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. Inter-copulatory 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 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 upsuck hypothesis proposes that the orgasm functions to suck up sperm during copulation (Fox et al. 1970). In an elaboration of the upsuck hypothesis, Singer (1973) proposed that orgasms could be typed by whether they involved contractions of the uterus as well as the vagina. Uterine orgasms were suggested to facilitate conception whereas non-uterine orgasms did not. Singer further proposed that by a systematic shift from one type of orgasm to another a female could, consciously or subconsciously, influence the probability of conception. The occurrence of female orgasms in quadrupeds (Evans 1933; Ford & Beach 1952; Hartman 1957) is

inconsistent with the poleaxe hypothesis. Nevertheless, in this paper, we provide the first direct test of both of these hypotheses.

Non-copulatory orgasms are usually considered either to be substitutes for copulatory orgasms or to represent mechanisms by which a female can train her body to orgasm during copulation (Lopiccolo & Lobitz 1972). Neither hypothesis, however, can explain why masturbation is more frequent when copulation is more frequent (Baker et al. 1989). Moreover, the 'substitute' hypothesis cannot explain why copulatory and masturbatory orgasms show different patterns in the female menstrual cycle (Baker et al. 1989).

Our own hypothesis (Baker et al. 1989) is much more firmly based in behavioural ecology. It is that the timing of orgasm, both during and between copulations, is the key feature of the mammalian female's armoury in male:female conflict and cooperation within the female tract. We propose that nocturnal, masturbatory and copulatory *orgasms are the primary mechanisms by which the* female influences the ability of sperm in the next and/or current ejaculate to remain in, and travel through, her reproductive tract. Thus, we predict that by altering the occurrence, sequence and timing of the different types of orgasm, the female can influence both the probability of conception in *monandrous situations and the outcome of sperm* competition in polyandrous situations. We also expect that as for the female's timing of copulation during the menstrual cycle (Bellis & Baker 1990), much of this influence will be cryptic to the male partner(s). This paper presents a test of this hypothesis and an exploration of the dynamics of *male:female conflict and cooperation over sperm.*

METHODS

Data

Our data came from four different sources: (1) *counts of sperm in whole ejaculates collected by* condom during copulation; (2) counts of sperm in 'flowbacks'; (3) subjective estimates of flowback volume; and (4) a U.K. nationwide survey of female sexual behaviour (Bellis et al. 1989; Bellis & Baker 1990). Full details of these different sources are presented in Baker & Bellis (1993) and here we give *only a brief resumé, describing in detail only those* methodological details that were not relevant to our previous study.

In our nationwide survey, 3679 females each answered 57 questions on their sexual behaviour, including information relating to their last copulation and to their last non-copulatory orgasm. This survey provided information on 2745 in-pair copulations and 126 extra-pair copulations. In our ejaculate study, 34 male–female human pairs (involving 32 males and 32 females) provided material or estimates relating to 323 in-pair copulations.

The methods for the collection, fixation, processing and counting of sperm followed the double-blind protocol used previously (Baker & Bellis 1989, 1993) based on the procedures described in the WHO Human Semen Manual (Belsey et al. 1987). All standard errors for sperm counts are within the range 5–25% and are not used further in this paper. A complete list of the number of whole ejaculates and flowbacks donated by each couple, plus the female's weight are given in tables in Baker & Bellis (1993).

Seven pairs, while willing to record details of in-pair copulations, preferred not to collect flowbacks directly but volunteered instead to estimate the volume of flowback subjectively. In addition, two pairs who collected flowbacks also made some subjective estimates of volume (Table I in Baker & Bellis 1993). All nine pairs recorded flowback volume as either 'normal' (for that female) ($=2$), heavier than normal ($=3$), lighter than normal ($=1$), or none ($=0$). Crudely, these estimates approximate to the volume of the flowback in ml. None of the subjects knew the results of the investigation of flowback samples that was being carried out simultaneously.

Statistics: Calculation of Probabilities

Throughout, to be consistent with our non-parametric statistics, medians are used instead of means. In Figures and Tables, the medians presented are the medians of medians (i.e. we first calculate the median for each contributing female, then calculate the median of the medians). Variation about the median is expressed in terms of inter-quartile range. On occasions when only one female contributed to a particular category, rather than give no indication of variability, we present the inter-quartile range for that female's data.

On two occasions we used the z-difference test (modified for two samples from Fugle et al. 1984) to calculate whether the difference between two

z-values is greater than expected by chance. Otherwise, to avoid making any assumptions concerning the normality of our data, we calculated probability values using only non-parametric statistical tests. In particular, we used Meddis' (1984) rank-sum test. The reasons and justification for our choice of test are given in detail in Baker & Bellis (1993). All analyses in this paper are 'blocked' by female unless stated otherwise. Results thus indicate whether within-female variation is also consistent between females. All probabilities associated with Meddis' non-specific tests (statistic $=H$) are two-tailed. Probabilities associated with Meddis' specific test (statistic $=z$) are one-tailed unless stated otherwise.

Statistics: Residuals and a Predictive Equation

As in our previous analyses (Baker & Bellis 1993), we used regression analysis to calculate values for the dependent variable with respect to one or more independent variables, and then calculated residuals. These residuals may then be analysed further for the influence of some other independent variable not included in the original regression. We also used regression and residual analysis to develop an equation to predict the number of sperm retained by females during in-pair copulations under different socio-sexual situations. The equations used in this paper are gathered together in Table I.

Male and Female Contributions to Sperm Retention

The number of sperm retained by a female from any given in-pair copulation is essentially the product of two influences. Insofar as the male inseminates a finite number of sperm, he places an upper limit on the number that may possibly be retained. The number actually retained then depends on what happens in the female reproductive tract. The behaviour of the sperm and/or the female's response to insemination may both influence the number of sperm actually retained.

The raw data on which this paper is based are counts of the number of sperm ejected in the flowback. Primary biological interest, however, lies not with the number of sperm ejected but with the number retained. Unfortunately, variation in the number of sperm ejected has no certain relationship with the number retained.

As an illustration, suppose that on two separate occasions the number of sperm in the flowback (in

Table I. Six equations used to calculate residuals or to predict number of sperm retained (for derivations, see Results)

Equations

(1) $\text{NINS} = \text{PV} - (((\text{PV} - \text{mid})/(\text{limC} - \text{mid}))^2 \times (\text{limC} - \text{limO}))$

(2) $\text{NSR} = -0{\cdot}9 + (0{\cdot}65 \times \text{NINS})$

(3) $\text{NSR} = 33{\cdot}4 + (0{\cdot}65 \times \text{NINS}) - (0{\cdot}71 \times \text{HEJ})$

(4) $\text{NSR} = -33{\cdot}7 + (0{\cdot}65 \times \text{NINS}) - (0{\cdot}71 \times \text{HEJ}) + (31{\cdot}2 \times \text{HLOR})$

(5) $\text{NSR} = -59{\cdot}7 + (0{\cdot}65 \times \text{NINS}) - (0{\cdot}71 \times \text{HEJ}) + (31{\cdot}2 \times \text{HLOR}) + (0{\cdot}6 \times \text{HFEV})$

(6) $\text{NSR} = (-34{\cdot}0 + 0{\cdot}65 \times \text{NINS}) - (0{\cdot}71 \times \text{HEJ}) + (31{\cdot}2 \times \text{HLOR}) + ((1\text{-ICM}) \times (1\text{-HLOR}) \times (\text{HFEV} \times 0{\cdot}60 - 34)) - (\text{ICM} \times 2)) \times (1\text{-PREG})$

NINS, Number of sperm inseminated in millions; PV, $1{\cdot}94 \times \text{HIPC} - 3{\cdot}40 \times \text{PCT} + ((2{\cdot}41 \times \text{HMAS} - 228) \times \text{MC}) - 1008 + 23{\cdot}37 \times \text{FW}$; HIPC, hours since last in-pair copulation up to 192 h (192 h is the longest time interval for which we have data and up to which analysis supports a linear relationship); PCT, the % time a pair have spent together since their last in-pair copulation; HMAS, hours (up to 72) since last masturbation; MC, 0 for IPC–IPC ejaculates and 1 for MAS–IPC ejaculates; FW, female weight (kg); mid, mid-point of number of sperm in observed ejaculates (350×10^6); limC, the minimum or maximum calculable limit to PV; limO, the minimum or maximum observed number of sperm in in-pair copulation (IPC) ejaculates; NSR, number of sperm (in millions) retained by the female after flowback; HEJ, hours since last ejaculation (range 1–72 h; values > 72 should be given a value of 72); HLOR, 1 when the orgasm regime at C_2 favours a high level of sperm retention and 0 when a low level; HFEV, hours to first event after C_1 (i.e. to first inter-copulatory orgasm or, in the absence of an inter-copulatory orgasm, to C_2; maximum value = 192); ICM, 1 if the female begins to menstruate between C_1 and C_2 and 0 when she does not; PREG, 1 if the female is pregnant, 0 if she is not. For derivation and use of equation (1), see Baker & Bellis (1993).

millions) was 100 and 200. If the number of sperm inseminated on these two occasions had been 150 and 300, respectively, the number of sperm retained (50 and 100) would have been positively associated with observed variation in the flowback. On the other hand, if the numbers inseminated had been 200 and 250, the number retained (100 and 50) would have been negatively associated with number in the flowback. Finally, if the numbers inseminated had been 150 and 250, the number retained would have remained constant despite variation in the number in the flowback.

It follows that, in order to draw biologically meaningful conclusions from flowbacks, it is essential that some estimate is made of the number of sperm retained. To do this, it is necessary to make some estimate of the number of sperm inseminated into the female during each of the in-pair copulations for which number of sperm in the flowback is known. The number of sperm inseminated is a measure of the male contribution to the number of sperm retained.

