

AFFILIATIVE AND SEXUAL DIFFERENCES BETWEEN A REPRODUCTIVE AND A NONREPRODUCTIVE RHESUS GROUP (*Macaca mulatta*)

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ABSTRACT: A heterosexual group of nonreproductive rhesus (*Macaca mulatta*) containing vasectomized males was compared with a matched control group containing intact males. Comparisons were made on data collected before the birth of the first infant in the control group. Three Darwinian *a priori* hypotheses were used to predict differences between groups. The first hypothesis correctly predicted more affiliative and sexual behavior among experimental heterosexual dyads. The results did not support the second hypothesis that predicted less affiliation between experimental males. The third hypothesis correctly predicted that heterosexual affiliation and sexual behavior would occur between more of the possible heterosexual dyads in the experimental group. Two-tailed tests showed the females in the reproductive group engaged in significantly less intrasexual affiliation. The results suggest failure to reproduce has a causal influence on the affiliative and sexual interaction patterns of rhesus macaques.

Studies of differences between contracepting and noncontracepting groups of nonhuman primates may help us to understand differences between our social and sexual behavior and that of our recent ancestors. The effects of contraception on humans may be so great that studies of natural groups of nonhuman primates may not shed much light on the behavior people in developed nations (Rasmussen, 1981a; Rasmussen, 1984; Rasmussen, Reinhardt & Goy, 1987; Rasmussen, 1994).

Empirical research on the behavioral processes associated with contraception must be matched with the development of evolutionary

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theory. Most evolutionary theory describes functions of human social and sexual behavior as if contraception were not used. Males, for example, are portrayed as more sexually ardent and indiscriminate since they may invest less in offspring. Females are depicted as more reluctant to engage in sexual behavior. This is particularly true in mammals since conception results in the necessary female investment of time and energy associated with gestation and lactation (Daly & Wilson, 1983; Hinde, 1984; Grammar, 1989).

Empirical support for this evolutionary theory generally is drawn from studies where sexual behavior retains its natural link with reproduction. These studies may be on animals in their natural habitats or on people in hunter-gatherer or agrarian societies not using contraception (Wilson, 1975). If applied to a contracepting population, evolutionary theory should, but usually does not, explicitly recognize changes in the balance of costs and benefits of sexual behavior (Tooby, & Cosmides, 1990). The contracepting female who copulates, for example, has a decreased probability of incurring the costs of gestation, lactation and infant care. Other things being equal, copulation costs less to contracepting females. Females may therefore copulate with males for reasons unrelated to conception (Broude, 1993).

Evolutionary and functional theories should be developed to understand and predict the behavior of individuals in contracepting populations. Such theory permits connection of our evolutionary past with our current behavior. The theory also holds the potential of predicting how behavior may be currently adapting to the changed contraceptive environment. To initiate the development of evolutionary theory we must first understand the selective factors that led to the current "design" of behavioral interaction patterns. We then must determine how this design would react to changes in the social environment associated with contraception. Thus we need to understand the adaptive behavioral patterns of the organism in the environment in which it evolved (Rasmussen 1981b, 1988), the "environment of evolutionary adaptation or EEA" (Tooby & Cosmides, 1990). With knowledge of the adaptive design of behavior we then must build testable theories and hypotheses about how the design would alter in the face of contraception.

This experimental study of rhesus, *Macaca mulatta*, was guided by this strategy for the development of evolutionary theory. Knowledge of the function of social and sexual interactions in natural environments was combined with knowledge of the effects of hormones and nonreproductive environments on behavior to develop

testable hypotheses. A frequent criticism of evolutionary theories of behavior is that they do not generate testable hypotheses (Brigham, 1991; Wright, 1994). This is clearly wrong (Tinbergen, 1965). The hypotheses described here are generated from evolutionary theory and are both testable and tested. Conception was prevented in the experimental group by performing vasectomies on the sexually mature males.

The analyses are focused on differences between an experimental group and a matched control group. Differences between the groups were predicted with three *a priori* functional hypotheses. The hypotheses were formulated before the experiment and are derived from those previously published (Rasmussen, 1981a, 1984). The theoretical and empirical support for the hypotheses are briefly summarized. A more thorough description of the theory and review of the literature will appear elsewhere.

Hypothesis 1: More male-female affiliative and sexual behavior was predicted in the experimental group.

Theoretical bases. We predicted the members of the nonreproductive group would not behave much differently than a normal group where females had potentially reproductive sexual cycles. The contracepting social environment was therefore predicted to deceive members of the nonreproductive group to engage in sexual behavior as if it were connected with reproduction.

Intrasexual competition for access to mates, and time and energy associated with courtship and mating, selects individuals to engage in such behavior when it is likely to result in conception (Michael & Zumpe, 1988). Periovoluntary periods in rhesus are accompanied by olfactory, visual, and behavioral stimuli (Keverne, 1983). More sexual and associated affiliative behavior were therefore predicted to occur in the experimental group since: First, copulation and associated affiliative behavior are precursors to reproductive success. Second, copulation is potentially risky and energetically expensive. Individuals would therefore be selected to engage in more sexual behavior when it has an apparently higher probability of leading to conception. Third, stimuli exist that are associated with ovulation. And fourth, more of these stimuli would be present in the experimental group because of the females' repeated nonpregnant menstrual cycles. In the nonreproductive group, the females' attractiveness, receptiveness and proceptivity (Beach, 1976) would all signal fertile matings were possible throughout the experiment.

