Reproductive Activity in Relation to Male Dominance and the Likelihood of Ovulation in Rhesus Monkeys

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Summary. Data on reproductive activity in one group of free-ranging *Macaca mulatta* were analysed in an attempt to assess the explanatory power of male dominance for mate selection when male reproductive performance is weighted in relation to the likelihood of ovulation and conception. In the present study, ovulation was assumed to have taken place during the four-day period preceding the 'attractiveness breakdown', that is, the moment in the menstrual cycle presumed to coincide with the onset of the luteal phase, the diagnostic criterion being the termination of consorting activity.

Positive correlations were found between the dominance rank of males and both their copulatory frequencies and the time which they spent consorting during ovulatory periods. However, the comparison of the data with the predictions of a version of Altmann's (1962) 'priority of access model' shows that male rank does not explain all the variance in male reproductive activity. Deviations due to male abstention, male selectivity and female choice are discussed in the context of a number of asymmetries in the competitive ability of males (other than dominance) and in payoff from consorting. Female choice appeared to provide a payoff asymmetry which could not be easily overcome by the rebuffed suitor. This suggests that the observed positive correlation between male rank and reproductive performance resulted from male-male competitive interactions *acting concurrently* with the capacity of males to influence female choice (e.g. through interferences in the consortships of lower-ranking males).

Introduction

Observational studies focusing on the relative importance of male dominance as a factor regulating reproductive activity in multi-male primate groups fall into two categories depending on whether the reproductive performance of males could be weighted in relation to the likelihood of ovulation or not. Among the species for which this was possible (e.g. on the basis of the swelling stage of the sex skin) the importance of male dominance in mate selection was found to be species-specific, with reproductive performance correlating positively with rank among male baboons (Hall and DeVore 1965; Hausfater 1975; Seyfarth 1978; Packer 1979a; with the exception of Saayman 1971) but not among male chimpanzees (Tutin 1979). The evidence on the relation between male dominance and reproduction in species (mostly macaques) where stages of estrus could not be differentiated is more equivocal. While Carpenter (1942), Conoway and Koford (1964), Kaufmann (1965), Lindburg (1971), Tokuda (1961/62), Hanby et al. (1971), Stephenson (1974), Enomoto (1974), Taub (1980) and Struhsaker (1967) all reported that higher-ranking males were more active sexually in rhesus, Japanese and Barbary macaques and in vervets, Loy (1971) and Eaton (1974) did not find such a relation and Drickamer (1974) reported that although he found a positive correlation between male rank and reproductive activity in rhesus monkeys, this correlation vanished when male differential observability was controlled for. The latter finding suggested that the importance of dominance in reproduction might have been greatly overemphasized in studies where males were differentially observable. However, recent paternity exclusion analyses based on biochemical data have revealed that male rank could be a good

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predictor of reproductive success (Duvall et al. 1976; Smith 1980, 1981; Witt et al. 1981).

The present analysis bears upon data on reproductive activity in one group of provisioned rhesus monkeys ranging freely over the island of Cayo Santiago, Puerto Rico. Its aim is to assess the explanatory power of male dominance for mate selection when the reproductive performance of males is weighted in relation to the likelihood of ovulation. Because rhesus monkeys do not exhibit regular patterns of morphological changes associated with estrous stage, other criteria were used to delimit the period in the menstrual cycle when ovulation was most probable. A major assumption of this study is that ovulation is most likely to occur over the four-day period preceding the abrupt termination of consorting activity and female attractiveness. This assumption makes it possible to reassess the importance of male dominance for mate selection in a species where reproductive activity had so far been analyzed independently of stages of estrus.

In a first stage, reproductive *activity* is analyzed on the basis of time spent consorting, copulatory frequencies and consort interferences. A version of Altmann's (1962) 'priority of access model', which states that differences in the dominance rank of males can explain all the variance in male reproductive activity, is tested on the basis of time spent consorting during the presumed periods of ovulation. In a second stage, male reproductive *success* is estimated on the basis of copulatory frequencies and time spent consorting during the presumed conception periods of 18 females who conceived.

The emphasis on male dominance throughout this paper does not stem from the belief that this variable is the single, or most important, determinant of mate selection. Many studies have shown that male rank explains only part of the variance in male reproductive activity even in species where estrous stages can be differentiated and male dominance has a high explanatory value (e.g. Hausfater 1975; Packer 1979a). The purpose of the present focus on dominance is to make it possible to compare its explanatory value when male reproductive activity is analyzed in relation to the likelihood of ovulation and when it is not. The results are then discussed in the context of (i) other asymmetries in male competitive ability and (ii) asymmetries in payoff from consorting.

Materials and Methods

Study Site and Subjects. Cayo Santiago is a heavily forested, 38-acre island off the southeastern coast of Puerto Rico. In January 1978 there were 518 rhesus monkeys on Cayo Santiago, all descendants of a stock imported from India by C.R. Carpenter and introduced by him on the island in 1938. A detailed history of the population can be found in Altmann (1962), Koford (1965), Carpenter (1972) and Sade et al. (1977). The monkeys were free-ranging and organized into six naturally occurring social groups. The population was provisioned daily with commercial monkey chow, while water catchments insured a constant supply of water. Yearlings are trapped every year to be tattooed and ear-notched for individual recognition. All monkeys are known by age, sex and maternal relatedness, these records extending back to 1956.

The present analysis is based on data on group F, collected during the 1978 breeding season (end of July – end of November). At the end of the birth season in June 1978, group F consisted of four matrilines totalling 80 natal individuals and 17 non-natal males. Male membership varied greatly during the breeding season as a result of emigration and immigration. Well-defined, linear dominance relations could be determined from the distribution of submissive behaviors among mature males (data in Chapais 1981). Table 1 gives the sequence of rank orders for mature males during the breeding season. (Fourteen males that are not listed in this table were nevertheless present in group F for various periods of time during the breeding season. They all remained at the periphery of the group so that neither the duration of their stay nor their dominance rank could be assessed precisely. Most of them ranked below the males ranking lowest in Table 1.) Group F included 19 adult females (aged 4 or older) and 11 females aged 3 throughout the breeding season, for a total of 30 sexually mature females.

