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Human sperm competition: ejaculate adjustment by males and the function of masturbation

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Abstract. Sperm competition theory argues that the number of sperm inseminated into a female by a male is a trade-off between two opposing pressures. On the one hand, the risk that sperm may find themselves in competition with the sperm from another male favours the male inseminating more sperm. On the other hand, ejaculates are costly to produce and males are favoured who economize over the number of sperm inseminated. This paper analyses: (1) sperm numbers and other ejaculation data for 35 human couples; and (2) data relating to the most recent copulation reported by 3587 women. Three sets of predictions based on sperm competition theory are tested. These are that the number of sperm inseminated should be a function of: (1) risk of sperm competition; (2) female reproductive value; and (3) optimum partitioning of ejaculates between successive in-pair copulations. During in-pair copulation the male used successive inseminations to 'top-up' the population of sperm in his female partner. In accordance with sperm competition theory: (1) individual males inseminated more sperm when the pair had spent a smaller proportion of their time together and hence risk of sperm competition was greater; and (2) larger females were inseminated with more sperm than smaller females. In apparent contradiction to sperm competition theory, the number of sperm inseminated did not vary according to female orgasm pattern or the probability of conception. This apparent failure of the theory may instead be due to the male's lack of necessary information. Paradoxically, male mammals seem to waste huge numbers of sperm through spontaneous emission and self-masturbation. Such shedding of sperm could be adaptive if it led to more competitive and/or more fertile inseminates at the next copulation. The data showed that a recent male masturbation reduced the number of sperm inseminated at the next copulation but not the number retained by the female. It is concluded that masturbation is a male strategy to increase sperm fitness without increasing sperm numbers in the female tract. The possibility that, in the absence of sperm competition, the probability of fertilization decreases if too many sperm are inseminated is discussed. This latter factor may be more important than ejaculate cost in favouring male restraint over the number of sperm inseminated.

It is conventional, for species in which males and females form long-term pair bonds with some form of mate guarding, to distinguish between in-pair copulations and extra-pair copulations (i.e. with an individual other than a long-term partner). A particular category of extra-pair copulation is 'double-mating' which occurs when a female mates with a second male while still containing fertile sperm from one or more previous males. The result is 'sperm competition' (Parker 1970a) as the sperm from different males compete to fertilize the female's egg(s).

There is some debate over whether sperm competition takes the form of a lottery (Parker 1982, 1984) or warfare (Sivinski 1980; Silberglied et al. 1984; Baker & Bellis 1988, 1989b; Harcourt 1991). On either mechanism, however, it is predicted that sperm competition will favour males who inseminate larger ejaculates (i.e. more sperm/ejaculate; Parker 1990). Although individual males differ in the general competitiveness of their sperm, the more sperm inseminated from an individual male, the greater his chances of success in sperm competition (Martin et al. 1974).

Current sperm competition theory states that the number of sperm a male inseminates into a female is a trade-off between two opposing pressures. On the one hand, the risk of sperm competition favours an increase in the number of sperm inseminated (Parker 1982); on the other, as sperm are inseminated in 'packages' (=ejaculates), non-trivial costs involved in ejaculate production (Dewsbury 1982)

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require restraint over the allocation of sperm to individual ejaculates. The predicted result is that males will inseminate a female with the number of sperm that is the optimum trade-off between the risk of sperm competition and the need for economy.

This theory has generated at least three predictions: (1) the greater the risk of sperm competition, the more sperm should be inseminated (Parker 1982); (2) the greater the reproductive value of a female, the more a male should invest in sperm competition and hence the more sperm should be inseminated (Dewsbury 1982); and (3) under some circumstances males do better in sperm competition to partition sperm between a succession of in-pair copulations rather than inseminate all available sperm in a single in-pair copulation (Parker 1984).

The first of these predictions (that males should inseminate more sperm when the risk of sperm competition is greater) has now been tested at three levels: interspecific (butterflies: Svard & Wiklund 1989; birds: Møller 1991; primates: Harvey & Harcourt 1984; and ungulates: Ginsberg & Rubenstein 1990); intraspecific (beetles, *Tenebrio molitor*: Gage & Baker 1991; flies, *Ceratitis capitata*: Gage 1992; rats, *Rattus norvegicus*: Bellis et al. 1990; and humans: Baker & Bellis 1989a); and intra-male (beetles, Gage & Baker 1991). So far, all tests are consistent with the predictions of sperm competition theory: males inseminate more sperm when the risk of sperm competition is higher.

In contrast to the number and variety of tests of this first prediction, there has been minimal attempt to test the second (that males should invest more in sperm competition when the female's reproductive value is higher). One initial problem is that the two predictions may sometimes be difficult to separate. For example, females of greater reproductive value may be inseminated by more males and thus offer greater risk of sperm competition. Even so, there are some circumstantial data consistent with the prediction, at least for insects. Thus, male dung flies, *Scatophaga stercoraria*, copulate for shorter periods with females containing fewer eggs (Parker 1970b). Male mormon crickets, *Anabrus simplex*, are less likely to transfer a spermatophore to lighter females containing fewer eggs (Gwynne 1981). In both cases, it seems likely that, on average, females containing fewer eggs are inseminated with fewer sperm.

Female mammals may differ in their reproductive value in many ways. In this paper we consider four: (1) body size; (2) sperm retention; (3) stage of menstrual cycle; and (4) use of oral contraception.

In many animals heavier females contain more eggs (Halliday 1983). Insofar as dizygotic twinning rates are higher in heavier human females (MacGillivray & Campbell 1978) the same may, on average, be true for humans. In addition, heavier human females have reduced risk of miscarriage during pregnancy, faster growth of the fetus and heavier birth weight (Lechtig & Klein 1981; Bongaarts & Potter 1983; Garn & LaVelle 1983; Gray 1983). In some societies, heavier women have higher offspring survival and, at any one time, more living children (Hill & Kaplan 1990). A male preference for larger females is reported to exist, both in humans (Ford & Beach 1952; Mulder 1990) and other animals (Halliday 1983) and male humans are reported to compete more for, and to show greater defence of, more fertile and fecund women (Flinn 1988). Sperm competition theory would predict, therefore, that males inseminate larger females with more sperm.

The function of the female orgasm in humans is discussed in detail in a separate paper (Baker & Bellis 1993). There we show a significant association between sperm retention and the occurrence and timing of the female orgasm relative to the timing of male ejaculation. It follows that, at any given copulation, the timing of female orgasm is likely to have some association with the reproductive value of the female to the male. We might expect males to vary the number of sperm inseminated accordingly.

Both stage of menstrual cycle and use and efficacy of contraception influence the probability of conception and hence, at any given copulation, the reproductive value of the female to the male.

Conventionally, studies of the menstrual cycle of human females use conversion to a standardized 28-day cycle (McCance et al. 1937). This standardized cycle may be divided into three major hormonal phases (Hawker 1984): I (days 1–5, menses); II (6–14, proliferative); and III (15–28, secretory). In this standardized cycle, ovulation occurs on day 14 and copulations are fertile on days 9–14 (peak fertility = day 12; Barrett & Marshall 1969). The rank-order of the three phases for fertility is II > I > III (i.e. phase II is the most fertile).

As far as contraception is concerned, the probability of conception (expressed as % pregnant women in 100 fertile women-years; i.e. 100 women for 1 year or 10 women for 10 years) is 5–30% when

couples use a condom and $<1\%$ when the female uses an oral contraceptive (combined pill; Johnson & Everitt 1988). When couples use both a condom and an oral contraceptive, the probability of conception should be correspondingly lower than when either method of contraceptive is used on its own. We might expect males to adjust the number of sperm inseminated in response to these altered levels of probability of conception.

The third prediction made by sperm competition theory is that males should partition sperm numbers strategically between successive in-pair copulations during the course of their partner's reproductive cycle. The most detailed consideration of the optimum strategy was by Parker (1984) though other authors (e.g. Ginsberg & Rubenstein 1990) have at least made assumptions as to how partitioning would influence the course of sperm competition. As yet, however, there has been no empirical study of the allocation of sperm to successive in-pair copulations which might allow the theoretical models to be evaluated.

In this paper we present data on the number of sperm inseminated by humans that allow us to test all three types of prediction derived from sperm competition theory. Thus, we evaluate predictions concerning: intra-male variation; variation in female reproductive value; and the partitioning of sperm between successive in-pair copulations.

In contrast to the wide range of evidence that increased risk of sperm competition favours larger ejaculates, there is as yet no unequivocal evidence that the cost of producing ejaculates is the major restraining factor in determining the number of sperm inseminated per ejaculate. On the contrary, behaviour exists, so far unconsidered, that is intuitively inconsistent with ejaculate cost being a major factor favouring male restraint, at least in mammals. Thus, male mammals appear to be extremely wasteful of sperm. Not only do they void large numbers of sperm in their urine (Mann & Lutwak-Mann 1981) but they also shed vast numbers during spontaneous (in humans, usually nocturnal) emissions and through the more directed behaviour of self-masturbation.

Such shedding of sperm is a characteristic of all male mammals studied (e.g. rhesus monkeys, *Macaca mulatta*: Carpenter 1942; cats, *Felis catus*: Rosenblatt & Schneirla 1962; deer, *Cervus elaphus*: Darling 1963; cattle, *Bos taurus*: Hafez et al. 1969a; horses, *Equus caballus*: Hafez et al. 1969b; and rats: Beach 1975) and is a virtually universal facet of the sexual behaviour of male humans (Kinsey et al. 1948). Such spontaneous and/or deliberate shedding of sperm is by no means restricted to males denied access to females, either in humans or other mammals. Thus, stags with harems frequently shed whole ejaculates following antler rubbing (Darling 1963) and dominant male rhesus monkeys masturbate to ejaculation even with full access to oestrous females (Carpenter 1942).

