The Ontogeny of Sex Differences in the Behavior of Patas Monkeys

T. E. Rowell[1] and Janice Chism[1]

Many studies of sex differences in primates have been based on small experimental groups of peers in which only a limited range of social behavior could be expressed. In addition, the first few months of life are often the focus of such studies, with relatively little attention paid to older juveniles. In this study, 11 male and 9 female juvenile patas monkeys, living in a captive social group with all age–sex classes available, were observed between 1 and 4 years of age. A subset of seven patas monkeys was also observed between birth and 1 year of age. Here, we report the development of sex differences in independence, play, grooming, positioning behavior, and aggression over the juvenile period. Juvenile male patas monkeys played more and in longer bouts than females, but wrestling (rough-and-tumble play) was not more common among males. There were few differences in behaviors directed to male and female juveniles by other group members. Distinct differences emerged only in the behaviors of the juveniles themselves, with females being more active participants in social and aggressive interactions than males. In general, sex differences in patas monkeys show a mixture of patterns, some of which are predictive of adult sex differences and some of which appear to be specific to the particular demands of the juvenile period in this species

KEY WORDS: sex differences; juvenile behavior; patas monkeys.

[1]Department of Zoology, University of California, Berkeley, California 94720.

83

INTRODUCTION

Adult male and female mammals differ in their social behavior, not only in those aspects immediately concerned with their different reproductive functions. In some species, sex differences are apparent as soon as infants begin to engage in social interactions. Interest in the origin and function of sex differences in behavior derives from two types of approaches. The first, a comparative approach, is instrumental in understanding human behavioral differences and how far these might be responses to particular cultural or economic environments (cf. Mead, 1935, 1949; Maccoby, 1966). The second, a developmental approach, investigates the role of hormones relative to that of genes or experience in the organization of the nervous system.

Boys and girls under 7 years of age have different modal patterns of play and other social interactions (for example, Blurton-Jones and Konner, 1973; Brindley et al., 1973) and there are obvious cultural pressures in the direction of the observed differences. Rhesus monkeys under 1 year also show differences in play behavior, with males doing more active rough-and-tumble play (Hansen, 1966; Harlow and Lauersdorf, 1974; but see also Seay, 1966). These differences were found among infants which had been reared from soon after birth in a "culture-free" environment (i.e., without any contact with adults). Goy and Phoenix (1972) found that infant female rhesus which had been anatomically masculinized by intrauterine treatment with androgens showed play patterns intermediate between those of males and those of females; similar results have been reported by Ehrhardt (1974) for girls with congenital adrenal hyperplasia. The adult behavior of rats and guinea pigs can be permanently modified by treatment of neonates and intrauterine embryos, respectively, with steroids (Phoenix et al., 1959; Gorski and Barraclough, 1961; Pfaff and Zigmund, 1971), and this whole body of data suggests that some sex differences in behavior are "prewired" into the nervous system according to the hormonal environment of the brain long before there is any possibility that social interactions can provide experiential means of modifying behavior.

In both macaque and human social groups, members inspect a new infant as soon as possible after birth, paying particular attention to its genitals. In both genera the genitals of males are conspicuous at birth, so the sex difference is visually obvious. Human and macaque adults treat male and female infants differently (e.g., Moss, 1967; Mitchell and Brandt, 1970). Thus, one mechanism for the development of sex differences in behavior may be the responses of conspecifics to the anatomical differences induced by hormones during prenatal development. Some preadolescent sex differences in behavior may thus be the result of the different social environments of the sexes.

These two processes might reinforce each other, or some behavior might be differentiated via one process (effects of hormones on neural organization) and some by the other (social induction). Which process is given a greater explanatory emphasis will lead to rather different expectations of the origins of sex differences and, hence, of factors which might modify them. The first process leads to the expectation that sex differences which will have adaptive significance for adults develop at a very much earlier stage, where they have no adaptive significance—indeed, they could even be somewhat maladaptive at that stage. In the second process, the animal is seen as responding primarily to its immediate needs and to its social and physical environment. Consequently one would expect sex differences to be correlated with environmental differences. Whereas these views need not be mutually exclusive, an emphasis on one or the other, by policy makers in education and other aspects of human welfare, can have profound effects on society.

Although direct extrapolation from findings on macaques to humans would be unwise, as Lehrman (1974) pointed out, a comparative approach can lead to insights if it is broad enough. Primates offer for study a variety of species-typical differences in the behavior of the sexes as adults. Comparison of the juvenile and adult behavior of males and females of species with different social organizations should allow a test of whether there is a correspondence between juvenile and adult sex differences and, hence, differentiate between the alternative routes of development of sex differences.

Although sex differences could not be found in captive baboons under 3 months, whether reared by their mothers in mixed-age groups or bottle-fed and housed in groups of peers (Young and Bramblett, 1977), differences have been reported for baboons in field studies by Owens (1975), Nash (1978), and Cheyney (1978). Jay and Bishop (1970) described sex differences in the play of young langurs. In all these studies, sex differences (where found) were in the direction of more frequent and rougher play by males than females.