Sampling Methods and Behavioral Measures. At any moment in time during the breeding season, a number of females (up to 14) were receptive and consorted by males. Changes of consort partners occurred however, and the distribution of males among receptive females changed accordingly. Because time spent consorting (i.e. having priority of sexual access to a female) is an essential component of reproductive success, an important goal in the present study was to determine as precisely as possible the hour of the day at which changes of consort partners had taken place. Since most consortships were stable over several hours or several days (especially during the period when ovulation appeared most likely to occur), long periods of focal sampling (Altmann 1974) on one estrous female at a time would have been relatively inefficient in this respect. Accordingly, the observations were designed to maximize the circulation of observers in the group in order to obtain a number of point-samples separated by the shortest possible intervals for each estrous female.

The group was watched alternately by two observers (the author and a research assistant) from 07:15 to 11:45 h and from 13:00 to 18:00 h on weekdays, and from 08:00 to 13:00 h on Saturdays and Sundays. Data were recorded on checksheets. The 19 adult females were the main focus of attention since the present data were collected as part of a global study on adult female-female and male-female relationships begun in January 1978. Five-minute long focal samples were performed by the author on each adult female two or three times a day, following a random order of observation. The procedure used by the research assistant differed in that each adult female had to be localized twice every hour and observed for one minute. For their part, the 11 3-year-old females were localized every hour by either observer. Male-female interactions taking place during focal periods but not involving the focal female were also recorded. Observability samples were taken in an attempt to estimate the relative observability of individuals during such

Table 1. The sequence of rank orders for the mature males present in group F during the breeding season. N denotes a male born in group F

Rank of males	July 25–July 30	July 31–Aug. 5	Aug. 6–Aug. 14	Aug. 15–Sept. 3	Sept. 4–Sept. 10	Sept. 11–Sept. 19	Sept. 20–Nov. 30
1	415 (N)	415 (N)	415 (N)	415 (N)	415 (N)	580 (N)	580 (N)
2	580 (N)	580 (N)	580 (N)	580 (N)	580 (N)	EE	EE
3	EE	Z2	EE	EE	EE	TJ	TJ
4	TJ	339	TJ	TJ	TJ	1J	Z2
5	1J	433	1J	1J	1J	Z2	339
6	Z2	481	Z2	Z2	Z2	339	433
7	339	557	339	339	339	433	481
8	433	282	433	433	433	481	285
9	481	440	481	481	481	285	491
10	557	N8	557	285	285	491	557
11	282		282	557	491	557	282
12	440		440	282	557	282	284
13	N8		N8	284	282	284	4T
14				440	284	4T	279
15				4T	4T	279	N8
16				279	279	N8	
17				N8	N8		

concurrent sampling. On the 4th min of each period of observation, all the monkeys aged 3 or older that could be seen around the focal female were recorded. Finally, male-female interactions were recorded ad libitum outside focal periods.

The present analyses were performed on data from all sampling sources combined. Therefore, rates of copulations and consort interferences could not be obtained. However, within-individual comparisons, the use of observability measures and the stability of consortships all contributed to minimize this problem. Consort interferences have been described by Altmann (1962). Copulations include all instances of series mounts ending with ejaculation and all sightings of coagulated semen on a female's labiae, which could be attributed with certainty to specific males (criteria: the male had been seen series mounting the female or consorting her just before the sighting). The duration of consortships was estimated only for the 4-day period of the cycle when ovulation was assumed to have occurred. Altmann's (1962) 'priority of access model' was tested on only the first half of the breeding season (July 24–September 30) because the observability of the monkeys worsened considerably in October and November mainly as a result of changes in weather conditions. In any case, more than three-fifths of all estrous periods began and ended during the first half of the breeding season, and no estrous period extended from September to October (Fig. 1).

Results

The Timing of Ovulation

A consistent pattern observed in group F was the abrupt termination of estrous periods following intense consorting activity. The 'attractiveness breakdown' refers to the onset of changes indicating the return to anestrus. These transitions, which usually took place over one night, are thought to correspond to the passage from the follicular to the luteal phase of the menstrual cycle and to be

homologous to the onset of deturgescence of the sex skin in baboons. Their most striking feature, or diagnostic criterion, was the cessation of consorting activity. After the attractiveness breakdown, mating could occur sporadically but was mostly initiated by females. All males would then exhibit little interest in the female they were actively soliciting the day before.

The assumption that the attractiveness breakdown coincides with the onset of the luteal phase enables one to delimit the period of ovulation by backdating a few days from the onset of the attractiveness breakdown. Because laboratory studies indicate that fertilization in rhesus monkeys is most likely to occur over a period of two days (Catchpole and Van Wagenen 1978) shortly followed by a sharp decline in female receptiveness and attractiveness (Czaja and Bielert 1975; Keverne 1976), the period of ovulation (termed the OV-1 period) was defined as covering the four days preceding the attractiveness breakdown. Consortships were often observed on the day immediately following the OV-1 period that is, on the day of the onset of the attractiveness breakdown, but they were markedly less intense and of shorter durations (Fig. 1).

