THE POTENTIAL FOR CRYPTIC FEMALE CHOICE IN PRIMATES: BEHAVIORAL, ANATOMICAL, AND PHYSIOLOGICAL CONSIDERATIONS

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INTRODUCTION

Primate mothers are heavily invested in each of their offspring, with high levels of energy required for both gestational and postpartum development. Many of the factors that contribute to these high energetic demands are related to the relatively high neonatal brain weight:body weight ratio in primates [Martin, 1995]. Because fetal development of a large brain is energetically costly, and requires more time than the development of a small brain, primate mothers expend more energy per pregnancy than other mammals of similar body size. Even though the brains of primate infants are relatively large, at birth infants are semi-precocial and typically require considerable and prolonged parental care. As a result primates are relatively slow breeders. Outside of several prosimians, which give birth to 2-3 offspring, and the marmosets and tamarins, which typically twin, most primate pregnancies result in a single offspring. Additionally, sexual maturity is delayed in a variety of species, such that offspring that would otherwise be capable of reproducing remain as non-breeders in their social group. This combination of energy-demanding infants and low reproductive output results in a relatively large investment per offspring by primate mothers. Moreover, paternal care is absent in the majority of species [Kleiman & Malcolm, 1981; Dunbar, 1988; Wright, 1990], resulting in an even greater maternal burden. Given this investment, female primates ought to be very choosy about their sexual partners. Concomitantly, male primates ought to compete at high levels for access to females and to their limited and precious eggs [Williams, 1966; Trivers, 1972].

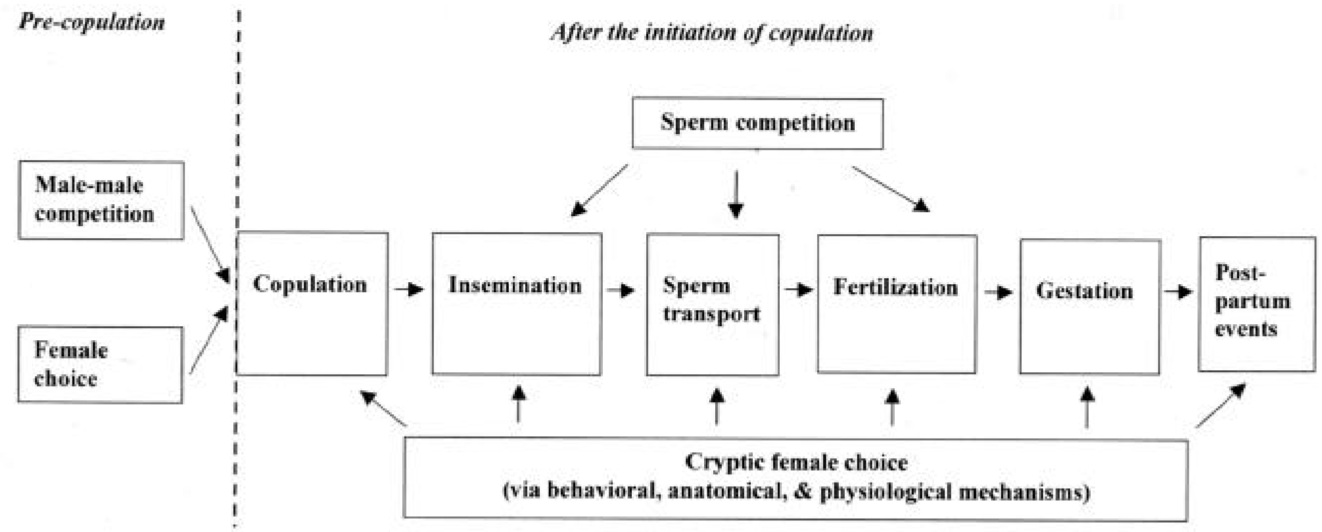
In the classic Darwinian view, both of these processes, female choice and male-male competition for access to females, are important and underlie evolution by sexual selection. As first discussed in Crook's seminal paper on sexual selection in primates [Crook, 1972], and as evinced by the many chapters in this text, these pre-copulatory processes have clearly played an important role in primate evolution. However, a male that successfully competes for and/or is chosen to copulate with a female is not necessarily ensured paternity. This is especially true when a female mates with more than one male, as occurs in many primate species. To account for this discrepancy, modern views recognize that sexual selection can also occur *after the initiation* of copulation, via sperm competition (SC) and cryptic female choice (CFC; Figure 1). Parker [1970] was the first to recognize that males can compete after copulation and insemination via competition between their sperm for the fertilization of a given egg or set of eggs. However, this process does not occur in a vacuum as female attributes also play a role in determining paternity. CFC, as broadly defined, occurs when female behaviors, anatomy, or physiology selectively bias paternity in favor of conspecific males with particular traits over others that lack such traits, after copulation has begun [Thornhill & Alcock 1983; Eberhard, 1996, 1998].

Just as female choice was once overshadowed in the literature by male-male competition, SC has received much more attention than CFC. Indeed, there has been little to no work on CFC in primates, but a fair amount of work on SC. For example, Bellis and Baker [1990], in their study of human sexual behavior, recognized that females may be the ones driving the timing of extra-pair copulations, but suggested that this served to promote SC, without any mention of CFC. There are several possible reasons for this generalized bias. One reason is that models of SC [e.g., Parker, 1990a] typically view the female reproductive tract as a passive vessel in which males compete cryptically. However, nothing could be further from the truth, as the female reproductive tract can indeed be a complex and harsh environment. In the words of Dixson [1998, p 276]:

> “Sperm competition should not be viewed as a ‘sprint-race’ between the gametes of rival males, but rather as a race over hurdles. The hurdles are the anatomical and physiological barriers provided by the female’s vagina, cervix, utero-tubal junction, and oviduct, as well as by the ovum and its vestments. At all these levels, the possibility of sexual selection by cryptic female choice exists in female primates…”

A second reason for this bias is that, historically, just as the female reproductive tract was considered a passive vessel for active sperm, female sexual behavior, especially in primates, was also considered passive [Small, 1993; Hrdy, 1999]. However, the biased treatment of SC versus CFC has occurred not only because of biased views of female reproductive processes, but also because it is difficult to demonstrate that CFC occurs (see discussion in Birkhead & Møller [1993], Birkhead [1998]). Even Darwin [1871, 1874] recognized that the distinction between sexual selection due to male-male competition versus that due to female choice was difficult to make. The difficulty in distinguishing between intrasexual and intersexual selection is magnified when considering sexual selection that occurs after the initiation of copulation. Additionally, just as pre-copulatory male-male competition and female choice are not mutually exclusive; neither are SC and CFC. In fact, in those species in which sexual selection after the initiation of copulation has acted, SC and CFC have undoubtedly co-evolved. The resulting relationship between SC and CFC in any given species can be variable and complex, representing a balance between potentially conflictual interests of males and females at the cryptic level [Eberhard, 1996, 1998; Alexander et al., 1997; Moore et al.,

Figure 1. Classic Darwinian sexual selection via male-male competition and female choice versus sexual selection that occurs after the *initiation* of copulation via SC and cryptic female sexual selection.



2001; Andrés & Arnqvist, 2001]. Eberhard [1996, 1998], who provided a detailed and thorough discussion of the relationship between SC and CFC, argued that CFC is in fact a common feature of evolution. Further discussion of this relationship and of the benefits obtained by females that mate with multiple males is found in Jennions and Petrie [2000], who concluded that postcopulatory SC and CFC allow for better selection of genetically compatible mates than pre-copulatory mate choice, which may be limited by a variety of factors.

As SC in mammals and even in primates has been well reviewed [e.g., Harvey & Harcourt, 1984; Ginsberg & Huck, 1989; Dixson, 1998; Gomendio et al., 1998], this chapter focuses on CFC in primates, with the aim of raising the topic from a footnote to a pursuable course of study. The first portion of the chapter describes specific mechanisms through which a female primate could theoretically bias paternity after copulation has begun. Although this discussion will highlight numerous possible mechanisms, we are **very far** from conclusively demonstrating that CFC actually occurs in any primate. It is therefore useful to highlight those systems in which CFC is most likely to occur. As will be discussed, these processes are likely to occur when fertile females mate with more than one male, as is the case in multimale-multifemale mating systems, such as that found in chimpanzees (*Pan troglodytes*), and in dispersed mating systems, such as those found almost exclusively in the nocturnal prosimians. However, as we shall see, there is a growing recognition that many primate mating systems are more plastic than previously thought and that extra-pair copulation occurs in many species. In fact, Hrdy [1999, 2000] argues that a polyandrous component resides in virtually all female primates, including human females. Given this, the potential for post-copulatory sexual selection in primates may be greater than previously thought. Of course, it is not just who a female mates with, but when that determines paternity. A discussion of the timing of mating and any potential order effects on paternity addresses this issue. This is followed by a discussion of specific female anatomical and physiological processes that could influence paternity. Finally, the chapter will elucidate the criterion necessary to establish CFC, concluding with a general discussion of the potential for CFC in primates.

It is important to note that this is a relatively new field, especially for primatology. Writing this chapter necessitated gathering data from a variety of disciplines, not all of which speak the same language, and many of which were generated before the concept of CFC fully emerged. My goal was to compile and integrate the various pieces of evidence relevant to CFC so as to facilitate further discussion and possible research into this field in primates. At times, this compilation may approach rampant speculation and even storytelling. When it does, I have tried to be overly generous in the use of qualifying terms such as “could”, “potentially”, “theoretically”, etc. Readers are urged to use caution so as not to over-interpret these statements and the data presented herein. While I hope to have highlighted the many intriguing possibilities for CFC in primates, most of the data needed to critically evaluate these possibilities do not **yet** exist. Additionally, where data do exist they are often buried in the literature. As a complete review of all primate data would have constituted a book in and of itself, many relevant papers are likely not cited herein.

POTENTIAL MECHANISMS OF CRYPTIC FEMALE CHOICE IN PRIMATES

In his seminal book, Eberhard [1996] described 20 potential mechanisms by which CFC could occur. While some have equated CFC with specific postcopulatory mechanisms such as sperm selection [e.g., Birkhead, 1998], a general definition of CFC [*sensu* Thornhill & Alcock 1983; Eberhard, 1996] is adopted here, where CFC is broadly defined as any behavioral, physiological, or morphological/anatomical mechanism that occurs after the *initiation* of copulation and that allows a female to bias paternity in favor of one male over another. In all animals, and especially in primates, where investment in each offspring after it is born is high, male reproductive success should be measured not just by paternity, but rather by the number of offspring that survive to reproduce. Hence, the definition of CFC should be extended to include any mechanism that occurs after infant birth that allows a female to bias male reproductive success towards males that possess a particular trait. Because primates have a relatively high investment per infant, one might expect that detrimental or differential care of infants would not be a feasible mechanism for females. However, differential care and even abuse of infant primates has been documented (especially in captivity) and thus these potential mechanisms of CFC should be explored. In practice, even if not explicitly stated, the expanded definition of CFC is the definition employed by Eberhard [1996], as he included investing less in offspring after they are born as a mechanism of CFC. By this definition, CFC can occur prior to fertilization, during pregnancy, and/or after infant birth (Figure 1). While many of Eberhard's mechanisms are generally applicable to all animals, some are taxon specific and do not apply to primates (e.g., removing a spermatophore before sperm transfer is complete), or only partially apply to primates. Those of Eberhard's mechanisms as well as several others that could theoretically apply to primates are discussed. For each of these mechanisms, which are roughly placed in the timeline shown in Figure 1, I will describe potential examples or provide arguments as to why the mechanism is unlikely to occur in primates. It is important to note that, in reality, many of these mechanisms may overlap and interact in complex ways.