Males of most primate species are more likely than females to leave their natal group before adulthood (Moore, 1984). Among baboons and macaques, adult males are more aggressive than females and rank above them in groups. Adult females, on the other hand, attend to infants and groom others far more than do males. Studies of rhesus indicate that infant males are more independent of mothers and are more often rejected by them (Mitchell and Brandt, 1970), that juvenile females groom more (Harlow, 1965), and that female, rather than male, juveniles interact with infants when present (Chamove et al., 1967). These findings provide support for the conclusion that the behavior of young rhesus monkeys is a precursor of adult patterns of social behavior including dominance and aggression (Hansen, 1962), and this view has been widely accepted.

Among talapoin monkeys (*Miopithecus talapoin*), adult females are not submissive to adult males; on the contrary, they are intolerant and aggressive toward them except when sexually receptive (Dixson *et al.,* 1975; Wolfheim, 1977a). In a study of juvenile talapoins, Wolfheim (1977b) found that female talapoins groomed more and preferred to do so with other females, and this pattern continued into adulthood. Juvenile male talapoins, however, played more and were avoided more than females, just as in those species with a pronounced male dominance among adults. She concluded that such behavior in juvenile males cannot be universally regarded as "practice for or predictive of adult male behavior" (Wolfheim, 1977b, p. 122). Similar results are reported for the squirrel monkey (*Saimiri sciureus*) by Coe and Rosenblum (1974), another species in which adult males do not dominate adult females (Baldwin, 1968). Among vervet juveniles (*Cercopithecus aethiops*) observed by Raleigh *et al.* (1979) in a mixed age group, males played more than females, but with a *lower* proportion of rough-and-tumble play, and males were also alone more. Females groomed more, approached others more, and interacted more with infants. There was no sex difference in aggressive behavior. Among adult vervets, males are not able to dominate females, which rely on coalitions to control the behavior of the other group members (Lancaster, 1971). Sex differences in vervet juveniles are more similar to those found in adults than was the case for the talapoins, but the pattern of sex differences is not the same as that found among macaques.

Thus, among a rather small sample of monkey species we see a variety in patterns of development of sex differences, with both the direction and the amount of difference between the sexes changing with age and from species to species. Behavioral sex differences among immature monkeys may be important primarily because they are precursors of adult sex differences and are in essence being "readied" for their presumably adaptive functions in adulthood. This would be a logical interpretation of the pattern found in species such as rhesus macaques, where juvenile sex differences are in the same direction as adult differences. Another possibility is that some juvenile sex differences are adaptive to the particular circumstances of the juvenile period itself. This may explain instances of seeming reversals of patterns of sex differences between juveniles and adults [e.g., talapoins (Wolfheim, 1977b)]. Of course these two possibilites need not be mutually exclusive; indeed, we might expect the patterns of juvenile sex differences in most species to be a mixture of the two.

Patas monkeys (*Erythrocebus patas*) are closely related to vervets but have a very different social organization. For most of the year only a single adult male associates with a group of females and juveniles, although this pattern may break down during the brief mating season. Juvenile males leave the natal group before reaching sexual maturity and, thereafter, live alone

or in small groups of males until they are able to enter heterosexual groups as adults (Gartlan and Gartlan, 1973). An adult male living in a group with females has a very low rate of interaction compared with that of the females, outside the mating season. Males are groomed infrequently, almost never groom others, and are often at the edge of their groups, whereas females frequently sit with and groom each other and juveniles. Thus, the difference between the sexes in adult social behavior is pronounced. In captivity males are extremely intolerant of each other and are aggressive toward each other (Kummer, 1974), especially in the presence of females.

The genitals of infant patas, like those of vervets, have no conspicuous features comparable to the enlarged scrotum of the newborn macaque or the brightly contrasting penis of the newborn baboon. Newborns are upended for inspection but not with the persistence seen among baboons or macaques (personal observation). As in other guenons, but unlike baboons and macaques, we have not seen males with erections before puberty.

Patas monkeys have an unusually short juvenile period. Females usually become pregnant at 2.5 years, but they may conceive as early as at 18 months and successfully rear an infant (Chism *et al.*, 1984). Rhesus females are juvenile for a full year longer, typically conceiving first at 3.5 years. Talapoins and some other guenons (Bramblett *et al.*, 1975; Rowell and Richards, 1979) usually extend the juvenile period at least a year beyond that. Young male patas monkeys can sire offspring before they are four, but would not normally have the opportunity to mate before about 5 years in wild groups. Thus young patas monkeys achieve a wide sexual divergence of behavior in an unusually short time, and the pattern of adult divergence is different from that of the multimale, male-dominant baboons and macaques. Thus, juvenile sex differences in patas promised to be especially interesting for the question of their function.

A previous study by Seay *et al.* (1972) compared patas infants, less than 6 months old, with crab-eating macaque infants in a playpen test. They found fewer sex differences in the patas than in the macaques, but they found that males of both species did more contact play than females, suggesting that the few sex differences apparent at that age were in the same direction in patas and macaques.