The assumption of a concordance between the OV-1 period and ovulation is supported by an examination of the temporal relation between the OV-1 periods and the approximate conception dates of the females who gave birth following the 1978 breeding season. The conception dates (indicated by dark circles in Fig. 1) were obtained by backdating 168 days (the mean duration of pregnancy in rhesus monkeys; Stolte 1978) from the

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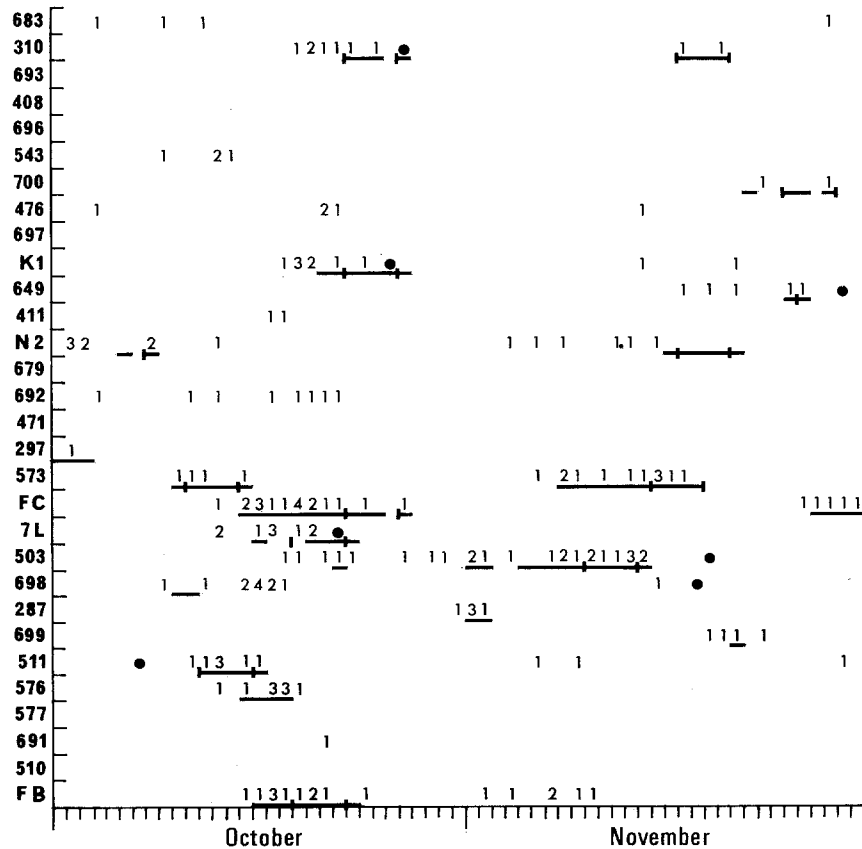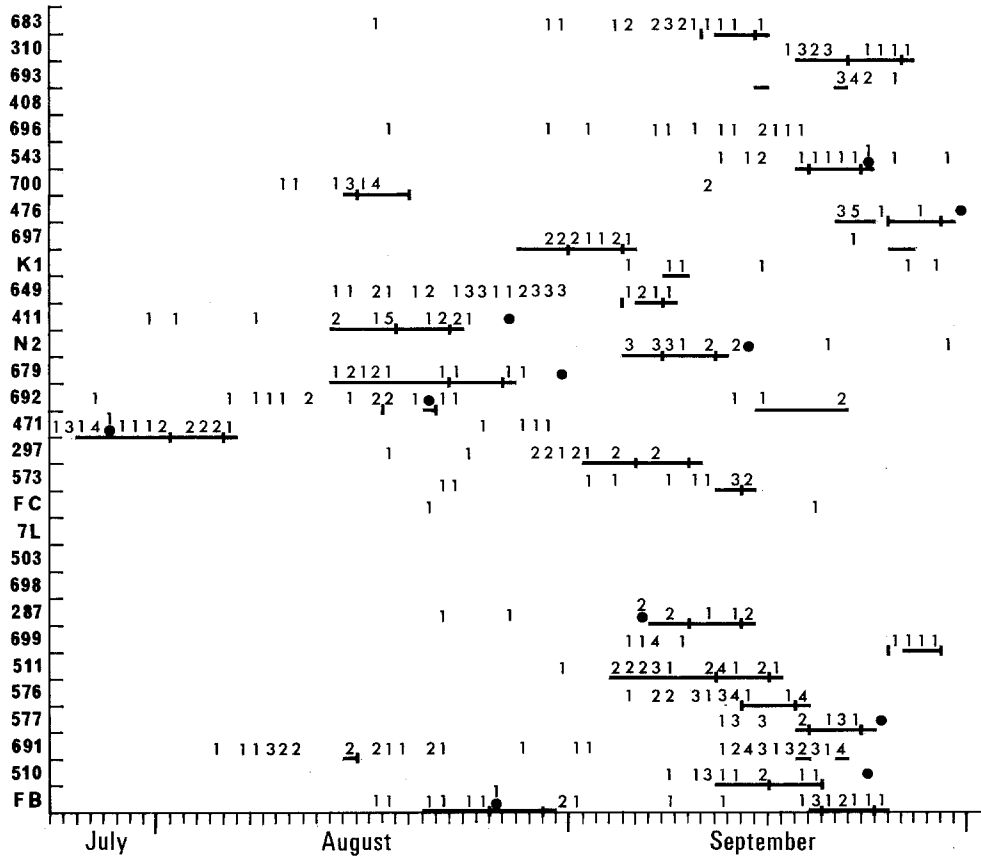
Fig. 1. The course of the estrous periods of the 30 sexually mature females (aged 3 or older) of group F during the 1978 breeding season. Females were consorted over the periods of time covered by *thick, continuous lines*. Figures refer to the daily number of recorded copulations per female (all sampling sources combined). *Bars* delimit OV-1 periods. *Dark circles* indicate approximate conception dates (the date of parturition minus 168 days). Females are arranged in ascending rank order (FB: alpha). The females whose names begin with a 6 were 3 years-old. All other females were 4 or older

known parturition dates. If the hypothesis of a concordance between OV-1 periods and ovulation is wrong that is, if conceptions actually occurred outside OV-1 periods, they should precede rather than follow OV-1 periods since relatively little reproductive activity took place after the attractiveness breakdown (see above and Fig. 1). An examination of Fig. 1 reveals that backdated conception dates precede OV-1 periods in only three cases (females 471, 287 and 511), whereas they coincide with OV-1 periods in four cases and follow them in the remaining 11 cases. Therefore, these data do not support the hypothesis that conceptions took place before OV-1 periods. The fact that many backdated conception dates follow the attractiveness breakdown suggests that in group F the average duration of pregnancies was greater than in the laboratory.