1. Forcefully terminate copulation before sperm are transferred

Female morphology and the need for females to cooperate in the process of mounting and intromission suggests that females could select for or against males at this point in mating. For example, bonnet macaque (*Macaca radiata*) females sometimes struggle after copulation has begun and may terminate copulation prior to ejaculation [Nadler & Rosenblum, 1969]. This mechanism is most likely to be useful for those species in which complex and prolonged copulatory patterns are found. In primates, Dixson has categorized 26 species (for which there are data) as having either multiple brief intromissions or a single prolonged intromission lasting at least three minutes [Dixson 1998; tables 5.5 and 5.6, pg. 120-121; see also Dewsbury & Pierce, 1989]. In these species and in the many others that likely display these patterns, ample opportunity for a female to terminate copulation is present. For example, Figure 2 shows the timing of a representative copulatory sequence for a rhesus monkey (*Macaca mulatta*), in which an average of 8.5 mounts and 42 intromitted thrusts is the norm [Shively et al., 1982]. A female rhesus monkey could choose to terminate the copulatory bout at any time before the final ejaculatory mount, thereby exerting CFC, that is, choice against this male after copulation was initiated. In a study of sexual behavior in the closely related Japanese macaque (*Macaca fuscata*), which also displays multiple brief intromissions, only 34% of copulations progressed to ejaculation [Hanby et al., 1971]. Although harassment from other group members and termination by the male accounted for some of these copulatory failures, withdrawal of the female from the male also occurred. Both single prolonged intromissions and multiple brief intromissions are thought to be beneficial to males. Single prolonged intromission may serve as part of a mate guarding strategy, to keep the ejaculate in contact with the os cervix, and/or to assist in sperm transport. Multiple brief intromissions may serve to dislodge copulatory plugs or coagulated semen from previous matings and may induce sperm transport. Both copulatory patterns may enhance female neuroendocrine responses [Dixson, 1998]. Thus, interruption of either of these copulatory sequences is a powerful mechanism by which a female can modulate the male's control over the reproductive process. In fact, termination of copulation prior to ejaculation has been described in several species (Table I) and undoubtedly occurs in many others.

2. Alter male physiology and/or subsequent reproductive behavior by varying behavioral and sensory cues

Male primates typically find female primates maximally attractive during the periovulatory period, when visual cues such as sexual skin swellings are maximal, and when olfactory cues are presumably the greatest (e.g., rhesus monkeys [Bonsall et al., 1978]; Tonkean macaques, *Macaca tonkeana,* [Aujard et al., 1998]; but for high variability of ovulation within the period of tumescence in bonobos (*Pan paniscus*) see Heistermann et al. [1996]). Not surprisingly, exposure to females in several species of rodents, rabbits, ruminants, and primates leads to an increase in luteinizing hormone and testosterone secretion (as reviewed by Graham and Desjardins [1980], Harding [1981], and Hart [1983]). Elevated testosterone secretion subsequently results in increased sensitivity and responsiveness of penile reflexes and more developed penile spines, both of which potentially facilitate SC and CFC via increased sperm transport and the dislodging of copulatory plugs. In addition to - or instead of - increased visual and olfactory cues, the heightened display of proceptive or sexually soliciting behaviors by a female during the periovulatory period likely serves to increase her attractiveness [Wallen, 1990; Dixson, 1998; Carosi et al., 1999]. By enhancing attractiveness via the display of proceptive behaviors, a female can then conceivably modify the male's level of physiological arousal and subsequent reproductive behavior. Of particular interest here, such behavioral influences on male physiological arousal and reproductive behavior are not limited to the precopulatory period, but are also influential after the initiation of copulation.

In many anthropoid primates, females are not passive during copulation but rather communicate with the male via facial expressions and vocalizations and often actively

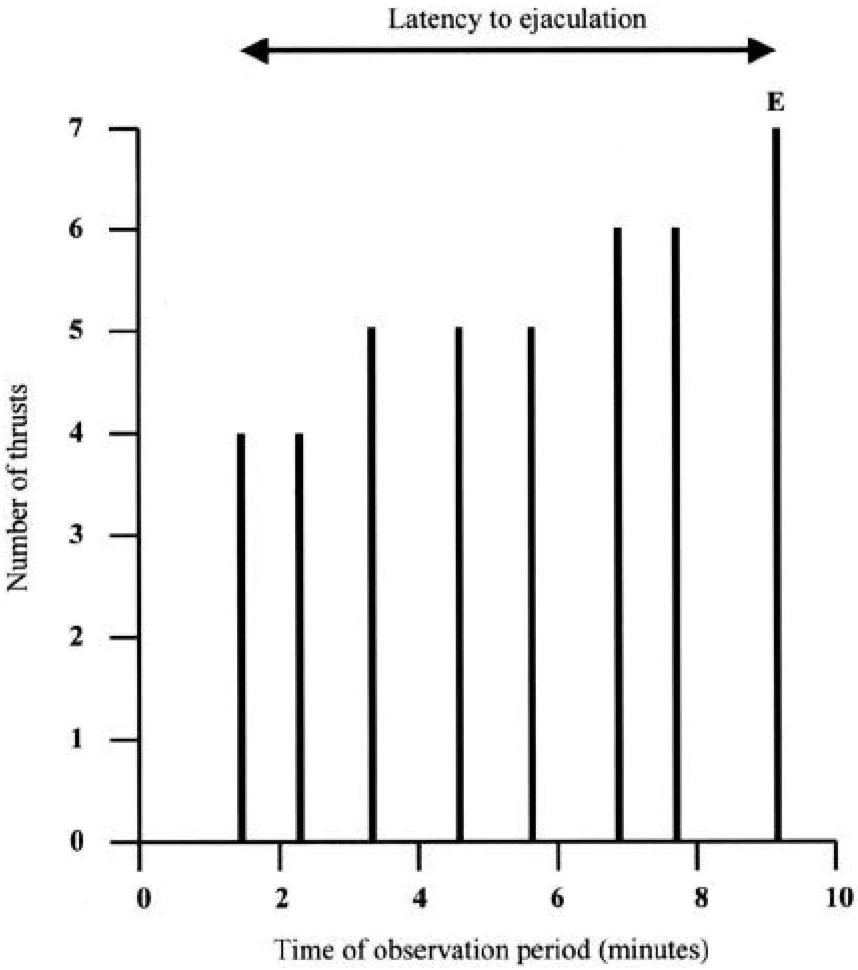


Figure 2. Idealized copulatory pattern for rhesus monkey (*Macaca mulatta*), in which multiple intromissions with thrusting (indicated by vertical lines) are performed prior to a final ejaculatory mount (based upon [Everitt & Herbert, 1972; Shively et al., 1982; Dixson 1998]).

participate in copulation (Table I). In each of these cases, it is possible that the female's behavior in some way influences the quality of the copulatory bout by facilitating thrusting and ejaculation and by increasing physiological arousal. Absence of such facilitative behavior may bias paternity against a mate. For example, Wallis [1983] reported that female gray-cheeked mangabeys (*Lophocebus albigena*) often look back at the male during copulation and sometimes grasp the male's thigh. In this study, copulations initiated by females resulted in ejaculation in 95% of the observations,

Table I. Examples of female copulatory behaviors that potentially bias paternity

Species	Terminate copulation prior to ejaculation	Facial communication during copulation	Vocal communication during copulation	Other active behaviors during copulation	Source
New World Monkeys					
Callimico goeldii		Eye contact; tongue flicking			Heltne et al., 1981
Callithrix jacchus		Eye contact; mouth opening; tongue flicking			Kendrick & Dixson, 1984
Callithrix pygmaea		Eye contact; rare tongue flicking			Soini, 1988
Leontopithecus rosalia		Eye contact	Yes		Kleiman et al., 1988
Saguinus fuscicollis		Eye contact; single recording of tongue flicking			Snowdon & Soini, 1988
Cebus capucinus			'chirp', 'warble', twitter or whine vocalizations	Reaches back to clutch male	Freese & Oppenheimer, 1981
Cacajao calvus				Female thrusting	Fontaine, 1981
Ateles belzebuth		Eye contact; protruded lips and semi-closed eyes		Head shaking; Rubs male's upper leg or back	van Roosmalen & Klein, 1988
Brachyteles arachnoides		Eye contact; grimace	'twitter' or chatter vocalization	Touches male's genital region prior to end of intromission	Milton, 1985; Strier 1992
Lagothrix lagotricha		Eye contact; display with lips retracted; lip smacking	'click' or 'tooth-chatter'	Female mounting and thrusting	Ramirez, 1988; Nishimura, 1988

Table I. (Continued)

Species	Terminate copulation prior to ejaculation	Facial communication during copulation	Vocal communication during copulation	Other active behaviors during copulation	Source
Old World Monkeys					
Lophocebus albigena		Eye contact		Reaches back to clutch male	Wallis, 1983
Macaca arctoides		Eye contact; open mouth 'O' shape ('climax face')	Yes	Reaches back to clutch male	Slob et al., 1978
Macaca fascicularis			Yes		Dixson, 1998
Macaca fuscata	Yes	Stare	Cackling vocalization, squawk or squeak	Reaches back to clutch male	Hanby et al., 1971; Wolfe, 1984; Oda & Masataka, 1992
Macaca mulatta		Eye contact		Reaches back to clutch male	Hinde & Rowell, 1962
Macaca nigra		Eye contact; lipsmack		Reaches back to clutch male	Dixson, 1977
Macaca silenus		Repeated glances	'ho-ho-ho' vocalization	Reaches back to clutch male	Kumar & Kurup, 1985
Mandrillus sphinx		Eye contact			Dixson, 1998
Miopithecus talapoin		Eye contact; grimace	'screeching' vocalization	Reaches back to clutch male	Dixson et al., 1975; Rowell & Dixson, 1975
Papio anubis			'series of loud grunts'		Smuts, 1985
Papio ursinus	Yes	Eye contact	'staccato grunts to panting barks'		Saayman, 1970; Hamilton & Arrowood, 1978
Piliocolobus badius			'quaver' vocalization		Struhsaker, 1975
Piliocolobus preussi			'quaver' vocalization		Struhsaker, 1975

Table I. (Continued)