We report here a study of patas immatures living undisturbed in a captive group with all age–sex classes available to them for interaction. We considered four categories of social behavior by juvenile patas monkeys. The first was play, since it is the most characteristic behavior of juvenile monkeys and has been found to differ in males and females of several species. Play is barely represented in the adult repertoire but has been regarded as preparation for later patterns of behavior. Our other categories were chosen because they showed large differences between the sexes in adults, and here we are

"hunting back" for the origin of the differences. Grooming is a typical behavior of adult females, rarely seen in adult males, and adult females are the object of most grooming by females. A divergence might, thus, be expected in the juvenile period. Since adult males in captivity (and this study concerns captive animals) are extremely and persistently aggressive to each other, while females show relatively low levels of aggression compared to baboons and macaques, we expected a difference in the development of aggressive behavior. Finally, much of the striking difference between adult male and female patas monkeys can be expressed in terms of interindividual proximity: adult females spend time close to other adult females and immatures, while males are frequently solitary or in rather loose association with other males or females. We looked for signs of the development of this difference.

ANIMALS AND METHODS

Juvenile patas monkeys were born into a small colony housed in a 900-m^2 grassy enclosure, which included a 60-m^2 covered and heated area in which the group was confined at night in winter. Chow and water were always available. Study animals were born between 1973 and 1980. During the study period, the group size averaged 15 animals, including a single adult male and between 5 and 8 adult females, plus their infant and juvenile offspring. Twenty juveniles (11 males, 9 females) were included in the study. Seven of these juveniles (four males and three females), were subjects of an earlier study of infant development, during which they were each observed for 6 hr a week for the first 3 months of life and 6 hr a month in months 4 through 11. At 1 year each infant was observed for 20 hr during a 1-month period. Information on sex differences during the first year is derived from observations of these seven individuals. All subjects were observed between 1 and 3 years of age, and three of the males and two of the females were observed during the first quarter of their fourth year. The intention was to watch each animal for at least 6 hr during each quarter-year, and only 3 of 90 quarters fell below this criterion. Not all quarter-years were covered for all juveniles, however, because of lack of manpower. More than 6 hr were available on some animals in some quarters because of overlap with other studies. The distribution of observations on each individual is shown in Table I.

Observations were recorded using checksheets divided into half-minute intervals, in sessions lasting at least 60 min. Individual behaviors were scored as often as they occurred in each half-minute and are reported as the frequency of occurrence per hour of observation. The duration of bouts of grooming, play, and sitting with or near other animals was recorded to the nearest half-minute. Some measures of infant behavior were scored using a one–zero sampling method described elsewhere (Chism, 1986).

Table I. Hours of Observation of Each Juvenile in Each Quarter[a]

	Age: quarter beginning month									
	12	15	18	21	24	27	30	33	36	Total
Males										
AM	14									14
HD	20					4.5	16			40.5
TH	20					20.5				40.5
AV	21				5	15	13	12.5	12	78.5
HJ	19				10					29
AY	20				6	6	6			38
NS	20				6	6	6			38
GR		6	6	6	6	6	6	6		42
NY	6	6	6	6	6	6	28	24	33.5	121.5
PD	6	6	6	6	6	6	6	35	23.5	100.5
KP	6	6	6	6	6					30
Total	152	24	24	24	51	70	81	77.5	69	
Females										
TP	6.5									6.5
NE	20					4.5	15.5			40
BK	18				6	6	6			36
PC	20									20
AW	6	6	6							18
BO			6	6	6	6	6	16	40	86
AL	6	6	6	6	6	6	6	6	24.5	72.5
NM	6	6	6	6	6					30
PS	6	6	6	6	6					30
Total	88.5	24	30	24	30	22.5	33.5	22	64.5	

[a]Juveniles with the same first initial have the same mother.

Differences between the sexes were assessed by ranking all the juveniles according to the frequency with which they performed a given behavior and using the Mann–Whitney U to test for significance. Differences were accepted and are described in the Results if the probability of their having occurred by chance was less than 0.05. We wanted to identify the timing of ontogenetic change as precisely as possible, so scores were tested by months or quarter-years. Such an analysis necessitates a large number of Mann–Whitney U tests and we recognize that this results in significant alpha slippage. We have confidence, however, in the biological significance of the observations. Age changes were assessed by comparing the scores of each animal in its second and third years and scoring whether increases or decreases occurred.

RESULTS

Sex Differences in the First Year

With seven animals, the Mann–Whitney U test gives a significance level of $P = 0.028$ if there is no overlap at all between scores for the two sexes, while one overlapping score gives $P < 0.057$, just short of acceptable significance. We present here results which reach the $P = 0.028$ level of significance, as well as some trends which are suggestive even though they did not reach significance in all months.

Mother–Infant Contact Behavior

Male infants were nursed more than females late in the first year (significant differences in months 10 and 11). No differences were found in nursing at earlier ages and there were no sex differences in clinging to the mother or resting in contact with her.

Proximity and Proximity Regulation

There were no sex differences in being within arm's length of the mother, within 3 m, or more than 3 m from her. Male and female infants did not differ in being in proximity to their mothers or at a distance from them. There were sex differences, however, in how mother–infant proximity was regulated.

Female infants were somewhat more likely than males to be responsible for moving away from their mothers, while males were more likely to be responsible for reestablishing proximity, although this pattern was reversed

at the end of the first year. For the proportion of all departures by a member of the mother–infant dyad which were due to the infant, female median scores were higher in all months after the first except for month 4. Differences were significant in months 7, 10, and 11. For the proportion of all approaches which were due to the infant, males had lower median scores in months 3 through 9. In month 10 the medians were the same for both sexes, and in month 11 females approached their mothers more.