Male Dominance and Reproductive Activity

Consorting Activity

In order to verify if male rank explained all the variance in male consorting activity, a version of Altmann's (1962) 'priority-of-access model' was tested. Altmann's model originally stated that if (i) dominance consistently confers priority of access to females, (ii) females cycle independently of each other and (iii) the duration of estrus is a constant, it follows that the probability that at least r females are simultaneously in estrus equals the probability that a male of rank r will be in consortship, and is given by the cumulative binomial distribution. Translating this prediction into time, Hausfater (1975) pointed out that each such probabilities corresponded to the proportion of total estrous time when at least r females were simultaneously in estrus, and consequently to the proportion of total estrous time when a male of rank r had access to estrous females. In the present study, Altmann's model was tested on the basis of time spent by males consorting on the OV-1 days of all cycles (fertile + non-fertile) of the first half of the breeding season. The number of hours during which at least r females were simultaneously going through their OV-1 period and were consorted, was compared to the number of hours males that occupied rank r had consorted these females. The present test of the model did not require two of its original assumptions (females cycle independently of each other and the duration of estrus is constant) and included one additional prediction, namely that males would attempt to concentrate their reproductive effort on OV-1 days.
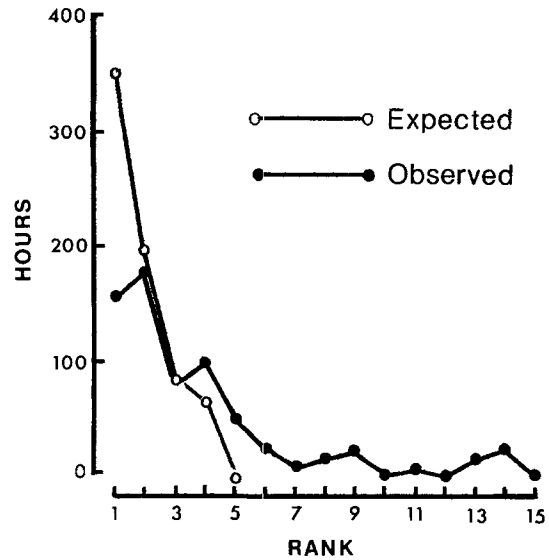

Fig. 2. Testing Altmann's 'priority of access model'. Expected and observed rank-specific numbers of hours during which males consorted females on the OV-1 days of all cycles of the first half of the breeding season (see text)

Figure 2 compares graphically the expected and observed rank-specific amounts of time spent by males in consortship with females on OV-1 days. Although there is a positive correlation between male rank and time spent consorting on OV-1 days ($r_s = 0.79$, $P < 0.01$), the alpha males consorted OV-1 females less often than expected whereas males ranking lower than third consorted these females more often than expected (χ^2 on first 4 ranks = 156.8, $P < 0.001$).

The behavior of males departed from the two main predictions of the present version of Altmann's model. First, males did not always consort the female which seemed the most likely to be ovulating. For example, male EE consorted the alpha female FB on 15 days during her first estrus even if females 679 and 411 (consorted by lower-ranking males) appeared more likely to be ovulating before the onset of FB's OV-1 period. Similarly, male 415 consorted female 297 at a time when female 697 appeared more likely to be ovulating; and male TJ preferred female 679 over female 411.

Second, male rank did not consistently confer priority of access to receptive females. In some cases, males abstained from consorting seemingly available females. For example, the alpha male 415 spent only one third of the 36 days on which he could have been active sexually (i.e., before he got tetanus) in consortships with group F females. On the 24 remaining days, females 471, FB, 700, 697, 411 and 697 went through their presumed period of ovulation and were consorted by other males.

Table 2. The distribution of all recorded copulations among males and females. *Vertical lines* delimit matrilines. Males and females are arranged in descending rank order (415: alpha male; FB: alpha female)

Males	FB	510	691	577	576	511	699	287	698	503	7L	FC	573	297	471	692	679	N2	411	649	K1	697	476	700	543	696	408	693	310	683	Total	Observability[a]
415	1													10				1	1												13	1,040
580						2		1		10	10	13	3	2	12	5	3	5	9	13	7	3	10	8				7	3		126	758
EE	21				1				1				11	4			9	1	2	6									3		56	879
TJ	4				5				1				3				7	4	1		5	4							3		37	719
1J	2				1	7										2		2	1												15	417
Z2	4			1	2	2	2	6		4				5	2	7		1							1				1		38	619
339	2	4		6		6	1			1			1	3															2		26	596
433		1	1	1	1	3	1		1				1										1						1	1	14	560
481						3	1							1	1										1	1	1				9	291
285	1	3	9	2	1	1								2			1	1	1												22	292
491	1	3			1	2				1												5	1	4					2		20	217
557	1	1	1	1												1	1	1				1	1	1	2					2	14	85
282	2	5		7		1	2							1	1								1						4	1	25	574
284				3		1				1				1																	6	291
440																															0	60
4T	2	6				1	1	1								15	6			1	2	1						1			37	311
279						1																									1	105
N8						1											6	2	12	1											22	106

a Frequency of appearance of males in the observability samples

Male EE also abstained for one week from consorting receptive females for a few days. In some other cases, females actively preferred lower-ranking male suitors. For example, females 510, 576 and 511, when receptive, each showed much interest (many approaches, followings and grooming episodes; few leavings) in males ranking lower than other male suitors which were in turn almost entirely responsible for the maintenance of proximity to these females. The rebuffed suitors usually followed the consort pair, directing friendly and submissive behaviors to the female.