This apparent paradox could be resolved if masturbation and spontaneous emissions produced a future ejaculate with a fitness enhanced beyond the level necessary to offset the numeric and energetic costs of the lost sperm. Previous authors have suggested that sperm have a limited 'shelf-life' and, if not used within a certain storage time, become suboptimal (e.g. Smith 1984). Masturbation is thus suggested to be a mechanism for shedding suboptimal sperm and reducing the mean age of sperm inseminated at the next copulation. The advantage to the male could be that younger sperm are more acceptable to the female and/or are better able to reach a secure position in the female tract. Moreover, once retained in the female tract, younger sperm could be more fertile in the absence of sperm competition and/or more competitive in the presence of sperm competition. Finally, if younger sperm live longer in the female tract, any enhanced fertility and competitiveness would also last longer. However, no evidence exists that either masturbation or spontaneous emission improves the fitness of a future ejaculate. The only support for the 'sperm age' hypothesis is the observation that after collection rabbit, *Oryctolagus cuniculus*, sperm aged outside of the male rapidly become poorer at competing for eggs against sperm from freshly collected ejaculates (Roche et al. 1968).

The data presented in this paper allow the first empirical test of the 'sperm age' hypothesis. The result of our analysis is the emergence of another potential constraint on number of sperm inseminated that we suggest may be more important than the cost of ejaculate production.

METHODS

Our data come from four different investigations: (1) counts of sperm in whole ejaculates collected by condom during either copulation or male masturbation; (2) counts of sperm in 'flowbacks' (the mixture of seminal fluids, sperm, female secretions

and female tissue that flows back out of the vagina after copulation); (3) subjective estimates of flowback volume; and (4) a U.K. nationwide survey of female sexual behaviour.

In our nationwide survey, 3679 females each answered 57 questions on their sexual behaviour, including information relating to their most recent copulation. The copulations for which we obtained data included 2744 in-pair copulations and 126 extra-pair copulations (of which 76 were double-matings).

In our ejaculate study, 35 male–female human pairs (involving 33 males and 33 females; two male and two female contributors changed partners during the study) provided material or estimates relating to 323 in-pair copulations and 67 male masturbations. Our 66 volunteers were recruited through staff, postgraduates and undergraduates in the School of Biological Sciences at the University of Manchester. Pair codes and the number of different types of usable samples and/or estimates they each provided are listed in Table I.

Whole Ejaculates

Whole ejaculates were collected in condoms during copulation or masturbation. Subjects were provided with a 'kit' containing instructions and all necessary equipment, including a mixture of lubricated (non-spermicidal) and non-lubricated condoms. Ejaculate collection and fixation and the counting of sperm followed the double-blind protocol used previously (Baker & Bellis 1989a), based on the World Health Organization Human Semen Manual (Belsey et al. 1987).

In addition to information relating to each sample, volunteers were asked their age, weight and height. Males also measured the length (L) and width (W) of their left testis in centimetres (to one decimal place), using callipers. Volume (V cm^3) was then calculated using the formula for a spheroid: $(\pi/6) \times L \times W^2$.

Flowbacks

The detailed instructions given to volunteers for the collection of flowbacks are published in full in Baker & Bellis (in press). The flowback emerges 5–120 min after copulation as a relatively discrete event over a period of 1–2 min in the form of three to eight white globules (for further details see Baker & Bellis 1993). With practice, females can recognize the sensation of the beginning of flowback and can collect the material by squatting over a 250 ml glass beaker. Once the flowback is nearly ready to emerge, it can be hastened by, for example, coughing. If the flowback has not yet emerged, it invariably does so at the female's first urination after copulation and on these occasions the flowback is often ejected with some force (cf Ginsberg & Rubenstein 1990 for zebra *Equus* spp). Again with practice, the female can collect the flowback during urination with minimal, or no, contamination from urine. Volunteers were asked to record which method of collection was used.

After flowback collection, the protocol followed was the same as for whole ejaculates.

Estimates of flowback volume are not used in this paper, but we do use the associated information on the in-pair copulations recorded (Table I).

Nationwide Survey of Sexual Behaviour

Our survey was based on a questionnaire developed between 1987 and 1989 in three pilot studies (two self-selected; one by interview), involving 250 females (Baker & Bellis 1989a). The final version (seeking 57 answers) was distributed throughout Britain in March/April 1989 by *Company* magazine (Bellis et al. 1989). Female readership of the relevant issue was estimated by the publishers to be 439 000. Our 3679 replies (excluding seven overtly spoilt) therefore represent 0·84% of the potential respondents who were themselves roughly 5% of the U.K. population of females of reproductive age. Ninety-two respondents claimed to be virgins leaving a sample of 3587 sexually experienced females aged between 13 and 72 years (mode = 21 years). Other major characteristics of our sample have been published elsewhere (Baker et al. 1989; Bellis & Baker 1990).

Statistics: Calculation of Probabilities

Throughout, medians are used instead of means. Variation about the median is expressed in terms of inter-quartile range. In figures and tables, as appropriate, the medians presented are the medians of medians (i.e. the median value is calculated for each male or female, then the median is calculated for the group). The calculation of probabilities, however, uses the techniques described below.

At one point, we used the *z*-transformation test (Sokal & Rohlf 1981) to compare correlation coefficients. Otherwise, to avoid making any

Table I. Codes and number of different types of samples provided by couples collecting whole ejaculates and/or flowbacks

Couple	Male	Female	No. of samples			
			Masturbation ejaculates	In-pair copulation ejaculates	Flowbacks	
					Samples	Estimates
A	A	A	6	4	9	0
B	B	B	17	27	93	8
C	C	C	1	2	0	0
D	D	D	1	1	0	0
E	E	E	1	1	0	0
F	F	F	1	1	0	0
G	G	G	2	1	1	0
H	H	H	1	2	1	0
I	I	I	1	1	0	0
J	J	J	1	1	0	0
K	K	K	1	1	0	0
L	L	L	2	3	0	0
M	M	M	1	1	0	0
N	N	N	2	22	2	0
O	O	O	0	1	0	0
P	P	P	1	1	0	0
Q	Q	Q	1	1	1	0
R	R	R	0	1	8	0
S	S	S	2	1	6	0
T	T	T	5	3	0	0
U	U	U	1	3	0	0
V	V	V	0	2	0	0
W	W	I	0	0	3	0
X	X	X	8	0	0	0
Y	Y	Y	2	1	0	0
Z	Z	Z	0	0	2	26
AA	A	W	0	0	1	0
AB	O	C	8	2	0	0
AC	AC	AC	0	0	0	19
AD	AD	AD	0	0	0	6
AE	AE	AE	0	0	0	14
AF	AF	AF	0	0	0	6
AG	AG	AG	0	0	0	16
AH	AH	AH	0	0	0	4
AI	AI	AI	0	0	0	16
Totals (pairs:ejaculates/flowbacks)			22:67	24:84	11:127	9:115

assumptions concerning the normality of our data, we calculated probability values using only non-parametric statistical tests.

We consider (following Siegel 1956 and Meddis 1984) that the use of parametric statistics requires justification on each application. This justification should involve demonstration that the data are significantly similar to a normal distribution, not merely that they do not significantly depart from a normal distribution. Not only could we not justify the use of parametric statistics, in some parts such statistics were clearly unjustified due to skewed, bi- or multi-modality etc., unsuitable for transformation. We particularly wished to avoid any reliance on some unspecified 'robustness' of parametric tests. For all of these reasons, we considered a distribution-free test to be essential. The only such test with the power and elegance to cope with the complexity of our data and analysis is the Meddis rank sum test (Meddis 1984).

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

	Equation
(1)	$NSM = 12 + 4{\cdot}63 \times HEJ$
(2)	$NSC = 452 - 2{\cdot}92 \times PCT$
(3)	$NSC = 357 + 1{\cdot}94 \times HIPC - 3{\cdot}40 \times PCT$
(4)	$NSC = 357 - 3{\cdot}40 \times PCT + 1{\cdot}94 \times HIPC + ((2{\cdot}41 \times HMAS - 228) \times MC)$
(5)	$NSC = 1{\cdot}94 \times HIPC - 3{\cdot}40 \times PCT + ((2{\cdot}41 \times HMAS - 228) \times MC) - 1008 + 23{\cdot}37 \times FW$
(6)	$NSC = PVequ5 - (((PVequ5 - mid)/(limC - mid))^2 \times (limC - limO))$

NSM, Number of sperm ejaculated during masturbation in millions; NSC, number of sperm inseminated during in-pair copulation in millions; HEJ, hours since last ejaculation; 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, % 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); PVequ5, the predicted value for NSC from equation (5); mid, mid-point of number of sperm in observed ejaculates (350×10^6); limC, the minimum or maximum calculable limit to NSC from equation (5); limO, the minimum or maximum observed number of sperm in in-pair copulation ejaculates. When: PVequ5 > mid, maximum limits should be used (see Table XII); PVequ5 < mid, minimum values should be used. When female weight is not available, equation (4) may be used to calculate PVequ5 instead of equation (5).

Statistics: Residuals and Predictive Equations

When the data allowed, we used Meddis' blocking technique to provide statistical control for one variable while analysing for an independent influence of another. Most often, however, we used regression or multiple regression to calculate values for the dependent variable with respect to one or more independent variables, then calculated residuals. These residuals were then analysed further for the influence of some other independent variable not included in the original regression. This procedure removed the influence of those independent variables included in the regression. However, even when we have used the parametric procedures of regression and multiple regression as intermediate steps in data handling, we still base probability statements only on non-parametric tests, for the reasons given above. It seems unlikely that any autocorrelation in the residuals would cause a problem for the Meddis procedures though we know of no formal analysis of this possibility.

