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Social Segregation in Male, but not Female Yearling Rhesus Macaques (*Macaca mulatta*)

Janice M. Hassett¹, Heather A. Rupp^{1,2}, and Kim Wallen¹

¹ Yerkes National Primate Research Center, Center for Behavioral Neuroscience, Department of Psychology, Emory University, Atlanta, GA, 30322

Abstract

Males and females of many species sex-segregate, ranging from complete separation of habitats to social segregation within the same space, sometimes varying across seasons and lifespan development. Mechanisms for such segregation are not well understood, though some have suggested that sex differences in preferred juvenile behaviors lead to greater behavioral compatibility within than between sexes. This within-sex behavioral compatibility may be the source of sex-segregation. Since juvenile behavioral sex differences are well-documented in rhesus monkeys, we examined sex-segregation patterns of yearling rhesus monkeys engaged in three different types of behavior: rough play, parallel play, and grooming. We observed male and female rhesus yearlings from five stable long-term age-graded social groups of 67–183 animals. Behavioral observations were designed to collect equal numbers of rough play, grooming, and parallel play bouts. In addition, sex composition and proximity to adults was recorded for each bout. Across all behaviors, more all-male groups and fewer mixed sex-groups were observed than expected by chance. All-female groups occurred at the level expected by chance. Thus, males sex-segregated regardless of type of behavior, while females did not sex-segregate. Female groups were observed in proximity to adults more often than expected by chance. These results suggest that behavioral compatibility may produce sex-segregation in male yearling rhesus monkeys, possibly preparing males and females for different social roles and segregation as adults.

Keywords

social segregation; sex; juvenile behavior; rhesus; primate

INTRODUCTION

Segregation of males and females occurs in many species, including fish, birds, ungulates, and primates. Males and females may spend the majority of their time in separate habitats, as in many ungulate species [Conradt 2005; Du Toit 2005; Main et al. 1996]. Other animals, including many primates [Watts 2005], segregate within the same space or habitat. Investigations into why such segregation occurs have been the focus of considerable theory and research, although the causes are still not entirely understood. The underlying mechanisms driving social segregation remain unclear in cases in which social segregation occurs in the absence of habitat segregation. In this study, we seek to understand the

Corresponding author: Janice M. Hassett, Emory University, Department of Psychology, 532 N. Kilgo Circle, Atlanta, GA 30322; jhasset@emory.edu; Phone: 404-727-4133.

²Current address: The Kinsey Institute for Research in Sex, Gender and Reproduction, Indiana University, Morrison Hall 313, Bloomington, Indiana 47405

relationship between sex differences in social behavior and sex-segregation in yearling rhesus macaques (*Macaca mulatta*).

One common explanation for persistent social sex-segregation is that animals of different sizes (based on age or sex) spend varying amounts of time engaged in activities required to fulfill physiological needs, consequently spending more time around those individuals most like them [Conradt 1998; Ruckstuhl 1998]. One alternative is that sex differences in juvenile behavior might lead to segregation based on differences in behavioral compatibility; the notion that individuals may interact with one another because they engage in similar kinds of behavior in similar ways [Bon and Campan 1996; Guilhelm et al. 2006]. Thus, one consequence of males and females engaging in different behaviors may be sex-segregation.

Juvenile rhesus monkey males engage more frequently in rough-and-tumble play than do juvenile female rhesus monkeys [Brown and Dixson 2000; Goldfoot et al. 1984; Lovejoy and Wallen 1988; Wallen 1996]. By contrast, juvenile female rhesus monkeys, like females of other primate species [Chamove et al. 1967; Lancaster 1971], spend more time touching and playing with infants than do juvenile male rhesus [Herman et al. 2003]. They also spend a greater proportion of their time approaching adult females and infants [Lovejoy and Wallen 1988]. Young females might be predicted to engage in more social grooming, a behavior commonly observed among adult female macaques and towards infants [Butovskaya and Kozintsev 1996; Nakamichi and Yamada 2007]. However, examinations of specific age groups and species reveal variable findings, with no difference reported in yearling rhesus [Lovejoy and Wallen 1988], significant differences at puberty in rhesus (2.5–4.5 years) [Bernstein et al. 1993], and significant differences reported from 28 weeks through the first year for Japanese macaques (*Macaca fuscata*) [Eaton et al. 1985].