Species	Terminate copulation prior to ejaculation	Facial communication during copulation	Vocal communication during copulation	Other active behaviors during copulation	Source
Apes & Humans					
Gorilla beringei		Eye contact	'rapid, pulsating whimpers'	Female thrusting; holding hands	Harcourt et al., 1981
Gorilla gorilla			'cooing'	Female thrusting	Nadler, 1976
Pan paniscus	Yes	Eye contact; grimace	Occasional 'nasalized scream'	Female thrusting; Grab testicles	Savage & Bakeman, 1978; Thompson-Handler et al., 1984
Pan troglodytes	Yes		'squeals'		Goodall, 1986
Pongo pygmaeus		Eye contact		Interrupts copulation to manually and orally manipulate penis	Nadler, 1977, 1988; Schüurmann, 1982

whereas those initiated by males only ended in ejaculation in 69% of the observed copulations. Differential female behavior was also demonstrated in Nadler's [1977, 1988] studies of captive orangutans (*Pongo*). In these studies, females that were able to control whether or not mating occurred frequently responded to male penile displays by making eye contact and by mounting him and thrusting. Females that were forcibly mated by males were less responsive and even indifferent to the males. In a wild population of orangutans, Schürmann [1982, p 279] observed a female who "often interrupted the copulation for a short while, manipulating *Jon's* penis with her hand, licking it or putting it in her mouth before mounting again". Although one should not draw conclusions based upon the observations of one animal, it is certainly plausible and in fact likely that this female's behavior increased male arousal. It is important to point out that for all species these behaviors are not necessarily conscious decisions on the part of the female but are also likely mediated by the qualities of the male and by the social, environmental, and neuroendocrine environment. Additionally, communication and other facilitative female copulatory behaviors are not reported for all species and thus this potential mechanism of CFC likely does not act in all species. This is especially true in the prosimians as female sexual behavior in several prosimian species appears to be reflexive and includes lordotic posturing (e.g., ring tailed lemurs, *Lemur catta* [Evans & Goy, 1968]).

3. Discard sperm of current male

The discarding, "dumping", or "flowback" of sperm has been demonstrated in a variety of mammalian taxa (e.g., swine [Sumption, 1961], rabbits [Morton & Glover, 1974], sheep [Tilbrook & Pearce, 1986], and zebra, *Equus grevyi* [Ginsberg & Rubenstein, 1990]). Within primates, flowback has been documented in rhesus monkeys [Kaufmann, 1965] and undoubtedly occurs in many other species. Much of the interesting data on sperm dumping in primates comes from Baker and Bellis's [1993] study of human sexual behavior. They found that, on average, 35% of sperm were ejected, with a mean time to the emergence of the flowback of 30 minutes after ejaculation. In 12% of the 127 cases for which flowback data were available, virtually 100% of the sperm were ejected, indicating that human females are capable of total ejection of ejaculates. In this study, sperm retention was influenced by the occurrence and timing of female orgasm: high retention occurred when the female's orgasm climaxed between one minute prior to and 45 minutes after male ejaculation. Low retention of sperm occurred when females either climaxed more than 1 minute prior to male ejaculation or failed to climax at all. Baker and Bellis [1993] argued that these data support the hypothesis that orgasm serves to generate an "upsuck" mechanism, first proposed by Fox et al. [1970; who called it "insuck"], that transfers the contents of the upper vagina (in this case sperm and seminal fluids) up into the cervix. Interestingly, women with more than one sexual partner retained higher levels of sperm from the extra-pair male's inseminate than from her main partner's inseminate. Baker and Bellis believed that this was primarily caused by increased levels of overt copulatory orgasm with the extra-pair male. While this fascinating line of research raises some very intriguing possibilities, the assumptions upon which it is based have not been conclusively demonstrated (see Hrdy [1999], p 222) and the possible link between female orgasm and sperm retention has not been shown in any other study. Clearly more research is needed.

Of course, these female controlled mechanisms are also potentially influenced by the sexual behavior and the physical characteristics of the male. For example, in humans, Thornhill et al. [1995] demonstrated that the probability of female orgasm was greater when her partner's fluctuating asymmetry index was low. Such symmetry may be associated with greater viability [Polak & Trivers, 1994; Watson & Thornhill, 1994] and is favored in human mate choice studies [Gangestad et al., 1994; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1994; but see Jones, 1996, who failed to find a significant relationship between symmetry and attractivity in a cross-cultural study and who suggested that fluctuating asymmetry is more important in terms of attractiveness in populations under significant stress]. Another example of male influence on female orgasm and thus potentially on sperm retention comes from Japanese macaques, where the probability of female orgasm (as indexed by the frequency of the clutching reaction, which may or may not truly indicate orgasm) is positively related to male dominance status and stimulation levels during copulation [Troisi & Carosi, 1998]. Additionally, in the brown greater galago (*Otolemur crassicaudatus*), intromission with bouts of thrusting is maintained for up to 260 minutes after ejaculation [Eaton et al., 1973], which could potentially serve to facilitate female orgasm and thus sperm retention. The production of copulatory plugs, which occurs in at least a handful of primate species (see mechanisms 7 and 8, below), likely serves to hinder flowback [McGill et al., 1968].

Whereas absence of female orgasm may mean that more sperm are discarded from the current mate, overt female behaviors may also influence whether sperm are retained or discarded. For example, in several Old World species (e.g., grivets, *Chlorocebus aethiops* [Gartlan, 1969]; Angolan talapoin, *Miopithecus talapoin* [Dixson et al., 1975]; chacma baboons, *Papio ursinus* [Saayman, 1970; Hamilton & Arrowood, 1978]; and chimpanzees, [Goodall, 1968, 1986]), females rush off or forcefully bound away from the male following ejaculation. Such behavior could conceivably facilitate the discarding of sperm by encouraging flowback of the ejaculate.

4. Remate with another male

When females mate with more than one male within a short time period, the likelihood of a given male fertilizing her egg decreases [Gomendio et al., 1998]. Given the variability in male fertility and semen quality, copulation with multiple males is theoretically advantageous to females in that it facilitates SC and CFC [Sivinski, 1984; Parker, 1992; Keil & Sachser, 1998; Jennions & Petrie, 2000] and increases female fitness [Loman et al., 1988]. Although it is possible for males to decrease the likelihood that a female will remate with another male, primarily by mate guarding or the use of copulatory plugs, such mechanisms are not always feasible. In fact, mating with more than one male within a single ovulatory cycle has been described for a number of primate species (Table II). As an extreme example illustrating this point, Goodall [1986, pg. 446] described how a single female chimpanzee copulated 50 times in one day with as many as 14 different males. A similar phenomenon has been documented in female muriqui (*Brachyteles*), with a single female mating with four males during an 11 minute period [Strier, 1992; see description under mechanism 8, below]. Yet another striking example is provided by the ring-tailed lemur, in which Koyama [1988] recorded one female receiving a total of 27 ejaculations from five males over a four hour period of sexual receptivity.

Rather than being passive participants in the reproductive process, females may actively solicit multiple mating via extravagant signals such as sexual skin swellings, chemical cues, copulatory calls, and proceptive behaviors. Additionally, females may compete for mating via dominance interactions with other females. In many primates, females produce context specific copulatory calls, with the supposed function of inciting multiple males to copulate with her (e.g., chacma baboons [Hamilton & Arrowood, 1978; O’Connell & Cowlishaw, 1994]; Barbary macaques, *Macaca sylvanus* [Semple, 1998]). In support of this, Semple et al. [2001] demonstrated that the copulatory calls of female yellow baboons (*Papio cynocephalus*) contain information about the female’s reproductive state and about the rank of male with whom she is currently copulating. Calls that occur while mating with one male and that result in the female being mated by a second male might result in postcopulatory CFC against the first male. Beyond calling, other proceptive displays on the part of the female facilitate mating (see review in Dixson [1998, p 96-101]).

Mating with additional males is physiologically facilitated by the Coolidge effect [see Dixson, 1998]. Following copulation, both sexes are in the refractory phase in which sexual receptivity is low. For females, this is likely adaptive because it allows them to reduce the dangers of courtship and copulation and refocuses their attention on critical activities such as feeding and predation avoidance. However, when it is to a female's advantage to mate with another male, the Coolidge effect, in which the refractory phase is shortened in response to a new mate, allows the female to become sexually receptive to a second male earlier than she would have otherwise. It is important to note that the Coolidge effect is a response to novelty and not necessarily a response to a trait specific to the second male. Thus, in and of itself the Coolidge effect does not constitute CFC. Rather, the Coolidge effect facilitates the female's ability to exercise the CFC mechanism of choosing to mate with another male, which would decrease the likelihood of paternity for the previously mated male. If, for example, a female were to mate first with a male of mediocre quality in a particular trait, but then have the opportunity to mate with a male that is superior in that trait, the Coolidge effect would allow her to shorten her refractory period and mate with the "superior" male. In rats, females solicit additional intromissions sooner after mating with a subordinate male than if they had first mated with a dominant male. This would allow not only for SC between the two males, but also for the cessation of sperm transport for the first (inferior) male [McClintock et al., 1982]. Similar mechanisms may occur in primates, particularly among those with multiple matings in a short period of time.

5. Destroy sperm of previous male

As discussed above, in humans, orgasm that occurs during copulation may facilitate the transfer of sperm from the vagina into the cervix via an "upsuck" mechanism. In contrast, orgasm that occurs outside copulation would likely suck-up both cervical mucus and vaginal secretions, serving to lower the pH of the cervix. This would result in a harsh, debilitating environment for any sperm remaining in the reproductive tract or for sperm retained from the next ejaculation. Thus, the presence or absence of orgasm and its timing relative to ejaculation are potentially powerful mechanisms by which a female can manipulate the ability of sperm to reach the egg. In women with multiple male partners, Baker and Bellis [1993] were able to show that women retained less sperm from their main partner's inseminates in comparison to monandrous females. Females presumably achieved this change in retention by varying the frequency of inter-copulatory orgasms cryptically from their main partner. This could be achieved by orgasms that occurred during sleep or during self or other stimulation outside of copulation. Whether or not this causal relationship truly holds or whether similar mechanisms occur in nonhuman primates is unknown.

6. Selectively discard sperm of previous male(s)

In species where females store sperm and mate with multiple males, the female might be able to manipulate stored sperm. Although it has been suggested that uterine

Table II. Species with documented cases of females mating with more than one male.