Copulations

Table 2 presents the distribution of the 481 recorded copulations irrespective of estrous stage, cycle type and male differential observability. There is a positive correlation between male rank and such raw copulatory frequencies ($\tau = 0.45$, $P < 0.01$). (Although male 415 was present in the group, he was excluded from these calculations because he became inactive sexually after contracting tetanus at the end of the first third of the breeding season.) However, males were more visible (i.e. appeared more frequently in the observability samples) the higher their dominance rank, as shown by a positive correlation between rank and observability ($\tau = 0.64$, $P < 0.01$). When the effect of male differential observability on the relation between rank and copulatory frequencies is par-

Table 3. Percentages of copulations performed by males on OV-1 days (fertile and non-fertile cycles) out of all copulations per rank. Percentages were calculated for rank-specific copulatory frequencies exceeding 10, a criterion which excluded four ranks. For a minority of estrous periods, the onset of the attractiveness breakdown could not be determined with certainty. These estrous periods (691's 1st, 699's 1st, 287's 2nd, FC's 2nd, 297's 2nd, KI's 1st, 697's 2nd, 310's 2nd, 693's and 696's) were either short postconception estrus, perimenstrual estrus (as assessed by their timing in relation to mid-cycle estrus; Loy 1970), incompletely sampled estrus (continuing after the end of observations) or otherwise atypical estrus (discontinuous or lacking consortships). The corresponding copulations were included in the 'All' category

Rank of males	Copulatory frequencies		%
	OV-1	All	
1	40	73	54.79
2	37	92	40.22
3	9	46	19.57
4	11	36	30.56
5	11	35	31.43
6	5	26	19.23
7	7	29	24.24
8	1	20	5.00
9	2	11	18.18
10	0	16	0.00
11	5	34	14.71
12	3	11	27.27
13	0	13	0.00

tialed out, the correlation between these two variables vanishes (Kendall's partial rank correlation $\tau = 0.07$). Assuming that males copulated as frequently when they were not observable as when

Table 4. The distribution of consort interferences according to the rank of male interferers, the rank of interfered males and the sex of targets

Male interferers	Interfered males																		Total	Sex of targets		
	415	580	EE	TJ	1J	Z2	339	433	481	285	491	557	282	284	440	4T	279	N8		F	M	?
415		6	2		2	1						1	1						13	5	8	0
580	3		8	1	8	1	3	3				8	2			2		1	40	29	8	3
EE				2		3				1			2						8	5	3	0
TJ					2	18	7		1	3	3	4				2			40	24	16	0
1J	1					1	1	3		1				1			1		9	7	2	0
Z2	1						1	5		3		5		1					16	8	5	3
339								6	1	2	3	5	1			1	1		20	16	3	1
433				1					2	4	1	3	4			1	1		17	15	1	1
481											2	2	5			2			11	9	2	0
285													13	5		4		1	23	21	2	0
491																			0	0	0	0
557	1																		1	1	0	0
282														1					1	1	0	0
284																4			4	4	0	0
440																1			1	1	0	0
4T																			0	0	0	0
279	1				1											1			3	3	0	0
N8																			0	0	0	0

they were, these results suggest that lower-ranking males did copulate as frequently as higher-ranking males.

In order to verify if males nevertheless copulated with different frequencies depending on the stage of estrus, the copulations of each male were partitioned according to their temporal relation with the attractiveness breakdown. The data of Table 3 show that there is a positive correlation between the dominance rank of males and the proportions of copulations performed during OV-1 periods out of all copulations per rank ($r_s = 0.75$, $P < 0.01$). Thus, even assuming that all males copulated with comparable frequencies, the copulations of higher-ranking males fell more often within the presumed ovulation periods.

Consort Interferences

Males were observed to interfere aggressively in the consort relationships of other males on 207 occasions. 30.6% of these interferences were executed at the sight of a copulation going on, whereas the remainder (69.4%) were performed at times when the consort partners were sitting in proximity, grooming, or just after they had copulated. Most often the interferer vigorously lunged at or chased one of the two partners. He much less frequently just threaten the pair from a distance or went as far as biting the target.

In the great majority of cases (Table 4), the interferer was dominant over the male consort. In the few cases where the male interferer was subordinate, he always attacked the female rather than the male. These data show that males interfered in consort relationships at little risk to themselves. Retaliation by subordinate males was never observed. Typically, interfered partners would separate and then disappear out of sight, pursued by the interferer. Not infrequently, however, the consort partners were observed to be reunited after an interference. They would approach each other cautiously, often sitting at a distance and looking around before resuming the approach. Without doubt, interferences had at least the immediate effect of reducing the amount of time consort partners spent together and possibly, as a result, the frequency with which they mated.

The relation between the identity of a male's mating partners and the identity of the females he interfered with suggests some possible selective advantages of consort interferences. A first possibility is that males interfered more often in the consort relationships of the females they also mated with in order to increase their probability of fertilizing these same females. Another possibility is that they interfered randomly among receptive females. These two hypotheses can be tested. There were 48 estrous periods during the breeding season (Fig. 1). Whether a male mated with a female during a specific estrous period and whether he interfered in the consort relationships of this same

Table 5. The relationship between the identity of the females with whom a male mated and the females whose consortships he interfered in (see text for explanation)

Males	Number of estrous periods with interferences	Number of estrous periods with mating	Expected number of estrous periods with both mating and interferences	Observed number of estrous periods with both mating and interferences
580	22	23	10.54	13
415	7	4	0.58	2
EE	8	15	2.5	6
TJ	22	18	8.25	6
1J	5	5	0.52	2
Z2	12	19	4.75	7
339	15	16	5.0	8
433	15	12	3.75	6
481	7	10	1.46	4
285	7	13	1.90	6

female during the same estrous period was noted on a one-zero basis for each male-estrous period pair (Table 5). For example, male 580 was seen to interfere at least once in 22 estrous periods and to mate at least once in 23 estrous periods. Therefore, the expected number of estrous periods in which 580 both mated and interfered with the same female is given by $22/48 \times 23/48 \times 48 = 10.54$. A significantly greater number of males (9:1) interfered more often in the consort relationships of females they also mated with (Table 5; two-tailed sign test, $P < 0.05$).