We used five different equations to generate residuals. Derivation of the equations is described under Results and the equations are collected together in Table II. To avoid giving undue weight to samples from the more active couples, equations were calculated from only the first sample in a category provided by each couple. Similarly, when necessary to avoid pseudoreplication of data, we followed our previous procedure (Baker & Bellis 1989a) and made between-couple comparisons also using only the first sample from each couple. Finally, we used regression and residual analysis to develop an equation to predict the number of sperm inseminated by males during in-pair copulation in different socio-sexual situations (Table II; equation 6).

RESULTS

Risk of Sperm Competition and Number of Sperm Inseminated

As previously (Bellis & Baker 1990), we take the conservative view that human sperm remain competitive for only 5 days (ca 7–9 days; Smith 1984). For humans, therefore, a double-mating is a copulation with one male within 5 days of copulation with a different male. Claimed total number of male sexual partners in life (so far) per female and the proportion of women who claimed ever to have double-mated (data from our nationwide survey) increased in relation to sexual experience (i.e. number of lifetime copulations; Table III).

The probability for a female of (1) having more than one current male partner, (2) the last copulation being an extra-pair copulation, and (3) the

Table III. Lifetime number of male sexual partners/female and number of females who have ever double-mated in relation to sexual experience

Lifetime number of copulations	*N*	Total number of male sexual partners: Median (inter-quartile range)	Total number of male sexual partners: >1 partner (%)	Total number of male sexual partners: >50 partners (%)	Number of females having double-mated at least once (%)
⩽50	481	2 (1–4)	64·5	—	17·5
51–200	796	4 (2–7)	80·6	0·5	36·3
201–500	896	5 (3–10)	86·9	0·8	49·4
501–1000	631	7 (3–13)	92·7	1·9	61·9
>1000	585	8 (4–20)	93·9	5·6	71·8

Double-mating = copulation with one male within 5 days of copulation with a different male.

Table IV. Influence of % time with male partner on incidence of extra-pair copulation and double-mating by human females

	Time spent with main male partner (%)										Meddis' specific test	
	100–91	90–81	80–71	70–61	60–51	50–41	40–31	30–21	20–11	10–0	*z*	*P*
Lambda	1	2	3	4	5	6	7	8	9	10		
Total sample												
N	26	52	189	228	381	361	269	534	454	314		
>1 male partner (%)	3·8	3·8	5·8	8·3	6·7	5·8	5·2	7·1	7·9	13·7	3·04	0·001
Last copulation an Extra-pair copulation (%)	0·0	0·0	3·2	4·0	1·8	4·2	2·0	5·1	5·6	9·8	4·69	<0·001
Double-mating (%)	0·0	0·0	1·1	1·3	1·3	2·8	1·2	1·5	1·8	4·0	2·17	0·015
Females not using contraception												
N	4	13	28	28	55	65	26	67	69	52		
>1 male partner (%)	0·0	7·7	7·1	3·6	5·5	6·2	11·5	7·5	10·2	19·2	2·36	0·009
Last copulation an Extra-pair copulation (%)	0·0	0·0	3·6	7·1	1·8	3·1	3·8	9·1	3·3	20·5	2·85	0·002
Double-mating (%)	0·0	0·0	0·0	0·0	1·8	1·6	4·0	0·0	1·7	9·1	2·12	0·017

last copulation being a double-mating were all significant negative functions of the average proportion of time (including sleeping time) the pair spent together (Table IV). The functions remained significant even when restricted to those 407 females who claimed that their last copulation was unprotected by contraception (Table IV). We conclude that there is a negative association between the proportion of time a pair spends together and the probability that the female will engage in extra-pair copulation (including double-mating).

Twenty-five couples contributed 84 ejaculates collected in condoms during in-pair copulation (Table I). Of these ejaculates, 50 (from 15 males) were preceded by an ejaculate also produced during in-pair copulation (henceforth IPC–IPC ejaculates). Median time interval between in-pair copulations for these 50 ejaculates was 48 h (inter-quartile

Table V. Variation in number of sperm inseminated during in-pair copulation (IPC) by five males in relation to % time with partner (IPC–IPC ejaculates only)

Time together since last IPC (%)	No. of sperm (millions) inseminated									
	Pair A		Pair B		Pair N		Pair T		Pair V	
	N	Median	*N*	Median	*N*	Median	*N*	Median	*N*	Median
1–20	1	507			1	296				
21–40					6	196 (147–319)				
41–60			1	495	6	210 (194–231)				
61–80	1	220	8	477 (268–530)	2	143 (128–159)	1	109	1	341
81–100			5	206 (143–219)	4	67 (48–82)	2	183 (161–205)	1	32

Inter-quartile range is shown in parentheses. IPC–IPC ejaculate: in-pair copulation ejaculate with no inter-IPC masturbation.

range = 25–70 h). Five males contributed more than one IPC–IPC ejaculate ($N = 40$). The clear tendency (Table V) for individual males to inseminate fewer sperm as % time with partner increased is highly significant ($z = 3{\cdot}535$, $P < 0{\cdot}001$). In part, this tendency is due to an equally strong tendency for inter-copulation intervals to be shorter when couples spent more time together ($z = 3{\cdot}830$, $P < 0{\cdot}001$). However, the former is not an artefact of the latter. When the data are blocked to remove the influence of time since last copulation, the association between % time together and number of sperm inseminated remains highly significant ($z = 2{\cdot}438$, $P = 0{\cdot}007$).

We conclude that for any given time interval since last in-pair copulation, individual males inseminate more sperm per ejaculate if they have spent less time with their partner and hence, on average, the risk of sperm competition is higher.

Time Since Last In-pair Copulation and Number of Sperm Inseminated

On average, human pairs engage in in-pair copulation at median intervals of about every 3 days (72 h; Britain: U.K. Family Planning Research Network 1988; U.S.A.: Kinsey et al. 1953). Our own nationwide survey produced a slightly longer median interval of 90 h (inter-quartile range = 51–184 h; $N = 2835$) whereas the 34 couples in our in-pair copulation and flowback studies showed a slightly shorter median interval of 62 h (inter-quartile range = 43–119 h).

Table VI shows the first IPC–IPC ejaculate produced by each of 15 males in relation to % time with partner and inter-copulation interval. Even for this small subset of our data, when the influence of inter-copulation interval is removed by blocking, % time together is still significantly negatively associated with the number of sperm ejaculated during in-pair copulation ($z = -1{\cdot}854$, $P = 0{\cdot}032$). The converse Meddis analysis (blocking to remove the influence of % time together) shows that time since last in-pair copulation is also a significant influence on the number of sperm ejaculated ($z = 1{\cdot}976$, $P = 0{\cdot}024$). We conclude that % time together and inter-copulation interval have significant but independent influences on the number of sperm ejaculated during in-pair copulation.

Next, we calculated the least squares regression line for the 15 IPC–IPC ejaculates in Table VI relating number of sperm inseminated during in-pair copulation to % time together (Table II; equation 2). We assumed a straight-line relationship (see Baker & Bellis 1989a). We then applied equation (2) to the complete set of 50 IPC–IPC ejaculates and calculated residuals for each ejaculate. This procedure removes the confounding influence of % time together.

Figure 1 shows the relationship between the residuals from equation (2) and time (h) since last in-pair copulation. Five males produced more than one IPC–IPC ejaculate (total = 40 ejaculates). We divided these ejaculates according to time since last in-pair copulation (≤ 24 h; 25–48; ... 169–192 h)

Table VI. First IPC–IPC ejaculate contributed by each of 15 males in relation to % time together and inter-copulation interval

Male	Time since last IPC (h)	Time with partner since last IPC (%)	No. of sperm inseminated ($\times 10^6$)	No. of sperm inseminated/h since last IPC ($\times 10^6$)
A	60	20	570	9·5
B	149	98	219	1·5
D	70	50	485	6·9
F	168	50	516	3·1
K	48	20	448	9·3
L	32	100	60	1·9
M	48	2	282	5·9
N	56	37	455	8·1
P	31	30	76	2·5
Q	38	45	228	6·0
R	48	75	76	1·6
T	54	75	109	2·0
U	32	60	295	9·2
V	48	80	341	7·1
Y	44	75	225	5·1

IPC = in-pair copulation. IPC–IPC ejaculate = in-pair copulation ejaculate with no inter-IPC masturbation.

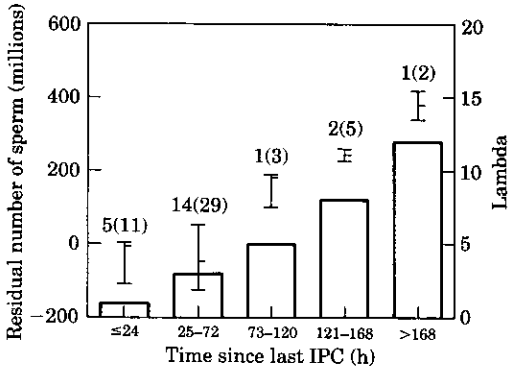

Figure 1. Variation in number of sperm ejaculated during in-pair copulation with time since last in-pair copulation. Bars show the median and inter-quartile range residual number of sperm after application of equation (2). Histograms show lambda coefficients which maximize z in a Meddis' specific test after blocking by couple. Numbers above bars: number of pairs (number of in-pair copulations).

and block by male (five blocks) to test for within-male variation. Time since last in-pair copulation has a significant positive association with the number of sperm ejaculated during in-pair copulation ($z = 2{\cdot}232$, $P = 0{\cdot}013$). z is maximized by rank order lambda coefficients which specify that, within the range of inter-copulation intervals in our data (1–192 h), males continued to increase the number of sperm inseminated the longer the time since the last in-pair copulation. We cannot determine from our samples whether the number inseminated would level off after in-pair copulation intervals greater than 8 days (192 h).