Maternal Behavior

Males were, on the whole, cradled (clasped against the ventrum) more throughout the year and these differences were significant in months 7, 9, 10, and 11. No female infants were cradled by their mothers after month 8, while three of four males continued to receive more cradling through the end of the year. There were no sex differences in infants being groomed, restrained, or retrieved by their mothers. Males were rejected more from 6 months on (differences were significant in months 6 and 7 and at 1 year). Weaning rejections were most frequent for both sexes in months 8 and 9, although nursing scores had already fallen to a low level by the fifth month. Thus, the higher nursing scores for male infants in months 10 and 11 occurred in spite of their being rejected more frequently at the time and in the preceding four months.

Behavior of Other Group Members to Mothers and Infants

General olfactory investigations probably function to identify newborns. Among patas monkeys, where newborns are extensively handled and frequently carried away from their mothers (to distances of up to 100 m or more in the wild), olfactory recognition of infants, by both mothers and other group members, appears to be very important. We frequently observed mothers sniffing their infants carefully before retrieving them from other animals, and occasionally, when a mother hurriedly picked up an infant from a group of infants, we saw her sniff it and then "trade" it for another infant. In such cases the implication that she had retrieved the wrong infant was unavoidable. Careful sniffing and nuzzling of an infant by other group members often preceded attempts to take infants from their mothers as well.

If the function of these olfactory investigations is identification, there should be no sex difference in the frequency with which infants receive such investigations. A sex difference might be predicted in the frequency of genital inspection if the genitals of one sex or the other are more attractive to group

members. We found no sex difference in the frequency with which infants received general olfactory investigations. We also found no significant sex differences in the frequency with which infants received genital inspections, although, in our sample of six infants (data on inspections were not available for one male infant), we found that the three female infants received a higher frequency of such inspections than did two of three male infants (the third male's scores fell within the range of the scores of the females). Infants received both general olfactory investigations and genital inspections from adult females and immatures of both sexes, but no adult male ever inspected infants.

Male and female infants were equally often held, controlled, carried, and groomed by other group members in the first and second months, when allomaternal behavior is especially frequent among patas monkeys. Mothers of males and females were groomed equally often by other females.

Play

There was no sex difference in the amount of play by male and female infants. We did not separate types of social play in the analysis of the first year's data.

Sexual Behavior

Mounting was first seen in the four males and in one female early in the third month. The other two females were not observed to mount until months 9 and 12, respectively. Mounting by male infants was 3.5 times as frequent as mounting by females, but it was never a frequent component of play, being recorded at an overall rate of once in every 6 hr of observation. Males were mounted slightly more frequently than females, but the choice of partner seemed to depend mainly on who was available. After the first appearance of mounting behavior, there were long periods during which an infant was not seen to mount, and bouts of mounting by infants frequently coincided with mating among the adults. Female proceptive behavior was not identified, even in incomplete form, in infant patas monkeys.

Sex Differences Among Juveniles

We have placed the division between infancy and the juvenile period at 12 months because the following sibling of most patas infants is born at that time, and the young monkey necessarily enters a new stage of independence. The end of the juvenile period is marked by reproductive maturi-

ty and its timing may be more variable. Four of the females in this sample first showed sexual behavior in their third year, and three of them gave birth soon after their third birthdays. Three did not become pregnant until after the end of this study; one became pregnant in her second year and was dropped from the sample before she gave birth soon after her second birthday. (Two females died in their second year.) Studies of males were terminated when the resident adult male became intolerant of them: for seven of them this occurred during the third year; for three, early in the fourth year (one was then retained as the resident adult male).

Play

At 12 months there was overlap in the amount of time spent in play by males and females, but overall, males played more than females. During the second year the amount of play by both sexes decreased (Fig. 1), but up to and including month 24 males played more than females, with no overlap in scores between the sexes. In the third year, play by males decreased quickly to a rate similar to that of females, about 6 min/hr, and there were no further differences between the sexes in the amount of play.

Males played in longer bouts than females, with no overlap from 12 to 24 months. After that the difference disappeared: while the median bout length continued to be higher for males than for females, female scores became more variable and some encroached on the male range of values. The overall median bout length for females was about 1 min; for males, 1.25 min: the difference, although consistent, was not large (Table II).
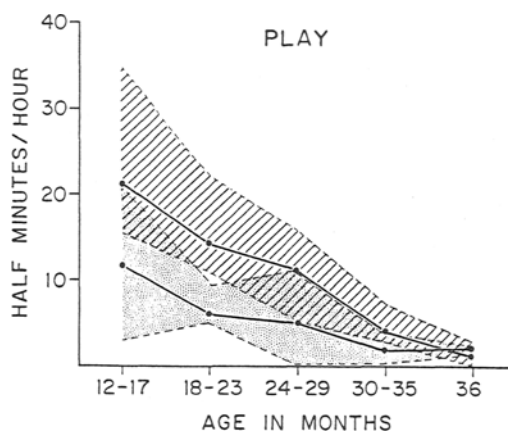

Fig. 1. Play by juvenile patas monkeys; median scores and ranges. Cross-hatch, males; stipple, females.