We have shown in our companion paper (Baker & Bellis 1993) that equation (1) (Table I) explains 58% of the observed variance in number of sperm ejaculated during 84 in-pair copulations by 24 couples (see Fig. 5 in Baker & Bellis 1993). In our study of flowbacks, we used equation (1) to calculate the number of sperm inseminated into the female at each in-pair copulation. We then estimated the number of sperm retained by the female by subtracting the number of sperm observed in the flowback from the number calculated to have been inseminated. In the remainder of this paper, to avoid unnecessarily long phrases, we refer simply to 'the number of sperm inseminated' and 'the number of sperm retained' even though both of these measures are the result of calculation rather than direct sampling.

There is a significant positive relationship between the number of sperm inseminated and the number of sperm in the flowback on the one hand and the number of sperm retained on the other ($N = 11$; first sample per couple; Table II). Blocking

Table II. Relationships between the number of sperm inseminated into a female during in-pair copulation and number of sperm ejected, number of sperm retained, and volume of flowback (analysis of only the first sample from each couple, $N = 11$ for sperm number, $N = 9$ for flowback volume)

	Sperm number		Flowback volume
	Ejected	Retained	Ejected
Correlation			
r_s	0·655	0·791	−0·113
P_1 one-tailed	0·026	0·004	0·560
Regression			
Intercept	0·90	−0·90	
Slope	0·35	0·65	
Percentage explained	24	58	
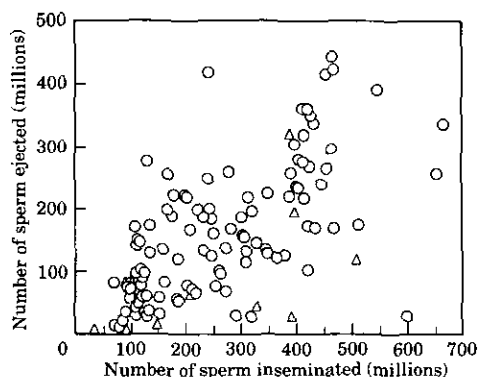
Figure 1. Relationship between number of sperm inseminated and number ejected in the flowback. △: First sample from each of 11 females; ○: subsequent samples.

by couple to test for within-couple response, both relationships are still highly significant (versus number in flowbacks: $z = 6·062$, $N = 11$ females, 127 in-pair copulations, $P < 0·001$, Fig. 1; versus number retained $z = 6·500$, $P < 0·001$). Both between and within couples, therefore, the more sperm that are inseminated the more are ejected and the more retained.

We exploited this positive relationship to remove the influence of the male on the number of sperm retained. Using only the first sample produced by each couple (to avoid pseudoreplication from the more prolific couples), we calculated the least squares regression line for numbers of sperm ejected and retained against numbers inseminated (Table II). We then applied these regression lines to each of the 127 in-pair copulations in our total

data set and calculated residuals. Variation in these residuals is thus independent of the variation in the number of sperm inseminated by the males and the residuals are, in effect, a measure of variation in the female's contribution to sperm retention.

Use of residuals to measure the female's influence on sperm retention has a number of advantages over the alternative which would be to use percentage sperm retention. Residuals are more robust, being less prone to wild fluctuations when the denominator is numerically small. Even so, at the end of our analyses, we checked the conclusions reached using residuals against percentage retention as reassurance that our major conclusions are not dependent on the parameter analysed.

The regression equations for sperm ejection and retention (Table II) are mathematically dependent (intercepts sum to zero; slopes sum to one). There is no value, therefore, in analysing residuals from both. Thus, we begin this paper by using residuals from equation (2) (Table I) as a measure of the female's contribution to the fate of the inseminated sperm. Discussion of this contribution is thus phrased in terms of the female's contribution to sperm retention rather than sperm ejection.

Correcting for the Age of Sperm

We have shown (Baker & Bellis 1993) that younger sperm are retained in the female tract in relatively, but not absolutely, greater numbers than older sperm (assuming that hours since last ejaculation is a measure of the age of the sperm inseminated; $z = 3·039$, $P = 0·002$, two-tailed). z is

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Table III. Number of sperm (millions) inseminated, ejected and retained by 11 pairs (127 in-pair copulation flowbacks)

Pair	N	No. inseminated		No. ejected		No. retained		Percentage retained	
		Median	(Inter-quartile range)	Median	(Inter-quartile range)	Median	(Inter-quartile range)	Median	(Inter-quartile range)
A	9	508	(211–546)	173	(73–257)	206	(138–339)	61	(46–66)
B	93	242	(121–388)	158	(83–224)	67	(26–136)	35	(14–50)
G	1	398		194		204		51	
H	1	90		7		83		92	
N	2	343	(293–393)	28	(27–28)	315	(265–366)	92	(90–93)
Q	1	147		14		133		90	
R	8	185	(117–206)	60	(32–67)	124	(66–134)	71	(49–75)
S	6	214	(101–309)	81	(27–115)	101	(16–194)	66	(16–76)
W	3	80	(72–80)	13	(11–44)	69	(59–286)	86	(82–87)
Z	2	81	(69–92)	84	(83–85)	−3	(−13 to 8)	−6	(−19 to 8)
AA	1	311		130		181		58	
Overall		214	(90–343)	81	(14–158)	124	(69–204)	66	(51–90)

Negative values for number of sperm retained (e.g. pair Z) occur when, owing to sampling error, the number of sperm in the flowback exceeds the number calculated to have been inseminated.

maximized (at 3·091) by a model that assumes there is no further influence of sperm age once time since last ejaculation exceeds 72 h.

It is a moot point whether the age of sperm is a male or female influence on sperm retention. Younger sperm may be more acceptable to the female (female influence) or they may be better able to attain a position in the female tract that makes them more resistant to ejection (male influence; see Discussion in Baker & Bellis 1993). Either way, before analysing contributions to sperm retention that are clearly female, such as timing of orgasm, it is necessary to correct the residuals from equation (2) to make them independent of sperm age. For this, we used equation (3) (Table I). Residuals from equation (3) are thus independent of both the number of sperm inseminated and sperm age.

Analysis Check

In unravelling the influence of female orgasm on the number of sperm retained, we made ever-increasing use of residuals from increasingly elaborate equations as different influential factors were identified and controlled (Table I). Such an approach is essential if artefacts are not to appear in our analysis due to cross-correlation of independent variables. However, our approach brings its own dangers in that mathematical artefacts may appear

that generate their own spurious, non-biological relationships. The further the dependent variable departs from the raw data, the greater the danger becomes. As a final check on our conclusions, therefore, we return to the raw data and consider the extent to which the apparent influence of female orgasm is evident in the variation of sperm numbers directly measured in the flowbacks.

RESULTS

Human Flowbacks: General Features

All 127 of the flowbacks collected contained sperm and 94% (103/109) of the in-pair copulations monitored subjectively for flowback volume were followed by noticeable flowbacks (i.e. value >0).

Sperm numbers in the 127 flowbacks we examined ranged from 7×10^6 to 443×10^6. Number of sperm inseminated, ejected and retained by each couple (Table III) suggest that humans have a median retention of about 65%.

There was a significant association between the number of sperm inseminated and both the number of sperm in the collected flowbacks ($z = 6·062$, $N = 11$ females, 127 flowbacks, $P < 0·001$) and the subjectively estimated volume of flowback ($z = 1·922$, $N = 9$ females, 109 flowbacks, $P = 0·027$).

Median time to emergence of the flowback after male ejaculation was 30 min (inter-quartile

range = 15–44; calculating the median for each of the 17 females who recorded time to flowback, then calculating the median for the group) with a range of 5–120 min. The number of sperm ejected in the flowback was not a linear (rank-order) function of the time-interval from ejaculation to flowback collection ($z = 1.608$, $N = 11$ females, 127 flowbacks, $P = 0.108$, two-tailed), the non-significant trend being for more sperm to be ejected the longer the time to ejection. In contrast, the volume of flowback was a significant negative function of time to flowback collection ($z = -2.844$, $N = 8$ females, 103 flowbacks, $P = 0.004$, two-tailed) suggesting that there is either a gradual loss or resorption of fluid without sperm before the main flowback emerges. Finally, time to flowback was not a function of the number of sperm inseminated ($z = 0.936$, $N = 18$ females, 230 in-pair copulations, $P = 0.350$, two-tailed), the non-significant trend being for the time from ejaculation to flowback to be longer when fewer sperm were inseminated.

We calculate that 12% (15/127) of all of the in-pair copulations for which we have flowback samples were followed by virtually 100% ejection of sperm (i.e. < 1% retained). Females thus appear capable of total or near-total ejection of in-pair copulation ejaculates.

Oral Contraceptives, Pregnancy and Flowbacks

Most of the flowbacks collected (11 females, 112 flowbacks) and all of those estimated for volume (nine females, 109 flowbacks) were from females who were taking oral contraceptives. However, three of the females volunteered to collect flowbacks ($N = 9$) when, for different reasons, they were not using oral contraceptives. Of these, two became pregnant. One of the two females who became pregnant then volunteered to collect six further flowbacks. As this female had monitored her cycle using the basal temperature method (Parsons & Sommers 1978), time of conception could be estimated to within ± 24 h. Ultrasonic scan of the fetus after 14 weeks provided strong support for the estimate. Two pregnancy flowbacks were collected in the first week after conception, four 35–42 days after conception. These six pregnancy flowbacks could be matched with seven flowbacks collected by the same female while not taking oral contraceptives (four pre-conception, three post-partum).

This albeit limited data set shows a significant reduction in sperm retention during pregnancy

($z = 2.143$, $N = 1$ female, 13 in-pair copulations, $P = 0.032$). The estimated median number (millions) of sperm actually retained were: pre-conception/post-partum (68; inter-quartile range = 11–139), 1 week post-conception (116; 75–157) and 5–6 weeks post-conception (-42; -178 to $+3$). In a Meddis' specific test of residuals, z is maximized (at 2.239) by a model that assumes retention during the first week post-conception is intermediate between retention levels pre-conception and 5–6 weeks post-conception.