Species	Mating System	Documented mating with > 1 male?*	Source
Prosimians			
Lemur catta	Multimale-multifemale	(S)	Koyama, 1988
Propithecus verreauxi	Multimale-multifemale	(S)	Richard, 1979
Daubentonia madagascariensis	Dispersed	(S)	Sterling & Richard, 1995
New World Monkeys			
Cebus apella	Multimale-multifemale	(S)	Freese & Oppenheimer, 1981; Janson, 1984
Saimiri sciureus	Multimale-multifemale	(S)	Baldwin & Baldwin, 1981
Callicebus cupreus	Unimale-unifemale	(S)	Reeder et al., unpub. data
*Callicebus ornatus***	Unimale-unifemale	(U)	Mason, 1966
Cacajao calvus	Multimale-multifemale	(U); semi-natural habitat	Fontaine, 1981
Alouatta palliata	Multimale-multifemale; unimale-multifemale	(S)	Carpenter, 1934; Jones, 1985; Dixson, 1998
Ateles paniscus	Multimale-multifemale	(S)	van Roosmalen & Klein, 1988
Brachyteles arachnoids	Multimale-multifemale	(S)	Milton, 1985; Strier, 1992
Lagothrix lagotricha	Multimale-multifemale	(S)	Ramirez, 1988; Nishimura, 1988
Old World Monkeys			
Cercopithecus ascanius	Unimale-multifemale with influx of extra males into group duirng mating season	(U)	Cords, 1987

Table II. (Continued.)

Species	Mating System	Documented mating with > 1 male?*	Source
Old World Monkeys (cont.)			
Cercopithecus mitis	Unimale-multifemale with influx of extra males into group during mating season	(U)	Cords, 1987
Chlorocebus aethiops	Multimale-multifemale	(S)	Andelman, 1987
Erythrocebus patas	Unimale-multifemale with influx of extra males into group during mating season	(S)	Chism & Rowell, 1986; Harding & Olsen, 1986; Ohsawa, 1991; Ohsawa et al., 1993
Lophocebus albigena	Multimale-multifemale	(S)	Wallis, 1983
Macaca fascicularis	Multimale-multifemale	(S)	van Noordwijk, 1985; de Ruiter & van Hooff, 1993
Macaca fuscata	Multimale-multifemale	(S)	Wolfe, 1984; Inoue et al., 1991
Macaca mulatta	Multimale-multfemale	(S)	Carpenter, 1942; Conoway & Koford, 1965; Southwick et al., 1965; Loy, 1971; Lindburg, 1983; Manson, 1992
Macaca nemestrina	Multmale-multifemale	(S)	Tokuda et al., 1968
Macaca radiata	Multimale-multifemale	(S)	Sugiyama, 1971; Glick, 1980
Macaca sylvanus	Multimale-multifemale	(S)	Taub, 1980; Ménard et al., 1992
Mandrillus sphinx	Multimale-multifemale; unimale-multifemale?	(S)	Dixson et al., 1993
Miopithecus talapoin	Multimale-multifemale	(S)	Rowell & Dixson, 1975
Papio anubis	Multimale-multifemale	(S)	Scott, 1984; Smuts, 1985
Papio cynocephalus	Multimale-multifemale	(S)	Altmann & Altmann, 1970; Hausfater, 1975
Papio ursinus	Multimale-multifemale	(S)	Hall & DeVore, 1965

Table II. (Continued.)

Species	Mating System	Documented mating with > 1 male?*	Source
Apes & Humans			
Hylobates lar	Unimale-unifemale	(S)	Reichard, 1995
Symphalangus syndactylus	Unimale-unifemale	(U)	Palombit, 1994
Gorilla beringei	Multimale-multifemale	(S)	Robbins, 1999
Pan paniscus	Multimale-multifemale	(S)	Kano, 1982; Furuichi, 1987
Pan troglodytes	Multimale-multifemale	(S)	Goodall, 1986; Hasegawa & Hiraiwai-Hasegawa, 1990
Homo sapiens	Highly variable; but unimale-multifemale polygyny and monogamy most common	(S)	Bellis & Baker, 1990; Baker & Bellis, 1993; Hrdy, 1999; many others

Data in this table in part adapted from Dixson [1998], Table 3.5. As this sort of information is often deeply buried in the primary literature, this is undoubtedly an incomplete list.

[a] (S) refers to documented mating with more than one male in a single ovarian cycle, (U) refers to documented mating with more than one male, but reproductive status of female at time of mating unknown. Copulations that occurred during known pregnancy are not considered here.

[b] Note that this is not *Callicebus moloch*, as has been commonly cited in the literature.

glands and/or cervical crypts may act as sperm storage sites in mammals, several recent reviews [Mortimer, 1995; Gomendio et al., 1998] concluded that sperm inside the glands or crypts are likely “trapped” and will never take part in fertilization. In the short term, the mammalian isthmus of the oviduct plays the role of a sperm reservoir during the hours preceding ovulation. However, outside of bats, there is no evidence for long-term sperm storage in mammals [Birkhead & Møller, 1993; Gomendio et al., 1998]. Given the lack of demonstrated sperm storage sites, the ability of a female mammal, including a female primate, to preferentially utilize or to discard the sperm of a previous male is presumably limited.

7. Remove copulatory plug

Males of many primate species deposit substances that form a copulatory plug following ejaculation. For example, plugs are found in golden angwantibos (*Arctocebus calabarensis* [Manley, 1967]), gray slender lorises (*Loris lydekkerianus* [Manley, 1967]), mouse lemurs (*Microcebus* [Martin, 1973]), and tarsiers (*Tarsius* [Hill, 1955]), all of which display dispersed mating systems [Dixson, 1998]. Copulatory plugs are also found in lemurs (e.g., brown lemurs, *Eulemur fulvus* [Brun et al., 1987]; ring-tailed lemurs [Dixson, 1998]); stump-tailed macaques (*Macaca arctoides* [Dixson, 1998]); rhesus monkeys [Loy, 1971]; chimpanzees [Tinklepaugh, 1930, Dixson & Mundy, 1994]; and muriqui [Strier, 1992]. Although not all species form copulatory plugs, this list of species is undoubtedly an underrepresentation of the presence of copulatory plugs in primates as the observation of such is a chance occurrence outside of captive studies.

As has been speculated for mice (*Mus musculus*), copulatory plugs may serve several purposes, such as reducing sperm loss [McGill et al., 1968], stimulating ovulation [Leckie et al., 1973], and/or blocking subsequent intromission by other males [Voss, 1979]. Following copulation, females choose to either remove the plug or allow it to remain in the vaginal opening (e.g., paca, *Agouti paca* [N. Smythe, *in* Eberhard, 1996]; squirrels, *Sciureus niger* and *S. carolensis* [Koprowski, 1992]). In primates, copulatory plug manipulation by female muriqui has been observed, where plugs are either removed immediately after mating or allowed to remain in the vagina for a few days [Strier, 1992]. Plug removal by females has also been documented in chimpanzees [Goodall, 1986]. Although it has never been demonstrated in primates, copulatory plug removal could presumably increase sperm loss by facilitating flowback. Thus, plug removal would potentially select against the sperm of the plug's depositor, whereas allowing a plug to remain would presumably increase the likelihood of fertilization by the plug's depositor.

8. Allow or impede plug removal by another male

Not only female, but also male muriqui manipulate copulatory plugs. A striking example of this was documented by Strier [1992, p 72-73]:

> " All of the males were resting in a nearby tree, and one of them, Clyde, swung over to Cher to inspect her as she lay sprawled on the branch. A moment later, he was mounting her, in one of the quickest copulations I have ever seen. Within 2 minutes it was over, and I could see the fresh ejaculate blocking Cher's reproductive tract.
>
> "Clyde swung out of the tree, and now Cutlip joined Cher. He pulled out Clyde's ejaculate, which he began to eat. Cher took a small piece of this solid material from his hand, and another dropped to the ground below…
>
> " Within 2 minutes Cutlip has disengaged himself and swung off in the direction that Clyde had gone just a few minutes earlier. Cher had another plug in her, this time it was Cutlip's.
>
> " Next, Preta was walking along the branch toward Cher. When he reached her, he pulled out Cutlip's plug and began to eat it, with Cher taking bites while other bits dropped to the ground. Again I collected what had fallen, only to look up and find Cher mating again. When Preta moved off to follow Clyde and Cutlip, Scruff approached Cher and repeated his predecessor's performance. Within 11 minutes, four different males had copulated with

> Cher, and three had removed and eaten the ejaculate of the male before them. Only Scruff's plug, the last of the sequence, was still intact."

The removal of copulatory plugs by males should, in most cases, require female cooperation (at least in terms of staying still). In the case of Cher, the removal of the copulatory plugs of all but the last male potentially favored his sperm over the others. Although female muriqui can and do remove copulatory plugs themselves, and could prevent their removal by other males, Cher did not do so in this case. Such overt behavior on the part of the female thus has potentially profound effects on male paternity. In some species such as bonnet macaques, females regularly allow anogenital exploration by males, and removal of "coagulated sperm…attached to the vagina" by both subordinate and dominant males has been observed [Sugiyama, 1971]. Observations of similar behavior in other species would be very useful in terms of assessing the relative frequency or feasibility of this mechanism in primates with copulatory plugs.

9. Fail to transport sperm to storage organs or fertilization sites

Although there is no evidence that primate females store sperm (see above), they could still fail to transport sperm to fertilization sites [Mortimer, 1995]. One mechanism by which sperm transport is achieved is via the vaginal contractions and orgasm triggered by copulation. Sperm transport may also be affected by the timing of mating. For example, McClintock et al. [1982] demonstrated that female rats that receive intromissions within 10 minutes of receiving an ejaculation halt transport of the previous male's sperm. Whether or not a similar phenomenon occurs in primates that mate with more than one male in succession is unknown.

10. Biased use of stored sperm

As previously discussed, there is no evidence that primate females store sperm in the classical sense. Additionally, there are little data available on the fertile lifespan of sperm in mammals, and this is especially true for primates [Gomendio et al., 1998]. In those mammalian species for which there are data, sperm fertile lifespans range up to 48 hours. In humans, sperm remain fertile for an estimated 33.6 hours [Weinberg & Wilcox, 1995]. Thus, in theory, any sperm present in the primate female during the window of potential fertilization are available for SC *sensu strictu* and differential use by the female. The potential physiological mechanisms by which a female could differentially utilize sperm from different ejaculates are discussed below (mechanism 13).

11. Allow or impede induced ovulation

As a general rule, all primates are considered to be spontaneous ovulators. However, even among species where spontaneous ovulation has been documented, including rhesus monkeys, squirrel monkeys (*Saimiri*), and possibly humans, copulation or copulation-like stimuli can lead to earlier ovulation than would have otherwise occurred (see Jöchle [1975] for review). This effect presumably comes about through physiological mechanisms, such as a surge in luteinizing hormone (LH) following mating, as discussed by Zarrow et al. [1968] and Milligan [1982]. In addition to the stimulatory influences of copulation, substances in the ejaculate have the potential to affect ovulation as well, as has been demonstrated in pigs [Claus, 1990] (see also discussion under **Anatomical and Physiological Considerations**). In order to utilize CFC in this scenario, females of a given species would have had to evolve mechanisms that either allow and possibly even facilitate these male influences for preferred males or that counteract these influences for less desirable males. A graded response to male stimulation could potentially achieve this effect.

12. Fail to prepare uterus for embryo implantation

There is no evidence to date that female primates ever fail to exhibit a spontaneous luteal phase following ovulation, which prepares the uterus for embryo implantation. Thus this mechanism seems unlikely for primates.