Empirical bases. Females in the control group were expected to conceive. Rhesus sexual behavior decreases after conception (Chambers & Phoenix, 1982; Wilson, Gordon, & Chikazawa, 1982; Hill 1986). The males in the experimental group could not fertilize the females. The females would therefore have repeated nonpregnant ovulatory cycles and a breeding season of greater length (Mallow, 1981). Experimental females would therefore have more periovulatory days than their controls. Rhesus sexual behavior and heterosexual grooming are usually found to occur at highest rates during periovulatory days (Gordon, 1981; Michael & Zumpe, 1988, Hill, 1986).

Hypothesis 2: Less affiliation between males was predicted the experimental group.

Theoretical bases. More heterosexual affiliative and sexual interactions in the experimental group were predicted by hypothesis 1. These interactions were expected to be accompanied by more competition between males and therefore with less affiliation.

Hypothesis 2 is based on a theoretical continuum. This continuum is of the degree to which interactions may be competitive, and decrease the recipient's inclusive fitness, or beneficial, and increase the recipient's inclusive fitness (Rasmussen, 1988). The term beneficial is used to encompass altruism, cooperation, helping (Brown, 1983) and other behavioral patterns that increase the recipient's inclusive fitness. Patterns of affiliation are used as measures of beneficial behavior.

Empirical bases. A previous study that compared a heterosexual group of bonnet macaques (*M. radiata*) in which all females were ovariectomized and a matched control group containing intact females found that there was more agonistic behavior and less affiliation between males housed with the intact and sexually cycling females (Rasmussen, 1984). Aggression between rhesus males has also been shown to increase during breeding seasons (Wilson & Boelkins, 1970; Gordon, Rose, & Bernstein, 1976).

Females are excluded from hypothesis 2 for a theoretical reason: Aggression between females might not be expected to be greatest during sexual behavior. There are other periods in the female reproductive cycle when aggression received by females could have a stronger negative impact on their reproductive success (Silk, Clark-Wheatley, Rodman, & Samuels, 1981; Small & Smith, 1982; Michael & Zumpe, 1984). More information is needed on changes in

affiliation between females as a function of their reproductive cycle. Female-female affiliation is therefore compared between groups and subjected to two-tailed tests of significance.

Hypothesis 3: Affiliative and sexual liaisons were predicted to form between a greater proportion of the possible heterosexual dyads in the experimental group.

Theoretical bases. When copulation does not result in conception, both males and females might increase their reproductive success by copulation with different partners since their previous mates, rather than themselves, could be sterile (Rasmussen, 1981a). In the face of failure to reproduce, an adaptive response of an organism thus would be to increase the number of heterosexual partners in sexual liaisons since copulation with previous partners did not result in conception.

This hypothesis was formulated since the experimental group was expected not to be entirely deceived into acting as if sexual behavior results in conception. Feedback information does show intersexual affiliation and sexual behavior do not have a reproductive payoff: In an intact group most ovulating females conceive during their first few sexual cycles. Repeated nonpregnant ovulatory cycles are not the norm in the EEA (Short, 1974). Instead most of a rhesus female's life is spent either pregnant or lactating. Macaques may prefer some sexual partners over others (Zumpe & Michael, 1989; Huffman, 1991). If hypothesis 3 were not true, then it is possible that increased sexuality in the experimental group predicted by hypothesis 1 would result in more sexual activity between the same preferred sexual partners. Hypothesis 3 predicts, instead, that the increased sexuality associated with failure to reproduce will be associated with a greater variety of sexual partners.

Empirical bases. The presence of sterile or sub-fecund individuals could exert selective pressure for a tendency to form liaisons with more individuals. Menarche may precede initiation of ovulation in rhesus (Schwartz, Wilson, Walker & Collins, 1988). Mounts and intromissions may therefore occur during pubertal sterility. Pubertal sterility thus could select for this hypothesized tendency. The occurrence of sterile and sub-fecund adult macaques is documented (Small, 1982; Lindburg, 1983, Walker, 1995). Evidence suggests they have existed in natural troops during evolution (Moore & Ali, 1985). Sterile and sub-fecund adults also could select for this hypothesized tendency. Repeated miscarriages and infant deaths due

to the many possible mortality factors (Dittus, 1980) and other sources of variation in female reproductive success (Hrdy, 1986) would also select for liaisons with different partners (Rasmussen, 1981a).

Hypothesis 3 is consistent with decreased sexual behavior observed between rhesus pairs. These pairs were placed together weekly over a 3½ year period (Michael & Zumpe, 1978) and the females did not conceive.

Strong correlations between fertility and both marital stability and duration have been consistently reported in human demographic literature (Rasmussen, 1981a). We are only distantly related to rhesus and often form sexual, reproductive and infant care pair-bonds of much longer duration than rhesus consortships. The persistent finding of these relationships in many populations with the large sample sizes provided by censuses indicates, however, that in at least one species of primate, *Homo sapiens*, there is a correlation between the duration and stability of an affiliative and sexual relationship, marriage, and reproduction. There are, of course, difficulties in determining the causality of these correlations (Bumpass & Sweet, 1972). These difficulties underscore the need of experimental and comparative studies of nonhuman primates. Such studies may help determine the causality of behavioral processes associated with differences in number of offspring born per female.

METHOD

Group Composition and Subject Matching

The experimental group was composed of a 5-year-old vasectomized male, a 4-year-old vasectomized male, an intact 2-year-old male, four 4-year-old females, one 3-year-old female and three 2-year-old females. The control group was sex and age matched. Young rhesus were used so experimental subjects could be more closely matched to their paired controls by previous social experience. All females were nulliparous and therefore did not vary in parturitional, lactational, or infant rearing experience.