Insofar as the median retention is negative, these data suggest a virtually 100% ejection of sperm even as early as 5–6 weeks after conception. This assumes, of course, that males do not inseminate more sperm in in-pair copulations during their partner's pregnancy. Unfortunately, no condom samples were collected during the female's pregnancy so we cannot test this assumption with our current data.

Females taking oral contraceptives showed no significant variation in retention or ejection during the 'menstrual' cycle, the tendency being to retain more sperm on days 6–15 (day 1 = first day of bleeding) than at other times ($z = 1.091$, $N = 11$ females, 110 in-pair copulations, $P = 0.276$, two-tailed). The three females not taking oral contraceptives, however, showed a significant decrease in retention during their most fertile phase (days 6–15; $z = 2.443$, $P = 0.016$, two-tailed). Finally, when taking oral contraceptives, the same three females tended to retain more sperm than when they were not taking oral contraceptives, though the difference was not significant ($z = 0.911$, $P = 0.362$).

Are Male Strategies Generally Successful?

Our previous studies of whole ejaculates (Baker & Bellis 1989, 1993) identified three male strategies involving adjustment of the number of sperm inseminated during in-pair copulation. First, the number of sperm inseminated is a positive function of time since last in-pair copulation. Adjustment of sperm numbers fits best a model based on the male 'topping-up' his partner to a particular level, inseminating only enough to make up the number of sperm likely to have died since the last insemination. Second, males top-up larger females with more sperm. Third, males top-up females with more sperm when the male spends a lower proportion of his time with his partner and thus, on average, the risk of sperm competition is higher.

Table IV. Male and female influence on sperm ejection and retention in relation to male strategies concerning % time with partner, inter-IPC interval and female weight (Meddis' specific test)

	Percentage time together		Inter-IPC interval		Female weight	
	z	P	z	P	z	P
Male influence						
Number inseminated	−7·109	<0·001	8·637	<0·001	3·876	<0·001
Female influence						
Residual no. retained	−0·519	0·604	−1·429	0·154	−1·218	0·224
Result						
Number retained	−5·704	<0·001	6·327	<0·001	2·861	0·004
Number ejected	−3·549	<0·001	5·723	<0·001	3·241	0·002
Volume of flowback	−1·749	0·040	1·930	0·027	No data	

Meddis' test: blocked by pair. Positive z-values indicate that an increase in time together, inter-IPC interval, or female weight are associated with an increase in number of sperm or volume of flowback; negative z-values indicate the converse. P-values are one-tailed against the hypothesis that the more sperm a male inseminates, the more will be ejected, the more will be retained and the greater will be the volume of flowback (except for analysis of female influence for which P-values are two-tailed). Analysis is based on 121 flowback samples from 11 females and 109 estimates of flowback volume from nine females. Figures for male influence are calculated from number of sperm inseminated, equation (1). Figures for female influence are calculated from residuals from equation (3). Other figures are calculated from raw data for numbers ejected and retained.

On any given occasion, it appears quite possible that females could override any attempt by the male to place more sperm in her tract in response to a particular socio-sexual situation. On average, however, we should expect male strategies to be successful otherwise they would not have been promoted by natural selection. This appears to be the case (Table IV). Thus, on average, males did succeed in placing more sperm in the tract of larger females, when % time together was lower, and when time since last in-pair copulation was greater. On average, when males inseminated more sperm, more were ejected in the flowback but more were also retained. The volume of flowback showed the same response as number of sperm in the flowback. As a function of time since last in-pair copulation, z is maximized (at 2·326) by the model that volume of flowback increased only for the first 72 h after the last in-pair copulation, thereafter remaining constant.

Patterns of Female Orgasm

We now have data on orgasm pattern from two sources: (1) our nationwide survey of the most recent orgasm, if any, reported by 3679 females (Bellis et al. 1989); and (2) the details returned by 22 'experimental' females who recorded orgasm pattern in the course of collecting or observing ejaculates and flowbacks. There were no significant differences in orgasm pattern between the two groups of subjects (Table V). The most striking features are that nearly 50% of female orgasms occurred in the absence of a male, around 35% of copulations did not involve a female orgasm (even during foreplay or postplay) and, when copulatory orgasms did occur, the female most often (>50% of copulatory orgasms) climaxed before the male ejaculated.

In our nationwide sample, 81% of females had experienced at least one non-copulatory orgasm while they were still virgin but only 7% experienced orgasm at their first copulation. After 50 lifetime copulations, 92% had experienced orgasm at some time but only 53% had done so during copulation. After 500 copulations, the figures had increased to 98% and 84%, respectively.

Test of the poleaxe theory

We tested three predictions of the poleaxe theory (using residuals from equation (3), Table I, for tests involving sperm retention).

Table V. Relative incidence of different types of orgasm reported by two groups of females: nationwide (U.K.) and 'experimental'

	Relative incidence (%)		Meddis' non-specific test	
	Nationwide ($N=3679$)	'Experimental' ($N=22$)	H_1	P
Non-copulatory				
Nocturnal	3	7	1·171	0·279
Self-masturbation	52	43	0·480	0·504
Male partner	44	50	0·178	0·677
Female partner	1	0	0·004	0·951
Copulatory				
Before male ejaculates	55	52	0·014	0·903
Simultaneous	26	24	0·074	0·782
After male ejaculates	19	24	0·204	0·657
Last orgasm with male present	56	56	0·001	0·969
Last copulation not involving female orgasm	37	41	0·114	0·735

Data refer to the most recent non-copulatory and copulatory orgasms for the nationwide sample and to the first non-copulatory and copulatory orgasms for the 'experimental' sample (i.e. each female contributes up to one non-copulatory and up to one copulatory orgasm to the analysis).

(1) Time from male ejaculation to flowback should be longer if the female has a copulatory orgasm than if she does not ($z = 1·643$, $N = 12$ females, 210 in-pair copulations, $P = 0·050$).

(2) More sperm should be retained if the female has a copulatory orgasm than if she does not ($z = 0·841$, $N = 8$ females, 106 in-pair copulations, $P = 0·200$).

(3) The longer the time-interval from male ejaculation to flowback, the more sperm should be retained ($z = -1·953$, $N = 7$ females, 117 flowbacks, $P = 0·975$).

On the whole, therefore, there is no support for the poleaxe theory in our data. Although time to flowback may be longer after an orgasm, there is no corresponding increase in the number of sperm retained nor is there any positive association between time to flowback and number of sperm retained.

Female Orgasms and Sperm Retention at C_2

Consider two successive in-pair copulations, C_1 and C_2, hours, days or weeks apart. The female may or may not experience a copulatory orgasm at either of these in-pair copulations and, in addition, may or may not experience one or more non-

copulatory orgasms in between. This section is concerned with the residual (equation 3; Table I) number of sperm retained at C_2 in relation to events between the beginning of foreplay at C_1 to the moment of flowback at C_2. As such, therefore, it is concerned specifically with female manipulation of the C_2 ejaculate, not with actual numbers of sperm retained or ejected.

We analysed only those 121 flowbacks collected by non-pregnant females.

Test of the upsuck hypothesis

The upsuck hypothesis (Fox et al. 1970) for the function of the female copulatory orgasm would predict that orgasm should be associated with greater sperm retention only if sperm are already present in the female tract.

In this analysis, six categories of female copulatory orgasm were recognized: (1) CX = no orgasm between the beginning of foreplay and ejection of the flowback; (2) BC = orgasm before copulation (i.e. during foreplay; penis not in vagina); BE = orgasm during copulation but before ejaculation (penis in vagina); DE = during ejaculation (i.e. simultaneous climax; penis in vagina);

AE = after ejaculation (penis in vagina); AC = after copulation but before flowback (penis not in vagina).

As already shown in testing the poleaxe theory, whether the female has a copulatory orgasm (BC, BE, DE, AE or AC) or not (CX) has no significant influence on residual number of sperm retained. However, if a copulatory orgasm does occur, the timing of the female climax relative to copulation and male ejaculation (i.e. comparison of BC, BE, DE, AE, AC) has a highly significant influence on the residual number of sperm retained ($H_4 = 13.567$, $N = 10$ females, 88 in-pair copulations, $P = 0.009$). The variation is also significant against the specific test that the residual number of sperm retained changes in a linear, rank-order, sequence from the earliest timing for female climax (BC) to the latest (AC) ($z = 3.495$, $N = 10$ females, 88 flowbacks, $P < 0.001$, two-tailed). The direction of the relationship is for the female to retain relatively more sperm when she climaxes later in the sequence than when she climaxes earlier.

In our flowback data, the earliest that a female experienced a copulatory orgasm during an in-pair copulation episode was 45 min before the male ejaculated and the latest was 45 min after (i.e. -45 min to $+45$ min, using negative numbers to indicate a female climax before the male ejaculates and positive numbers to indicate a climax after the male ejaculates). The frequency distribution of the timing of orgasm for our 11 flowback donors shows the typical pre-ejaculation peak (Fig. 2).

Our data fitted best the model shown in Fig. 3 and are almost entirely consistent with the upsuck hypothesis. Essentially, climaxes earlier than 1 min before the male ejaculates were associated with low sperm retention. Maximum sperm retention was associated with climaxes from > 0 to 1 min after the male ejaculated onwards. If the female climaxed earlier than -1 min, female influence on sperm retention was no better than if she failed to climax altogether ($z = 0.873$, $N = 8$ females, 76 in-pair copulations, $P = 0.382$, two-tailed). Only climaxes that occurred between -1 min and emergence of the flowback (up to $+45$ min) were associated with a significant increase in the residual number of sperm retained compared with having no orgasm at all ($z = 1.997$, $N = 10$ females, 82 in-pair copulations, $P = 0.046$, two-tailed).