Table II. Play by Juvenile Patas Monkeys[a]

	Age (months)									
	12-17		18-23		24-29		30-35		36	
	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
0.5 min/hr										
Males	21	16-35	14	11-22	11	5-16	4	3-7	1	0.2-3
Females	11.5	3-21	6	5-9	5	0-11	2	0.3-4		2-3
Mean bout length: (half-min)										
Males	3.2	2.2-4.0	2.6	2.3-2.9	2.7	2.4-3.9	2.5	1.9-3	2	1.3-3.1
Females	1.9	1.5-2.3	2	1.3-2.0	1.6	0-3.6	1.7	1.0-2.2		1.5-1.6
Wrestling/bout										
Males	0.64	0.55-0.82	0.7	0.59-0.79	0.75	0.67-1.0	0.68	0.39-0.85	0.86	0.83-0.88
Females	0.63	0.46-0.84	0.77	0.64-0.85	0.66	0-1.0	0.75	0.61-0.76		0.4-0.5
Chasing/bout										
Males	0.58	0.3-0.71	0.34	0.3-0.68	0.41	0.25-0.67	0.37	0.21-0.56	0.17	0-0.36
Females	0.37	0.22-0.55	0.17	0.1-0.33	0.29	0-0.57	0.21	0.05-0.31		0.35-0.38

[a]Wrestling and chasing are expressed as the proportion of play bouts which included them.

Patas monkey play consists predominantly of wrestling and chasing and we scored these two types of play separately. Wrestling is the equivalent of macaque "rough-and-tumble" play, described by Harlow (1965), and was equally common in the play of both sexes through the second and third years. (Three males wrestled more than two females at the beginning of the fourth year.) On the other hand, there was a difference in chasing: males chased more than females in both the second and the third year by a large margin (Mann–Whitney U, $P = 0.02$) (Table II).

Grooming

There was no difference in the amount of grooming mothers gave to sons and daughters, although we found a difference between families. Two of the colony's founder females and their daughters frequently groomed their offspring, and offspring of these families occupied all but 1 of the 11 highest ranks for the frequency of being groomed by their mothers. Offspring of two other females occupied six of the eight lowest ranks. Most juveniles were groomed less by their mothers in the third year than in the second (seven of nine males and four of six females for which comparisons could be made). Juvenile females, however, groomed their mothers more than did males in both the second and the third year (Mann–Whitney U, $P < 0.001$). Both sexes tended to increase the frequency with which they groomed their mothers as they grew older. Six of eight females did so, the exceptions being the two daughters of female BB, which were already grooming their mother at high frequencies in the second year. Seven of nine males also groomed their mothers increasingly as they aged, although their grooming frequencies remained very low.

Females groomed their offspring more than did all the other adult females in the group combined, until the end of the third year. The one exception was female AA, which groomed all her offspring very little. Other adult females groomed juveniles of both sexes equally often. When juveniles groomed adult females other than their mothers, sex differences were larger than when they groomed their mothers, and in the same direction. Thus, juvenile females groomed other adult females more than did males, and overall, there was more grooming of other females in the third year than in the second by both sexes. Four of six females increased their grooming of other adult females in their third year; the other two already had higher scores in their second year. Three of nine males were never seen to groom other adult females in either year; four of the six remaining increased their grooming in the third year, although grooming always occurred at low frequencies. Where data were available, these trends appeared to continue into the fourth year.

Female juveniles groomed other juveniles 10 times as frequently as did males, and females groomed about twice as often as they were groomed. Thus females groomed males more often than the reverse, but for the most part, juvenile females groomed other juvenile females. Infants less than 3 months old were rarely groomed by juveniles, but young infants were infrequently groomed by any animals, even their mothers. Five of nine females groomed infants for a total of 7.5 min in 339 hr (0.02/hr). No male was ever seen to groom an infant of less than 3 months. Six juvenile males groomed older infants (aged 4–11 months) for a total of 7 min (0.01/hr) and were groomed by the infants at about the same low rate. Five of the juvenile females groomed older infants for a total of 72 min (0.2/hr), and their frequency of grooming infants was similar in their second and third years. Infants groomed juvenile females at about the same low rate that they groomed juvenile males.

To summarize, grooming by juveniles showed a clear sex difference but there was no such difference in the grooming they received (Fig. 2). By their third year, juvenile females were grooming at rates within the range found for adult females by Rowell and Hartwell (1978).
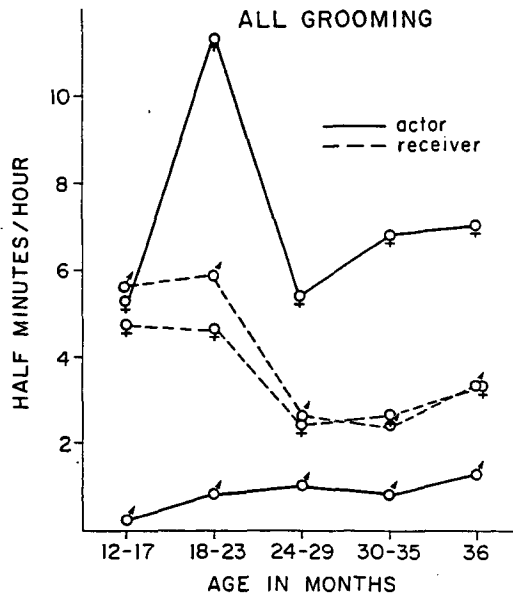

Fig. 2. Grooming by juvenile patas monkeys; all part-
ners combined.