The 5 and 4-year-old males in both groups engaged in adult ejaculatory mounts of females and the 3-year-old female in the control group conceived. While young, all group members, except 2-year-olds, were sexually mature to the extent that they could potentially reproduce.

The females were selected from those who could be most closely

matched by age, weight and housing history. One of each pair of matched female subjects was randomly assigned to the experimental or control group.

Vasectomies were used to prevent reproduction since they have less direct effects on the hormones and behavior of the sterilized male (Phoenix, 1973) than other methods. Vasectomy of the two potentially reproductive males was also the procedure that could be used on the fewest subjects and yet prevent conceptions in the nonreproductive group. Group differences could therefore be most directly attributed to the differences in the reproductive cycles of the females: In the control group the females would experience repeated nonpregnant ovulatory cycles. In the experimental group the matched controls of the females were expected to rapidly conceive.

The vasectomized males were matched to controls by age, housing history, size and estimated agonistic rank in previous social groups. The vasectomies were done on the experimental 5 and 4-year-old males 3 months before data collection.

Hypothesis 1 was based on our expectation that the experimental females would have more nonpregnant ovarian cycles. This expectation was fulfilled: All 3 and 4-year-old females in the experimental group menstruated and there were 24 ovarian cycles in that group. The females experienced a mean of 4.8 ovarian cycles ($SD = 2.17$). In the control group all but one sexually mature female rapidly conceived. Three of the five conceived during their first ovarian cycle. There were only 4 ovarian cycles in the control group. Both of the two control females observed to menstruate were 4-year-olds. One had three ovarian cycles and the other had one cycle before conception. Sexually mature control females experienced a mean of 0.8 ovarian cycles ($SD = 1.3$).

Housing

The identical indoor chain-link pens housing the groups were 6.7 m long, 2.5 m wide and 2.6 m in height. Lights were turned on at 6 am and turned off at 6 pm. Two frosted windows next to the pens let in ambient light.

More sexual behavior was expected to occur in the experimental group containing females with continuous nonreproductive ovulatory cycles. This could potentially influence the males' testosterone level (Vandenbergh & Drickamer, 1974). The control group was housed close to groups containing cycling females to control this potential group difference. Housing all male rhesus groups near heterosexual

groups results in a seasonal increase of levels of testosterone in the all male groups. This increase is indistinguishable from levels in heterosexual groups (Gordon, Bernstein & Rose, 1978). The groups were housed in adjacent pens separated by a minimum distance of 1.2 m. The pens were in a room housing two additional identical pens containing breeding rhesus groups.

Rhesus sexual behavior during the breeding season is associated with increased male testosterone (Gordon, Rose & Bernstein, 1976). The groups were therefore simultaneously observed from the peak of the breeding season (January 2) to the onset of the birth season (June 1).

Behavioral Variables

Rationale

The hypotheses are based on influences of behavior on reproductive success and inclusive fitness. Ideal behavioral measures used to test these hypotheses would have only positive or negative influences on fitness. The actual influence of a behavior on fitness is, however, influenced by social and environmental context. A behavior may be sexual in one context, affiliative in another and aggressive in a third. Theoretically defined concepts such as sexual and beneficial behavior may therefore only be imperfectly assessed with empirical measures.

The measures selected were those that seemed to most accurately assess affiliative, sexual, and beneficial behavior as used in the a priori hypotheses. An evaluation of the relationships between the affiliative variables, and the influence of social context on their interrelationships has been published elsewhere (Rasmussen, 1994).

A functional definition of sexual behavior was used (Scott, 1956; Tinbergen, 1965): Sexual behavior is behavior that has been associated with conception in the EEA, the environment of evolutionary adaptation (Rasmussen, 1984). Although it may be impossible to find a behavioral pattern that has only beneficial consequences, typical measures of affiliation do assess interactions that may benefit the recipient (Crooks & Rasmussen, 1991). Affiliative behavioral patterns were therefore used to assess beneficial behavior.

Sampling

All behavioral data was collected by the author. Observations used in the analyses were collected until the day before the birth of

the first infant in the control group. Sampling sessions were conducted for 14 min on individual focal subjects. During sampling sessions, focal samples (Altmann, 1974) were collected on variables requiring constant monitoring of the subject. Concurrent sampling (Hausfater, 1975) was conducted of all occurrences (Martin & Bateson, 1993) of behavioral variables that could be accurately assessed for all group members. Instantaneous, frequency and I/O sampling methods (Altmann, 1974) based on 2 min intervals were used to assess the variables. The data base used here has 163 hours of 2 min interval samples collected during 14 min sampling sessions. Further description of the sampling methods appear elsewhere (Rasmussen, 1993, 1994).

Matching of Subjects and Dyads

Tests of the hypotheses require comparison of experimental and control subjects. Each subject in the experimental group was matched to a subject in the control group. Comparisons could therefore be made between subjects matched by sex and age.

Most of the comparisons between groups used here are comparisons of the interactions between pairs of individuals matched between groups. For example, the oldest male in the experimental group was matched with the oldest male in the control group. The oldest experimental female was also matched with the oldest control female. Comparisons could therefore be made between the matched dyads composed of the oldest experimental male and female and the oldest control male and female. Hypothesis 1, for example, predicts more male-female affiliative and sexual behavior in the experimental group. Application of this hypothesis led to the prediction that heterosexual dyads in the experimental group should engage in more affiliative and sexual behavior than the dyads to whom they were matched in the control group. The oldest female in the experimental group was therefore expected to groom the oldest male in that group more than the oldest female in the control group groomed the oldest male in that group.