13. Select for or against sperm during capacitation or hyperactivation

In most eutherian mammals, including primates, semen is deposed in the anterior part of the vagina during copulation. From here, sperm must travel through the female reproductive tract in an effort to eventually reach the site of fertilization (see **Anatomical and Physiological Considerations**, below). Before they are able to fertilize the ovum, newly deposited sperm must first undergo a series of physiological changes, collectively called capacitation (see review in Yanagimachi [1994]; Figure 3). Even though the necessity of this process has been recognized since 1951 [Austin, 1951; Chang, 1951], it is still not fully understood. We do know that there are a variety of molecular events that occur during capacitation, including changes in intracellular ions, metabolic activity, cAMP activity, and changes in the plasma membrane. These changes in the plasma membrane, which occur in the presence of uterine fluid, include the simultaneous release of several proteins and adsorption of several proteins, indicating male-female interaction [Yanagimachi, 1994].

After capacitation has occurred, sperm in some species, including primates, undergo a process called hyperactivation, in which they begin to move much more actively than before (see Yanagimachi [1994, p 219-220] for movement patterns). As with capacitation, the physical and chemical environment play a large role in the initiation and maintenance of hyperactivation. Additionally, there is a close correlation between the ability of a spermatozoa to fertilize an intact egg and its ability to display hyperactivated motility [Fraser & Quinn, 1981], suggesting that both processes are necessary (Figure 3). That both capacitation and hyperactivation appear necessary for successful fertilization and that the uterine and oviductal chemical environments play a role in these processes indicate that females can potentially select for or against the properties of certain sperm at this stage. Clearly a greater understanding of the mechanisms involved in these processes will help us understand the female's role in them.

14. Choose among sperm that have reached the egg

Images from *in vitro* fertilization, in which numerous sperm simultaneously reach and compete for penetration of the ovum misrepresent the true nature of the final

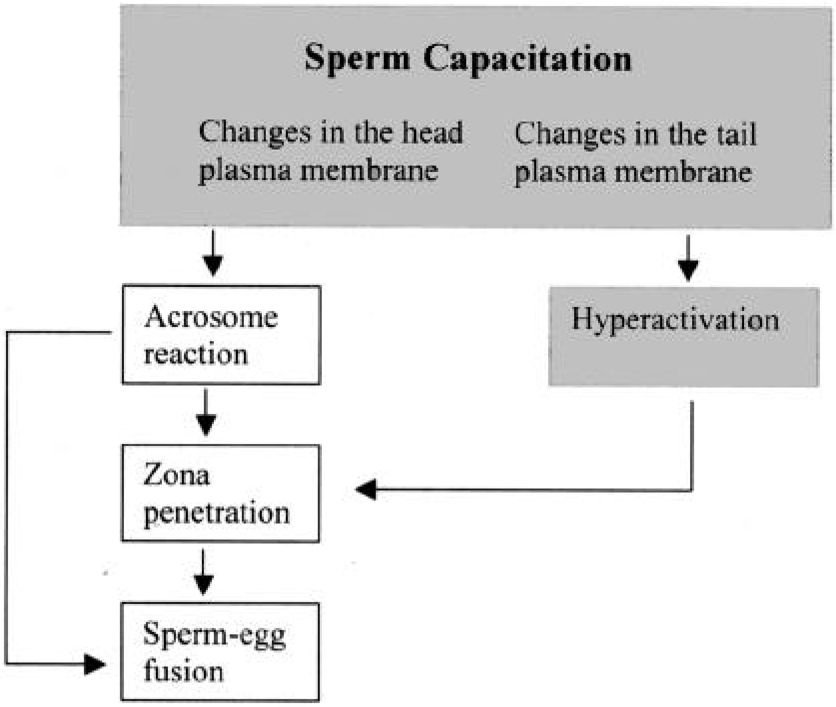


Figure 3. Spermatozoon processes presumably necessary for successful fertilization. Areas in gray indicate pre-fertilization processes in which females could potentially choose among sperm by selecting for or against the properties of certain sperm. Areas in white indicate processes that occur once a single spermatozoa has contacted a single ovum; sperm can still be selected against during these processes due to incompatibility. Redrawn in part from Yanagimachi [1989].

sperm/ovum interaction [Gomendio et al., 1998]. In those species in which *in vivo* studies have been carried out (e.g., hamsters, rats, mice, guinea pig, and rabbit; as reviewed by Hunter [1993]) the ratio of sperm to ova in the ampulla is roughly 1:1. However, it is important to note that all of the species in which this type of study has been carried out give birth to more than one infant. This necessitates that more than one sperm reach the ampulla. Thus, one cannot assume that the sperm:ova ratio in primates is necessarily 1:1, as most primates give birth to only a single infant. In fact, these data suggest the contrary, that more than one sperm (but certainly not a high number) can reach the single primate ova.

Of course reaching the egg first does not ensure paternity as there are still a number of complex processes that must take place. Once a spermatozoa that has already undergone capacitation and hyperactivation reaches the ovum, the acrosome reaction must take place, in which the outer or acrosomal membranes of the sperm are altered so as to render the sperm head able to penetrate the cumulus oophorus and the zona pellucida. Following this, the sperm and the egg must fuse, the egg must be activated, additional sperm must be blocked, and sperm nucleus decondensation, meiosis, pronuclei development and syngamy must occur [Yanagimachi, 1994]. At each of the stages there is room for failure, presumably at least in part due to some feature of the spermatozoa.

15. Abort zygotes (including the Bruce Effect)

Even achieving fertilization does not ensure reproductive success as abortion is relatively common. For example, in humans, approximately 78% of pregnancies spontaneously abort, most often in the absence of pregnancy detection [Wasser & Isenberg, 1986]. Spontaneous abortion in nonhuman primates has been described in a number of species (e.g., common marmosets, *Callithrix jacchus* [Jaquish et al., 1996]; squirrel monkeys [Diamond et al., 1985]; three striped night monkeys, *Aotus trivirgatus* [Rouse et al., 1981]; hamadryas baboons, *Papio hamadryas* [Colmenares & Gomendio, 1988]; olive baboons, *Papio anubis* [Fortman et al., 1993]; southern pigtail macaques, *Macaca nemestrina* [Sackett et al., 1975]; and rhesus monkeys [Hertig et al., 1971]) and presumably occurs in all species. Spontaneous abortion occurs for a number of reasons [Clark & Chaouat, 1989; Baines & Gendron, 1990; Gill, 1999; Clark et al., 1999], and is often but not always linked to defect and/or the maternal immune response. Of particular interest to the topic of CFC, the sharing of certain major histocompatibility (MHC) alleles is positively correlated with spontaneous abortion in both humans [Ho et al., 1990] and pigtailed macaques [Knapp et al., 1996]. The sharing of MHC-linked alleles has been associated not only with increased abortion rates but also with somatic defects and increased prevalence of cancer [Gill, 1999]. Rejection based upon MCH similarity thus allows a female to selectively abort the offspring of a particular male, which would likely be inbred and of low reproductive value [Verrell & McCabe, 1990]. Clark et al. [1999] pointed out that the abortion of these ‘weaker’ embryos is more likely to occur when the mother is stressed. They go on to say (p 16): “To make a selection amongst embryos of differing genotype, under stressful conditions, the mother must ‘know’ the father.” That paternal alloantigens are expressed on the trophoblast while the maternal allele is suppressed supports the idea that females can identify the father at this stage [Gill et al., 1993; Clark et al., 1999]. Although CFC in this case is relative in that it is tied to the degree of similarity in the MHC-linked genes between the male and female and thus somewhat different from selecting on some absolute male trait such as body size, the definition of CFC is still met. Not surprisingly, detection of MHC similarity via olfactory cues also allows the female primate to exercise pre-copulatory choice for males with whom she is not related and against males with whom she shares alleles [Grob et al., 1998].

Beyond physiological measures like MHC, social influences play a large role in spontaneous abortion [Wasser & Barash, 1983; Wasser & Isenberg, 1986]. Based upon the belief that reproductive failure, which presumably occurs in all mammals, can be adaptive, Wasser and Barash [1983] proposed the Reproductive Suppression Model.

This model argues that reproductive failure (including not only abortion but also problems such as infertility and amenorrhea) can in many cases be considered a filtering mechanism that inhibits or terminates reproduction when conditions suggest that it is unlikely to succeed. Wasser and Isenberg [1986] reviewed the human literature on psychosocial stress and reproductive failure. They found a number of studies in which characteristics or conditions related to males, including rape, infidelity, death of a spouse, discontent with one's partner, and low levels of social support from the spouse, played a role in reproductive failure of one type or another. Their review was largely restricted to those studies that they believed adequately controlled for the effects of a variety of other factors, including age, parity, disease, smoking, drinking, marital status, race, and socioeconomic status. Nevertheless, human psychological studies are complex and often retrospective – thus caution is suggested in interpreting these studies in terms of selection via CFC.

Male primates could in theory derive reproductive benefits from the ability to induce abortions, as has been shown via the Bruce effect in multiple rodent species (as reviewed by Eberhard [1996]). Although it is theoretically possible and even perhaps likely in certain systems, as of yet, there have been no systematic studies of the Bruce effect in primates. However, the existence of the Bruce effect in Hanuman langurs (*Semnopithecus entellus*) was suggested by Agoramoorthy et al. [1988]. Additionally, Colmenares and Gomendio [1988] were able to demonstrate that, within one captive colony of hamadryas and hybrid baboons, the introduction of novel males was followed by reproductive changes in the resident females, including the spontaneous abortion by one female during early pregnancy. They argued that these changes in reproductive state were spontaneous female responses to male novelty, rather than impositions due to male aggressive behavior. Some would argue that the response to novelty, in and of itself, would not constitute CFC as the male trait of "novelty" is theoretically random and not necessarily associated with genetic differences. However, immigration of a new male in a natural primate population is a far cry from the introduction of a random novel male in the laboratory. I would argue that, in fact, males that successfully immigrate into a primate group are not a random selection of possible immigrants, but rather possess particular traits that enable them to better take over a group of females. Males with these traits would then be selected for as females aborted the progeny of others. Whether or not a female in this scenario would be responding simply to novelty or to these other traits remains an interesting question.

Another example of female modulation of abortion comes from the common marmoset, where twinning is the norm. Several studies have shown that litter size can be reduced during pregnancy, with loss occurring both during and after the embryonic phase [Jaquish et al., 1996; Nubbemeyer et al., 1997; Windle et al., 1999]. Both Jaquish et al. [1996] and Windle et al. [1999] suggested that this ability to adjust litter size allows for a variable response to proximate environmental factors. Although this is an intriguing possibility, it has yet been documented and clearly warrants further study. This potential flexibility on the part of common marmoset mothers would theoretically also allow for changes in litter size in response to characteristics of the male, who typically provides more parental care than she does [Tardif et al., 1986].