Agonistic Interactions

We compared rates with which males and females were initiators or receivers of overt aggression such as hits, threats, and chases. We also analyzed avoidance interactions in which avoiding followed a simple approach by another monkey without a display of any overt aggression. Such avoiding occurred twice as frequently as interactions involving overt aggression and is presented first.

Overall there were more interactions in which juvenile males avoided another animal (1066) than interactions in which females did so (631), and females were avoided more often (in 894 interactions) than males (528 interactions). Despite the large differences in male and female total scores for avoiding and being avoided, individual scores showed considerable overlap between 12 and 24 months of age, whereas after 27 months patterns of avoidance changed. To make comparisons between the sexes clearer, we have omitted the period of transition (21–27 months) and compared the first 9 months of the second year with the last 9 months of the third year (Fig. 3).

Between 12 and 21 months, although males collectively avoided more than females, when individuals were ranked by rate of avoiding, rate of be-
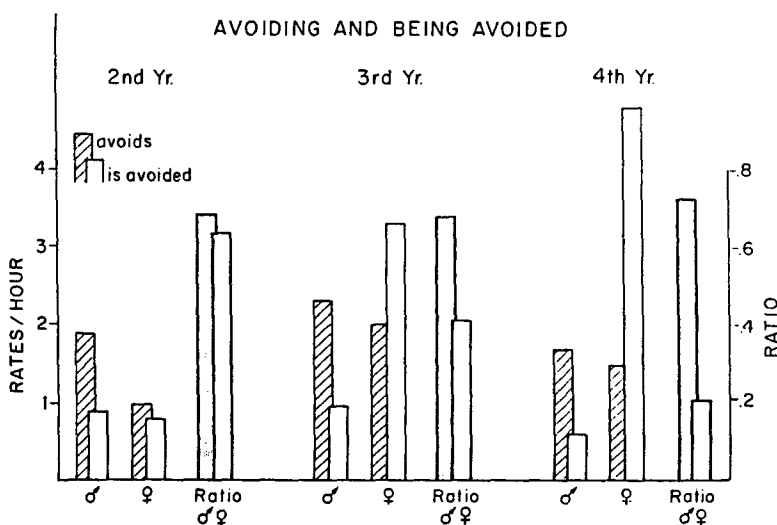

Fig. 3. Avoidance behavior of juvenile patas monkeys. The median rates for avoiding and being avoided are shown for each sex, as well as the median proportion of avoiding in total approach–avoid interactions (ratio). 2nd Yr., months 12–20; 3rd yr., months 27–34. The "4th Yr." data derive from a small sample of observations involving monkeys 36–38 months of age (cf. Table I).

ing avoided, or relative proportion of avoiding to being avoided, there were no significant sex differences. Between 27 and 36 months both males and females avoided more than they had done in the second year. In this period, although males continued to be avoided at about the same rate as in the earlier period, females were avoided at a much higher rate (Fig. 3). There was no overlap in rates of being avoided for males and females during the third year, but there was no sex difference in rates of avoiding for this period. In the fourth year the sex difference in being avoided was further accentuated in the small sample.

There were fewer interactions which included overt aggressive behavior, but these showed a pattern similar to that seen in avoidance interactions. After 27 months of age, females increased the frequency of their aggressive behavior and all females gave more aggression than they received. In general males decreased the frequency of aggressive interactions in which they were involved in the third year; only one male consistently gave more aggression than he received, and he did so in all three years.

Positioning Behavior

Adult males and females differ most obviously in their positioning relative to other patas monkeys. Adult females spend their lives in groups with other females, accompanied for much of the time by a single adult male, although he may often be spatially or socially peripheral. When not resident in groups with females, males live alone or in association with a few other males. Thus measures of being alone, of being in proximity (within 1 m) to another patas monkey of a particular age or sex, and of behavior by which these relative positions are established, such as approaching and following, should clearly differentiate between adult males and females. Are these differences apparent among juveniles also?

Approaching. There was no difference in the rate with which males and females were approached by their own mothers. Mothers were approached by their juvenile offspring more than three times as often as they approached: the juveniles were responsible for maintaining proximity to their mothers. The rate of approaching between mothers and juveniles did not change with age. Adult females, other than their mothers, also approached male and female juveniles equally often. Female juveniles approached adult females significantly more than did males, and this difference was even larger in the third year than in the second.

Following. We defined following as moving behind another animal within 3 m. By this criterion there was no difference in following by males and females in either year or in the proportion of an individual's following

that was directed to its mother. Our impression had been that males follow-ed their mothers more than females, and followed her even more persistent-ly during the third year, especially when the adult male was being aggressive toward the juvenile male [which, in captivity, occurred in bouts lasting a few days and interspersed with calm periods; see Gutstein (1983)]. We believe that the definition of the measure used was inadequate to capture this dif-ference, because the distance criterion was too short.