Directional dyadic interactions are matched between groups by the age and sex of subjects within dyads. The directional dyad composed of 5-year-old male => 4-year-old male interactions in the experimental group was, for example, matched to the identical directional dyad in the control group¹. It was therefore possible to determine if, as predicted by hypothesis 2, the 5-year-old experimental male groomed the 4-year-old experimental male less than the 5-year-old control male groomed the 4-year-old control male. There were 110 possible

matched directional dyads (11 subjects x 10 cage mates in each group). Directional dyadic interactions were compared between groups for the variables ALF, grooming, grooming presents, presents, mounts, and ejaculation.

Distances between individuals are not directional since the mean distance of "A"=>"B" is the same as the mean distance of "B"=>"A". There were 55 matched non-directional dyads "A"<=>"B" that could be compared in the two groups for the distance variables. The direction of consorts were not scored since they were due to the behavior of both the male and female.

Neither the recipients of threatening away nor the consort partners from whom the threats were directed away were recorded. Comparisons of threatening away were therefore made between matched subjects.

Variable Descriptions

Many of the variables, or variables like them, are among those most frequently found in studies of sexual and affiliative behavior of nonhuman primates. The time and space is taken here to describe these variables since nuances of variable definition, their sample and the descriptive statistics used to summarize the variables can have a substantive influence on results and their interpretation. The variables, the unit of observation and the sampling used to assess the variables are listed in Table 1. Further description of the variables, and references to previous use of the variables, appear elsewhere (Rasmussen 1984, 1993, 1994).

Neighbor distances. Distances between individuals have been used as indirect measures of affiliation since Galton (1884). Mean distance between macaques has been shown to correlate strongly and negatively with affiliative interactions (Rasmussen, 1984): individuals whose mean nearest neighbor distance is small tend to engage in more affiliative behavior.

Instantaneous samples of the coded estimated distance of the nearest neighbor male and female to the focal subject were collected at the beginning of each 2 min interval. The coded distances were as follows: 0=contact, 1=not touching to 1/3m, 2=1/3-2/3m, 3=2/3-1m, 4=1-4/3m, 5=4/3-5/3m, 6=5/3-2m, 7=greater than 2m. When

1. => indicates a directional behavioral interaction. Male grooms of females are indicated as male => female grooming. <=> is used to indicate bidirectional behavior or a measure of the distance between a dyad. When, for example, analyses are focused on grooming of males by females and grooming of females by males this is indicated as male <=> female grooming.

Table 1. Variables, Observation Unit and Sampling Method. Focal: the focal subject of the 14 minute sampling session; group: all individuals in the focal subject's group.

Variable	Observation Unit	Sampling Method
Nearest Neighbor Distance (NN)	focal	instantaneous
Close Distance to Nearest Neighbor (CD)	focal	instantaneous
Approaches, Leaves & Follows (ALF)	focal	frequency
Grooming	group	concurrent 1/0
Grooming presents	focal	frequency
Presents	focal	frequency
Mounts	group	concurrent frequency
Consorts	group	1/0 per sampling session
Threatening away	group	concurrent frequency
Ejaculation	group	concurrent frequency

individuals were engaged in agonistic behavior with the focal subject they were excluded as nearest neighbors since neighbor distances were used to assess affiliation (Rasmussen, 1984).

Two measures of mean distance were calculated: Nearest neighbor distance (NN) was the mean ordinal distance between a given dyad across all samples. When the focal subject had a nearest neighbor all other group members of the same gender as the nearest neighbor were given a coded distance of 7 from the focal subject for that 2 min interval. Close neighbor distance (CD) was the mean distance between a dyad during those intervals when members of the dyad were nearest neighbors. NN was thus a measure of the distance between a dyad during all sampling and CD a measure of the mean distance between individuals when they were nearest neighbours.

Approaches, leaves and follows (ALF). Approaches, leaves and follows are sensitive measures of rhesus affiliation (Chapais, 1986). The frequency of these variables was assessed for focal subjects during the 2 min intervals. These three strongly and positively correlated variables (Rasmussen, 1994) were combined in a composite variable, ALF. ALF rates were calculated as the number of times "A" approached, left or followed "B" divided by the focal samples on "A" and "B".

Grooming. Grooming, picking through the hair or skin of another with fingers or teeth (Rasmussen, 1984), was also used to assess affiliation. Data on grooming were collected with 1/0 concurrent sampling. Rates of 1/0 "A" => "B" grooming were calculated by dividing the sum of intervals with "A" => "B" grooming by the number of 2 min intervals of observation on their group.

The focus of the analyses is neither on true frequencies nor durations. The focus is on differences between matched directional dyads. Since 1/0 samples are strongly correlated with both true frequencies and durations (Martin and Bateson, 1986), differences between groups assessed with 1/0 samples, true frequencies, and durations seem likely to be in same direction.

Grooming presents. An "A"=>"B" grooming present was recorded when "A" approached "B" and exposed a body part at 1/3 m or less of "B's" hands or mouth. The frequency of grooming presents involving the focal subject was assessed throughout the 2 min intervals. Grooming present rates were calculated as the number of times "A" grooming presented to "B" divided by the focal samples on "A" and "B".

Presents. An "A"=>"B" present was scored when "A" oriented its anogenital region towards the face of "B" when "B" was within 2 m of "A". Present rates were calculated as the number of times "A" presented to "B" divided by the focal samples on "A" and "B".

Mounts. An "A"=>"B" mount was scored when "A" climbed on top of "B", placed both hands on "B"'s back and the anogenital regions of "A" and "B" were aligned as during copulation. Concurrent samples were collected on the frequency of all mounts in the focal subject's group. Rates of "A" mounting "B" were calculated as sum of these mounts divided by the 2 min intervals during which their group was observed.