Based on the occurrence of these sexually dimorphic behaviors, behaviors which occur with greater frequency in one sex than the other, we predict segregation of male and female yearling rhesus monkeys living in a naturalistic social context. Yearlings are a good age group for studying patterns of social segregation because most individuals are completely weaned and exhibit high levels of independence from the mother. There is also minimal size dimorphism between males and females at this age. Moreover, little research in rhesus monkeys has focused on yearlings, and data on segregation patterns at this age could help us understand potential developmental mechanisms that lead to adult segregation.

Studies investigating partner preferences of rhesus monkeys support the hypothesis that young rhesus monkeys will segregate by sex. Work using a preference apparatus suggests that rhesus monkeys as young as nine months seek proximity to same-sex over opposite-sex peers [Suomi et al. 1970]. In more naturalistic settings, differences in partner preferences emerge in a more complex manner. In focal observations on a free-ranging birth cohort of 14 male and six female Japanese macaques through the first four years of life, males were often observed in proximity to same-age males starting at approximately two years of age. Although females in this study preferred to associate with other females, they did not display a same-age preference and interacted with females of all ages [Nakamichi 1989].

Although these studies support the likelihood of juvenile sex-segregation in rhesus monkeys, neither investigated the social context in which peer same-sex proximity was observed or what behavior the monkeys engaged in when with peers. Relying on focal observations will bias evidence of sex-segregation towards those behaviors which occur at the highest frequencies. Similarly, group scans will bias observations towards the most active and attention-getting of behaviors. Identifying sex-segregation in a specific behavioral context requires a substantial sample of peer groups engaged in that behavior, ideally comparable numbers of behavioral events should be collected for each behavior. Because neither routine

focal observations nor group scans guarantee comparable numbers of behavioral events, we explicitly sampled rough-and-tumble play, grooming, and parallel play equally to correct for potential observational bias. The sex composition of each behavioral bout was recorded to investigate sex bias in the expression of each behavior. We report here that yearling male but not female rhesus monkeys show evidence of social segregation and that males segregate across different behavioral contexts.

METHODS

Subjects

A total of 43 male and 54 female rhesus monkey (*Macaca mulatta*) yearlings (approximately 10–14 months of age) were potential participants. Observations occurred within five stable age-graded social groups. The number of male and female yearlings within each of the five social groups ranged from seven to 12 males ($M = 8.6$), and from two to 17 females ($M = 10.8$). The ratio of yearling males to females varied between groups. This was statistically controlled for during data analysis by calculating expected frequencies of sex-segregation within each social group based on each group's yearling sex composition, described in more detail below. Members of the social groups included infants, other same-age juveniles, older adolescents, and adults. Non-yearling monkeys were both male and female, with roughly equal numbers of each except for adults in which there were many adult females and only two adult males in each group. Social groups were housed at the Yerkes National Primate Center Field Research Station in large indoor-outdoor compounds ($38 \times 38\text{m}$, or $30 \times 30\text{m}$) with attached heated and air conditioned indoor quarters. Water was continuously available. The monkeys were fed monkey chow twice daily, supplemented once per day with fruits and vegetables. All research was conducted under an approved Institutional Animal Use and Care protocol, in accordance with the *NIH Guide for the Care and Use of Laboratory Animals*, and in accordance with legal requirements of the United States.

Data Collection

All data collection took place between June 12, 2002, and July 19, 2002. The observed units of yearling peer social interactions were referred to as 'bouts'. A bout was defined as the social interaction of two or more yearling rhesus monkeys. Bouts, as described below, were balanced across behaviors. We used this unit of measurement rather than a focal method to guarantee an equal representation of all behaviors across many subjects. Using the bouts as the data points did not artificially distribute the observations equally across all yearlings. The identities of individual yearlings were not recorded, making it possible that individual dyads might be over-represented in the data set. To investigate this possibility, we used 5600 bouts of rough-and-tumble play collected using focal observations of yearlings from a previous study of two rhesus monkey social groups to investigate the relationship between number of play bouts and number of play partners. We found that as the number of play bouts that any one individual engaged in increases, the number of play partners also increases in an almost 1:1 relationship (Social group 1: $r = .91$, $p < .001$, $r^2 = .83$; Social group 2: $r = .95$, $p < .001$, $r^2 = .90$). Thus, the likelihood that a randomly selected dyad would account for a significant portion of the total data was exceedingly small. The methodology utilized here likely provided a reasonable random sample of the behavior of individuals within each social group.