Proximity. Three levels of proximity were considered for juveniles: be-ing "near" (within 3 m), "sitting with" (within 1 m), and being in contact with another monkey. Proximity was scored only when the animals were not interacting in any other way; grooming, for example, was a separate activi-ty, not included in sitting together or in contact. Males and females spent the same amount of time near, sitting with, and in contact with their mothers and other adult females. Infants under 3 months were not always available in the group, but male and female juveniles had the same number of infants available to them and the same number of quarter-year time blocks in which to interact with infants. In the second year, the average time females spent sitting with infants was half again as much as the time spent by males, but individual variation was such that there was no sex difference when they were ranked. In the third year, females sat with infants four times as often as did males, and the difference between the sexes was significant (Mann–Whitney U, $P < 0.01$).

Alone and Inactive. Males and females spent about the same time sit-ting alone and inactive at the beginning of the second year (Fig. 4). Both sexes increased the amount of time they spent alone in the third year, males by far more than females. The sex difference reached significance in the begin-ning of the third year (Mann–Whitney U, $P < 0.05$), and there was no overlap in rates of sitting alone by males and females in the second half of the third year.

Sexual Behavior

Female proceptive behavior, which is conspicuous and elaborate in patas monkeys (Hall *et al.*, 1965), was first seen when the females began to solicit adult males for copulation shortly before they conceived for the first time. This behavior has been seen only in females and was not identified, even in incomplete form, as a component of play.

Young males have a suite of behavior patterns with which they approach an adult male. This includes reaching for the blue scrotum, a characteristic tail position, and a "finger-chewing" gesture. These are also used when harass-ing a copulation. In a variant of this suite, a young male picks up an infant
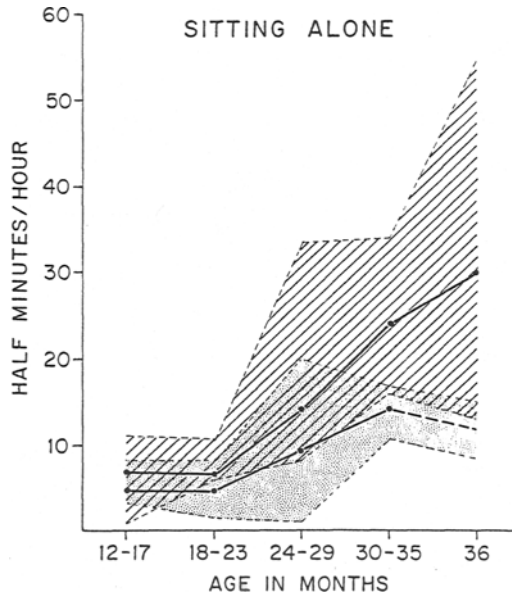
Fig. 4. Time spent sitting alone and inactive, juvenile patas monkeys: median scores and ranges for each sex. Cross-hatch, males; stipple, females.

and runs bipedally toward the adult male, holding the infant out in front of him as if offering it. The juvenile male squeals at the same time and the infant is usually also screaming and wriggling to be free (Chism, 1986). Young males show such behavior toward the adult male in their first year and also join older male juveniles in bouts of harassing sexual behavior. We have not seen females behaving in this way.

After the first year there was no further elaboration of male sexual behavior during the juvenile period. Males continued to mount occasionally, particularly when adults were copulating. Female juveniles were not seen to mount after the first year.

DISCUSSION

The classical studies of sex differences in young monkeys used small experimental groups of peers in which only a limited range of the social repertoire could be expressed. Many of these studies focused on the first 6 months and there has been relatively little written about older juveniles. In contrast, most sex differences in patas monkeys appeared after infants had achieved

some independence from their mothers. Apart from play, the clearest differences between males and females appeared in their behavior toward other monkeys older and younger than themselves: the environment of a complete social group was necessary for their expression. Differences in the social environment and age of subjects make it difficult to compare our results with those obtained for other species, but it does seem that there are some basic differences between patas and (for example) macaques.

The sex differences in infant scores for nursing, cradling, and rejection in our samples appeared to indicate that females became independent of their mothers more readily than did males. The higher nursing scores for males at the end of the first year might be due to higher caloric needs. Reiter *et al.* (1981) and Clutton-Brock *et al.* (1982) have suggested that mothers invest more in milk for sons because rapid early growth will ultimately confer a greater adult weight and fighting ability and, therefore, a greater reproductive success on sons, which must compete with other males to breed at all. A similar argument might be made for patas monkeys, but it would not explain why patas males are dependent longer than females, while macaque males, which must also compete as adults, become independent earlier than females. The higher male scores for cradling and rejection among patas monkeys seem contradictory, as if mothers were both abetting and objecting to the greater demands of their male offspring. During "weaning" episodes, however, patas mothers typically respond to infants' attempts to suckle by first rejecting infants and then cuddling them if they persist (Chism, 1986).

Loy and Loy (1986) studied 12 patas infants in a captive group over their first 10 months. With this rather larger sample, they found some sex differences in contact, grooming, and play which, in general, parallel the differences we found among juveniles. They concluded that what sex differences are apparent during the first year presage the incorporation of females into the stable adult female nucleus of the group. Males showed less tendency to establish bonds with females and more interest in males, even at this early age. We did not find differences in grooming and play so early, but it may well be that the apparently easier and more rapid achievement of independence by females in our sample could be explained by their beginning to shift their focus of social activity from the mother to other adult females, to peers, and, later, to infants.