Intrasexual presents and mounts were used as measures of affiliation. Heterosexual presents and mounts (Michael, Wilson & Zumpe, 1974) were used as measures of affiliative and sexual behavior. These behavioral patterns were correlated with the other measures of affiliation used here (Rasmussen, 1994).

Consorts. A consort was recorded when a male was the nearest neighbor of a female for at least 5 min and the female's sexual skin indicated she was near the middle of her menstrual cycle (Czaja et al. 1977). The dyads in consort were recorded once each 14 min sampling session. Rates of "A" <=> "B" consorts were calculated by dividing their sum by the 14 min sampling sessions conducted on their group.

Threatening Away. Threatening away is strongly associated with the initiation of sexual interactions in rhesus (Zumpe & Michael, 1970). Threatening away was scored for "A" when "A" and "B" were in consort, separated by less than 1 m and a threat away from "B" was made by "A". The threat could be an eye threat or a yawn threat. When "A" eye threatened it raised its eyebrows, flattened its ears against the side of its head and stared. When "A" yawn threatened, it yawned with its mouth open and lips retracted so as to expose its teeth. The threat could also be a hand slap, head bob, or head duck as defined by Zumpe & Michael (1970). Recipients of threats were not recorded, as threatening away was sometimes not directed at another individual. Concurrent samples were collected on the frequency of threatening away by each individual in the focal subject's group. "A's" threaten away rate was the number of times "A" threatened away divided by the sum of the 2 min intervals during which "A's" group was observed.

Ejaculation. Ejaculation was recorded if a male paused after several penis thrusts into a female's vagina and maintained a rigid posture for 5 s or more or if, after intromission, fresh ejaculate was observed on the male's penis or the female's vagina. Concurrent samples were collected on the frequency of all ejaculations in the focal subject's group. The rate of "A"'s ejaculation in "B" was calculated as the sum of these ejaculations divided by the 2 min intervals during which their group was observed.

Tests of the Hypotheses

The ability of the three combined hypotheses to predict differences between groups was evaluated with a one-tailed sign test (Siegel & Castellan, 1988). The datum tested was whether a difference between groups was in the direction predicted by an a priori hypothesis. For example, hypothesis 1 predicted the oldest female in the experimental group would groom the oldest male in that group more than the oldest female in the control group groomed the oldest male in that group. The sign of this difference in rate of grooming between groups was positive. This comparison of matched dyads therefore supported hypothesis 1.

The data used to test the hypotheses were independent: Making a correct or incorrect a priori prediction of a difference between groups did not influence the likelihood of another prediction being either correct or incorrect.

An initial overall sign test was applied to the number of correct

predictions of differences between the experimental and control groups in (a) directional variables between the 110 matched directional dyads, (b) distance variables between the 55 matched non-directional dyads, (c) differences in threaten away between the 11 matched pairs of subjects and (d) the number partners in liaisons formed for each variable used to assess hypothesis 3. The significance of the initial overall test is used to protect the experimentwise significance level. In a manner analogous to the Fisher's protected t-test, subsequent tests of hypotheses 1 and 2 are only made if the overall test of the accuracy of the hypotheses is significant (Rasmussen, 1984).

Hypothesis 3 is focused on differences in the number of pairs that formed heterosexual affiliative and sexual liaisons in the experimental and control groups. The number of pairs who were ever close neighbors was the distance variable used to assess hypothesis 3, since all individuals had NN distances. The Wilcoxon matched-pairs signed-ranks test (Siegel & Castellan, 1988) was used to assess hypothesis 3.

The hypotheses were derived from theory concerned with intrasexual competition and the reproductive function of heterosexual affiliation and sexuality. The hypotheses therefore might be more accurate when restricted to sexually mature individuals. The hypotheses were therefore applied to these individuals after the accuracy of the hypotheses was assessed for all group members.

Affiliation Between Females

The significance of differences between groups in affiliation between females was determined with two-tailed sign tests. The data tested therefore shift from correct or incorrect predictions of group differences to the direction of differences between groups. Differences between groups are not necessarily independent: Interactions between one pair of individuals are socially and physiologically associated with interactions these individuals have with group members (Michael & Zumpe, 1988) or with other groups (Gordon, Bernstein & Rose, 1978).

The sign test does not assume outcomes are independent. It is used to determine if observed outcomes differ significantly from those of the binomial distribution (Sokal & Rohlf, 1981). There are many textbook examples of applications of the sign test to outcomes unlikely to be independent. These include repeated qualitative judgments by a group (Siegel & Castellan, 1988), successive choices

by a person in an experiment (Edwards, 1972), and presence of contagious disease in groups of insects (Sokal & Rohlf, 1981).

Statistical Control of Previous Familiarity

The groups were not perfectly matched by previous familiarity (Rasmussen, 1993). Regression was used to statistically control this nuisance variable. All variables were regressed on the linear and quadratic aspects of previous familiarity as measured by the mean of number of days dyads had been housed together before the experiment. Only grooming was strongly associated with the quadratic aspect of previous familiarity (linear $r=+0.27$; linear and quadratic multiple $R= +0.34$). Residuals from the regression of grooming on both linear and quadratic aspects of previous familiarity were therefore used in the analyses. For all other variables the residuals from regression on the linear aspect of previous familiarity were used in the analyses. The relationships between the variables and previous familiarity are tested for significance and interpreted elsewhere (Rasmussen, 1993).