Essentially, our analysis of female orgasm at C_2 identified two levels of sperm retention (henceforth, orgasm regimes) at C_2: a higher level associated
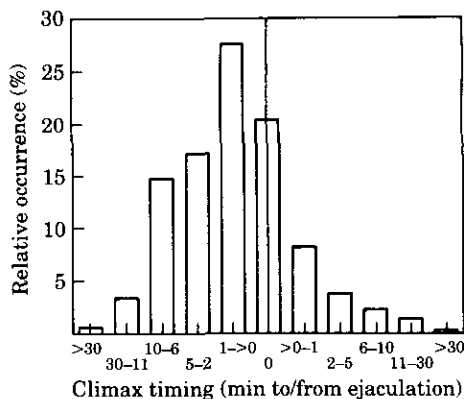
Figure 2. Relative frequency of timing of climax of female orgasm in relation to the timing of male ejaculation. Vertical line represents male ejaculation. Histogram bars to the left of this line show the frequency of orgasms that climax before the male ejaculates; bars to the right the same for orgasms that climax after the male ejaculates. Data for 10 females, 88 in-pair copulations.
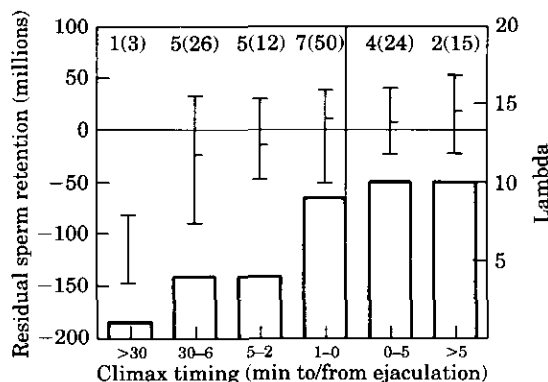
Figure 3. Influence of timing of climax of female orgasm on the number of sperm retained. Bars show median and inter-quartile range sperm retention (residuals from equation 3). Numbers above bars: number of females (number of in-pair copulations). Histograms show the lambda coefficients that maximize z in a Meddis' specific test when the data are blocked by couple to test for within-couple response. Lambda coefficients are the more accurate indicators of the form of the relationship between the timing of climax and sperm retention. Vertical line shows the timing of male ejaculation. Histogram bars to the left of this line show lambda coefficients for orgasms that climax before the male ejaculates; bars to the right the same for orgasms that climax after the male ejaculates.

with climaxes −1 min or later; and a lower level associated with absence of orgasm or orgasms earlier than −1 min.

C_1, inter-copulatory orgasms and sperm retention at C_2

We used residuals from equation (4) (Table I) to test for an influence of C_1 and inter-copulatory orgasms on sperm retention at C_2. We define an inter-copulatory orgasm as any female orgasm that occurs between the first withdrawal of the penis after male ejaculation at C_1 and the last insertion of the penis before male ejaculation at C_2. In this paper, we use five categories of inter-copulatory orgasm, two copulatory (AC_1 = during postplay at C_1; BC_2 = during foreplay at C_2) and three non-copulatory (NO = nocturnal/spontaneous; SS = self-stimulation in absence of male; PS = any stimulation, but not leading to copulation, in the presence of a male or female partner).

First, we considered whether the different types of inter-copulatory orgasm differ in influence on sperm retention at C_2. Analysis was restricted to those occasions on which there was no menstruation and only a single inter-copulatory orgasm between C_1 and C_2 (four females, 33 flowbacks). We divided the data into five samples according to the type of inter-copulatory orgasm (i.e. AC_1, NO, SS, PS or BC_2) and tested the residuals from equation (4) for heterogeneity. There was no significant heterogeneity between the five samples ($H_4 = 7 \cdot 308$, $P = 0 \cdot 119$), nor between the three types of non-copulatory orgasms (NO, SS, PS; $H_2 = 1 \cdot 628$, $N = 4$ females, 14 flowbacks, $P = 0 \cdot 553$). If inter-copulatory orgasms have any influence on the residual number of sperm retained at C_2, it is independent of the type of inter-copulatory orgasm. We therefore considered the five types of inter-copulatory orgasm as a single category.

Next, we restricted analysis to occasions on which the female neither menstruated nor had an inter-copulatory orgasm between C_1 and C_2 (10 females, 47 flowbacks). On such occasions, residual sperm retention at C_2 is a highly significant function of time since C_1 ($z = 2 \cdot 757$, $P = 0 \cdot 006$, two-tailed). Residual sperm retention was higher when inter-copulatory interval was longer, with no clear indication of any plateauing of the relationship up to the limit of our data (i.e. 192 h; = 8 days). The data suggest that C_1 sets up some form of block to sperm retention at C_2 and that this block persists with declining effectiveness for up to at least 8 days.
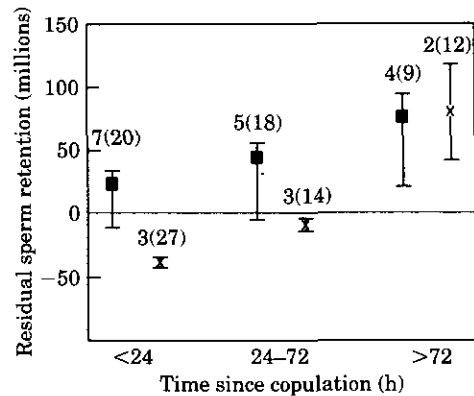
Figure 4. Influence of the time from C_1 to first inter-copulatory orgasm and from C_1 to C_2 (in the absence of inter-copulatory orgasms) on level of sperm retention at C_2 where C_1 and C_2 are consecutive copulations. Sperm retention is measured as residuals from equation (4). ■: Median number of sperm retained at C_2 for a particular time interval from C_1 to C_2 (in the absence of inter-copulatory orgasms); ×: median number of sperm retained at C_2 for a particular time interval from C_1 to first inter-copulatory orgasm. Error bars show inter-quartile ranges. Numbers above bars: number of females (number of in-pair copulations).

In contrast, on occasions when the female has a single inter-copulatory orgasm between C_1 and C_2, there is no significant association between residual sperm retention at C_2 and inter-copulation interval ($z = -0 \cdot 386$, $N = 4$ females, 33 in-pair copulations, $P = 0 \cdot 700$, two-tailed). Moreover, the relationship is significantly different from that when there is no inter-copulatory orgasm ($z_1 - z_2 = 2 \cdot 757 - (-0 \cdot 386) = 3 \cdot 143$; $z = 3 \cdot 143 / \sqrt{2} = 2 \cdot 222$, $P = 0 \cdot 026$, two-tailed; z-difference test). However, time from C_1 to first inter-copulatory orgasm does show a significant relationship with level of sperm retention at C_2 ($z = 2 \cdot 580$, $N = 4$ females, 52 in-pair copulations, $P = 0 \cdot 010$, two-tailed). Thus, both time to C_2 (in the absence of an inter-copulatory orgasm) and time to first inter-copulatory orgasm have a positive relationship with sperm retention at C_2 (Fig. 4), but an inter-copulatory orgasm removes any further influence of time to C_2. The implication is that an inter-copulatory orgasm effectively fixes sperm retention at a level that is a function of time from C_1 to the first inter-copulatory orgasm.

Crudely dividing time since C_1 into four categories (<2 h; 2–24 h; 25–72 h; >72 h), we compared the level of sperm retention at C_2 for occasions when either C_2 (in the absence of an

inter-copulatory orgasm) or the first inter-copulatory orgasm falls into a particular zone. There is no significant difference between these two types of occasions for either the <2 h ($H_1 = 1.699$, $N = 1$ female, 12 in-pair compulations, $P = 0.189$), 2–24 h ($H_1 = 0.533$, $N = 7$ females, 35 in-pair copulations, $P = 0.528$), 25–72 h ($H_1 = 0.001$, $N = 5$ females, 32 in-pair copulations, $P = 0.969$) or >72 h ($H_1 = 0.646$, $N = 5$ females, 21 in-pair copulations, $P = 0.573$) time categories. We conclude, therefore, that when an inter-copulatory orgasm occurs it effectively fixes the level of sperm retention at the next copulation at a level that is more or less the same as the level determined by the efficiency of the block established by the previous copulation.

These analyses combine to suggest that the level of sperm retention at C_2 is primarily a function of the time interval from C_1 to the next sexual event, either C_2 (in the absence of inter-copulatory orgasms) or the first inter-copulatory orgasm. Analysing all flowbacks (excluding those with inter-copulatory menstruation) for level of retention at C_2 in relation to time from C_1 to the next sexual event reveals a highly significant relationship ($z = 3.142$, $N = 10$ females, 100 in-pair copulations, $P = 0.002$).

In our flowback data, the maximum number of inter-copulatory orgasms between any two successive copulations was six. Using the residuals from equation (4) as the dependent variable, there is a very significant negative relationship between the number of inter-copulatory orgasms between C_1 and C_2 and the retention of sperm at C_2 ($z = -2.744$, $N = 10$ females, 115 in-pair copulations, $P = 0.006$, two-tailed); the more inter-copulatory orgasms, the lower the retention of sperm.

So far, our analysis has shown that copulation (C_1) apparently produces some form of block to sperm retention at the next copulation (C_2). This block gradually declines in efficiency, at least over the next 8 days, the time that sperm are known to remain alive in the cervix. An inter-copulatory orgasm fixes the level of efficiency of the block at about the level that it has reached during normal decline. The obvious implication is that this putative block is in some way due to the sperm from the C_1 ejaculate. Our data allow three tests of this hypothesis.

First, we have five flowbacks (i.e. at C_2) for which we can be reasonably certain that no sperm had been transferred at C_1 (or at any copulations within the 8 days prior to C_2) because the male either wore

a condom or withdrew the penis before ejaculation. This limited data set shows no association between sperm retention at C_2 and time from C_1 to the next sexual event ($z = 0.174$, $N = 2$ females, 5 in-pair copulations, $P = 0.431$).

