobos (*Pan paniscus*) but absent in orangutans (*Pongo pygmaeus*) and gorillas, *Gorilla gorilla* (Dixon, 1983).

Female copulation calls have been noted and studied primarily among the Papionini, and within this tribe, their taxonomic distribution overlaps with that of sexual swellings (see also van Schaik et al., 1999). As Table 2 illustrates, female copulation calls have now been reported in all species of *Papio*, *Theropithecus*, and *Cercocebus* for which information is available. In *Macaca*, copulation calls are present in all species of the *syvanus-silenus* group and in some species of the *fascicularis* group and are rare or absent in species of the *sinica* group. Female vocalizations associated with mating have also been reported in many other primate species (Dixon, 1998). For most of these other species, however, the acoustic characteristics of these vocalizations are very different from the copulation calls reported in most Old World monkeys and apes, and the timing of occurrence of the vocalizations relative to copulation is unclear. Obviously, there may be different types of female vocalizations associated with copulation across the more than 300 species in the Primate order, and these vocalizations probably serve different functions.

The taxonomic distribution of exaggerated sexual swellings in relation to mating and social systems across all primate species is consistent with the idea that they serve to encourage either male mating competition or sperm competition (as well as with other hypotheses; Dixon, 1983; 1998). Additional evidence in support of these hypotheses comes from the association between exaggerated sexual swellings and the intensity of mate guarding. For example, among the papionin monkeys, intensity of mate guarding is generally higher among baboons, in which all species have prominent swellings, than among macaques, in which only some species have swellings (see Manson, 1997, and commentaries). Among the macaques, mate guarding is more intense in species with large swellings such as liontail, pigtail, and tonkean macaques than in species with little or no swelling such as rhesus, longtail, or bonnet macaques (Manson, 1997 and commentaries).

Nunn's (1999) "graded signals" hypothesis proposes that exaggerated and prolonged swellings evolved to allow females to obtain multiple benefits. According to this hypothesis, maximum swellings indicate the highest probability of ovulation and thus increase the probability that higher-quality males will compete for and mate guard females when conception is most likely. Because there is a nonzero probability of conception during submaximal swelling, however, females may also entice other males to mate with them and thus obtain benefits such as paternity confusion or male protection during times when fertilization is less likely. Copulation calls as a female choice adaptation complement the graded signals hypothesis quite nicely (cf. Nunn, 1999: 241) as these calls may provide an additional signal to high-quality males that conception is likely and thus encourage mate guarding. Furthermore, females who mate with multiple males for nongenetic benefits have the greatest incentive to prolong and exaggerate their swellings (in order to obtain these benefits), but doing so diminishes the value of swellings for indicating the timing of ovulation and thus creates selection pressure for a supplementary signal.

The argument that copulation calls reflect postcopulatory female choice would be supported by their presence in species in which females have little direct control over choice of mating partners or in which female mate choice is

especially costly. This would occur in species in which males are much larger than females, and/or in species in which males are aggressive toward females in the context of mating. The macaques provide a good case in point. As Table 2 illustrates, the taxonomic distribution of both sexual swellings and copulation calls within this genus is accounted for by the main phyletic distinctions among subgroups of species, suggesting some degree of phylogenetic inertia in the evolution and maintenance of these traits. There are cases, however, of closely related species such as Japanese, longtail, and rhesus macaques (*Macaca mulatta*), in which some species show copulation calls (the Japanese and longtail macaques) and others do not (the rhesus). Rhesus macaques are characterized by low sexual dimorphism in body size relative to the other species (female body weight as percentage of male body weight; rhesus = 91.30%; Japanese = 84.54%; longtail = 69.40%; data from Napier and Napier, 1967; see also Smith and Jungers, 1997) and by a high degree of female control over mating and conception (see Wallen, 1990; Zehr et al., 2000). For example, male aggression toward females in the context of mating has been reported in Japanese macaques but is virtually nonexistent in rhesus macaques (Smuts and Smuts, 1993). Other macaque species in which female copulation calls have been reported, such as pigtail macaques, are also characterized by relatively large and aggressive males (female body weight as percentage of male body weight = 74.97%; Napier and Napier, 1967; Oi, 1996).

Outside of the *Macaca* genus, chimpanzees and bonobos provide another potentially relevant comparison. Both species exhibit promiscuous mating and exaggerated female sexual swellings, and therefore, there is potential for mating and sperm competition (Dixon, 1983). However, chimpanzee males are larger, more aggressive toward females, and in control of mating to a greater extent than bonobo males are (Nishida and Hiraiwa-Hasegawa, 1987; Wrangham, 2002). Therefore, the female choice hypothesis would predict that female copulation calls should occur in chimpanzees but not, or to a lesser extent, in bonobos. Female copulation calls have been reported in chimpanzees (Hasegawa and Hiraiwa-Hasegawa, 1990; Hauser, 1990), whereas it is not clear whether the "nasalized screams" occasionally given by bonobo females in the context of mating (Thompson-Handler et al., 1984) are acoustically and contextually similar to the copulation calls of other species.

As illustrated by the macaque and the chimpanzee/bonobo examples, the female choice hypothesis provides a reasonable explanation for the presence or absence of female copulation calls in closely related species with a similar mating system and a similar potential for sperm competition. Such species differences in female copulation calls are not readily accounted for by the sperm competition/paternity confusion hypothesis or other previously proposed hypotheses. Clearly, the examples discussed above are meant to generate hypotheses and encourage further comparative research on female copulation calls in primates rather than to provide confirmatory evidence for our hypothesis. The information on the occurrence of female copulation calls in many primate species and their characteristics is too incomplete and preliminary to allow for a strong test of the female choice hypothesis using the comparative method. It is clear, however, that any evidence provided by empirical tests of this hypothesis in any primate species will have to be complemented by comparative research across the whole Primate order to guarantee the general validity and applicability of this hypothesis.

In conclusion, the female choice hypothesis makes a number of testable predictions about the occurrence and distribution of female copulation calls both within and

between primate species. This hypothesis is compatible with a number of previously advanced hypotheses about the function of copulation calls but arguably accounts for the characteristics of these vocalizations to a greater extent than most other hypotheses. The female choice hypothesis is consistent with the sperm competition/paternity confusion hypothesis in suggesting that copulation calls may play an important role in postcopulatory sexual selection, but the two hypotheses postulate opposite functions for copulation calls (minimizing versus maximizing the likelihood of sperm competition). The two hypotheses, however, are not entirely mutually incompatible and might apply differentially to different primate species. Future studies of female copulation calls could provide valuable information on the use and function of mating-related signals and on the dynamics of postcopulatory sexual selection in primates.

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