Because of the greater investment per offspring in primates relative to other mammals, one could argue that "spontaneous" abortion in the absence of obvious defect in the infant should be a relatively rare occurrence. Hrdy [1979, p 32] reflected this view in stating "If abortion of a nondefective infant is ever selected for among primates one would expect it to be an option of 'last resort'." However, given what we now know about the prevalence of social effects on reproduction, and the ability of some primates to potentially respond to environmental cues (e.g., the marmosets' ability to selectively reduce litter size), I would argue that abortion in response to social and/or environmental cues has likely been selected for in some systems. Clearly, in terms of managing reproductive potential, the ability to terminate pregnancy is much more energy efficient and effective than modulation of reproductive success by infanticidal counterstrategies and/or differential care of young.

Human females are in the unique position of being able to make conscious decisions regarding abortion and a variety of abortion methods are described from multiple cultures. Of particular interest here, abortion in the case of some form of illegitimacy is recorded for numerous primitive societies (as reviewed by Devereux [1976]). Abortion was historically a common practice in some Western societies as well (e.g., nineteenth-century Britain [Sauer, 1978]), particularly in the case of illegitimacy. The availability of voluntary, legal, and relatively safe abortion in modern human societies has provided a new scenario in which women can more freely demonstrate choice against the progeny of a particular male after copulation. Indeed, Lycett and Dunbar [1999] demonstrated that human females were more likely to abort if they were single than if they were married, thereby selecting against the progeny of those males unwilling or unable to support them through marriage. The conditions under which human females will exert choice after conception have been examined in the psychological literature and further integration of the psychological and evolutionary perspective as well as direct investigation of abortion as a mechanism of choice against particular males would be fruitful.

16. Allow or impede infanticide

Infanticide as a means of birth control has been practiced in a number of human societies, where illegitimacy is one reason for its occurrence. When performed because of illegitimacy, infanticide results in selection against those fathers not likely to provide support (see reviews in Minturn and Stashak [1982], Scrimshaw [1984], Voland and Stephan [2000]). Among nonhuman primates, infanticide is a relatively rare behavior, described from approximately 7-10% of all species (see reviews by Hrdy [1979], Struhsaker and Leland [1987], Bartlett et al. [1993]; van Schaik [2000]). Infanticide has been largely explained by the sexual selection hypothesis [Hrdy, 1974, 1977, 1979; van Schaik, 2000] in which infanticidal behavior by an immigrant male results in a quick return to estrus for the infant's mother and hence greater paternity for that male. Females subject to infanticide display a wide variety of behaviors (see recent comprehensive reviews in Treves [2000], Sterck and Korstjens [2000], and van Schaik et al. [2000]), including actively avoiding immigrant males (e.g., gray or Hanuman langurs [Hrdy, 1977]; western red colobus, *Piliocolobus badius* [Struhsaker & Leland, 1985]), forming coalitions against the male (e.g., blue monkeys, *Cercopithecus mitis* [Butynski, 1982]), and abandoning their infants (e.g., purple-faced langurs, *Trachypithecus vetulus* [Rudran, 1973] - formerly called *senex*; see Groves, in press]). It is reasonable to expect that mothers would be more successful in protecting their infants against males of lower quality than against males of higher quality. Given this, it is theoretically possible that mothers may protect their infants more vigorously against intruder males of lower quality whereas females confronted by high quality males may resist less. If, in fact, differential levels of protection from infanticide exist and are related to the qualities of the intruding male, this could constitute CFC against the previous male. While the **overt** female counterstrategies discussed above are, in fact, rarely successful [Hrdy, 1974, 1977; Hausfater, 1984; Crockett & Sekulic, 1984], more **covert** counter-strategies [see van Noordwijk & van Schaik, 2000], which have been less studied to date, could also constitute CFC.

17. Invest less in each offspring after birth

As previously discussed, reproductive success for the male primate is not equivalent to mating success, but rather requires that the male's sperm successfully fertilizes an egg. To extend this argument, the true measure of reproductive success is not simply achieving paternity, but rather requires that one's offspring live to reproduce themselves. By this standard, many things can happen in the life of a young primate that could either increase or decrease its likelihood to survive and reproduce successfully, resulting in greater or lesser reproductive success for its father. As the primate mother is the primary caregiver in the vast majority of species, and as her behavior is directly related to the infant's survival and success, maternal behavior is a potential mechanism through which CFC can act. Although infant-directed detrimental behaviors (including variations in anti-infanticidal protection, see above) would seem maladaptive given the relatively high investment in primate infants, they nevertheless do occur and we would do well to dispel the myth that all mothers are loving and attentive to all offspring. For an iteroparous, long-lived primate mother, the value of each offspring is assessed in terms of current and future energetic and social circumstances. In the words of Hrdy [1999, p xviii] "Mothers [are] multifaceted creatures, strategists juggling multiple agendas. As a consequence, their level of commitment to each offspring born [is] highly contingent upon circumstances." Accordingly, the primate mother, depending on a variety of factors, can increase or decrease the amount of resources allocated to a given infant. If a primate mother differentially allocates resources in a way that biases male reproductive success, then these behaviors serve as cryptic mechanisms for female choice. Such differential care has been described in humans. For example, in some Tibetan societies where fraternal polyandry is the norm, abuse of illegitimate children by mothers is accepted [Levine, 1987a], and infanticide has been known to occur. In at least one Tibetan society (the Rongphug), Levine [1987b, p 275] reported that "some women do not mask their preferences [for particular husbands and children], sleeping mostly with one brother, arranging that their favourite receives the easier work assignments and best food, treating his children best."

In both human and nonhuman primates, age at weaning affects offspring health. In common marmosets, earlier weaning was associated with slower subsequent growth [Tardif et al., 1998], while in humans, early weaning and the introduction of solid foods significantly increased the risk for respiratory illness [Wilson et al., 1998]. Premature weaning may also be a strategy of defense against potentially infanticidal males [Hrdy, 1977]. If this occurs in response to a specific, heritable characteristic of infanticidal males, then it constitutes CFC against the father of the weaned infant (see **Establishing Cryptic Female Choice**, below). In addition to feeding, the quality of maternal care influences infant health, with outright infant abuse also occurring, at least in captivity (see review in Nicolson [1987]; Maestripieri [1998]). For example, juvenile and adolescent common marmosets that experienced abusive caregiver-infant interactions (such as rejection, rubbing off, and biting) during their first few weeks of life were significantly smaller than infants not subject to abuse [Johnson et al., 1996]. Although it is theoretically possible, as of yet, there is no evidence from nonhuman primates of a relationship between the identity and characteristics of a given father and differential infant care either in terms of early weaning or abuse.

FURTHER BEHAVIORAL, ANATOMICAL, AND PHYSIOLOGICAL CONSIDERATIONS

Mating/Social Systems

The ability of a female to select for or against the sperm of a particular male after the initiation of copulation should be especially beneficial to females that routinely mate with more than one male. Unfortunately, for the vast majority of primate species, data available for mating systems describe group composition/social organization, rather than actual mating patterns. Moreover, there are a surprising number of primates for which we know little or even nothing about their behavior (e.g., *Pseudopotto martini*; the false potto; known only from type specimens). This is especially true today, as recent taxonomic splits and the discovery of at least 23 newly described species in the past decade brings the current total number of primate species to over 350 [Groves, in press].

In the absence of actual mating data for most species, information about their group composition or social organization can still be helpful. For example, routine mating with more than one male is most likely to occur in those species with multimale-multifemale, dispersed, and polyandrous mating systems (for reviews of primate social organization/ mating systems see Dunbar [1988], Rowe [1996], Dixson [1998]; see also appendix in Plavcan [1999]). It is important to remember, however, that social organization can be complex and highly variable, both between and within species (for example, the simakobou or pig-tailed langur, *Simias concolor*, can be found in one male-one female, one male-multifemale, and multimale-multifemale groups [Watanabe, 1981]). Furthermore, although the social organization of a given species is a good indicator of mating patterns, they are clearly not synonymous - being found in a multimale-multifemale group does not necessarily mean that females mate with more than one male. For example, despite residing in multimale-multifemale groups, both female Verreaux's sifakas (*Propithecus verreauxi*) and female Venezuelan red howlers (*Alouatta* *seniculus*) apparently only mate with the dominant male during the mating season [Richard, 1979; Pope, 1990]. In the multimale-multifemale saddleback tamarin (*Saguinus fuscicollis*), as in some of the other callitrichids, only the dominant male and female typically breed, with sexual behavior in subordinate animals suppressed behaviorally and physiologically [Abbott, 1993; see Saltzman, this volume]. A final example comes from capuchins (*Cebus*), where all species are found in multimale-multifemale groups; for at least one species (weeper capuchin; *Cebus olivaceus*), a single breeding male within the hierarchy has been described [O'Brien & Robinson, 1993].

On the other hand, even though we can point out which primate species are organized in such a way as to allow females to mate with more than one male, demonstrating that they do so is another matter. Nevertheless, for a number of species, copulation of one female with more than one male has been documented, both during a single breeding season and even within a single ovulatory cycle (Table II; see also Gomendio et al. [1998], van Schaik et al. [1999]). Because the observation of copulation in the field is difficult and biased in many respects, this table likely underestimates the number of species in which females mate with more than one male. As an illustration of this point, Ohsawa et al. [1993] demonstrated that patas monkey (*Erythrocebus patas*) infants were sired by extra-group males in two of four cases in which no extrapair copulations had been observed. Likewise, Dixson et al. [1993] demonstrated inconsistencies between behavioral observations of male mandrill (*Mandrillus sphinx*) sexual and mate guarding behavior and paternity.

When considering sexual selection that occurs after the initiation of copulation, it is tempting to ignore those species typically characterized as being found only in one male-multifemale polygynous groups or in "monogamous" one male-one female groups. However, females in groups classified as one male-multifemale may very well be mating with more than one male (see also Table II), as has been documented in red-tailed monkeys (*Cercopithecus ascanius)* [Cords, 1987], blue monkeys [Cords, 1987], and in patas monkeys [Chism & Rowell, 1986; Harding & Olson, 1986; Ohsawa, 1991], where influxes of additional males in the breeding season occur. For patas monkeys, Ohsawa et al. [1993] documented multiple matings within a single ovarian cycle and were able to demonstrate via DNA typing that extra-group copulations resulted in mixed paternity. As has been shown in birds, being typically found in a one male-one female group does not preclude the possibility of mating with more than one male. In fact, in numerous species of "monogamous" birds extra-pair copulations have been shown to result in mixed paternity (as reviewed by Wink and Dyrcz [1999]). Classic precopulatory female choice and even possibly CFC, again considered more likely in polygynous species, appear to be demonstrated by some monogamous birds (e.g., widowed collared flycatchers, *Ficedula albicollis* [Sheldon et al., 1999]). Thus, it is not unreasonable to suggest that female choice (both pre- and post-copulatory) might also occur in "monogamous" primates. In fact, copulations outside of the group have been documented in several "monogamous" primates (e.g., titi monkeys, *Callicebus ornatus* [Mason, 1966]; siamang, *Symphalangus syndactylus* [Palombit, 1994]; and lar gibbons, *Hylobates lar* [Reichard, 1995]).