At a proximate level, the simplest hypothesis is that of short-term effects of repeated consort interferences on the copulatory frequencies of lower-ranking males. A somewhat more sophisticated hypothesis is that of female conditioning with interferences as negative reinforcers. As stated by Altmann (1962): "females learn that they can mate with impunity if they consort with dominant males" (p. 393). That it is the female vs the male which should be conditioned is justified on the grounds that it is more economical in terms of a male's energy to condition *one* receptive female rather than a *number* of male consorts. According to this hypothesis, the inhibiting effect of interferences would be longer-lasting. If it is correct, one would expect (i) females to be the targets of interferers more often than their male consort (22 out of the 28 interfered females verify this predictions; two-tailed sign test, $P < 0.01$) (ii) interferences to take place in contexts other than copulations (69.4% of recorded interferences took place in such other contexts) and (iii) as a result of the conditioning process, females to prefer the highest-ranking suitor (only infrequently did females prefer lower-ranking suitors).

In summary, consort interferences appear as an extension of consorting behavior, leading females to prefer higher-ranking males as consort partners.

Table 6. Number of hours spent by males consorting the 18 (to-be-pregnant) females during their fertile OV-1 period. *Total* total number of hours during which group F was under observation during the female's fertile OV-1 period. *Not visible* number of observation hours during which the interactions of the female with males could not be adequately observed. Males and females are arranged in descending rank order (415: alpha male; FB: alpha female)

Females	Total	Not visible	Males												
			415	580	EE	TJ	1J	Z2	339	433	481	285	491	557	282
FB	29	0		29											
510	30	8					6			10	6				
577	40	0						20	20						
511	28	7						4	17						
287	35	0		10			15	10							
503	23.5	0		18.5				3	2						
7L	28.5	11		17.5											
471	29	4		25											
692	27	14		6					7						
679	35	0		26		7								2	
N2	30	0		18		12									
411	25	0	3.5	14.5	1		6								
649	14	6		1.5		3			3.5						
K1	15	0		1		14									
697	20	0		14		6									
476	28	0		16		2							10		
543	38	0		33										5	
310	14	1								13	1				

Male Dominance and Reproductive Success

Eighteen females gave birth following the 1978 breeding season. One other female (697) was clearly pregnant but probably aborted. Fertile OV-1 periods could be defined for 697 and for 17 of the 18 females who gave birth (the fertile OV-1 period of 698 could not be delimited) (Fig. 1). Table 6 compares the consorting activity of males with the 18 females whose conception periods were defined. The proportion of hours a male spent consorting a female, out of the total number of hours during which the observers watched group F during the OV-1 period of this female, was assumed to correspond to this male's probability of fertilizing the female. Because males underwent changes in rank during the breeding season (Table 1), rank-specific, versus male-specific, reproductive success was calculated. Rank-specific reproductive success was obtained by summing up for all the males that had occupied the same rank the probabilities that they had fertilized females when occupying this rank (Fig. 3). There is a positive correlation between male rank and time spent consorting ($r_s = 0.90$, $P < 0.01$).

In accordance with the latter finding, there is a positive correlation between the dominance rank of males (415 excluded, see above) and the frequencies with which they copulated during the fertile OV-1 periods of the 18 females that became pregnant (Table 7; $r_s = 0.76$, $P < 0.01$). Male differential

Fig.3. Rank-specific reproductive success estimated on the basis of time spent by males consorting the 18 (to-be-pregnant) females during their fertile OV-1 period (see text and Table 6)

observability could hardly account for this result given that consortships were long-lasting on OV-1 days, a fact which minimized the number of opportunities for low-ranking males to copulate furtively.

Discussion

Previous studies on the reproductive behavior of the Cayo Santiago rhesus monkeys did not assess

Table 7. Male copulatory frequencies during the fertile OV-1 period of the 18 (to-be-pregnant) females. Males and females are arranged in descending rank order (415: alpha male; FB: alpha female)

Males	FB	510	577	511	287	503	7L	471	692	679	N2	411	649	K1	697	476	543	310	Total
415																			0
580				1	4	4	3	1	2		4	5	1		4	3	7		39
EE	1											3							4
TJ														1	2				3
1J																			0
Z2				1	2	1													4
339		1	4	4													1		10
433		1																	1
481				1					1										2
285																			0
491																			0
557										1							1		2
282																			0
284																			0
440																			0
4T																			0
279																			0
N8																			0

the likelihood of ovulation, and produced contradictory results with respect to the relative importance of male dominance in mate selection (see Introduction). In the present study, positive correlations were found between the dominance rank of males and their reproductive performance on the four days preceding the attractiveness breakdown of (i) 18 fertile cycles and (ii) all cycles of the first half of the breeding season. However, not all the variance in male reproductive activity could be explained on the basis of male dominance relations. Other factors will be discussed below. But first, the two major assumptions of the present study, namely that OV-1 periods coincide with ovulation and that male reproductive performance was measured accurately, will be examined in more detail.