We recorded the sex composition of 150 bouts and sampled equally across the five social groups. Three bout types were studied: rough-and-tumble play, parallel play, and grooming. These three types of behaviors were chosen to cover a range of relatively frequently occurring behavior in juvenile rhesus monkeys that encompasses different aspects of their

social behavior. We defined rough-and-tumble play (rough play) as an active and high-energy contact play [Goy et al. 1974]. Parallel play was defined as no contact low energy play, usually involving object manipulation in which subjects are in arms length of each other [Serbin et al. 1977]. Although parallel play shares much in common with solitary play, it differs in that it is play in a social context. With 67–183 animals in a group and 900m²–1400m² available for social interaction, proximity to another monkey was unlikely to occur accidentally and thus likely only occurred if sought out. Therefore, yearlings engaged in parallel play are participating in a social activity based on their solicitation of proximity to another yearling. The final behavioral category, grooming, was defined as the manipulation of the fur or body of another animal with hands or mouth [Lovejoy and Wallen 1988].

A bout began with the observation of a social interaction including two or more yearlings, and ended when one subject left or a new monkey joined the originally observed yearling subgroup. Only subgroups composed exclusively of yearling rhesus monkeys were included. For each bout, we recorded the sex composition of the yearling subgroup and whether the interaction occurred within proximity (arms length) to an adult. For all bouts, a single trained observer located the yearling social subgroup while another experimenter videotaped and timed the bouts at the direction of the primary observer. After each observed rough play event, we scanned for a parallel play or a grooming bout. The same set of observers collected all of the data according to this method. No more than 4 of each bout type were collected from a social group in one day, and the data represent 44 total hours of observation. Sexes of the individuals involved in the bouts were recorded at the time of observation and verified with the videotaped recordings. Male yearlings were distinguished from female yearlings due to the noticeable presence of a scrotum.

Data Analysis

The expected probability of same- or mixed-sex groups for each type of bout was derived from the yearling sex ratio within each social group. For example, a group with two males and three females can potentially form one unique male same-sex dyad, three female same-sex dyads, and six mixed-sex dyads. Thus one would expect by chance that 10% of juvenile groups would be male same-sex dyads, 30% female same-sex dyads, and 60% mixed-sex dyads. The expected percentages were then used to determine expected frequencies based on the total number of observed bouts. Each of the five large social groups was initially treated separately to obtain the expected and observed frequencies according to the unique yearling sex ratio of the group. The observed and expected frequencies were then combined and compared to the observed distributions of male same-sex, female same-sex, and mixed-sex peer social groups using Chi-Square tests of independence. Because our unit of measurement was the bout rather than the individual yearling, the data were considered independent and a Chi-Square test was statistically appropriate. A p-value less than 0.05 was considered significant. Chi square tests were completed using SPSS and Microsoft Excel.

RESULTS

Although 150 play bouts were collected, 145 were included in the analysis because we limited analysis to dyads or triads and five of the bouts (all rough play) involved groups of four or five subjects. The breakdown of social subgroups observed was 45 rough play, 50 parallel play, and 50 grooming bouts. Across all behavior types we observed 72 male same-sex, 25 female same-sex, and 48 mixed-sex dyads or triads.

For the following results dyads and triads were combined. An overall Chi-Square totaled across all bouts comparing the expected frequency of same- and mixed-sex group compositions, based on the sex ratio of the social groups, revealed that bouts were not evenly distributed across the three possible group compositions ($\chi^2(2, N = 145) = 88.6, p < .$

001). There were significantly more male same-sex bouts than expected by chance (50% vs. 19% expected; $\chi^2(1, N=72) = 71.72, p<.05$), and significantly fewer mixed-sex bouts than expected by chance (33% vs. 54% expected, $\chi^2(1, N=48) = 11.73, p<.05$). However, female same-sex bouts (17% vs. 27% expected; $\chi^2(1, N=25) = 0.59$ did not differ significantly from chance. A difference from a random distribution of the sex composition of the bouts was also seen according to behavior type (Table 1). Male same-sex bouts occurred significantly more often than expected by chance for all three types of bouts; rough play, parallel play, and grooming. Mixed-sex bouts were observed significantly less frequently than expected by chance for rough play and grooming. Female same-sex bouts were observed significantly less often than expected by chance for rough play, but did not differ from chance for grooming and parallel play bouts.