RESULTS

Of the 295 applications of the hypotheses to differences between groups, 183 (62%) were correct ($p<.001$). When applied to sexually mature group members, 101 of 153 applications of the hypotheses (65%) were correct ($p<.001$).

Hypothesis 1

Experimental heterosexual dyads had higher rates of affiliative and sexual behavior in 63% of the between group comparisons (Table 2). Heterosexual grooming, grooming presents, and presenting occurred at significantly higher rates in the experimental group. For all variables except CN distance more of the heterosexual dyads in the experimental group had higher levels of affiliative and sexual behavior.

There were higher rates of affiliative and sexual behavior in 69% of the experimental heterosexual dyads composed of sexually mature individuals ($p<.0001$, Table 3). ALF and presents occurred at higher rates in significantly more of the experimental dyads. For all the variables more of the experimental dyads had higher rates of

Table 2. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Data are shown for all Heterosexual Dyads. Correct/Incorrect: the number of differences between groups that were in the direction predicted compared to the number of differences between groups that were not in the direction predicted; Proportion Correct: the number of correct predictions divided by the number of predictions; *p* Value: the probability of obtaining this number of correct predictions by chance alone; *: $p < .05$.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> value
1. Nearest Neighbor Distance	14/10	.58	0.2707
2. Close Neighbor Distance	10/13	.44	not tested
3. ALF Rate	25/18	.58	0.1801
4. I/O Grooming Rate	30/16	.65	0.0277*
5. Grooming Present Rate	21/10	.68	0.0365*
6. Present Rate	25/11	.69	0.0152*
7. Mounting Rate	19/13	.59	0.1884
8. I/O Consort Rate	5/2	.71	0.2266
9. Threatens Away Rate	4/0	1.00	0.0625
10. Ejaculation Rate	5/2	.71	0.2266
Overall Sign Test	158/95	.63	$p < .0001$

affiliative and sexual behavior than their matched controls.

The greatest proportion of correctly predicted differences were for the variables most closely associated with conception: consorts (71%), threaten away (100%) and ejaculation (71%). These sexual behavior patterns only occurred between adults. These variables were not significantly different between groups since they occurred between only a few individuals. When these variables are pooled they occurred at higher rates in significantly more of the matched dyads in the experimental group (14 of 18 matched dyads, $p = 0.015$).

Adult female => adult male affiliative and sexual behavior occurred at higher rates in the experimental group in only 60% of the interactions ($p > .05$). Adult male => adult female affiliative and sexual behavior occurred at higher rates in 74% of the experimental dyads (Table 4, $p < .001$). When ejaculations are excluded so these interactions include the same variables as those directed by

Table 3. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Data from all sexually mature dyads. See Table 2 for explanation of column labels. Consorts, Threatens Away and Ejaculations are identical to Table 2 since they only occurred in dyads not containing 2 year olds.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
1. Nearest Neighbor Distance	8/2	.80	0.0547
2. Close Neighbor Distance	6/4	.60	0.3770
3. ALF Rate	4/5	.74	0.0318*
4. 1/0 Grooming Rate	14/6	.70	0.0577
5. Grooming Present Rate	11/7	.61	0.2403
6. Present Rate	14/5	.74	0.0318*
7. Mounting Rate	10/8	.56	0.4073
8. 1/0 Consort Rate	5/2	.71	0.2266
9. Threatens Away Rate	4/0	1.00	0.0625
10. Ejaculation Rate	5/2	.71	0.2266
Overall Sign Test	91/41	.69	<i>p</i> <.0001

Table 4. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Behaviour Directed by Adult Males to Adult Females. See Table 2 for explanation of column labels.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
3. ALF Rate	7/2	.78	0.0899
4. 1/0 Grooming Rate	7/3	.70	0.1719
5. Grooming Present Rate	7/2	.78	0.0898
6. Present Rate	8/2	.80	0.0547
7. Mounting Rate	6/3	.67	0.2539
10. Ejaculation Rate	5/2	.71	0.2266
Overall Sign Test	40/14	.74	<i>p</i> <0.001

Table 5. Tests of Hypothesis 2: Less Affiliative Behaviour Between Males in the Experimental Group. Data from all Dyads. See Table 2 for explanation of column labels.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct
1. Nearest Neighbor Distance	2/1	.67
2. Close Neighbor Distance	3/0	1.00
3. ALF Rate	4/2	.67
4. 1/0 Grooming Rate	4/2	.67
5. Grooming Present Rate	3/2	.60
6. Present Rate	1/4	.20
7. Mounting Rate	1/4	.20
Overall Sign Test	18/15	.55 ($p=0.3639$)

adult females to adult males, 75% of the comparisons were greater in the experimental group.

Only 43% of the experimental dyads composed of an immature male and a mature female had higher rates of affiliative and sexual behavior than their matched controls ($p>.05$). In adult male and immature female dyads, 61% of the experimentals engaged in higher rates of affiliative and sexual behavior ($p>.05$). There were higher rates of affiliative and sexual behavior in the experimental group in 65% of the dyads composed of immature males and immature females ($p>.05$).

Hypothesis 2

There was less affiliation between experimental males in 55% of the dyadic comparisons (18 of 33, $p>.05$, Table 5). Further tests were not conducted since the initial test was not significant.

Descriptive analyses of the data were conducted: Counter to hypothesis 2, there was more affiliation between the sexually mature experimental males for every variable except close neighbor distance. As predicted by hypothesis 2, in the experimental group there was less affiliation between the immature male and the two older males for all variables except presents and mounts.