The multiple regression that best describes the number of sperm inseminated in terms of time since last in-pair copulation and % time together (first in-pair copulation per couple; Table VI) is equation (3) (Table II). Although equation (3) is the best to express the association between sperm number, % time together and time since last in-pair copulation, some later discussions are facilitated by considering the number of sperm inseminated during in-pair copulation for each hour since the last in-pair copulation. This rate is not fixed but is significantly negatively correlated with % time together ($r_S = -0{\cdot}587$, $P = 0{\cdot}011$, one-tailed; data from Table VI). When % time together is $\leqslant 25\%$, the rate of insemination is 9·3 (inter-quartile range = 5·9–9·5) million sperm/h since last in-pair copulation. Percentage times together of 25–75% and $\geqslant 75\%$ are associated with insemination rates of 6·5 (inter-quartile range = 3·1–8·1) and 2·0 (1·6–

5·1) million sperm/h, respectively (from data in Table VI).

Reproductive Value of Female and Variation in Number of Sperm Inseminated

We applied equation (4) to our 84 in-pair copulation (50 IPC–IPC; 34 MAS–IPC; see section on masturbation) ejaculates and calculated residuals. These residuals were then used as the dependent variables for tests of the prediction that the number of sperm inseminated should vary according to the reproductive value of the female.

Seven couples returned 30 in-pair copulation ejaculates complete with information on the occurrence and timing of female orgasm during the copulation sequence. We could find no evidence that the numbers of sperm (residuals) inseminated varied in relation to occurrence and timing of orgasm. There was no significant heterogeneity across six categories (no orgasm; orgasm during foreplay; during copulation but before ejaculation; during ejaculation; during copulation but after ejaculation; after copulation) whether we analysed the first sample in each category by each couple ($H_5 = 3{\cdot}662$, $P = 0{\cdot}602$) or blocked by couple to test for within-couple variation ($H_5 = 5{\cdot}575$, $P = 0{\cdot}350$). Exploratory post-hoc analyses comparing different orgasm categories with each other (e.g. orgasm versus no orgasm; orgasm during foreplay versus no orgasm during foreplay; etc.) and using different dependent variables (raw data; residuals from equation 5; etc.) also failed to find any significant differences in number of sperm inseminated. We conclude that the number of sperm inseminated does not vary in association with variation in the occurrence and timing of female orgasm.

Similarly, we could find no evidence of variation in the number of sperm inseminated at different phases (I, II, III; see Introduction) of the menstrual cycle. We restricted analysis to those five pairs (52 ejaculates) who provided multiple samples while the female was not using oral contraceptives and who was thus on an unaltered hormonal cycle. Blocking by male to test for within-male response, neither analysis of residuals ($z = -0{\cdot}630$, $P = 0{\cdot}736$) nor of actual sperm numbers ($z = 0{\cdot}191$, $P = 0{\cdot}425$) shows a significant positive association with the relative fertilities of the different phases.

Of the 23 first ejaculates provided by each male, 14 were collected at a time when the female partner was also taking an oral contraceptive. There was no significant difference in the number of sperm (residuals) inseminated by males whose female partner was taking an oral contraceptive and those whose partner was not ($H_1 = 1{\cdot}433$, $P = 0{\cdot}230$). The trend was for females to be inseminated with more sperm when they were taking oral contraceptives. Three of the males produced ejaculates ($N = 34$) before and after their female partner changed from taking to not taking an oral contraceptive or vice versa. Blocking by male to test for within-male response, there is no significant difference in number of sperm (residuals) inseminated ($H_1 = 0{\cdot}305$, $P = 0{\cdot}588$). The trend was for females to be inseminated with more sperm when they were not taking oral contraceptives.

In contrast to the failure of predictions that the number of sperm inseminated should vary according to female orgasm pattern and/or probability of conception, the prediction that the number inseminated should be a function of female body size is strongly supported. There is significant heterogeneity between the 24 pairs who contributed in-pair copulation samples in the number of sperm inseminated during in-pair copulation ($H_{23} = 38{\cdot}50$, $P = 0{\cdot}022$; Table VII). Using the residuals from equation (4) as the dependent variable, the different couples as samples, and stature measurements (Table VIII) as lambda coefficients, we tested the prediction that there would be a positive association between female body size and between-pair variation in number of sperm inseminated (Fig. 2). A very significant association was found (Table IX), female weight showing a slightly greater association with sperm number than height. Comparison of pairs with the influence of female weight removed (residuals from equation 5; Table II), shows that there is no longer a significant heterogeneity in the number of sperm inseminated during in-pair copulation ($H_{23} = 29{\cdot}354$, $P = 0{\cdot}173$).

The Dynamics of Male Self-masturbation

Pattern of timing of masturbation

Figure 3 shows the frequency distribution of in-pair copulations preceded by male masturbation in relation to inter-copulation interval. When the inter-copulation interval was less than 72 h (3 days), the incidence of masturbation by males was low (< 5%). There was then a sharp rise to around 50% once time since last in-pair copulation exceeded 96 h (4 days). All 18 of the in-pair copulations for which the inter-copulation interval was more than

Table VII. Median observed and residual number of sperm ejaculated during in-pair copulation by 24 pairs

		No. of sperm ($\times 10^6$)			
		Observed		Residuals (from equation 4)	
Pair	*N*	Median	(Inter-quartile range)	Median	(Inter-quartile range)
A	4	514	(220–570)	80	(−59 to 92)
B	27	393	(244–507)	81	(1 to 133)
C	2	305	(301–308)	−174	(−222 to −126)
D	1	485		162	
E	1	422		−127	
F	1	516		3	
G	1	244		293	
H	2	65	(46–83)	−140	(−531 to 251)
I	1	525		−95	
J	1	55		44	
K	1	448		66	
L	3	39	(2–60)	−233	(−407 to −233)
M	1	282		−161	
N	22	175	(128–231)	−56	(−150 to 15)
O	1	213		−179	
P	1	76		−239	
Q	1	228		−50	
R	1	76		−119	
S	1	87		−129	
T	3	161	(109–205)	63	(−98 to 63)
U	3	283	(193–295)	80	(24 to 80)
V	2	182	(32–341)	86	(9 to 163)
Y	1	225		38	
AB	2	242	(173–310)	−109	(−148 to −70)

240 h (10 days) were preceded by the shedding of sperm through masturbation. When masturbation did occur, there was rarely a gap of more than 72 h (3 days) between in-pair copulation and the last masturbation (Fig. 4). On over 50% of occasions, this time interval was less than 48 h (2 days).

We conclude that when time since last copulation exceeds 72 h, males become increasingly likely to shed sperm through masturbation before they next copulate. On the majority of occasions, their last masturbation is within 48 h of their next in-pair copulation.

Number of sperm ejaculated during masturbation

We could find no association between the percentage of time a male had spent with his partner since their last in-pair copulation and the number of sperm ejaculated during either: (1) self-masturbation in the absence of a female ($r_S = -0{\cdot}193$, $N=20$, $P=0{\cdot}415$, two-tailed); or (2) masturbation (by self, partner or both) in the presence of a female ($r_S = 0{\cdot}190$, $N=8$, $P=0{\cdot}762$, two-tailed; data from Table X; cf Baker & Bellis 1989a). There is no significant difference between the two correlation coefficients ($z=0{\cdot}762$, $P=0{\cdot}448$, two-tailed, *z*-transformation test). Six males contributed masturbation ejaculates under both circumstances (female present, $N=17$; female absent, $N=24$). Blocking by individual male to test for within-male variation, there is no significant difference in the number of sperm ejaculated according to whether the female partner was present or absent ($H_1 = 1{\cdot}088$, $P=0{\cdot}297$). The non-significant trend is for more to be ejaculated when the female was present. Thus, for the remainder of this analysis, no distinction is made between whether the female partner was present or absent.

The number of sperm ejaculated during masturbation shows a highly significant correlation with time since the male's last ejaculation, both between males (analysis of first sample from each male:

Table VIII. Age and stature details for males and females of all pairs who contributed in-pair copulation and masturbation ejaculates

	Female			Male			
Pair	Age (years)	Height (cm)	Weight (kg)	Age (years)	Height (cm)	Weight (cm)	Testes (cm^3)
A	25	170	64	25	188	95	28
B	24	175	58	44	180	79	20
C	22	180	57	20	185	76	—
D	27	183	66	30	183	67	—
E	26	163	54	25	183	67	14
F	30	166	59	32	175	73	18
G	20	173	63	31	180	75	31
H	21	164	57	24	175	70	15
I	20	155	56	18	178	75	23
J	21	163	54	28	173	68	—
K	31	170	57	31	180	76	—
L	27	152	52	31	174	67	7
M	19	163	54	19	163	57	12
N	19	163	54	22	185	73	17
O	22	165	54	20	180	70	12
P	21	170	53	21	180	67	—
Q	21	170	54	21	172	71	—
R	21	166	56	21	166	60	—
S	26	168	58	26	174	86	29
T	22	171	56	22	187	64	11
U	19	157	52	23	183	68	15
V	—	—	—	21	—	—	—
X	—	—	—	20	—	—	—
Y	—	—	—	20	—	—	—
AB	20	180	57	20	180	70	12

Measurements refer to time of contribution of first sample.

$r_S = 0{\cdot}558$, $N = 22$, $P = 0{\cdot}003$, one-tailed) and within males ($z = 2{\cdot}853$, $N = 10$ males, 55 ejaculates, $P = 0{\cdot}002$). z is maximized by lambda coefficients which specify that the number of sperm ejaculated continued to increase linearly with time since last ejaculation, at least up to 9 days (216 h) after last ejaculation. The best fit to the masturbation data in regression analysis (using only the first masturbation ejaculate produced by each of our 22 males) is given by equation (1) (Table II).