Mating with more than one male by females in both one male-multifemale and one male-one female groups suggests that the potential for CFC exists in all primate species. Despite this potential, selection via CFC is most likely to have occurred in those species where females *routinely* mate with more than one male. However, variability in which social system is expressed is common and can be attributed, at least in some cases, to changes in environmental conditions and to changes in the demographics of a given population [Lott, 1984; Ferrari & Lopes Ferrari, 1989]. Given this, it is difficult to say with certainty what social system(s) have been expressed throughout evolutionary time. Not only are social systems not fixed, but in many species their basic characteristics and degree of variability are not well enough described. Thus, we can only make an educated guess about the selection pressures that may or may not have existed for a given species.

Timing, Order, and Patterns of Mating

To add another layer of complexity, it is not just who a female mates with, but when she mates that can bias paternity. Despite the fact that females in some species will mate for days or weeks on end (e.g., rhesus monkeys [Carpenter, 1942]; bonobos [Kano, 1982; Furuichi, 1987]; Hanuman langurs [Heistermann et al., 2001]), which may serve functions other than conception (such as paternity confusion), mammalian ova remain maximally fertile for only approximately 24 hours [Gomendio et al., 1998]. Accordingly, there is an optimum period for mating in mammals and the male that copulates within that period is most likely to fertilize the egg [Gomendio & Roldan, 1993; Gomendio et al., 1998]. Thus, it appears that the best strategy for a male is to copulate with a female prior to ovulation, leaving enough time between copulation and ovulation for sperm capacitation to occur (Figure 4). Whether or not competition between sperm from rival males occurs depends upon when these males mated with the female and upon sperm lifespan, which averages approximately 48 hours in mammals [Gomendio et al., 1998]. Given this, males should compete to mate with females most heavily in the periovulatory period, as has been demonstrated for the olive baboon [Bercovitch, 1989]. In the yellow baboon, the copulatory advantage of high ranking males is most pronounced during the few days prior to female sexual skin detumescence, when ovulation is most likely to occur [Hausfater, 1975]. Clearly, classic precopulatory male-male competition and female choice should be most pronounced during this short window of time and the same is to be expected of SC and CFC. The exertion of female choice during this time period, including the decision to remate during this short window of time, could potentially allow a female to cryptically bias paternity. Additionally, the precise pattern of mating, which is largely controlled by the female, potentially affects paternity. For example, sperm count significantly decreases over multiple ejaculations (e.g., rams [Synott et al., 1981]; chimpanzees [Marson et al., 1989]), thus female alteration of the number and spacing of ejaculations could potentially allow for cryptic choice for one male versus another. Although many female primates advertise their ovulatory state via sexual swellings and changes in proceptive behavior, the timing of ovulation in most species is less obvious, at least to the human observer [Dixson, 1983]. Despite the controversy as to whether or not true concealed ovulation exists in female primates, the lack of visual ovulatory indicators and the prolonged period of

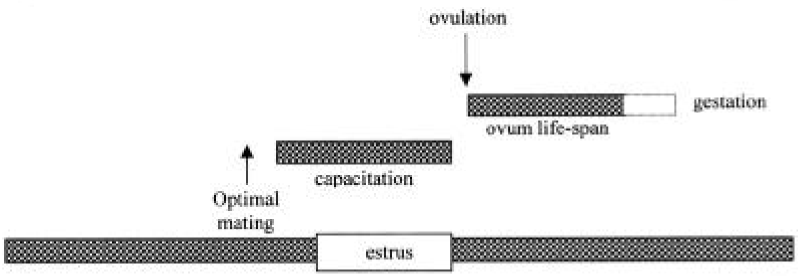


Figure 4. Schematic of optimal timing of mating in order to ensure fertilization. Redrawn in part from Gomendio and Roldan [1993].

mating in some species (as occurs for example in muriqui [Strier & Ziegler, 1997] and rhesus monkeys [Carpenter, 1942]) would allow the female primate to select for or against the sperm of a given male, even after she has copulated with him.

Within mammals, demonstrating a role for the order of mating in post-copulatory selection has been variable and has appeared to be species specific. In some induced ovulators, such as rabbits, the male that mates first gains the reproductive advantage. In prairie voles, also induced ovulators, the second male fathered more offspring. In other species, such as rats, there appears to be no order effect [Dewsbury, 1984; Birkhead, 2000a]. The discrepancy between species has now been largely resolved by the realization of the optimum period for mating such that the male that copulates within this period is most likely to fertilize the egg, regardless of the order of mating [Birkhead & Hunter, 1990; Gomendio & Roldan, 1993; Gomendio et al., 1998]. In those species, such as muriqui [Milton, 1985; Strier, 1992] and chimpanzees [Goodall, 1986], where multiple males mate within a very short window of time, sperm *may* compete via a "lottery" or "raffle" system [Parker, 1990a, 1990b]. However, given how little we know about the timing and reproductive physiology of most primate species and given the evidence that copulation may induce ovulation in some circumstances [Jöchle, 1975], judgment as to order effects and other paternity influences should be reserved.

As previously described, female primates can choose to terminate copulation once it has begun (e.g., bonnet macaques [Nadler & Rosenblum, 1969]). Thus, it may be necessary for males to continue to court females during copulation ("copulatory courtship" *sensu* Eberhard [1996]) in order to ensure ejaculation and sperm transfer. Eberhard [1985] was first to suggest that the penis functions not just to transfer sperm, but also as an 'internal courtship device' to facilitate sperm transport and fertilization. As such, penile morphology and the accompanying copulatory patterns have been subject to sexual selection. Although primates display either single or multiple intromissions, multiple thrusts prior to ejaculation are ubiquitous among primates and may even occur after ejaculation [as reviewed by Dixson, 1998]. For example, in the brown greater galago, intromission and intermittent thrusting can occur for up to 260 minutes after ejaculation [Eaton et al., 1973]. In most cases, intromission and thrusting only occur when the female allows them. In Japanese macaques, the number and frequency of intromissions and thrusts increased the likelihood of female orgasm, as indexed by the frequency of the clutching reaction [Troisi & Carosi, 1998]. The presence of orgasm could strongly influence the likelihood of fertility by facilitating sperm transfer (both via the potential "upsuck" mechanism described above and through uterine smooth muscle contractions facilitated by the neuropeptide oxytocin). Additionally, oxytocin released during orgasm has been shown to facilitate affiliative behavior [Carter et al., 1992]. Thus, whether a female facilitates or blocks intromission and thrusting could affect relative male reproductive success. Dewsbury [1988] suggested that multiple intromissions and prolonged mating function to allow the female to choose strong, dominant males, as less dominant males are more likely to be interrupted before ejaculation. This argument may apply to rhesus monkeys, as low ranking males ejaculate more quickly than dominant males [Curie-Cohen et al., 1983], presumably to avoid aggressive encounters with more dominant males [Manson, 1994].

Anatomical and Physiological Considerations

The competition of sperm within the female's often hostile and complex reproductive tract and the potential favoring of one male's sperm over another's on the part of the female may be related to a number of anatomical and physiological adaptations in both males and females (see reviews in Dixson [1998] and Gomendio et al. [1998]). As previously discussed, many species of Old World monkeys and apes exhibit sexual swellings, where changes in the coloring and swelling of skin surrounding the anogenital region roughly track the ovarian cycle. There exists a fair amount of variation in the appearance of sexual swellings (see Dixson [1998, p 202] and Nunn [1999]), which appears highly subject to phylogenetic inertia. Variation also exists as to the relationship between the day of ovulation and the stage of the swelling [Heistermann et al., 1996]. Despite this variability, sexual swellings in female primates serve, at least in part, as an indicator of the probability of ovulation (the graded-signal hypothesis [Nunn, 1999]). In a similar manner, the hypertrophied clitoris of ateline primates likely advertises the female's state as it distributes urine droplets in the environment [Klein, 1971; Dixson, 1998]. Such advertisement facilitates mating with multiple males, thus allowing the female greater choice regarding when and with whom to mate, which in turn potentially affects both overt female choice and CFC (see above), as well as SC.

Given the multiple mechanisms by which a male's paternity can be influenced after copulation is initiated, it makes sense that he continue to "convince" the female of his worthiness after the initiation of copulation, via behavior, anatomy, and physiology. For example, some have suggested that the presence of female sexual swellings, which elongates the vaginal entrance, has selected for long penises in male primates [Dixson, 1987, 1998; Dixson & Mundy, 1994]. Although these sorts of analyses have inevitably suffered from the lack of controlling for phylogenetic inertia (see the multiple chapters in Lee [1999] for examples of correct methodologies), such a relationship clearly seems plausible. Likewise, CFC may be the selective force behind the diversity of male genitalia, including variation in baculum length, glans penis length, length of the erect penis, and the presence and types of penile spines. In fact, it was the lack of adequate explanations for complex male genital morphology that led Eberhard to first propose CFC as a selective mechanism [Eberhard, 1985]. Although most of Eberhard's ideas were developed by comparing invertebrate species, Eberhard's idea that the penis can function as an "internal courtship device" to facilitate sperm transfer, transport, and fertilization is certainly applicable to primates, where variation in male genitalia is high (see review in Dixson [1998, chapters 8 & 9]; see also Dewsbury [1988]). Likewise, selection for seminal products that enhance fertilization and that potentially affect female reproductive physiology has undoubtedly occurred (see also mechanism 11, above). The primate ejaculate contains a large array of chemical products. Some of these constituents serve as transportation medium for sperm, as nutrients for sperm [e.g., fructose, Harper, 1994], or as the basis for the coagulate or the copulatory plug. Other constituents likely serve to influence female physiological processes, for example, by buffering the normally acidic intrauterine environment [Masters & Johnson, 1966; Fox et al., 1973], which is detrimental to spermatozoa [Harper, 1994]. Prostaglandins are released in high quantities at ejaculation as well, and are known to cause contractions of uterine and oviductal musculature. However, a definitive relationship between prostaglandins and male fertility has yet to be established [Harper, 1994].

From the discussions in the chapter thus far, it should be clear that initiating copulation with a female is only the first step for a male in terms of his reproductive success. To gain access to the egg, sperm must navigate the somewhat hostile and complex physical and chemical vaginal, cervical, and intrauterine environment (see Figure 5). As discussed above, the chemical environment of the vagina is normally very acidic, ranging from 3.5 to 4.0 prior to mating [Masters & Johnson, 1966]. Constituents of the ejaculate serve to buffer this environment, but these buffering abilities decline with repeated ejaculations. Although the acidic environment likely exists in part to ward off infection [Yanagimachi, 1994], Dixson [1998, pg. 269] suggested that vaginal pH might serve "to 'test' the ejaculates of rival males and to discourage the onward migration of poor quality gametes." Once inside the female reproductive tract, sperm face not only a highly acidic environment, but are also under phagocytotic attack by the female's immune system, as females respond to the appearance of sperm with a leucocytic invasion [Barratt et al., 1990]. Anatomically, increased vaginal length might have evolved via CFC, but there does not appear to be any relationship between residual vaginal length and mating system once phylogenetic effects are controlled for [Dixson & Purvis, in Dixson, 1998]. Once sperm have traversed the length of the vagina they must pass through the cervix, which in some species is structurally complex. For example, in the crab-eating macaque (*Macaca fascicularis*), the convoluted cervical canal is lined with deep crypts containing thick mucous [Jaszczak & Hafez, 1973]. Although Dixson [1998] suggested that the cervical crypts found in some primates might serve to store sperm, Gomendio and Roldan [1993] and Gomendio et al. [1998] highlighted the lack of evidence for sperm storage in primates. Rather the cervical crypts and associated cervical mucous likely serve as yet another barrier that works to filter out less fit sperm.