Second, including these five occasions, we have 54 flowbacks (from C_2s) for occasions when we also have flowbacks and relevant details for the corresponding C_1 and are thus able to estimate the number of sperm retained by the female at C_1. On these occasions there is a significant negative relationship between the number of sperm retained by the female at C_1 and the residual (from equation 5) level of sperm retention at C_2 ($z = 1.721$, $N = 5$ females, 54 in-pair copulations, $P = 0.042$).

Finally, we used the same 54 in-pair copulations as above and crudely estimated how many sperm might still be present in the female tract from C_1. We made no allowance for sperm that may still be present from copulations before C_1 on the assumption that most will be dead by the time of C_2. We assumed a linear decline from the number of sperm retained at C_1 to zero 192 h later. We assumed that if an inter-copulatory orgasm occurs between C_1 and C_2 it 'fixes' the number of sperm at the level on this decline reached by the time of the first inter-copulatory orgasm. In the absence of an inter-copulatory orgasm, the number of sperm is determined by the inter-copulation time interval. Residual (from equation 4) level of sperm retention at C_2 is a significant negative function of the number of sperm remaining in the tract from C_1 ($z = -1.996$, $N = 5$ females, 54 in-pair copulations, $P = 0.023$; Fig. 5).

In summary, therefore, our data suggest that sperm transferred during C_1 interfere with sperm retention at C_2. As their numbers decline with time, the level of interference also declines. Inter-copulatory orgasms in some way (see Discussion) use the remaining sperm to fix the level of interference at roughly the point it has reached in its normal decline. The stability of this fixation can be tested by analysing level of retention at C_2 in relation to time since inter-copulatory orgasm.

We restricted analysis to occasions when there was only one inter-copulatory orgasm between C_1 and C_2. Up to 168 h (the longest time-interval in our data) after inter-copulatory orgasm, there is no significant change in residual (from equation 4) retention of sperm at C_2 with time since inter-copulatory orgasm ($z = -1.752$, $N = 4$ females, 33 in-pair copulations, $P = 0.080$, two-tailed). The
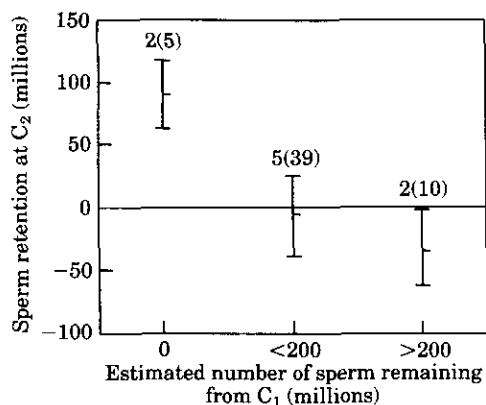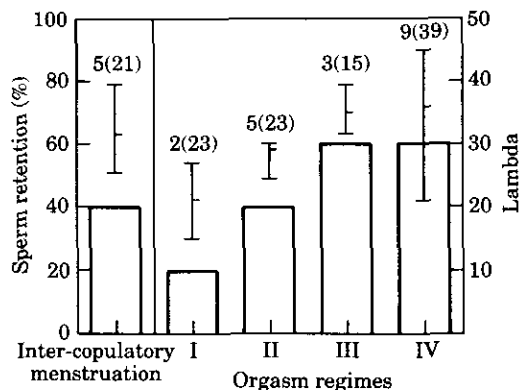
Figure 5. Influence of number of sperm remaining from C_1 on number of sperm retained at C_2 where C_1 and C_2 are consecutive copulations. Number of sperm retained at C_2 is measured as residuals from equation (5). Other conventions as in Fig. 4.

Figure 6. Percentage retention of sperm after an inter-copulatory menstruation compared with retention after four orgasm regimes. Bars show median and inter-quartile range sperm retention (residuals from equation 3). Numbers above bars: number of females (number of in-pair copulations). Histograms show the lambda coefficients that maximize z in a Meddis' specific test when the data are blocked by couple to test for within-couple response. Lambda coefficients are the more accurate indicators of the form of the relationship between the timing of climax and sperm retention. Regime I: low retention orgasm regime at C_2, $\leqslant 24$ h from C_1 to first inter-copulatory orgasm or (in absence of an inter-copulatory orgasm) C_2 where C_1 and C_2 are consecutive copulations. Regime II: low retention orgasm regime at C_2, $\geqslant 25 - \leqslant 72$ h from C_1 to first inter-copulatory orgasm or (in absence of an inter-copulatory orgasm) C_2. Regime III: low retention orgasm regime at C_2, > 72 h from C_1 to first inter-copulatory orgasm or (in absence of an inter-copulatory orgasm) C_2. Regime IV: high retention orgasm regime at C_2 (see Table VI).

non-significant trend for longer time intervals to be associated with reduced retention is very different from the positive trend from C_1 to C_2 in the absence of inter-copulatory orgasm.

Finally, we used the residuals from equation (4) as the dependent variable and tested for an interaction between the influence of C_1 and inter-copulatory orgasms on sperm retention at C_2 and the high/low retention orgasm regime at C_2. The normal relationship between sperm retention at C_2 and time from C_1 to first sexual event is present only when there is a low retention orgasm regime at C_2 ($z = 2 \cdot 936$, $N = 6$ females, 61 in-pair copulations, $P = 0 \cdot 002$). A high retention orgasm regime at C_2, however, seems to remove this relationship ($z = 0 \cdot 848$, $N = 10$ females, 39 in-pair copulations, $P = 0 \cdot 198$).

Orgasm regimes and levels of retention

In effect, our analyses have led us to recognize four regimes for sperm retention, based on the interaction of inter-copulation interval, time to first inter-copulatory orgasm, and orgasm regime at C_2. For ease of description, let FEV = the first event after C_1 (i.e. first inter-copulatory orgasm or, in the absence of an inter-copulatory orgasm, C_2). The four regimes are: (I) $\leqslant 24$ h to FEV with a low retention orgasm regime at C_2; (II) > 24 to $\leqslant 72$ h to FEV with a low retention orgasm regime at C_2; (III) > 72 h to FEV with a low retention orgasm

regime at C_2; and (IV) any time to FEV with a high retention orgasm regime at C_2.

The hypothesis that regimes I–IV show a rank-order linear decrease in levels of sperm retention, using residuals from equation (3) as the dependent variable (i.e. before any orgasm factors were controlled) is supported ($z = 3 \cdot 534$, $N = 11$ females, 100 in-pair copulations, $P < 0 \cdot 001$). z is maximized (at $3 \cdot 806$), however, by the hypothesis that regimes III and IV produce equal levels of sperm retention (see also Fig. 6) and, when compared directly, there is no significant difference in retention at these two levels ($z = 0 \cdot 996$, $N = 10$ females, 54 in-pair copulations, $P = 0 \cdot 320$, two-tailed).

The four orgasm regimes, therefore, impart three levels of sperm retention (levels I–III). These three retention levels are significantly evident even if we restrict analysis to only the first sample produced by each female ($z = 2 \cdot 032$, $N = 11$ females, 11 in-pair copulations, $P = 0 \cdot 021$).

Table VI. Definition of orgasm regimes and levels of sperm retention (identified in this study and used during discussion in text)

Orgasm regime	Time to FEV (h)	Retention level at C_2	Level of retention
I	$\leqslant 24$	L	I
II	$> 24 – \leqslant 72$	L	II
III	> 72	L	III
IV	any	H	III

C_1 and C_2, Consecutive copulations by a female. FEV, first sexual event after C_1 (i.e. either the first inter-copulatory orgasm or, in the absence of an inter-copulatory orgasm, C_2). L, low retention level at C_2 (no copulatory orgasm or a climax earlier than 1 min before the male ejaculates). H, high retention level at C_2 (climax some time between 1 min before the male ejaculates and flowback).

In the analyses and discussions that follow, we refer, for ease of description, to regimes I–IV and/or levels I–III. The definitions of these regimes and levels are summarized in Table VI.

Menstruation and sperm retention

If the number of sperm retained at C_2 is in part a function of the number of sperm remaining in the cervix from C_1, we should expect the normal relationship between retention at C_1 and C_2 to be changed if the female begins to menstruate between C_1 and C_2. Menstruation not only clears the cervix of the sperm present in the cervical mucus (but not necessarily of all those in the cervical crypts; Discussion), it also, at least temporarily, replaces them with various female tissues and cellular debris. The result should be a change in the normal relationship between C_1 and C_2 and perhaps a tendency to reduce sperm retention at C_2.

Our flowback data set included 21 in-pair copulations (from five females) which were preceded by menstruation between C_1 and C_2. Using the residuals from equation (5) as the dependent variable, sperm retention at C_2 tended to be lower after inter-copulation menstruation, though the difference is not significant ($z = 1·343$, $N = 5$ females, 107 in-pair copulations, $P = 0·090$). However, the normal influence of levels I–III on the residuals from equation (4) is obliterated ($z = -1·261$, $N = 5$ females, 21 in-pair copulations, $P = 0·896$) and changed significantly ($z_1 - z_2 =$

$3·142 - (-1·261) = 4·403$; $z = 4·403/\sqrt{2} = 3·113$, $P = 0·002$, two-tailed; z-difference test).

The level of sperm retention (residuals from equation 4) after menstruation tended to be greater than level I retention ($z = 0·600$, $N = 7$ females, 87 in-pair copulations, $P = 0·548$, two-tailed) but lower than level III ($z = -1·433$, $N = 6$ females, 29 in-pair copulations, $P = 0·152$, two-tailed). Menstruation thus appears to produce a block to retention that is intermediate in effectiveness between that associated with a cervix relatively full of sperm and a cervix relatively devoid of sperm (i.e. equivalent to level II; Fig. 6).