We applied equation (1) to our full set of 67 masturbation ejaculates, then calculated residuals. Seven males produced ejaculates in both IPC–MAS (masturbation preceded by in-pair copulation) and MAS–MAS (masturbation preceded by a further masturbation) categories. Blocking by male to test for within-male variation, there is no significant difference between the residual number of sperm in IPC–MAS and MAS–MAS ejaculates ($H_1 = 1{\cdot}364$, $N = 7$ males, 49 ejaculates, $P = 0{\cdot}241$). The non-significant trend is for males to ejaculate more when masturbations were preceded by a masturbation than when preceded by an in-pair copulation.

We conclude that the primary factor associated with the number of sperm ejaculated by a given male during masturbation is the length of time since the male's last ejaculation. The circumstances of the last and current ejaculation have no significant influence.

There is a just significant heterogeneity between males in the number of sperm ejaculated during masturbation when time since last ejaculation is controlled ($H_{21} = 33{\cdot}127$, $P = 0{\cdot}045$; residuals from equation 1; Table XI). However, when tested against measurements of male stature (Table VIII), these differences were not a significant function of male height ($z = 0{\cdot}916$, $P = 0{\cdot}180$), weight ($z = 1{\cdot}024$, $P = 0{\cdot}153$) or volume of testes ($z = -0{\cdot}066$, $P = 0{\cdot}526$). Only male age approached significance ($z = -1{\cdot}880$, $P = 0{\cdot}060$, two-tailed), the tendency

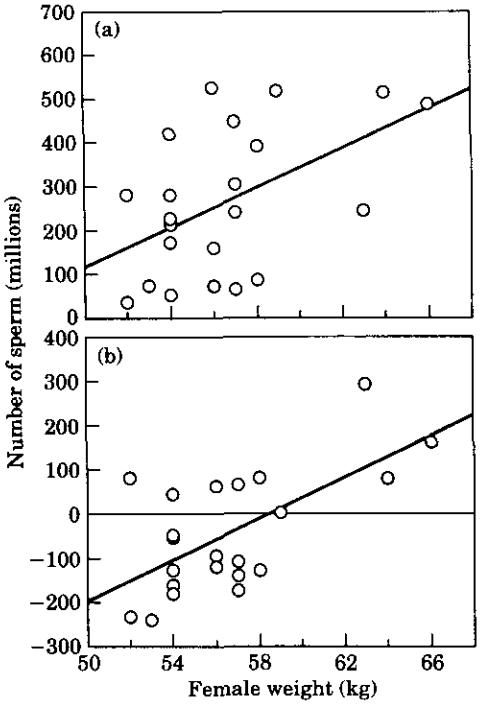

Figure 2. Variation in number of sperm ejaculated during in-pair copulation with weight of female. (a) Actual number of sperm: $r_S = 0{\cdot}484$, $P = 0{\cdot}012$; (b) residual number of sperm after application of equation (4): $r_S = 0{\cdot}504$, $P = 0{\cdot}009$.

Table IX. Analysis of number of sperm inseminated during in-pair copulation by 22 pairs in relation to male and female stature

Parameter	*N*		Meddis' test	
	Pairs	Ejaculates	*z*	*P*
Female weight	22	81	3·902	<0·001
Male weight	22	81	2·824	0·003
Female height	22	81	3·038	0·001
Male height	22	81	0·897	0·185
Testis volume	15	73	3·181	0·001

No. of sperm inseminated = residual from equation (4). Stature measurements from Table VIII.

being for older males to ejaculate fewer sperm during masturbation. We conclude that although males may differ in the number of sperm ejaculated during masturbation, the differences are not associated with any of the factors we have so far investigated.

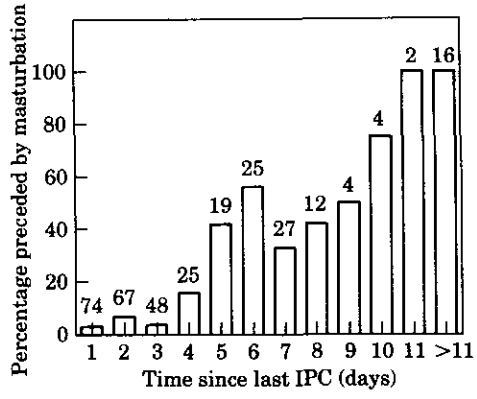

Figure 3. Frequency distribution of in-pair copulations (IPCs) preceded by male masturbation as a function of time since last in-pair copulation, based on 323 in-pair copulations recorded by 34 pairs. Numbers above bars: total number of in-pair copulations in time interval.

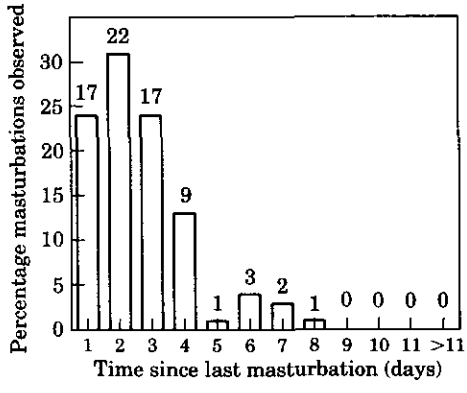

Figure 4. Frequency distribution of time intervals from male's last masturbation (MAS) to next in-pair copulation (IPC), based on 72 MAS–IPC events recorded by 34 pairs. Numbers above bars: total number of MAS–IPC events in time interval.

Masturbation and sperm at next in-pair copulation

During our study, 15 males produced 50 IPC–IPC ejaculates and 13 males produced 34 MAS–IPC ejaculates (MAS–IPC = in-pair copulations preceded by a masturbation; no cases of nocturnal emission were reported). Equation (3) (Table II) explains 73% of observed variation in sperm number in the first IPC–IPC ejaculates produced by each male and 76% of variation in all 50 IPC–IPC ejaculates. It is reasonable, therefore, to apply equation (3) to the 34 MAS–IPC ejaculates to predict the number of sperm that would have been

Table X. First masturbation ejaculate contributed in each of two circumstances (female partner present or absent) by 22 males

Male	Female absent			Female present		
	Time since last ejaculation (h)	Time with partner since IPC (%)	No. sperm ejaculated ($\times 10^6$)	Time since last ejaculation (h)	Time with partner since IPC (%)	No. sperm ejaculated ($\times 10^6$)
A	72	5	825			
B	103	68	415	53	81	235
C	81	33	168			
D	55	50	213			
E	24	30	61			
F	62	60	582			
G	24	90	20			
H	1	90	37			
I	9	37	12			
J	50	80	103			
K				24	75	205
L	20	5	150			
M	36	1	175			
N	48	8	52	70	30	87
O	15	20	112	14	11	155
P	23	30	110			
Q	34	62	228			
S	60	50	140			
T	36	20	102	48	70	343
U				17	65	112
X	48	1	213	27	1	261
Y	36	100	119	40	90	211

IPC = in-pair copulation.

inseminated had the male not masturbated in the inter-copulation interval (assuming that equation 3 is as applicable on the 34 MAS–IPC occasions as on the 50 IPC–IPC occasions). The difference between expected and observed numbers of sperm is then a measure of the influence of masturbation on the number of sperm inseminated during in-pair copulation.

When blocked by male to test for within-male variation there is a significant decrease in the difference between observed and expected number of sperm with increase in time since last masturbation ($z = 2{\cdot}274$, $N = 13$ males, 34 MAS–IPC ejaculates, $P = 0{\cdot}011$). z is maximized by lambda coefficients that specify that masturbation had no further influence on the difference between observed and expected number of sperm inseminated at the next in-pair copulation after 72 h. When masturbation preceded in-pair copulation by less than 72 h, the observed number of sperm in in-pair copulation inseminates was significantly lower than expected ($z = 3{\cdot}291$, $P = 0{\cdot}001$). After 72 h, however, there was no significant decrease ($z = -2{\cdot}087$, $P = 0{\cdot}982$). Allocating a value of 72 to times since last masturbation > 72 h, then performing regression analysis on the residuals (from equation 3) for the first MAS–IPC provided by each male allows calculation of a reduction factor. This reduction factor may then be used to modify equation (3) such that it becomes applicable to all in-pair copulation ejaculates whether or not they are IPC–IPC or MAS–IPC ejaculates. This modification of equation (3) gives equation (4) (Table II) which suggests that masturbation between in-pair copulations is associated with a reduction in the number of sperm the male inseminates into his female partner at the next

Table XI. Median observed and residual number of sperm ejaculated during masturbation by 22 males

		No. of sperm ($\times 10^6$)			
		Observed		Residuals (from equation 1)	
Male	*N*	Median	(Inter-quartile range)	Median	(Inter-quartile range)
A	6	195	(156–254)	117	(70 to 147)
B	17	323	(282–415)	−74	(−267 to −22)
C	1	168		−219	
D	1	213		−54	
E	1	61		−62	
F	1	582		283	
G	2	54	(20–87)	−60	(−103 to −18)
H	1	37		20	
I	1	12		−42	
J	1	103		−141	
K	1	205		82	
L	2	116	(82–150)	21	(−4 to 45)
M	1	175		−4	
N	2	70	(52–87)	−216	(−249 to −182)
O	8	97	(64–125)	−10	(−31 to 20)
P	1	110		−8	
Q	1	228		59	
S	2	118	(96–140)	−218	(−286 to −150)
T	6	236	(102–335)	−60	(−77 to 68)
U	1	112		21	
X	8	149	(83–185)	13	(−23 to 50)
Y	2	165	(119–211)	−23	(−60 to 14)

in-pair copulation by 228 million sperm minus 2·41 million sperm for every hour since last masturbation (up to 72 h).

Male masturbation and female sperm retention

In the rabbit, the number of sperm remaining in a female after flowback is a meaningful index of the number of sperm that attain functional positions within the female tract (Morton & Glover 1974a, b). In the following analysis, we assume that, on average, the same is true for humans. Full details of our flowback studies are given in our companion paper (Baker & Bellis 1993).