The Timing of Ovulation

Carpenter (1942), Kaufmann (1965) and Loy (1971) reported mean durations of estrous periods of respectively 9.2, 11 and 6.2 days for the Cayo Santiago rhesus monkeys. This indicates that female rhesus mate over a period of time that is much longer than the 2-day period when conception is most likely. Now, studies on baboons have revealed that high-ranking males are more active sexually than low-ranking males during the period of maximal turgescence of the sex skin, that is, when ovulation is most probable (Hall and DeVore 1965; Saayman 1971; Hausfater 1975; Packer 1979a). Taken together, these data suggest that the timing of ovulation might be an important variable affecting the dynamics of mate selection in rhesus monkeys. However, the absence of morphological changes reliably associated with hormonal changes in this species makes it difficult to assess the likelihood of ovulation. In the present study, the periods of ovulation were delineated on the basis of behavioral changes indicating the termination of a female's attractiveness. This decision was based on laboratory data showing that ovulation in rhesus monkeys is followed by abrupt behavioral changes. Czaja and Bielert (1975) found that the greatest number of conceptions occurred two or three days before a sharp decline in the amount of time females spent stationary close to restrained male partners, and with a marked increase in the latency of ejaculations. Similarly, Keverne (1976) reported a peak in operant responding during the expected period of ovulation, followed by a marked decline during the luteal phase of the menstrual cycle. In baboons, the passage from the follicular to the luteal phase of the

menstrual cycle, following ovulation, coincides both with the onset of deturgescence of the sex skin and with marked changes in the behavior of males and females. Hausfater (1975) described these changes for *Papio cynocephalus*, stating that the rate of all social interactions combined for estrous females declined rapidly with the onset of deturgescence and that only rarely did consortships continue after this time.

Two factors complicated the delimitation of ovulatory periods based on the present criteria. First, the attractiveness breakdown could not be identified for a small number of estrous periods which were characterized by discontinuous or short consortships or by the absence of consortships. It is noteworthy that the few females which exhibited such atypical (anovulatory?) estrous periods were all aged 3. Second, perimenstrual estrous periods (Loy 1970) might have been mistaken for mid-cycle estrus. This possibility is unlikely however, given that menstrual bleedings were observed in many cases and that perimenstrual estrous periods were characteristically shorter and less intense than mid-cycle estrus.

Although behavioral criteria are not ideal means for assessing the likelihood of ovulation, it is believed that the approximation which they lead to may shed more light on the dynamics of mate selection than approximations failing to differentiate stages of estrus altogether.

The Measures of Reproductive Activity

If two males (A and B) spend the same amount of time consorting the same number of equally fertilizable females, but male A copulates more often than male B, it does not necessarily follow that A's reproductive success is greater than B's. Provided that the intervals at which each male copulates are significantly shorter than the duration of sperm viability (up to 24 h in mammals in general; up to 52 h in *Macaca fascicularis* and *Macaca mulatta;* Dukelow and Brüggemann 1979), a more frequent copulator is not necessarily at an advantage. On the other hand, if the two males consort and mate with the same female alternately, the more frequent copulator has an advantage in the context of sperm competition. Ideally therefore, a male's reproductive performance would be assessed by the time he spends consorting *weighted* by his copulatory rate relative to that of other males. Computing such indices necessitates long periods of focal sampling and was not possible in the present study (see Sampling Methods). As a

compromise, both time spent consorting and copulatory frequencies were analysed separately.

These measures may have under-estimated the reproductive performance of lower-ranking males which might have mated furtively. On the other hand, such an effect was probably counter-balanced by an under-estimation of the copulatory frequencies of high-ranking males interfering frequently in the consortships of lower-ranking males, and sometimes mating with the consorted female.

Mate Selection and Factors Other Than Male Dominance

Male dominance explains approximately 81% of the variance in time spent consorting on fertile OV-1 days ($r_s = 0.90$) and 62% of the variance in time spent consorting on all OV-1 days (fertile and non-fertile) of the first half of the breeding season ($r_s = 0.79$). While these figures may indicate that males were able to differentiate ovulatory from nonovulatory cycles and that high rank conferred prior access to fertilizable females, they also show that male rank does not explain all the variance in male reproductive activity. First, high-ranking males did not, or were not able to, *maximize* the advantages conferred upon them by their rank; they were sometimes unsuccessful in their attempt to consort estrous females which were being consorted by lower-ranking males, or they simply ignored such estrous females. Second, they did not *always* prefer to consort OV-1 females; they sometimes preferred females which appeared less likely to be ovulating. These observations will now be examined in relation to a number of asymmetries which might affect the competitive relationships of males for females. Asymmetric contests are expected to be settled on the basis of inter-individual differences in Resource Holding Potential (RHP) and/or asymmetries in payoff from winning (Maynard Smith and Parker 1976; see also Hammerstein 1981 and Parker and Rubenstein 1981).

Asymmetries in RHP. Possible components of male RHP other than basic dominance rank (which is itself a composite of factors such as age, size, aggressiveness, fighting ability, etc.) are resistance to fatigue, experience, wounds, canine conditions, mobility and aid-enlisting capacity (Packer 1979a). None of these factors, however, could account for the unexplained portion of the variance in male reproductive activity. In all instances where OV-1 females were consorted by males ranking lower than expected on theoretical grounds, the higher-ranking non-consorting males did not appear to

be more tired, less experienced, more afflicted by wounds or have canines in worse condition compared to consorting males. Coalitions and required mobility cannot be invoked either, since group F males were never observed to enlist other males against the highest-ranking males.

Asymmetries in Payoff. Various factors may produce payoff asymmetries wherein the male which stands more to gain is expected to be ready to expend more fitness units in the contest for the female and, as a result, win the encounter without fighting. A first asymmetry in payoff may result from differences in the physiological capacity of sexually mature males to fertilize females. For example, sustained high copulatory rates may lead to sperm depletion. Such a male would have less to gain from consorting and mating compared to a male that is less active sexually. It is unlikely that this type of asymmetry could explain male abstention in group F because the males concerned had been moderately active sexually prior to abstaining.

A second type of asymmetry in payoff was suggested by Packer (1979a) as resulting from differences between males in prior reproductive investment in an estrous female:

"if n males had copulated with the female during her period of peak fertility, the nth male would have a $1/n$ chance of siring the resulting offspring, the $(n+1)$th male would have a $1/(n+1)$ chance, and since $1/n > 1/(n+1)$, the holder would always have higher prospects of paternity than the rival" (p. 41).

