11. HUMAN SPERM COMPETITION: EJACULATE MANIPULATION BY FEMALES AND A FUNCTION FOR THE FEMALE ORGASM

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ABSTRACT

Behavioural ecologists view monogamy as a subtle mixture of conflict and cooperation between the sexes. In part, conflict and cooperation is cryptic, taking place within the female's reproductive tract. In this paper the cryptic interaction for humans was analysed using data from both a nationwide survey and counts of sperm inseminated into, and ejected by, females. On average, 35% of sperm were ejected by the female within 30 min of insemination. The occurrence and timing of female orgasm in relation to copulation and male ejaculation influenced the number of sperm retained at both the current and next copulation. Orgasms that climaxed at any time between 1 min before the male ejaculated up to 45 min after led to a high level of sperm retention. Lack of climax or a climax more than 1 min before the male ejaculated led to a low level of sperm retention. Sperm from one copulation appeared to hinder the retention of sperm at the next copulation for up to 8 days. The efficiency of the block declined with time after copulation but was fixed at its current level by an inter-copulatory orgasm which thus reduced sperm retention at the next copulation. Inter-copulatory orgasms are either spontaneous (= nocturnal) or induced by self-masturbation or stimulation by a partner. It is argued that orgasms generate a blow-suck mechanism that takes the contents of the upper vagina into the cervix. These contents include sperm and seminal fluid if present; acidic vaginal fluids if not. Inter-copulatory orgasms will therefore lower the pH of the cervical mucus and either kill or reduce the mobility of any sperm that attempt to penetrate from reservoirs in the cervical crypts. Intercopulatory orgasms may also serve an antibiotic function. Copulatory and inter-copulatory orgasms endow females with considerable flexibility in their manipulation of inseminates. The data suggest that, in

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purely monandrous situations, females reduced the number of sperm retained, perhaps as a strategy to enhance conception. During periods of infidelity, however, females changed their orgasm pattern. The changes would have been cryptic to the male partners and would numerically have favoured the sperm from the extra-pair male, presumably raising his chances of success in sperm competition with the female's partner.

By definition, most mating by monogamous species is in-pair copulation. However, an apparently universal feature of such species (Mock & Fujioka 1990) is that from time to time both sexes engage in extra-pair copulation. A special category of extra-pair copulation is double-mating (the female mating with a second male while still containing fertile sperm from one or more previous males). The result is 'sperm competition' (Parker 1970) as the sperm from different males compete to fertilize the female's egg(s).

Models of sperm competition (e.g. Parker 1990) tend to view the female tract as a passive receptacle in which males play out their sperm competition games. Females have the potential, however, to influence the outcome of the contest in several different ways. The sequence and frequency with which the female mates with different males and the time interval between in-pair copulations and extra-pair copulations often have a major influence on the outcome of sperm competition (Birkhead & Hunter 1990). More directly, females eject sperm (e.g. birds: Howarth 1971; Davies 1983; mammals: Sumption 1961; Morton & Glover 1974; Tilbrook & Pearce 1986; Ginsberg & Huck 1989; Ginsberg & Rubenstein 1990). On average, about 80% of the sperm inseminated into the rabbit, *Oryctolagus cuniculus*, are ejected in the flowback (Overstreet 1983).

Female humans eject up to 3 ml of seminal fluid from their vagina after copulation (Baker & Bellis 1993). This 'flowback' emerges from the vagina as a discrete series of three to eight white globules and consists of a mixture of sperm, seminal fluid and female tissue and secretions. Flowback either occurs while the female is still horizontal after copulation, when she next begins to walk, or, perhaps most often and most forcefully, when she next urinates. No attempt has previously been made to determine the proportion of sperm ejected and retained by human females following normal copulation. Nor has any attempt been made to investigate variation in this proportion in relation to socio-sexual situation or in relation to female physiological events, such as the female orgasm.

Female orgasms occur in four main situations (Fisher 1973): (1) spontaneously during sleep (equivalent to the nocturnal emissions of males; see Wells 1986); (2) through direct self-stimulation (e.g. of the clitoris) in the absence of a male; (3) through stimulation (either by self and/or by a male or another female) in the presence of a partner but without copulation; and (4) through self, manual or penile stimulation as part of a copulation episode (orgasm occurring during foreplay, postplay, or copulation itself). For convenience, we refer to types (1) – (3) as 'non-copulatory' orgasms, and to type (4) as 'copulatory'. No study of humans, or other mammals, has yet attempted to quantify the relative occurrence of these four types of female orgasm.

Currently, there are two favoured hypotheses concerning the function of copulatory orgasms in females: (1) the 'poleaxe' hypothesis (Morris 1967); and (2) the 'upsuck' hypothesis (Fox *et al.* 1970). The poleaxe hypothesis proposes that, as humans are bipedal, it is important for the female to lie down after copulation in order to reduce sperm loss. The orgasm thus functions to induce fatigue and sleep (see Levin 1981). The