Once sperm pass through the internal os of the cervix, they must pass through the uterus, and then into the oviduct where capacitation and fertilization occur. Just as the

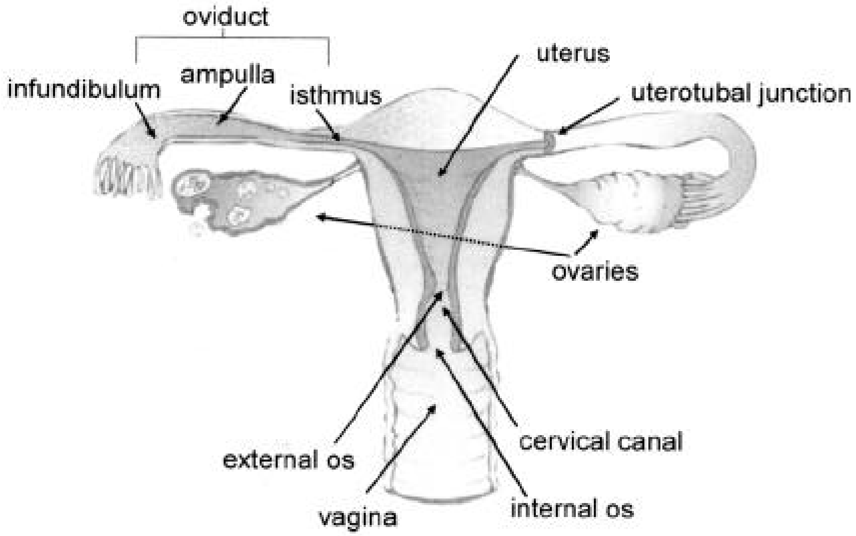


Figure 5. Anatomy of the female primate reproductive tract, showing the potential cites of "filtration" for sperm.

junctions between the vagina and the cervix and between the cervix and the uterus serve to filter sperm, so does the uterotubal junction between the uterus and the oviduct. With its convoluted walls and narrow diameter, robustly motile sperm with normal morphology stand a much greater chance of entering the oviduct than less vigorous and otherwise abnormal sperm [Katz et al., 1982, 1989; Suarez et al., 1990]. That all of these junctions indeed serve to filter sperm is supported by data from multiple species demonstrating that the number of sperm reaching the ampulla of the oviduct is a mere fraction of those in the ejaculate [see Harper, 1982, 1994]. Of the millions of sperm contained in each ejaculate, only a handful (approximately 2-20) reach the site of fertilization [Suarez et al., 1990]. Travel from the lower portion or isthmus of the oviduct to the ampulla is presumably facilitated by the oviductal contractions that occur during the periovulatory period [Battalia & Yanagimachi, 1980]. Not surprisingly, oviductal ciliation is greatest in the periovulatory period in the crab-eating macaque [Brenner & Slayden, 1994]. It is presumably within the oviduct that the processes of capacitation, hyperactivation, and fertilization occur. If capacitation and hyperactivation of sperm are dependent upon an interaction between some quality of sperm and the female's anatomy and physiology, then selection between the sperm of different males via CFC has acted (see mechanism 13, above). Once a sperm comes in contact with an ovum, the acrosomal reaction is very quick (one minute in crab-eating and rhesus macaques [Vandevoort et al., 1992] and approximately 3 minutes in humans [Yudin et al., 1988]), making it unlikely that any other sperm present in the ampulla would compete.

The seemingly lengthy journey from the vagina to the oviduct is in some cases assisted by rapid transport via vaginal and uterine contractions, which has been reported in a number of mammalian species [see Harper, 1982, 1994]. Although the mechanisms underlying rapid transport are not fully understood, the presence of rapid transport in species in which females mate with multiple males in a short time period would clearly facilitate both SC and CFC. Once again, in reality it is difficult to distinguish between the selective forces of SC and CFC, which have likely interacted throughout evolutionary time. Given the relative paucity of comparative physiological data from primates, teasing out male and female physiological processes within the female reproductive tract through which selection has acted to favor certain males and to select against others is currently out of reach.

ESTABLISHING CRYPTIC FEMALE CHOICE

Describing the multiple mechanisms by which CFC *could* function and the species and circumstances in which it is likely is a far cry from demonstrating that it has indeed operated. According to Eberhard [1996, p 80], the following conditions must be met in order to demonstrate that CFC has operated:

> “1. Female responses to some conspecific males differ from those to others (if females respond equally to all males, no selection can occur).
> 2. Such discrimination occurs under natural conditions (if females in nature mate only once, for example, cryptic choice among males in captivity would be biologically irrelevant).
> 3. The discrimination results in differences in reproductive success for the males involved (if, for instance, the first male to mate with a female always obtains all fertilizations, female discrimination among subsequent males would have no reproductive significance).
> 4. Female biases are associated with particular male characteristics (if female favoritism is bestowed randomly on different males, it will have no selective effect).
> 5. Variation among males in characters used by females to discriminate is associated with genetic differences (otherwise female discrimination will have no evolutionary effect on males).”

Eberhard considers the last criterion to be “optional” in that it need not be met to demonstrate that female choice occurred in the past. Unfortunately, there are very few systems, mammalian or otherwise, that meet all of these criteria. This failure to demonstrate CFC is due, however, not to contradictory evidence but rather to the lack of appropriate studies. Even when biased paternity is discovered, one must be able to hold the effects of SC constant in order to determine the relative importance of CFC, which is clearly difficult to do, especially for primates.

Our ability to examine the specific mechanisms underlying CFC is varied. Those mechanisms that occur inside the female’s reproductive tract are, at this point, very difficult to demonstrate due to the paucity of physiological and anatomical data for primates, and even for mammals in general. Nevertheless, thanks to advances in biomedical research, reproductive physiology in several species is well understood, including the common marmoset, squirrel monkeys, several species of macaques, and the chimpanzee. These species provide perhaps the best opportunity for exploring these questions, although our ability to perform comparative analyses to answer broader questions is limited given the small number of species available for study. Even if data from more species were available, these processes are strongly tied to the evolutionary history of the animal. As such, phylogenetic inertia places constraints on our ability to tease apart these processes, especially if one desires to distinguish between evolution due to SC and that due to CFC. That these internal physiological processes are difficult to examine is evinced by the great deal of debate in the literature on the necessary criteria for demonstrating the existence of female **sperm** choice [see discussions in Birkhead, 1998, 2000b; Eberhard, 2000; Kempenaers et al., 2000; Pitnick & Brown, 2000].

In contrast, those mechanisms that occur outside of the reproductive tract ought to be more readily available for study. For example, the termination of copulation prior to ejaculation has been documented in a number of species (see above; [Dixson, 1998]). Close examination of the conditions under which such rejection occurs and the attributes of the affected males would be very fruitful. Likewise, systematic examination of the conditions in which copulatory plugs are removed by females or by males with female “consent” might reveal specific attributes of the males being presumably selected against. The examination of the differential care of infants, including infanticide and for humans, abortion would also be very useful. For humans, integrating the psychological child abuse literature with evolutionary analyses is especially promising. For nonhuman primates, examining differential infant care in relation to traits of the father would be more difficult as it would require long-term comprehensive field studies combined with DNA analyses. Whatever the variable being examined, it is critical that once comparative datasets become available, these data must be analyzed with respect to the phylogenetic relationships of the species from which they are derived. Although many previous analyses of comparative primate data have failed to appropriately consider the evolutionary relationships between the species in question, methodologies that control for phylogenetic inertia are now readily available (as evinced by the many chapters in Lee [1999]) and should be employed.

CONCLUSIONS AND PROSPECTS

There are a number of conclusions that can be drawn regarding the potential for CFC in primates:

- Despite the challenges in demonstrating that CFC exists, there are compelling theoretical reasons as to why CFC is likely to act and have acted in primates.
- There are multiple mechanisms by which CFC can be accomplished. These mechanisms can act anytime after the initiation of copulation and even include post-birth events.
- CFC is at times co-existent with pre-copulatory female choice. For example, what may be pre-copulatory female choice towards one male may at the same be CFC against a previously mated male. Or, pre-copulatory choice on the basis of some male trait(s) can be followed by CFC based upon the same or different male trait(s).

- CFC is most likely to act in those species where females routinely mate with more than one male.

Despite what I believe to be the high potential for CFC in primates, it may in fact be very difficult to demonstrate unequivocally due to factors such as the generally small sample sizes of primate studies and the level of invasive work that may be required. Nevertheless, in many ways, the time is right to begin to explore this field. This comes about in large part by many recent methodological advances that allow us to approach this topic from a variety of angles. A particularly important advance of course is DNA analysis, which is becoming more routine and more accessible. Without the ability to assess paternity, the definitive demonstration of CFC in most cases is impossible. As with DNA analysis, our ability to track animals via telemetry has been around for some time, but is currently better than ever, with smaller and more reliable transmitters and tracking equipment. Field studies on primates are being carried out throughout the world, which should increasingly provide the broadly based comparative data needed to answer many questions about the behavioral, anatomical, and physiological components of CFC. The numerous studies conducted in captivity are also shedding light on the processes potentially underlying CFC. In particular, the advances made in understanding reproductive physiology by the biomedical community allow us to begin to explore things such as female influences on sperm transport. Information gathered through the use of all of these technical advances can be combined in a synergistic way such that we can now examine CFC from multiple perspectives. In fact, the study of CFC and its relationship to SC provides an excellent opportunity to integrate physiological and behavioral mechanisms with evolutionary theory [Gomendio & Roldan, 1993; Eberhard & Cordero, 1995].

As primatologists, we tend to draw our conclusions from what we observe, both in captivity and in the field. In this chapter, I hope to have illustrated how observed male mating success and male paternity can be two very different things, influenced in large part by interactions with the female's behavior, anatomy, and physiology. That this discussion of the potential for CFC has carried on for many pages, and even that it warrants a chapter in this text, is testament to the need to continue to recognize the active role that females play in reproduction. In the words of Eberhard [1996, pg. 420], "Abandoning the idea that females are morphologically and behaviorally passive and inflexible in male-female interactions promises to give a more complete understanding of sexual selection."

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