As the design of this study produced equal sampling of rough play, parallel play, and grooming, it would be expected that among each type of grouping (male-same sex, female same-sex, and mixed-sex), there would be an equal distribution of rough play, parallel play, and grooming bouts. An overall three-way chi-square (sex composition of group by behavior), showed that the three types of bouts were not randomly distributed within the male same-sex, female same-sex, and mixed-sex groups ($\chi^2(4, N = 145) = 16.3; p=.003$). Further analysis revealed that there were no significant differences for rough play, parallel play, and grooming within male same-sex and mixed-sex groups (Table 2). Female same-sex groups showed significantly more grooming and less rough play than expected by chance (Table 2).

Across all bouts, 37% occurred within proximity to an adult. A two by three way Chi-square (presence of adults by sex composition of the group) revealed that, across all bouts, proximity to adults was not evenly distributed ($\chi^2(2, N=145)=9.3, p=.01$). Chi-Square analyses within groups found that female same-sex groups were observed more often than chance in proximity to adults, and male same-sex and mixed-sex groups did not differ from expected frequencies (Table 3). Males' separation from adults was driven by rough and tumble play behavior, which occurred away from adult proximity in 28 of 31 cases ($\chi^2(1, N=31) = 20.16, p<.001$) all male parallel play ($\chi^2(1, N=19) = 0.47, p=.49$) and grooming ($\chi^2(1, N=22)=.18, p=.67$) bouts were observed in proximity to adults at levels expected by chance.

DISCUSSION

Male rhesus monkeys sex-segregate across both sexually dimorphic (rough play) and nondimorphic (grooming and parallel play) behaviors whereas female rhesus monkeys do not sex-segregate. Female same-sex social groups, when they do occur, are more likely to be in proximity to adults than are male same-sex groups. These findings are similar to those for Japanese macaques at two years of age [Nakamichi 1989], but reveal that the age and sex-segregation of rhesus males is present as early as one year of age, and occurs in different behavioral contexts.

The reasons why yearling male but not female rhesus monkeys sex-segregate remain unclear. The hypothesis that male sex-segregation reflects sex differences in juvenile behavior is not fully supported by our data. Yearling males sex-segregate during rough-and-tumble play, a behavior which yearling males participate in at much higher frequencies than do yearling females, supporting a behavioral compatibility interpretation of sex-segregation. By contrast, yearling males also sex-segregate in grooming and parallel play contexts which are not sexually dimorphic and thus do not support a behavioral compatibility interpretation. Young males might be drawn to each other initially for their interest in rough play, especially since rough play requires a high degree of behavioral coordination between the

participants. Males may continue to segregate in other behavioral contexts not requiring such a high degree of compatibility because of the familiarity resulting from engaging in rough play.

Lack of sex-segregation integrates young females into the social structure whereas male sex-segregation isolates them from the bulk of the social group. These patterns may facilitate divergent life-histories of males and females. Rhesus social groups are composed of a few adult males and many more adult females and their offspring [Dittus 2004]. While female rhesus monkey offspring remain in their natal social group, most males leave soon after puberty. Females form the stable core of the matriarchy with a dominance hierarchy in which offspring assume their mother's rank [Berman et al. 1994]. Offspring become integrated into the social hierarchy soon after birth [Berman et al. 1994], become attracted to other infants around the second week of life, and engage in social behaviors with peers around 8 weeks of age [Hinde et al. 1964]. They also substantially reduce the time spent with their mother and other relatives throughout their first year [Berman 1982; Hinde et al. 1964]. Thus, there is considerable opportunity for the social lives of male and female rhesus macaques to diverge starting early in life. One form of divergence is that males in large social groups gain independence from their mothers sooner than do females [Devinney et al. 2001]. Even when females show comparable maternal independence, they still spend more time near adult males and other females, and near or in contact with infants [Lovejoy and Wallen 1988].