Combined with equation (4) for those couples for whom female weight was unavailable, equation (5) explains 72% of the variation in the first in-pair copulation ejaculate contributed by each of our 24 couples and 56% of the total sample of 84 in-pair copulation ejaculates. We modified equation (5) to a form (equation 6; Table II) that always gives biologically realistic (i.e. never negative) predictions of the number of sperm inseminated during any given in-pair copulation. Naturally, equation (6) should be used only within the ranges and limits encountered in our study. These ranges and limits are listed in Table XII. Extrapolation beyond these limits should be done only with caution.

Figure 5 shows the relationship between predicted (from equation 6) and observed numbers of sperm in in-pair copulation ejaculates. This equation accounts for 76% of the observed variation in the first in-pair copulation ejaculate contributed by each of the 23 males in our study, 51% of all subsequent samples ($N=61$) and 58% of the total data set ($N=84$). We assume that equation (6) (while not necessarily the best) is sufficiently accurate and robust to be used as a tool to predict the number of sperm inseminated during in-pair copulation for pairs involved in our study. Whether it is robust for other groups of subjects remains to be tested.

We used equation (6) to estimate the number of sperm that should have been inseminated into the female during each of the 121 non-pregnancy in-pair copulations from 11 couples for which we

Table XII. Range of parameter values for which equation (6) was calculated

Parameter	Measure	Minimum value	Maximum value	Imposed maximum
Time together between IPCs	%	1	100	100
Time since last IPC	h	1	2500	192
Time since last masturbation	h	1	186	72
Female weight	kg	52	66	
Observed no. sperm	($\times 10^6$)	2	692	692
Calculable no. sperm	($\times 10^6$)	−359	919	919

IPC = in-pair copulation. Mid-point of observed ejaculates = 350×10^6 sperm. When ejaculate parameter exceeds the value of the imposed maximum, the imposed maximum value should be used. When female weight is outside the range of 52–66 kg, equation (6) may no longer be valid.

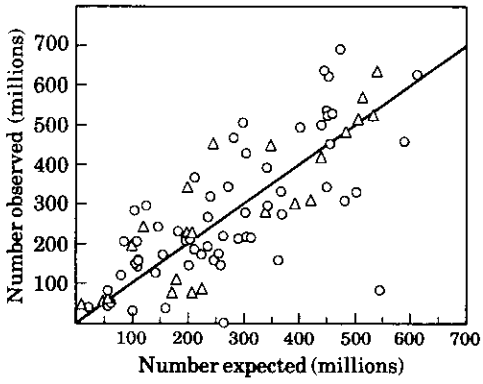

Figure 5. Number of sperm observed in 84 in-pair copulation ejaculates compared with the number predicted by equation (6). △: First sample contributed by each of 23 males; ○: subsequent samples. Diagonal line shows the expected 1:1 relationship.

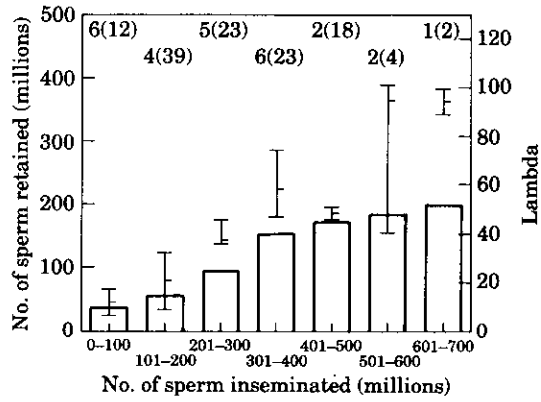

Figure 6. Influence of ejaculate size on number of sperm retained by the female during in-pair copulation. Number of sperm inseminated calculated from equation (6). Bars show median and inter-quartile range number of sperm retained. Histograms show lambda coefficients which maximize z in a Meddis' specific test after blocking by couple. Numbers above bars: number of females (number of flowbacks).

received flowback samples. Subtraction of the observed number of sperm ejected from the predicted number inseminated provides a measure of the number of sperm retained on each occasion.

Analysing just the first flowback from each couple, there is a significant positive correlation between the number of sperm predicted to be inseminated (equation 6) and both the number of sperm observed in the flowback ($r_S = 0{\cdot}655$, $P = 0{\cdot}026$, one-tailed) and the number calculated to be retained by the female ($r_S = 0{\cdot}791$, $P = 0{\cdot}004$, one-tailed). Using all 121 flowbacks and blocking by couple, we again find a significant increase in number of sperm retained with number of sperm inseminated ($z = 6{\cdot}666$, $P < 0{\cdot}001$), z being maximized by the lambda coefficients shown in Fig. 6. Over the whole range in our data, the more sperm the male inseminates, the more are retained.

We removed the influence of the number of sperm inseminated by the male in order to test for the relative retention of sperm by the female using the method described in detail in our companion paper (Baker & Bellis 1993). Briefly, we calculated the least squares regression of number of sperm retained on number of sperm inseminated, then calculated the residuals from that line for each in-pair copulation. Positive residuals indicate that the female retains an above average number of sperm; negative residuals that she retains a below average number. Actual regression lines and equations are given in Baker & Bellis (1993) along with a discussion of the merits of this measure of the female role

Table XIII. Median number of sperm retained and ejected by females following in-pair copulation as a function of whether the male's previous ejaculation was a copulation or masturbation

	Previous ejaculation							
	In-pair copulation				Masturbation			
Time since last ejaculation (h)	*N*	Sperm ejected ($\times 10^6$)	Sperm retained ($\times 10^6$)	Sperm retained (residual)	*N*	Sperm ejected ($\times 10^6$)	Sperm retained ($\times 10^6$)	Sperm retained (residual)
⩽24	7 (30)	21 (12–77)	64 (34–133)	61 (13 to 75)	3 (6)	121 (98–132)	120 (45–214)	55 (−20 to 69)
25–72	6 (26)	103 (85–130)	132 (42–180)	14 (−2 to 30)	3 (13)	167 (141–252)	155 (154–260)	−17 (35 to 14)
>72	5 (39)	186 (44–194)	203 (151–285)	−20 (−84 to 46)	1 (7)	224 (220–320)	68 (44–92)	−103 (−162 to −50)

Inter-quartile range is shown in parentheses. Format for sample sizes (*N*): number of females (number of flowbacks).

Table XIV. Influence of time since last ejaculation on number of sperm retained and ejected by females following in-pair copulation: results of Meddis' specific test on data in Table XIII

	Previous ejaculation					
	In-pair copulation ($N=97$)			Masturbation ($N=26$)		
	No. sperm ejected	No. sperm retained	Residual sperm retained	No. sperm ejected	No. sperm retained	Residual sperm retained
z	5·689	5·485	−1·888	3·429	−0·400	−1·805
P	<0·001	<0·001	0·029	<0·001	0·344	0·035

Positive *z*-values indicate that number increases with time since last ejaculation; negative *z*-values that number decreases. *P*-values for residual sperm retention are one-tailed against the specific hypothesis that a recent ejaculation improves sperm retention by reducing sperm age.

in sperm retention compared with the alternative measure of % retention.

Table XIII shows the number of sperm ejected and retained after in-pair copulation by females according to time since their partner's last ejaculation and whether that last ejaculation was the preceding in-pair copulation (IPC–IPC inseminates) or a masturbation (MAS–IPC inseminates). In Table XIV, the results are tested against the predictions of the sperm age hypothesis (see Introduction).

Whether the male's last ejaculation was an in-pair copulation or a masturbation, the number of sperm in the flowback increased significantly with increase in time since last ejaculation. The number of sperm we calculated to be retained by the female also increased with time since the male's last ejaculation if that ejaculation was during in-pair copulation but not if the male's last ejaculation was masturbatory. The number of sperm retained did not change significantly with time since last masturbation though the tendency was for more sperm to be retained the more recent the masturbation.

When we compare the number of sperm retained by the female following IPC–IPC and MAS–IPC inseminations, no differences are significant ($H_1 = 0{\cdot}201$, $P = 0{\cdot}659$; blocked by order). This remains true when blocked by time since last in-pair copulation ($H_1 = 2{\cdot}436$, $P = 0{\cdot}114$). On average, therefore, males suffer no disadvantage from masturbation in terms of the number of sperm retained by the female at their next in-pair copulation,

despite inseminating fewer (on average, by 228 million minus 2·4 million for every hour since last masturbation; equation 4). In fact, over all in-pair copulations, the non-significant trend is for more sperm to be retained when the male masturbates between copulations ($z=0·448$, $P=0·632$, two-tailed).

There is good support in Table XIV for the sperm age hypothesis. Assuming that the more recently the male has ejaculated, the younger the average age of sperm in the next ejaculate, there is a decline in residual sperm retention with age of sperm in both IPC–IPC and MAS–IPC inseminates. Over all inseminates, the greater relative retention of younger sperm is highly significant ($z=-3·039$, $N=11$ females, 121 in-pair copulations, $P=0·001$; blocked by female).

DISCUSSION

Partitioning of Sperm between Successive In-pair Copulations

There has been no previous study for humans of the relationship between time since last in-pair copulation and the number of sperm inseminated during in-pair copulation. However, there are four models of the possible relationship.

Fixed inseminate model

This assumes that males inseminate a relatively fixed number of sperm per in-pair copulation and are relatively unconstrained by rate of sperm maturation. On this model, the number of sperm inseminated at each in-pair copulation is relatively constant and the total number inseminated during a fixed interval is a function of the number of in-pair copulations during that interval. With some qualification, this is essentially the model assumed by Ginsburg & Rubenstein (1990) for zebras (*Equus* spp.).