Table 6. Tests of Hypothesis 3: More Heterosexual Liasons in Affiliative and Sexual Behaviour in the Experimental Group. Difference: is the difference between the residualized number of pairs who interacted by each variable in the experimental and control groups. A positive difference is in the direction predicted, that is, more liasons formed in the experimental group. The number of pairs was residualized on the mean number of days the dyads had spent together before the experiment. **: $p < .01$.

All Dyads	EXPERIMENTALS	CONTROLS
Corrected Variable	Difference from all Pairs	Difference between Sexually Mature Pairs
2. Close NN	0.67	1.34
3. ALF	4.07	4.39
4. 1/0 Grooming	1.21	8.50
5. Grooming Presents	-0.02	3.23
6. Presents	2.31	7.61
7. Mounting	3.23	6.62
8. 1/0 Consorts	3.88	7.45
9. Threat Away	2.57	3.22
10. Ejaculations	3.88	7.45
Wilcoxon matched pairs signed-ranks test	$p=0.0055^{**}$	$p=0.0039^{**}$

Hypothesis 3

More heterosexual dyads in the experimental group formed affiliative and sexual liaisons for eight of nine variables ($p=0.0055$, Table 6). There were more liaisons between experimental adult dyads for all nine variables ($p=0.0039$).

Affiliation Between Females

There was significantly more affiliation between experimental females in 56% of the matched dyads (Table 7). Presents and mounts occurred at significantly higher rates in more of the experimental dyads.

Table 7. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group for all Dyads.
*: $p < .05$; ***: $p < .001$.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
1. Nearest Neighbor Distance	11/17	.39	0.3447
2. Close Neighbor Distance	10/18	.36	0.1859
3. ALF Rate	30/25	.55	0.5896
4. I/O Grooming Rate	32/21	.60	0.1696
5. Grooming Present Rate	16/23	.41	0.3367
6. Present Rate	38/12	.76	0.0004***
7. Mounting Rate	29/13	.69	0.0206*
Overall Sign Test	166/129	.56	0.0361*

Table 8. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 3 and 4 year old female \leftrightarrow 2 year old female. See Table 2 for explanation of column labels. *: $p < .05$; **: $p < .01$.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
1. Nearest Neighbor Distance	4/11	.27	0.1185
2. Close Neighbor Distance	5/10	.33	0.3018
3. ALF Rate	15/14	.52	1.0000
4. I/O Grooming Rate	17/10	.63	0.2482
5. Grooming Present Rate	9/7	.56	0.8036
6. Present Rate	20/4	.83	0.0015**
7. Mounting Rate	15/2	.88	0.0023**
Overall Sign Test	85/58	.59	0.0297*

Affiliation between experimental adult females occurred at higher levels in 51% of the comparisons ($p > .05$). Affiliation between immature females occurred at higher levels in the experimental group in 63% of the comparisons ($p > .05$). Affiliative behavior was greater between experimental adult and immature females in more of the matched dyads (59%, $p < .05$, Table 8). Presenting and mounting

Table 9. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 3 and 4 year old females => 2 year old females. See Table 2 for explanation of column labels.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
3. ALF Rate	9/6	.60	0.6072
4. 1/0 Grooming Rate	8/6	.57	0.7905
5. Grooming Present Rate	5/4	.56	1.0000
6. Present Rate	10/2	.83	0.0386*
7. Mounting Rate	7/0	1.00	0.0156*
Overall Sign Test	39/18	.68	0.0231*

Table 10. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 2 year old females => 3 and 4 year old females. See Table 2 for explanation of column labels.

Corrected Variable (Residualized on Days Together)	Correct/ Incorrect	Proportion Correct	<i>p</i> Value
3. ALF Rate	6/8	.43	0.7905
4. 1/0 Grooming Rate	9/4	.69	0.2668
5. Grooming Present Rate	4/3	.57	1.0000
6. Present Rate	10/2	.83	0.0386*
7. Mounting Rate	8/2	.80	0.1094
Overall Sign Test	37/19	.66	0.0231*

occurred at higher rates in significantly more of these experimental dyads. Experimental adult female => immature female affiliation occurred at higher rates in 68% of the comparisons ($p < .05$, Table 9). Presenting and mounting occurred at higher rates in significantly more of the experimental dyads. Experimental immature female => adult female affiliation occurred at higher levels in 66% of the comparisons ($p < .05$, Table 10). Presents of immature females to adult females occurred at higher rates in significantly more experimental dyads.

DISCUSSION

Previous Familiarity

Previous familiarity was greatest between the control dyads (Rasmussen, 1993). In heterosexual dyads this was associated with more affiliative and sexual behavior (counter to hypothesis 1) and with more heterosexual liaisons (counter to hypothesis 3). Since hypotheses 1 and 3 were confirmed and hypothesis 2 was rejected, any influences of previous familiarity not removed with statistical control would have biased the data against this pattern of results. Differences between groups in previous familiarity between subjects therefore seems an unlikely cause of our results.

Hypothesis 1

Higher rates of affiliation and sexual behavior appear to be linked causally with reproductive failure. The repeated nonpregnant estrous cycles of the experimental females, and the conception and resultant gestation of their controls, were probably the major factors responsible for differences between groups.

The majority of heterosexual interactions in the experimental group were more affiliative and sexual by 9 of the 10 variables for all group members (Table 2). For adults the majority of heterosexual interactions were more affiliative and sexual in the experimental group for all 10 variables (Table 3).

These differences between groups gave a qualitative impression as great as that between different species of macaques. The experimental group was more heterosexually and sexually oriented. Yet the control group was not asexual. Heterosexual affiliative and sexual behavior remain salient and important aspects of social organization during periods when females cannot conceive (Chapais, 1986; Hill, 1986). There was a much greater difference between groups in adult male => adult female than adult female => adult male interactions. Group differences may therefore hinge more on differences in attractiveness and receptivity of the adult females than on females' proception.