Check on Conclusions

Our analyses have used dependent variables (residuals from predictive equations; Table I) that increasingly depart from our raw data (counts of sperm in flowbacks). Moreover, most of our flowbacks were from volunteers, some of whom were more prolific than others, and most were taken while the females concerned were using oral contraceptives. This section checks our conclusions concerning the existence of three levels of sperm retention (Table VI) controlling for these potential sources of error.

All aspects of the female's influence on sperm retention that were identified by our analysis of residuals are also apparent in the variation in actual numbers of sperm ejected and retained (Table VII). Any apparent inconsistencies in Table VII between trends in median values and the results of Meddis' test are due to the latter being blocked by female to test for within-female response.

We opted at the beginning of this paper, for the reasons given, to measure the female's influence on sperm retention using residuals rather than percentage retention. However, the influence of regimes I–IV (Table VI) and inter-copulatory menstruation are equally applicable (Fig. 6) to the percentage retention of sperm ($z = 3·310$, $N = 11$ females, 121 in-pair copulations, $P = 0·001$), even if we restrict analysis to the first sample provided by each subject ($z = 2·159$, $N = 11$ females, 11 ejaculates, $P = 0·015$).

Finally, but importantly, if we restrict analysis of retention level (Table VI) to those few flowbacks collected by females not using any form of contraceptive, the influence of regimes I–IV is still significant ($z = 1·776$, $N = 3$ females, 9 in-pair copulations, $P = 0·038$).

Table VII. Association between actual number of sperm inseminated, ejected and retained at C_2 and orgasm regime for sperm retention

	Orgasm regimes				Meddis' test	
	I	II	III	IV	z	P
Lambda coefficients	1	2	3	3		
No. females (flowbacks)	2 (23)	5 (23)	3 (15)	9 (39)		
Number inseminated						
Median	190	216	329	135	0·120	0·453
Inter-quartile range	(176–203)	(214–310)	(270–330)	(76–205)		
Number retained						
Median	100	128	167	96	2·727	0·003
Inter-quartile range	(75–125)	(101–181)	(156–226)	(71–105)		
Number in flowback						
Median	113	130	62	78	2·445	0·007
Inter-quartile range	(93–133)	(85–173)	(53–111)	(28–85)		
Volume of flowback						
Median	2·3	2·0	2·0	2·0	−0·099	0·539
Inter-quartile range	(1·0–3·0)	(1·5–2·0)	(1·5–2·0)	(2·0–2·0)		

P-values are one-tailed against the hypothesis that orgasm regimes with higher lambda coefficients will have larger numbers of sperm inseminated and retained and lower numbers and volume ejected. Positive *z*-values: trend consistent with hypothesis.

Flowback Volume

Flowback volume varied significantly with the % time the pair spent together and time since last copulation (Table IV). There was also a very strong influence of copulatory orgasm on flowback volume. The primary influence is that, when a copulatory orgasm occurred, the volume of the flowback increased significantly ($z = 2·980$, $N = 9$ females, 109 in-pair copulations, $P = 0·002$, two-tailed). z is maximized (at 3·135) by the model that flowback volume was greatest when orgasm occurred during foreplay. No other aspects of the timing of copulatory orgasms or inter-copulatory orgasms were significant and, in general, orgasm regimes that favoured sperm retention did not decrease flowback volume (Table VII).

Female Orgasm and Sperm Competition

In this section we analyse the way that the pattern of female orgasm varies in relation to socio-sexual situation, with particular reference to in-pair copulation and extra-pair copulation. The results are summarized in Fig. 7.

In our nationwide survey, the majority of subjects provided enough information relating to their last copulation and inter-copulatory orgasm

to allow us to estimate the level of sperm retention (in terms of levels I–III; Table VI). In evaluating female behaviour, however, we also determined the extent to which the level shown is a function of behaviour overt to her male partner (i.e. overt copulatory orgasms) or cryptic (inter-copulatory orgasms that are nocturnal, self-masturbatory, or encouraged by a female partner). It is known that these two elements of female sexual behaviour sometimes vary differently (e.g. through the menstrual cycle: Harvey 1987; Baker et al. 1989).

To reduce complexity, we present results only for hormonally 'normal' subjects (i.e. we exclude all females who were under an unusual hormonal regime, either taking oral contraception or depo-provera injections, or who had undergone hysterectomy). As shown above, an increase in cryptic inter-copulatory orgasms leads to a decrease in sperm retention at the next copulation unless it is counteracted by a high retention copulatory orgasm.

In-pair copulations and monandry

A total of 1207 hormonally 'normal' females provided information on their last in-pair copulation at times that they claimed they had no other
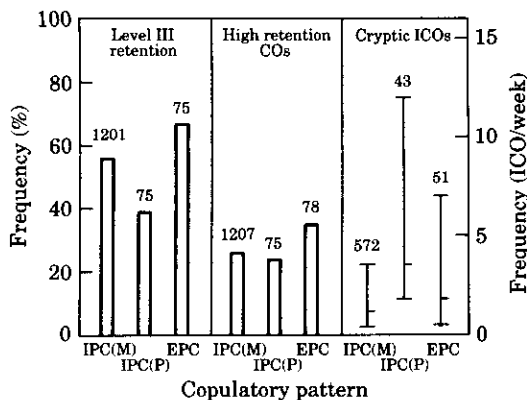
Figure 7. Variation in sperm retention, overt copulatory orgasms (COs) and cryptic inter-copulatory orgasms (ICOs) as a function of socio-sexual situation for hormonally 'normal' women. IPC(M), In-pair copulations by monandrous females; IPC(P), in-pair copulations by polyandrous females; EPC, extra-pair copulations (including double-matings). Sperm retention is illustrated as frequency (%) of level III retention; overt copulatory orgasms (COs) illustrated as frequency (%) of high level retention regimes; cryptic inter-copulatory orgasms (i.e. nocturnal, self-masturbatory and lesbian inter-copulatory orgasms) illustrated as median (and inter-quartile ranges) frequency/week. Numbers above bars: number of females providing all necessary information. Data from U.K. nationwide survey.

sexual partners. We refer to these as monandrous females.

A slight, but not significant, tendency for monandrous females to show an increase in high retention copulatory orgasms during the main fertile phase of their menstrual cycle (days 6–15) compared with the remainder of the cycle ($z = 1.185$, $P = 0.118$, two-tailed) is counteracted by a very significant increase in cryptic inter-copulatory orgasms ($z = 3.159$, $P = 0.002$, two-tailed; cf. Harvey 1987). The result is no change in retention level during the menstrual cycle ($z = 0.064$, $P = 0.950$, two-tailed).

Twenty-one of our monandrous females were pregnant. These showed no difference in orgasm regime, whether in overt copulatory orgasms, cryptic inter-copulatory orgasms, or overall retention level ($z = 0.427$, $P = 0.668$, two-tailed), relative to non-pregnant monandrous females.

In-pair copulations and polyandry

Seventy-five hormonally 'normal' females provided information on their last in-pair copulation at times that they also had one or more other male sexual partners. We refer to these as polyandrous females.

Compared with monandrous females, polyandrous females showed a significantly lower level (i.e. of levels I–III; Table VI) of sperm retention when copulating with their main partner ($z = 2.464$, $P = 0.014$, two-tailed). They achieved this change, however, not by any change in overt copulatory orgasms ($z = 0.293$, $P = 0.385$) but by a very significant increase in the frequency of cryptic inter-copulatory orgasms ($z = 4.192$, $P < 0.001$).

Extra-pair copulations

A further 75 hormonally 'normal', polyandrous females provided information on their last copulation when the latter was an extra-pair copulation. Behaviour during extra-pair copulation for these females can be compared with behaviour during in-pair copulation for the 75 other polyandrous females from the previous section (Fig. 7).

Level of sperm retention was significantly higher during extra-pair copulation than during in-pair copulation ($z = 3.242$, $P = 0.002$, two-tailed). This increase was achieved primarily by a difference in overt copulatory orgasms when females were copulating with their extra-pair male(s) compared with their partner ($z = 1.673$, $P = 0.047$). A slight tendency also to change the frequency of cryptic inter-copulatory orgasms before copulating with the extra-pair male was not significant ($z = 0.720$, $P = 0.236$).

Predicting the Number of Sperm Retained

During the course of this paper, we have identified a number of factors that significantly influence the retention of sperm during in-pair copulation. These may be combined into equation (6) (Table I) which explains 71% of the observed variation in number of sperm retained in the first in-pair copulation for which flowbacks were provided by our 11 females and 62% of the entire data set of 127 samples. The difference between number of sperm inseminated (equation 1) and number of sperm retained (equation 6) is the predicted number of sperm in the flowback. Figure 8 shows the relationship between the predicted and observed numbers of sperm in the flowbacks in this study. Our analyses explain 51% of the observed variation in number of sperm in the first flowback provided by each female and 55% of the total data set. Figure 8 shows a fit to the expected 1:1 relationship. The equation now needs
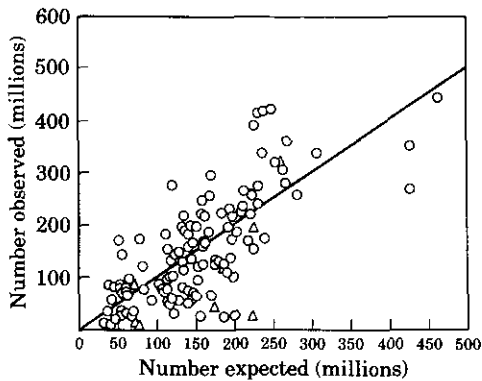
Figure 8. Numbers of sperm observed in 127 flowbacks from 11 females compared with the number predicted by equation (6) (Table I). △: First flowback contributed by each couple; ○: subsequent flowbacks. Diagonal line shows the desired 1:1 relationship.

to be tested for robustness with other groups of subjects.

DISCUSSION

Methodology

The methodologies associated with two of the investigations used in this paper (i.e. (1) the collection of whole ejaculates in condoms in the derivation of equation (1); and (2) our nationwide survey of sexual behaviour by questionnaire) have been discussed elsewhere (Baker & Bellis 1989; Bellis & Baker 1990) and need not be debated further here.