Our analysis has demonstrated a significant increase in the number of sperm inseminated with increase in time since last in-pair copulation. As such, the data are clearly inconsistent with the 'fixed ejaculate' model. Nevertheless, the form of the relationship (equation 3; Table II) means that the total number of sperm inseminated through in-pair copulation during a given time interval is slightly greater if there are more in-pair copulations during that interval. Thus, if we assume male and female spend 100% of their time together, we calculate that a male inseminates 1372 million sperm during a complete (28 day) menstrual cycle of his female partner if the pair have four in-pair copulations compared with 1440 million sperm if they have eight in-pair copulations. Doubling the in-pair copulation rate thus increases the total number of sperm inseminated by 5%. If male zebra show the same pattern as humans, our data provide some support for Ginsberg & Rubenstein's (1990) assumption that the number of sperm inseminated is a function of in-pair copulation rate. However, our data do not support their assumption that in-pair copulation rate is more important than any other adjustment the male may be making. Thus, for humans, relative to four in-pair copulations per menstrual cycle with 100% time together, halving the % time together raises the total number of sperm inseminated per menstrual cycle by 50% compared with the 5% increase due to doubling the in-pair copulation rate.

Physiological constraint model

This model assumes that, at each in-pair copulation, males inseminate all of the stored sperm mature enough to be ejaculated. On this model, number of sperm inseminated at each in-pair copulation will be a function of time since last ejaculation and the rate at which sperm mature. Total number of sperm inseminated during a fixed interval, such as one oestrous cycle or other fertile phase, will be the number of sperm matured during that interval.

Our data are not consistent with this model. The relationship illustrated in Fig. 1 suggests an increase in number of sperm inseminated of only about 57 million sperm per day since the last in-pair copulation. Yet adult human males probably manufacture nearly 300 million sperm per day (Johnson et al. 1980). Moreover, the number of sperm inseminated during in-pair copulation for each hour since the last in-pair copulation is not fixed but is significantly negatively correlated with % time together. Even the greatest rate of insemination (9·3 million sperm/h since last in-pair copulation when couples spend less than 25% of their time together) is lower than the estimated rate of sperm production by humans of 12·5 million/h (Johnson et al. 1980). It thus seems likely that observed insemination rates are in some way strategic and not simply due to physiological constraint.

Parker's partitioning model

Parker (1984) assumed that a given number of sperm are available for insemination during one fertile phase of the female partner. He then identified circumstances in which the optimum strategy for the male would be to use these sperm during in-pair copulation in a series of smaller inseminations spread through the female's fertile phase rather than in a single large insemination at the beginning of that phase. His model predicts that in species, such as humans, with cryptic ovulation and a sperm life that is short relative to the inter-ovulation interval, males should show multiple insemination. On Parker's model, the total number of sperm inseminated during one fertile phase is relatively constant and independent of the in-pair copulation rate. Number of sperm per insemination is given by the total number of sperm available divided by the number of in-pair copulations during the phase. On average, therefore, there must be a positive association between inter-IPC interval and number of sperm inseminated, as we have shown.

The 'topping-up' model

On our own 'topping-up' model, the total number of sperm inseminated during a given time interval is not fixed. Instead, males attempt to maintain an optimum-sized population of sperm in their partner's tract as a defence against sperm competition. Optimum size of sperm population will be a function of the risk of sperm competition. Successive in-pair copulations thus become 'toppings-up'. The number of sperm inseminated is that necessary either simply to replace sperm lost through death and phagocytosis since last insemination and/or, if risk of sperm competition has changed, to adjust the total size of the sperm population. On this model, number of sperm inseminated during in-pair copulation is a function of time since last in-pair copulation and risk of sperm competition. As in Parker's model, the total number of sperm inseminated during a fixed interval will be relatively independent of the in-pair copulation rate (as long as the in-pair copulation rate is greater than zero) but, rather than be fixed, will be a function of the risk of sperm competition.

The data are consistent with this 'topping-up' model. Thus, total number of sperm inseminated during a fixed time interval increase relatively little with an increase in the number of in-pair copulations during that interval. Instead, males appear strategically to adjust the number of sperm with which they inseminate their partner according to time since last insemination. The number of sperm ejaculated during any given insemination increases with time since last in-pair copulation for at least the 8 days (192 h) that some active sperm are known to remain in the female tract (Austin 1975). Any in-pair copulation less than 192 h since the previous in-pair copulation is effectively, therefore, a 'topping-up' to some particular level, rather than a complete insemination in its own right. To what level the male tops-up the female depends on the risk of sperm competition. From equation (3) (Table II), if we assume an 8-day (192 h) inter-IPC interval (to allow all sperm from previous inseminations to die), males inseminate 389 million sperm/ejaculate when % time with the female is 100% compared with 712 million/ejaculate when % time with the female is only 5%.

One possible implication of our data is that the concepts of extra-pair and in-pair copulation may be irrelevant to male strategies of sperm adjustment. Perhaps, when a male inseminates a female, his strategic concern is not whether she is or is not his partner. Rather, the number of sperm inseminated may instead be determined simply by how long it is since he last copulated with that particular female (if ever) and the extent to which he has associated with her within the past 8 days (the active life of sperm she may already contain).

Our data on top-up rates at different levels of association between male and female allow us to make one further calculation. The rate of sperm production in humans (12·5 million/h; Johnson et al. 1980) should allow a male to inseminate: (1) six females in a group such that he could associate with them all simultaneously and continuously (because of the 'topping-up phenomenon' this would be independent of inter-copulation interval with each female); (2) two spatially separate females between whom he equally divided his time; or (3) one female with whom he spent 70% of his time while, during the other 30%, seeking occasional extra-pair copulations with other females with whom he spends relatively little time. All of these patterns are found in the anthropological literature (see Smith 1984).

Sperm Number and Female Reproductive Value

Our demonstration that individual male humans vary the number of sperm they inseminate according

to the proportion of time they have spent with the female (and hence the risk of sperm competition) is the first demonstration of intra-male variation for a mammal. As such, it adds to the now considerable body of evidence that, in accordance with sperm competition theory, males inseminate more sperm when the risk of sperm competition is higher. In contrast, the prediction that males should inseminate more sperm when copulating with females of higher reproductive value has met with much more mixed success.

As predicted, heavier females are inseminated with more sperm (Table IX). Even this apparent success, however, has the caveat that the association between sperm number and female body size may be an artefact due to the influence of some third factor, such as male stature. The data suggest male stature may not be important as Table IX shows that female body size, particularly weight, has a stronger association with sperm number than any corresponding measure of the males. From our current data set, however, we are statistically unable totally to rule out a separate influence of male stature, particularly testis volume (Table IX).

The best test, of course, would be to investigate whether any given male inseminates more sperm into larger females. However, during our study, only one male (male O) changed partners, moving from a larger female (female C; height 180 cm; weight 57 kg) to a smaller (female O; 165 cm; 54 kg). Data are minimal (Table VII; pairs O and AB) though the trend is at least in the direction expected. Median number of sperm inseminated decreased (absolute numbers from 242 million to 213 million; residuals from −109 million to −179 million; Table VII).

Detailed consideration of the interaction between male and female stature must await further study and more data. Procedurally, however, we could find no statistical justification for adding any stature parameter to our predictive equation (equation 5; Table II) other than female weight.

In contrast to the positive association between sperm number and female weight, no association emerged between the number of sperm inseminated and the other measures of female reproductive value we considered. One possible explanation for this apparent failure of sperm competition theory is that whereas males can reliably judge female body size they cannot obtain reliable information concerning female orgasm and probability of conception.

As far as female orgasm is concerned, there is a major difference in sperm retention between a copulation involving no female orgasm and one with a female orgasm after male ejaculation (Baker & Bellis 1993). Yet unless, on ejaculation without a female orgasm, males could predict whether the female will or will not experience orgasm before flowback, there would seem to be no opportunity for the male to adjust sperm number appropriately. Similarly, the difference in sperm retention between an orgasm during foreplay and an orgasm within a minute of ejaculation is also major (Baker & Bellis 1993). However, in this context, the time available for the male to adjust sperm number is very short (a few minutes or even seconds). Add to these difficulties the possibility of the female 'faking' an orgasm and the opportunity of the male to make appropriate strategic adjustments in sperm number in response to the occurrence and timing of female orgasm seems minimal.

Similarly, there is some doubt over whether males can actually perceive when a female is fertile. The hypothesis that females produce pheromones that lead to synchronizaton of menstruation and which could be used by males to detect phase of cycle has been discounted (Little et al. 1989). Most authors now assume that ovulation by humans really is cryptic (e.g. Small 1989) and that such crypsis is a strategy which allows the female more control over the timing of copulations with different males than might be possible if a male partner could detect ovulation. We have shown previously that whereas in-pair copulations peak at the least fertile phase (phase III) of the menstrual cycle, extra-pair copulations, particularly double-matings, peak during the most fertile phase (phase II; Bellis & Baker 1990). Now it seems that in-pair males also fail to adjust the number of sperm inseminated at different phases of their partner's menstrual cycle. However, rather than represent a failure of sperm competition theory, these data could perhaps provide further indication that menstrual fluctuation in fertility of female humans really is cryptic to their male partner (Small 1989; Bellis & Baker 1990).

Finally, given the recent origin of modern contraceptive techniques, it is perhaps not surprising that males may not have the psychophysiological repertoire to vary the number of sperm inseminated according to the use of oral contraceptives by their female partner. Even if male humans had such a repertoire, adjustment of sperm number may not be advantageous. Even if the female has taken oral

contraceptives up to the moment of copulation, the male cannot be certain that she will continue to do so for the next 5–8 days while the sperm he inseminates are competitive. Thus, males can never assume that the sperm being inseminated have no chance of entering competition or no chance of fertilization.

Perhaps, therefore, our failure to find any association between number of sperm inseminated and either orgasm pattern, stage of menstrual cycle, or use of oral contraceptives should not be considered a failure of sperm competition theory. Rather it could reflect the extent to which males cannot obtain the information necessary for optimum adjustment of sperm number.