However, in order to assess an asymmetry in resource value on the basis of differences in prior investment, one has to compare the two contestants for their expected payoff from winning in terms of *future* reproductive benefits. In the present case, assuming that the two males could keep the female for the same period of time after the contest, the expected fitness accrual from winning (and copulating) is the same for both males. Now, since the holder's prior investment in the female represents a gain that is not transferrable (i.e., not lost to the rival) losing the female does not affect the holder's future reproductive success more than that of the rival (see Parker (1974) for a discussion of cases with payoff imbalances). Therefore, if the interest of the female is not taken into account (it will be below), the male which started consorting earlier does not appear to benefit from an asymmetry in resource value.

A third asymmetry in payoff may arise through differences between males in their degree of relatedness with estrous females. Breeding avoidance among close relatives is well documented in multi-

male primate groups (Sade 1968; Missakian 1973; Enomoto 1978; Packer 1979b; Baxter and Fedigan 1979; Pusey 1980). Thus, a male may be less willing to mate with a female relative compared to a male unrelated to this female. Two brothers (415 and 580) were members of the highest-ranking matriline of group F. They did not consort or mate with their female relatives (except 415 who mated once with his mother; Tables 2 and 6). However, it never happened that the females related to 415 and 580 were the only females in estrus at any singular moment in time. Consequently, the case never arose when males ranking lower than 415 and 580 had access to estrous females as a result of these two males avoiding incestuous relationships.

A fourth type of payoff asymmetry might result from males using different reproductive strategies dictated by different criteria of mate choice. For example, different males might attempt to concentrate their energy on different females (e.g. Packer 1979a) or on different groups of females (e.g. McMillan and Duggleby 1981) or not so much on different females but on different stages of estrus (e.g. Hausfater 1975). Packer (1979a) found that some male baboons preferred to consort certain females with whom they maintained affiliative bonds outside consortships, and that such male selectivity was not the result of female choice. In group F the highest-ranking non-natal male (EE) consorted assiduously the alpha female (FB) over her three estrous periods even though other OV-1 females were available. EE had maintained a long-term affiliative relationship with FB during the previous birth season but had done the same with other females which he did not consort. As another possibility, a particular form of mate selectivity was proposed by McMillan and Duggleby (1981) to explain their finding that the mean genetic distance between lineages of the same troop among rhesus monkeys on Cayo Santiago was not less than the mean distance between lineages belonging to different troops. They suggested that males would mate preferentially with females of a particular lineage and that, as a result, lineages of the same troop would remain differentiated. (The benefits accruing to males adopting such a restrictive mating pattern were not specified.) However, the data of Tables 2 and 6 do not support this hypothesis since males did not restrict their mating and consorting activity to particular matrilines. Finally, Hausfater (1975) observed that first-ranking males abstained from consorting certain females even if no other estrous females were present in the group, and that they concen-

trated their mating activity on the optimal day for fertile matings. He suggested that this type of selectivity might express a reproductive strategy minimizing the short-term negative effects of consortships. Although baboons and group F rhesus share the characteristic that males can sometimes ignore available estrous females, high-ranking male rhesus did not show a consistent pattern of cycle day selectivity since they sometimes ignored receptive females on all cycle days.

The four types of asymmetries in payoff discussed above are all independent of the females' interest and behavior. A fifth type of payoff asymmetry is provided by female choice. If a female shows a marked preference for male A over male B, the cost of consorting the female is higher for male B (e.g. Bachmann and Kummer 1980). Moreover, if the female mates furtively with other males while being consorted by B, or if she refuses to mate with B, the benefits of consorting are lower for B than for A, and may even be nil. The fact that females do play an active role in mate selection in multi-male primate groups was reported by Lindburg (1971), Stephenson (1974), Hausfater (1975) Packer (1979a), Tutin (1979) and Taub (1980). Given that a female prefers the lower-ranking of two male suitors, the dominant male has two alternatives. First, he may attempt to overcome the asymmetry by threatening away or chasing the subordinate male. However, even if the succeeds in doing so, this strategy is inefficient if the female maintains her preference for the subordinate male and refuses to mate with the dominant male. Second, the male may attempt to reverse the asymmetry in his favor either by being aggressive to the female or by courting her.

As seen above, group F males only rarely attacked the male when interfering in consort relationships, possibly because this could not prevent the female from maintaining her preference for the lower-ranking suitor. Rather, they acted as if attempting to induce the female to prefer them over the subordinate male. Two types of interactions are interpretable in these terms. First, the majority of consort interferences were directed at females, with the probable outcome that the latter came to prefer higher-ranking male suitors in most cases, as this is reflected in the positive correlations between male rank and reproductive activity. Second, males were observed to direct a mixture of friendly gestures (e.g. lip-smacking) and submissive behaviors (e.g. fear grimaces) to females preferring, and being consorted by, lower-ranking males. Such affiliative strategies may have been used when aggression had proven inefficient. The reasons why

females sometimes preferred lower-ranking males could not be identified. The small number of recorded instances could not be understood either in the context of longer-term relationships involving an exchange of benefits or in terms of incest avoidance.

Two conclusions may be drawn from the above discussion. First, unless the two major assumptions underlying this analysis are inaccurate, or there are some unknown adaptive advantages associated with male abstention and selectivity, the present data suggest that male-male competition for estrous females among group F rhesus monkeys was less stringent than expected on theoretical grounds. Second, it appears that a necessary condition to the existence of a positive correlation between male rank and reproductive activity is that female choice coincides with the interest of the highest-ranking suitor. Possibly in order to insure that this was the case, males interfered in the consortships of lower-ranking males and attempted to affiliate with the females from whom they were rejected. Thus, the explanatory power of male dominance for mate selection among group F rhesus monkeys would stem from male-male competitive interactions acting concurrently with the capacity of males to influence female choice.

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