Evolutionary theory added to the ability to predict group differences. Evolutionary theory also suggests the ultimate cause of the differences: Individuals in the experimental group continue to attempt behavioral patterns that have been selected since they could lead to conception in an intact group. The answer to the functional question: "Why is there more affiliative and sexual behavior in the experimental group?" is that group members have failed to reproduce but continue in

the attempt.

Hypothesis 2

Hypothesis 2 was not confirmed: there was less affiliation between only 55% of the experimental male dyads (Table 5). Hypothesis 2 was based on a theoretical continuum of the degree to which interactions are competitive or beneficial. The theory requires the net result of interactions between the experimental males to be more competitive. In retrospect the theory does not exclude the possibility that individuals who compete more also engage in more affiliation. Hypothesis 2 is therefore revised to predict a greater ratio of competitive to beneficial behavior in the experimental group. When analyses are focused on the interactions between the 5 and 4-year-old males, there were higher levels of affiliation between adult experimental males in 92% of the comparisons between groups. The adult males may have engaged in more conciliatory and reconciliatory affiliative behavior (de Waal & RenMei, 1988) because of more intrasexual competition in the experimental group.

In dyads composed of an immature and an adult male, 81% of the comparisons between matched dyads were in the direction predicted. Lower levels of affiliation between the immature male and the adult males in the experimental group may have been due to the immature male's inability to make serious reprisals to the frequent vicious attacks by adult males.

Hypothesis 3

Hypothesis 3 was confirmed for eight of the nine variables to which it was applied in all heterosexual pairs and for all nine variables for adult heterosexual pairs. Affiliative and sexual interactions occurred between more pairs in the experimental group. The experimental females had repeated nonpregnant menstrual cycles. The greater opportunities for sexual behavior in this group may have been a proximate cause of the greater number of partners in affiliative and sexual liaisons. It would, of course, be possible for the increased sexual behavior in the experimental group to have been instead associated with more frequent sexual and affiliative behavior between the same pairs.

Affiliation Between Females

There was more affiliation between experimental females primarily because of higher levels of affiliation between the adult and immature

females (Tables 8, 9 and 10). Increased presenting and mounting could be associated with higher levels of intrasexual competition between the adult and immature females. Female intrasexual competition seems likely to be greater due to the higher levels of affiliative and sexual behavior that occurred between the adult males and immature females in the experimental group.

Replication

Comparisons have often been made between two groups of nonhuman primates (Keverne, Meller, & Martines-Aria, 1978; Rasmussen 1984). Comparisons have been made when the groups are not closely matched or are composed of different species (Gordon, Bernstein, & Rose, 1978; Rosenblum & Paully 1984). Such comparisons have been subjected to statistical test (de Waal & RenMei 1988; Boccia 1989). The significant differences are, however, based on only two groups. The generality of the results of this, and other such studies, must therefore be regarded with caution.

This study must be replicated to determine the degree to which the hypotheses may be generalized to other groups of rhesus, and, with suitable modification, to species with different modal patterns of social organization (Rasmussen, 1981a). As R. A. Fisher (1951) noted: "In order to assert that a natural phenomenon is experimentally demonstrable we need, not an isolated record, but a reliable method of procedure". This paper describes such a method for comparison of reproductive and non-reproductive groups. Replicates, further comparative studies, and long term studies conducted on nonhuman primates certainly seem important for increased understanding of both proximate and selective consequences of the widespread use of contraception on human social behavior.

Potential Relevance to Human Behavior

In developed nations the mean number of children born per woman has steeply declined and the mean age at which a woman bears her first child has steadily increased over the past century (Short, 1974; May, 1978; Caldwell, 1982). Strong and consistent correlations have been found between changes in the number of children born by women and many changes in our premarital and marital social and sexual behavior as well as marital stability and duration (Thornton, 1977; Zelnik & Kantner, 1980; Clayton & Bokemeier, 1980; Rasmussen, 1981a; Lodewijckx, 1987; Martin & Bumpass, 1989). Decreased number of children born to women has, for example, been shown to be positively

correlated with decreased marital duration and stability (Rasmussen, 1981a). These are undoubtedly some of the most profound and far reaching changes in the natural history of the human animal within the last several centuries. These changes are similar in magnitude to other major alterations in the course of human history such as the industrial revolution, the rise of the nation state and global communication networks.

The decline in number of children born per woman, and increased age upon birth of their first child, is associated with modern fertility control methods that sever causal links between sexual and social behavior and reproduction (Montagu, 1969). It would not be ethical to conduct studies on many of the relationships between human reproduction and social behavior. When human studies are not ethical, studies conducted on nonhuman primates may sometimes contribute to comparative knowledge on biological processes similar to those in humans (Hinde, 1974). This experimental study suggests that the correlations between increased use of fertility control, decreased family size, and increased sexual interactions may be causal.

With further studies we may eventually have a strong theoretical and empirical understanding of the behavioral processes responsible for differences between groups of nonhuman primates in which sexual behavior has been uncoupled from reproduction and reproductive groups. This knowledge seems likely to increase our understanding of how differences in numbers of children born to women are linked with affiliative, sexual and marital differences between human populations. Without such an understanding, results from studies of natural reproductive groups of nonhuman primates (e.g. Rasmussen, 1979; de Waal, 1982; Goodall, 1986) are of limited use for understanding behavioral processes observed in human populations using effective means of contraception.

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