Of all of our investigations, the study of flowbacks was the most difficult and, as it was new, the most problematic. In particular, it was naturally impossible to standardize efficiency of collection in any precise way even from sample to sample by the same couple. However, there are several reasons to believe that the methodological problems were not severe enough to mask underlying biological effects. First, we obtained a strong correlation between the number of sperm we calculated to be inseminated by the male partner and the number of sperm collected by the female partner. Within-couple variation in collection efficiency was not, therefore, enough to mask biological variation from flowback to flowback. Second, the residuals (from equation 3) of sperm in the flowback correlate with female weight (Table IV). Inter-couple variation in collection efficiency was again, therefore, not enough to mask inter-couple biological

variation (unless it is proposed that larger females are more efficient at collecting flowbacks). Third, the six flowbacks collected during pregnancy suggest that virtually all of the sperm inseminated were successfully collected in the flowback.

All sperm counts were carried out blind (Baker & Bellis 1989). Estimation of sperm numbers could not, therefore, have been influenced by any preconceptions on the part of the investigators. None of the females who collected the samples or estimated volumes could have had any preconception of the patterns later revealed by the analysis of their samples. In most cases, the volunteers were even unaware of the precise aims of the study. The majority assumed they were simply making some general contribution to the study of human fertility. There was no opportunity, therefore, for subjects to bias results in any particular direction by putting more effort into collecting more of the flowback on some occasions than others. The possibility that the timing of orgasm influenced, not the size of the flowback, but the effort people put into the collection of the flowback, can also be ruled out. The difference between high and low levels of sperm retention was not a simple function of whether or not the female experienced an orgasm. Rather, retention was a fairly precise function of the timing of orgasm relative to the male's ejaculation (Fig. 3). It seems unlikely that any heterogeneity of effort in collection would show such a precise relationship.

Our conclusions concerning the volume of flowback and the number of sperm ejected derived primarily from studies of females using oral contraceptives. However, we had enough information to be able to demonstrate that orgasm regimes and retention levels have the same influence on sperm retention when the female is hormonally 'normal'. Thus, even though orgasm regimes may change in frequency when females take oral contraceptives (Baker et al. 1989), any given orgasm regime when it occurs appears to have the same influence on sperm retention whether the female is taking oral contraceptives or not. Our conclusions seem equally applicable, therefore, to hormonally 'normal' females.

Ideally much larger numbers of females should have been used to collect flowbacks. Not surprisingly, however, it was relatively difficult to recruit people to participate in the collection of material that many consider to be highly personal. The result was a relatively large sample of flowbacks but a skewed distribution between only 11 volunteers

(Table III). However, for the following reasons, neither skew nor small sample size appears to invalidate our conclusions.

The use of Meddis' blocking technique avoids the worst vagaries of skewed sample sizes. Nevertheless, wherever possible (e.g. when the whole data set was being analysed) we began with the first sample from each female before considering the biologically more meaningful tests of within-couple variation. Most importantly, however, our final conclusions concerning the influence of orgasm regimes on levels of retention significantly predicted variation in sperm retention in the first sample produced by each couple. The generality of our conclusions should not, therefore, be questioned on any grounds of skewed sample sizes and undue bias from the more prolific females. Figures and tables present medians of medians, again avoiding undue visual bias from the more prolific females.

The similarity in pattern shown by our flowback samples and the quite separate volume estimates from a further group of nine subjects (e.g. Table IV) gave some reassurance that our conclusions were not specific to our flowback contributors. Where differences do occur, as discussed below, they are reconciled by the fact that one group was providing sperm numbers, the other group, flowback volume. Also reassuring was the way in which the conclusions from our experimental subjects could then be applied in an apparently meaningful way to our nationwide sample of over 3000 females.

Finally, we were able to show that our main conclusion concerning levels of retention (Table VI) was independent of the analytical parameters and methods chosen. Our conclusions were equally applicable to other parameters (i.e. percentage retention; Fig. 6) and the raw data (i.e. number of sperm in the flowback; Table VII). Moreover, our final predictive equation, although mathematically not necessarily the best and although developed for sperm retention, nevertheless provided a significant fit to our raw flowback data (Fig. 8).

For all of the above reasons, we feel confident that our major conclusions concerning the influence of female orgasm patterns and sperm retention are real and not an artefact of either our sample of volunteers or our method of analysis. The main gap in our study is that, for obvious reasons, we do not yet have direct counts of the sperm content and volume of flowbacks from extra-pair copulations, particularly double-matings. We have been able to make inferences concerning what might happen on such occasions from our nationwide survey, but such indirect evidence is only an interim substitute for actual samples.

## Hypotheses of the Female Copulatory Orgasm

Our flowback data provide no support for the 'poleaxe' hypothesis of the female copulatory orgasm (Morris 1967; Levin 1981). On the other hand, they do provide the first direct evidence in support of the 'upsuck' hypothesis mooted by Fox et al. (1970). Highest levels of sperm retention (about 70%) occurred when the seminal pool was present in the upper vagina at the time the female climaxed (Fig. 6). The fact that improvement in sperm retention was observed when the female climaxed up to a minute before the male ejaculated (Fig. 3) suggests that the upsuck mechanism continues to function for at least 1 min after the female subjectively first experiences the climax.

We observed an increase in volume of the flowback if the female experienced an orgasm at any time during a copulation episode, the volume being greatest for orgasms during foreplay. The pattern suggests that the female adds some material, probably cervical mucus, to the seminal fluid in forming the flowback and that more is added if the female climaxes than if she does not. Climaxes during foreplay thus either add more material or add the same amount but without 'sucking' it back up to the same extent as when it is mixed with seminal fluid.

Inter-copulatory Orgasms: a Hypothesis

The penetrability of the cervical mucus to sperm from the next inseminate is a negative function of the density of cells and debris (Parsons & Sommers 1978; Belsey et al. 1987). Pregnancy, characterized by a large population of leucocytes and other cells in the cervical mucus (Davey 1986) irrespective of copulation and inter-copulatory orgasms, should be a time of maximum impenetrability, as our results indicate. Our results for non-pregnancy flowbacks also show that sperm retention seems to be a function of the number of sperm remaining from the previous copulation (Fig. 5).

If the upsuck mechanism applies to copulatory orgasms, it is likely also to apply to inter-copulatory orgasms. The difference would be that instead of sucking-up a mixture of cervical mucus and seminal
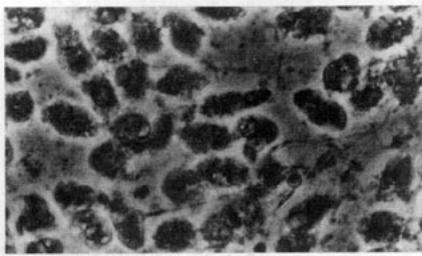
Figure 9. Human cervical mucus containing leucocytes and sperm. When cervical mucus contains a dense population of cells, the ease with which sperm can migrate through the channels is reduced.

fluid, inter-copulatory orgasms would suck-up a mixture of cervical mucus and vaginal secretions. This would lower the pH of the cervix and thus have far-reaching repercussions on the mobility and survival of sperm which would be consistent with our data.

Sperm are immediately immobilized in acidic environments at pH levels below 6·5. Even at a pH of 7·0 the ability of sperm to penetrate cervical mucus is minimal. Penetration is 'normal' at pH 7·5 and above normal at pH 8·25 (El-Banna & Hafez 1972). The pH of seminal fluid is normally in the range 7·0–7·8 (Raboch & Skachova 1965) and buffers the sperm from the vaginal environment which is acidic, and thus hostile, having a pH of between 5·8 and 3·5 (Duerden et al. 1987). Once sperm are no longer buffered by seminal fluid, they cannot live for more than a maximum of 10–12 h at the hostile pH levels found in the vagina (Vander Vliet & Hafez 1974). The pH of the cervical mucus can vary considerably from a favourable 7·4 to a hostile 4·0 (Kroeks & Kremer 1977), probably depending on the extent to which it has been mixed with material from the vagina.

Mixing cervical mucus and vaginal secretions via inter-copulatory orgasms should lower the pH of the cervix towards the acidic end of its observed range. This will slow down, or even immobilize, any sperm that subsequently enter the cervical mucus from reservoirs such as the cervical crypts. More may also die before reaching the uterus. Any hindrance to passage through the cervical mucus into the uterus may lead to the gradual accumulation of millions of sperm in the cervical mucus (Sagiroglu & Sagiroglu 1970). Here they attract an even larger population of scavenging, female-produced leucocytes (Fig. 9). The result could be that instead of declining with time since the most recent copulation

the population of sperm leucocytes and debris in the cervical mucus could remain constant or even increase, at least for as long as sperm continue to leave the crypts.

We suggest, therefore, that an inter-copulatory orgasm lowers the pH of the cervical mucus. In the context of the manipulation of sperm, the function is to slow down or prevent further passage of sperm already present in the cervix, promote a build up of cells and debris in the cervical channel, and thus to reduce sperm retention at the next copulation. As with all such blocks, however, this can perhaps be circumvented by a high retention orgasm at the next copulation which may take sperm directly to their storage sites, bypassing mucus penetrability.

Most medically significant infections of the female tract also prefer a more-alkaline environment (Duerden et al. 1987) and any increase in acidity due to inter-copulatory orgasms could have an antibiotic effect. In the absence of copulation (i.e. while still virgin or during temporary periods without insemination) and during pregnancy, the function of nocturnal, masturbatory and other non-copulatory orgasms could be as an 'antibiotic' mechanism aimed at combating cervical infection. Some support for this latter mechanism may be taken from our earlier finding that the frequency of non-copulatory orgasms is greater in females who also report having infection of the reproductive tract (Baker et al. 1989).