A greater separation of rhesus males from the social group has been observed from early infancy [Berman et al. 1994], to late juvenile stages [Herman et al. 2003; Lovejoy and Wallen 1988; Vessey and Meikle 1987], and into adulthood [Vessey and Meikle 1987]. Male transfer to a non-natal group appears to rely on their relationships with male peers within their natal group [Colvin 1986]. Colvin found that male peers treated one another differently based on relative rank in the peer group. Furthermore, relative rank at one year and three years predicted age at emigration. If male relationships are important for natal transfer, the development of those relationships may be facilitated by early behavioral compatibility between young males.

Here we have found that the rhesus monkey, a species which shows sexually differentiated juvenile behaviors and which forms stable mixed-sex groups, shows sex-segregation in yearling males. Yearling behavioral patterns alone, however, may not predict whether a species will establish groups which are sex-segregated or mixed-sex. While there are no mammalian species that sex-segregate as adults who do not do so as juveniles, the opposite is not true, bringing in to question the role that sex-segregation plays in social development. Something as simple as behavioral compatibility may drive juvenile sex-segregation, whereas sexual compatibility and mating systems drive adult integration or sex-segregation.

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Table 1

The distribution of same- and mixed-sex yearling rhesus monkey groups by activity type. Significant results ($p < .05$) are noted by a (*) for one-sample Chi-square comparisons.

Activity	Group type	% Observed	% Expected	Statistic
<i>Rough play</i>				
	Male same-sex	69	19	$\chi^2(1, N=31)=16.26^*$
	Female same-sex	2	27	$\chi^2(1, N=1)=124.32^*$
	Mixed-sex	29	54	$\chi^2(1, N=13)=9.82^*$
				Overall: $\chi^2(2, N=45)=74.4, p < .001$
<i>Parallel play</i>				
	Male same-sex	38	19	$\chi^2(1, N=19)=4.75^*$
	Female same-sex	20	27	$\chi^2(1, N=10)=1.23$
	Mixed-sex	42	54	$\chi^2(1, N=21)=1.71$
				Overall: $\chi^2(2, N=50)=11.7, p = .003$
<i>Grooming</i>				
	Male same-sex	44	19	$\chi^2(1, N=22)=7.10^*$
	Female same-sex	28	27	$\chi^2(1, N=14)=0.02$
	Mixed-sex	28	54	$\chi^2(1, N=14)=12.07^*$
				Overall: $\chi^2(2, N=50)=22.7, p < .001$

Table 2

The distribution of activity types within yearling rhesus monkey peer groups. Significant results ($p < .05$) are noted by a (*) for one-sample Chi-square comparisons.

Group	Activity Type	% Observed	% Expected	Statistic
<i>Male same-sex</i>				
	Rough play	43	33	$\chi^2(1, N=31)=2.04$
	Parallel play	26	33	$\chi^2(1, N=19)=1.04$
	Grooming	31	33	$\chi^2(1, N=22)=0.17$
				Overall: $\chi^2(2, N=72)=3.2, p=.20$
<i>Female same-sex</i>				
	Rough play	4	33	$\chi^2(1, N=1)=6.37^*$
	Parallel play	40	33	$\chi^2(1, N=10)=0.37$
	Grooming	56	33	$\chi^2(1, N=14)=4.01^*$
				Overall: $\chi^2(2, N=25)=10.6, p=.005$
<i>Mixed-sex</i>				
	Rough play	27	33	$\chi^2(1, N=13)=0.51$
	Parallel play	44	33	$\chi^2(1, N=21)=1.68$
	Grooming	29	33	$\chi^2(1, N=14)=0.21$
				Overall: $\chi^2(2, N=48)=2.4, p=.31$

Table 3

The distribution of adult proximity to yearling rhesus monkey groups by sex composition. Significant results ($p < .05$) are noted by a (*) for one-sample Chi-square comparisons.

Adult Presence	Group Type	% Observed	% Expected	Statistic
No				
	Male same-sex	68	63	$\chi^2(1, N=49)=0.29$
	Female same-sex	36	63	$\chi^2(1, N=9)=2.89$
	Mixed-sex	69	63	$\chi^2(1, N=33)=.25$
				Overall: $\chi^2(2, N=91)=26.73, p < .001$
Yes				
	Male same-sex	32	37	$\chi^2(1, N=23)=.50$
	Female same-sex	64	37	$\chi^2(1, N=16)=4.93^*$
	Mixed-sex	31	37	$\chi^2(1, N=15)=.43$
				Overall: $\chi^2(2, N=54)=2.11, p = .35$