Masturbation, Costly Ejaculates and Sperm Number

Our analysis of the dynamics and consequences of masturbation suggests that the behaviour is a functional strategy. The function, however, appears to be more to increase the 'fitness' of sperm retained by the female at the next in-pair copulation than to increase the number retained.

As time since last copulation increases beyond 72 h, males become increasingly likely to masturbate (Fig. 3) and are most likely to do so less than 48 h before their next in-pair copulation (Fig. 4). One implication is that they could be anticipating the next in-pair copulation. In any case, the result is a significant improvement in the residual number of sperm retained by the female at the next in-pair copulation (Table XIV). Thus, masturbation appears to remove from the next ejaculate sperm that are either less acceptable to the female and/or less able to attain a 'secure' position in the female tract. Either way, our analysis of flowbacks implies that the sperm removed by masturbation are in some way suboptimal and largely destined to be ejected by the female. Table XIV strongly implies that the primary, though not necessarily the only, way in which these sperm may be suboptimal is that they are older.

Suppose, at least for descriptive convenience, that sperm move along the male's production line on a 'conveyor belt' system and that ejaculation uses the oldest section of sperm. After development and maturation in the seminiferous tubules, vas eferens and early part of the epididymis (Mann & Lutwak-Mann 1981), sperm pass the point at which they are eligible for ejaculation at the rate of 12·5 million/h (Johnson et al. 1980). They then accumulate in the wider, distal end of the vas deferens. Some of these waiting sperm may be removed by phagocytosis (Mann & Lutwak-Mann 1981). At ejaculation, a segment of the waiting sperm is moved from the vas deferens and mixed with seminal fluid (Mann & Lutwak-Mann 1981).

The rate at which sperm become suboptimal through waiting to be ejaculated at the storage end of the conveyor belt is unknown. It should be less than 12·5 million/h otherwise there could be no build-up of usable sperm waiting for ejaculation. According to equation (1) (Table II), an extra 4·63 (say 5) million sperm are shed during masturbation for every hour since the male's last ejaculation. It is not unreasonable to suppose that this approximates to the rate at which unused sperm become suboptimal while waiting to be ejaculated (though, to this number, should be added the unknown number that are phagocytosed and voided in the urine).

We have shown that when a male inseminates a female he does not ejaculate all of the sperm available but instead inseminates a number that is a function of the risk of sperm competition inside that female. Thus, some sperm which could have been used are conserved and, we presume, move up on the conveyor belt to be next in line for ejaculation. The important question is why these sperm should be conserved instead of being inseminated at the current copulation. Essentially, interpretation rests on whether restraint generates: (1) a future advantage through use of the conserved sperm; and/or (2) an advantage or disadvantage at the current copulation.

Is there an advantage in saving sperm for a future copulation?

The sperm conserved by a male through restraint at the current copulation have four possible destinies. They may be: (1) inseminated into the same female in a future copulation; (2) inseminated into a different female in a future copulation; (3) shed in a future masturbation or nocturnal emission; or (4) phagocytosed or voided in the male's urine.

Clearly, if the conserved sperm are eventually shed or voided, their conservation was of no future advantage. Indeed, any cost attached to post-copulation storage and then shedding renders their conservation a disadvantage. Phagocytosis may recoup some of this cost. However, only if the

sperm are eventually inseminated into a female is there any real chance that their conservation could have been an advantage. In part, therefore, the value of conservation depends on the probability that the conserved sperm will be inseminated into a female rather than be shed or voided. In part, also, it depends on the value of the sperm for fertilization in a future copulation relative to what would have been their value in the present copulation.

We consider first the possible value of conserving sperm for a future copulation with the same female. For each hour's delay before the next copulation, at least 5 million of the conserved sperm will become suboptimal and, even if inseminated into the female at the pair's next copulation, will probably be ejected in the flowback. At least these sperm, therefore, were of no future value. Our data show that males top-up their female by between 2 million and 9 million sperm (depending on the proportion of time the pair are together) for each hour between copulations. Yet new sperm are becoming available at the rate of 12·5 million/h, more than enough to top-up the female at the next copulation, no matter what proportion of time the pair have been together. It seems unlikely, therefore, that males conserve sperm at one copulation for use at some future copulation with the same female.

This conclusion could be complicated by the possibility that, if the female subsequently engages in extra-pair copulation, the male (as for birds: Birkhead & Møller 1992) may need to show rapid 'unscheduled' in-pair copulation and inseminate large numbers of sperm to counteract the certainty of sperm competition. However, unlike birds which show a clear second male advantage (Birkhead & Møller 1992), mammals may show first male (house mice, *Mus musculus*), last male (prairie voles, *Microtus ochrogaster*) and often no order effects (rats and swine, *Sus scrofa*; see Dewsbury 1984), in which case, the male has little to gain from conserving sperm for insemination after the female has engaged in extra-pair copulation. This is especially so if any sperm conserved have, through greater age, a high probability of being ejected in the flowback.

The only possible use for conserved sperm, therefore, is to increase the chances of securing fertilization of a different female. To be beneficial, the conserved sperm must increase the chances and/or value of fertilization of the second female by more than they would have increased the chances and/or value of fertilization of the first female. A major factor will be the relative probability of sperm competition in the two females. However, even when the conserved sperm would be more beneficial in the second female than the first, this greater benefit has to outweigh three other factors: (1) the cost of storage; (2) the conserved sperm would be younger when inseminated into the first female; and (3) the conserved sperm must be inseminated into the second female before they become suboptimal, are shed, or are inseminated into the first female. As an initial approximation, they have at most about 3 days (median inter-copulation interval and time to increase in probability of masturbation; Fig. 3).

Without knowing the relative costs and benefits of these different parameters, no decision can be reached. Until it can, we have at least to entertain the possibility that conserved sperm are of no future advantage to the male and that the advantage of restraint may derive, not from economy and conservation, but from some direct benefit at the current insemination.

Is restraint an advantage or disadvantage at the current copulation?

There are several possibilities why males could use restraint to gain maximum advantage from the current copulation, irrespective of what happens in the future to any sperm conserved.

Our analysis of ejaculate adjustment has identified two main elements to male strategy. First, successive in-pair copulations are 'toppings-up' to some maximum level that is lower when risk of sperm competition is also lower. Second, masturbation seems to be a strategy to increase the fitness (perhaps longevity, competitiveness and/or fertility) of the sperm retained by the female at the next in-pair copulation without increasing the number retained. The overall impression is that there is some disadvantage to a male in placing too large a population of sperm in his partner's tract.

No data exist for any mammal on the relationship between large numbers of sperm in the female tract and the probability of fertilization. However, a known correlate of fertility impairment in humans is polyzoospermy (ejaculation of too many sperm; Wolf et al. 1984). At present, clinical diagnosis places the lower level of polyzoospermy at 250×10^6 sperm/ml of ejaculate (when inter-ejaculation interval is about 72 h and ejaculates are collected during masturbation). With an average ejaculate volume of about 3 ml, this density is equivalent to

an ejaculate containing about 750 million sperm. Why polyzoospermy should lead to impaired fertility is unknown. Apart from their concentration of sperm, polyzoospermic ejaculates have clinically normal parameters and, as long as concentration around the egg is controlled, their sperm fertilize eggs in vitro.

Our own data show that the more sperm a male inseminates, the more are retained (Fig. 6). It is also known that, in rabbits, the more sperm retained, the more are found at all positions throughout the female tract (Morton & Glover 1974a, b). The implication is that, on average, the more sperm are inseminated the more arrive at all positions in the female tract including, presumably, around the egg.

In vitro studies show clearly that there is an optimum sperm:egg ratio in the vicinity of the egg, above which the probability of obtaining a viable zygote declines. Thus, in laboratory mice the probability of fertilization peaks (78%) at sperm:egg ratios of about 16 000:1 (Tsunoda & Chang 1975). Increasing the sperm:egg ratio about ten-fold decreases the probability of fertilization by more than 50%. The optimum sperm:egg ratio for humans in vitro is around 50 000:1 (see Lee 1988).

There are at least two potential disadvantages of a high sperm:egg ratio. First, above a certain ratio, enzymes released by sperm have an increasing chance of killing the egg (Adams 1969). Second, the presence of too many sperm around the egg could lead to polyspermic fertilization and a non-viable zygote. In rats and rabbits, higher concentrations of sperm at the site of fertilization are associated with larger numbers of sperm in eggs (Braden & Austin 1954). In humans, the incidence of polyspermy in vitro is directly related to the concentration of sperm (Simpson et al. 1982; Wolf et al. 1984). In vivo, 10% of all first trimester abortions are polyploid (Simpson et al. 1982). A retrospective study of 1499 spontaneously aborted fetuses showed that 39% had abnormal karyotypes of which 25% were polyploid (Boue et al. 1975; see also Wolf et al. 1984). In other mammals, level of polyspermy in vivo is around 2% (Austin 1961).

Conclusion

We suggest that in the presence of sperm competition, a male's chances of fertilizing a female are increased by increasing sperm number but, in the absence of sperm competition, his chances are increased by decreasing sperm number to some optimum level. We suggest further that this latter factor (the optimum sperm number in the female tract for fertilization in the absence of sperm competition) could be a major constraint to insemination of too many sperm at any given copulation. On this model, the primary trade-off in determining ejaculate size is between the probabilities that the male will fertilize the female if the inseminate does or does not encounter sperm competition. Optimum number of sperm is thus determined for each inseminate simply by the risk of sperm competition.

At present, we cannot determine the relative importance of this factor and any constraint on sperm numbers due to the cost of producing ejaculates (Dewsbury 1982). Inevitably, ejaculate cost must have been a factor in the evolution of species-specific rates of sperm production. It is possible, however, that at least for mammals ejaculate cost could be less important than the factors discussed here in influencing restraint over the number of sperm inseminated on any given occasion.

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