Male–Female Conflict and Cooperation over Sperm

Although our data are consistent with the upsuck hypothesis as a mechanism for the female orgasm, both copulatory and non-copulatory, they also suggest a behavioural significance far more complex than simple assistance in sperm retention. The relatively high incidence of non-copulatory orgasms, copulations without orgasm, and copulatory orgasms which climax before the male ejaculates (Table V; Fig. 2) cannot simply be ignored as they have in most previous discussions of the female orgasm. Far from assisting sperm retention, all of these inter-copulatory events reduce sperm uptake at the next copulation, perhaps using the mechanisms just discussed. Yet their influence can be overridden by a high uptake copulatory orgasm at the next copulation. The whole pattern hints strongly at a female strategy to influence sperm retention differently at different copulations.

We are not suggesting, of course, that this strategy is necessarily conscious or that, like any other strategy, it is infallible and omnipotent. As in any other arms race, we should expect male and female strategies to interact and it is by no means inevitable that one sex will always prevail. Nevertheless, the occurrence, pattern and timing of female orgasms emerge from our analysis as part of a female strategy to influence sperm retention from any given copulation. As such, the strategy should influence both the probability of conception and the outcome of sperm competition contests between males.

Manipulation in the absence of sperm competition

In our companion paper (Baker & Bellis 1993), we concluded that, in the absence of sperm competition, both male and female partner may benefit from improved chances of viable conception if fewer sperm are taken into the female tract. The advantage of fewer sperm may either be through reduced risk of debilitating the egg or through reduced risk of pathological polyspermy, eggs fertilized by more than one sperm failing to develop into viable embryos (Englert et al. 1986). In this context, females who produce the optimum rate of arrival of sperm at the oviduct by manipulating both the number of sperm that enter the cervical crypts and the rate and length of time that sperm migrate through the cervical mucus will benefit both themselves and their male partner. We assume, however, that the more sperm the male inseminates beyond a certain optimum and/or the more are retained after flowback, the more difficult it is for the female to produce the optimum traffic of sperm.

Lack of orgasm during copulation or a climax more than 1 min before the male ejaculates is associated with low sperm retention (Fig. 3). It has long been known that copulatory orgasm is not essential for conception (Moghissi 1977). In our data we had a situation in which date of conception could be estimated to within $+24$ h and was attributable to one or other of two in-pair copulations, about 156 and 120 h before conception. The number of sperm inseminated on both occasions could be estimated (equation 1; Table 1) and both flowbacks were collected. The amount of information available for this natural conception is probably unique. Neither of the relevant in-pair copulations was associated with a copulatory orgasm and, summed for the two copulations, we estimated -6 ± 48 million sperm (i.e. near zero) to have been retained from a total insemination of 545 million sperm. Two non-copulatory orgasms occurred approximately 28 and 22 h before conception. This unique data point illustrates that neither a copulatory orgasm, nor any more than minimal sperm retention, is necessary for conception.

Sperm retention was significantly reduced during the fertile phase of our three flowback donors who were not taking oral contraceptives, two of whom conceived. This reduction was primarily the result of the timing of inter-copulatory orgasms, menstrual variation in retention no longer being significant once timing of inter-copulatory orgasm was statistically controlled. A significant increase in cryptic inter-copulatory orgasms during the fertile phase was also found not only in our nationwide survey but also by Harvey (1987). Overall, there was no indication in our nationwide survey of any increase in sperm retention (measured in terms of levels I–III; Table VI) by monandrous females during their fertile phase. Finally, there is a tendency for a reduction in sperm retention in hormonally normal females, both in our nationwide survey and in our flowback analysis, compared with those taking oral contraceptives. There is thus no indication in our data that monandrous females favour higher sperm retention when conception is more likely. On the contrary, the impression is that the favoured strategy associated with conception in a monandrous situation is to reduce the number of sperm retained. The results are therefore entirely in line with our previous discussion of ejaculate adjustment by males (Baker & Bellis 1993).

We are not suggesting, of course, that high retention copulatory orgasms never lead to conception. During in-pair copulation, such orgasms are, in any case, more often associated with occasions when the male inseminates relatively few sperm (Table VII). Any negative relationship between the number of sperm retained and the probability of conception (Baker & Bellis 1993) will be quantitative, not absolute (i.e. there is always some chance of conception, no matter how many sperm are retained).

Manipulation in the presence of sperm competition

Although a male's probability of fertilization from any given copulation may be increased by decreasing sperm number in the absence of sperm

competition (Baker & Bellis 1993), it is generally accepted that it is increased by increasing sperm number in the presence of sperm competition (Parker 1990).

The current explanation for concealed ovulation and continuous receptivity in some female mammals, such as humans, is that it allows the female to confuse the male over which copulations are likely to lead to paternity (Small 1989; Bellis & Baker 1990). In this way, females may manipulate the timing of inseminations from different males to suit their own priorities. Continuing copulation well into pregnancy maintains this deception by concealing the date of conception.

If females use copulation as a form of mate confusion, it is important that no aspect of their behaviour changes predictably with levels of infidelity and chances of conception. We have demonstrated that polyandrous females favour the extra-pair male (or males) not only by the timing of extra-pair copulations (Bellis & Baker 1990) but also by the relative level of sperm retention (Fig. 7). When females switch from a monandrous to a polyandrous situation (but still retaining a main partner), they reduce the level of sperm retention from their partner's inseminates but show a significantly higher level of retention from the extra-pair male's inseminates.

Our data show that females achieve the change in retention with their partner by varying the frequency of inter-copulatory orgasms cryptic to their partner while maintaining the same level of overt copulatory orgasms (Fig. 7). They achieve the difference in level of retention between males by varying the pattern of overt copulatory orgasms. The female response is exactly the one expected if the key factor in her behaviour were the deception of her primary partner. Add to these changes in pattern of real orgasms the possibility of females faking or hiding orgasms and the opportunity for males to detect any underlying female strategy is greatly reduced.

Sperm retention in the absence of fertilization

There are three situations in which manipulation of ejaculates by both males and females at first sight seems redundant: (1) during the infertile phase of the female menstrual cycle; (2) when either male or female is using contraceptives; and (3) during pregnancy.

A male's sperm remain fertile for at least 5 days after copulation (Barrett & Marshall 1969). In addition, our data suggest that his sperm, simply by being present in the cervix, can influence retention of sperm at the female's next copulation for up to 8 days (cf. Austin 1975). This in turn could mean that the sperm could indirectly influence retention at the copulation after that, and so on. Thus, sperm from one insemination could in principle have some influence on fertilization for up to at least 13 $(8 + 5)$ days and perhaps even longer. Rarely can males, or even females, predict whether or not the female will become fertile at some time during the next 13 or so days.

In a sense, with this time-scale in mind, discussion over why ejaculate manipulation should occur at times that conception is unlikely is largely unnecessary. The general answer is that it is very rare that any copulation has absolutely no chance of influencing fertilization. No form of contraception is perfect (Johnson & Everitt 1988), no phase of the menstrual cycle is absolutely infertile (Barrett & Marshall 1969; Jochle 1975), and even during pregnancy, spontaneous abortion followed by ovulation could occur within the period of influence of sperm.

As far as the male is concerned, a female has to be many months into pregnancy before her symptoms are unequivocal. As discussed above, pregnancy, like the menstrual cycle, is a phase when the female may benefit from confusion. During pregnancy, the vast majority of the sperm are apparently ejected in the flowback, no matter what the orgasm regime. Overt copulatory orgasms, therefore, seem to be functionless for sperm retention and we presume the main reason for overt regimes not to change during pregnancy is to maintain the efficiency of confusion. However, the frequency of cryptic orgasms also remains unchanged during pregnancy. Perhaps, as suggested for virgins, the functions of these cryptic orgasms during pregnancy is largely antibiotic.

Individual variation in female strategies

The greatest flexibility of ejaculate manipulation is shown by females who are capable of a varied range of orgasm patterns, both copulatory and inter-copulatory, including at times having no orgasm at all.

According to our nationwide survey, 84% of women, by the time they have had 500 copulations (henceforth, 'experienced' women), are using the whole range of ejaculate manipulation. Their

strategy is 'mixed', involving copulatory and inter-copulatory orgasms, as well as lack of orgasm. Only 2% of experienced women claimed never to have experienced any orgasm and thus to be using a 'no orgasm' strategy.

Sixteen per cent of experienced women in our survey claimed not to experience copulatory orgasms though the majority of these (88%) were experiencing inter-copulatory orgasms. Women with such an 'inter-copulatory orgasm dominated' strategy are less flexible in ejaculate manipulation than women with a fully 'mixed' strategy only insofar as they cannot convert a level I retention into a level III (see Table VI) during copulation itself.

Our analysis of flowbacks suggests that no matter whether a woman uses a 'no orgasm', 'inter-copulatory orgasm dominated', or a 'mixed' strategy, all are capable of manipulating sperm retention across the whole range from level I to level III (Table VI). Indeed, what 'no orgasm' and 'inter-copulatory orgasm dominated' strategies may lose in flexibility, they may recoup, at least partially, through greater crypsis.

Conclusion

Males adjust the number of sperm in their ejaculates according to the conflicting pressures of an advantage of low numbers for conception in the absence of sperm competition and of high numbers for competitiveness in the presence of sperm competition. On average, partly through female cooperation and perhaps partly through lack of total perfection in the female mechanism, when males inseminate more sperm, more are retained. On any one occasion, however, a female is capable of negating any male strategy through her implementation of different orgasm regimes to manipulate the male's inseminate. The most flexible strategy involves copulatory and inter-copulatory orgasms as well as occasional lack of orgasm. The conception strategy for females in monandrous situations seems primarily to be to favour low retention regimes. In polyandrous situations, females change their orgasm regimes on average to favour the extra-pair male in sperm competition. They do this by varying cryptic orgasms to reduce retention with their partner, then overriding this preparation with overt high retention orgasms should their next copulation be with an extra-pair male.

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