Sex differences in the amount of play and length of play bouts in patas monkeys were in the same direction as those reported for macaques (with males playing more and longer). The difference was transitory in patas, however, not appearing until the second year and disappearing by the middle of the third year. This is the age at which most females begin to show sexual behavior and at which males, in captivity, begin to be threatened by

the adult male; and it could be taken as the end of the true juvenile period if it were necessary to define such. That males play more than females seems to be a robust sex difference which has been found in most studies so far. It is, however, one of the few consistent sex differences in behavior, apart from copulation-related patterns, that has been reported, and it is a behavior which is a very minor part of the repertoire of adults.

Sex differences in types of play (males chase more but do not wrestle more) were opposite to those found in macaques and humans, where wrestling or rough-and-tumble was characteristic of male play. Chasing is a frequent component of male patas monkey aggression, as it is in the aggression of males of many species, but among macaques chasing was more typical of female play. The aggressiveness of male patas monkeys, at least toward other males as adults, is not in question. It would seem that more wrestling by immature males is not a necessary precursor of adult male aggression among monkeys, just as Wolfheim (1977b) showed that it is not necessarily predictive of the pattern of aggression and dominance among adults. Comparing patas social play with that of other species leads us to the conclusion that the function of play should be sought in the developmental stage in which it is a frequent, even characteristic behavior. Any effect continued into adulthood must be of a more general nature, and not related to the quality of play itself.

Juvenile female patas achieved rates of grooming within the ranges of those of adult females in their second year. Grooming by male juveniles was always infrequent, although possibly not as infrequent as that of adult males. Other monkeys, adults and infants, groomed juveniles of both sexes impartially, at a frequency which decreased as the juveniles grew older. Among adult patas monkeys grooming is not impartial: adult males are rarely groomed except by estrous females. It seems that grooming is highly sex dependent in this species, and the difference does not depend on any reciprocal response to a difference in grooming received. Whereas the females of most monkey species groom more than males, the difference in patas monkeys is extreme.

Adult females seemed interested in establishing the sex of new infants, as judged by their inspection of the genitals of newborns, and apparently recognized the sex, since female infants were inspected more than males. This information, however, hardly seemed to affect their later interactions, since we found few differences in the way infants or juveniles were treated by their mothers or other group members.

Infants and juveniles of both sexes were responsible for maintaining their links with their mothers, links which seemed equally important to both sexes into the third year. There was also no difference between males and females in initiating interactions with mothers. There were clear sex differences in the ways in which juveniles behaved toward other group members,

however. Females, unlike males, increasingly approached adult females to initiate interactions. In a cross-sectional study (Rowell and Olson, 1983) we found that the frequency of approaching by young female patas monkeys was high initially and continued to rise until the fifth year. Older females became increasingly passive recipients of interaction; females older than 10 years were approached more often than they approached others. Thus, young females seem to have an important role in group coherence, a role which begins before sexual maturity.

Female juveniles spent more time with infants than did males, especially in the third year. By the age of 1 year they shared the common adult female pattern of taking young infants from their mothers and carrying or cuddling them for long periods and were active in caring for their younger siblings. Males always showed only rudimentary infant-caretaking behavior [allomaternal behavior among patas monkeys has been described by Chism (1978, 1986)].

With regard to proximity patterns we had expected to find that juvenile females spent more time with other females, while males spent increasingly more time with their mothers: these had been our subjective impressions. The absence of a sex difference in proximity in our study may have been due to the tendency of juvenile females to groom adult females when they were near them, while males, if not being groomed themselves, just sat nearby. The difference in association patterns appeared in grooming, rather than in proximity per se.

The more active participation of juvenile females is apparent in agonistic interaction patterns also. Since female juveniles were avoided more than they avoided others, they might be described as being, as a class, high-ranking or dominant. We think that would be a valid description only in the narrowest sense. Young females' active, importunate insistence on interaction seemed to annoy the adult females, which consequently avoided them. The effect is less marked in wild groups, probably due to the need to spend more time foraging for food.

In general, among adult patas monkeys, males are aggressive toward males and females are aggressive toward females and immatures. Between the sexes aggression is infrequent and males rarely initiate aggression toward females. A female that attacks a male is generally supported by other females, and the male retreats. For the most part, males avoid females. It may be that the aggressiveness of males is so specific to adult males that a juvenile male has hardly any appropriate object for aggression in a group composed mainly of females and young. While it would clearly be foolhardy to attack directly the very much larger resident male, incompletely suppressed aggression could perhaps be the origin of the harassment behavior which juvenile males direct toward the adult male.

The differing patterns of social interaction shown by male and female patas juveniles may also be viewed in relation to the timing of the events accompanying the onset of sexual maturity in each sex. Patas females reach sexual maturity at 2.5 years and thus have a very short juvenile period in which to establish lifetime relationships with the adult females of their group. The aggressive, interactive juvenile and young adult patas female described here is very different from the timid and frequently supplanted juvenile female toque macaques described by Dittus (1977) or the socially peripheral bonnet macaque juvenile females (Clarke, 1978). Comparable behavior has been described for young female langurs by Hrdy and Hrdy (1976) and for baboons by Cheney (1978). The Hrdys ascribed the aggressive behavior of young female langurs to their high reproductive potential, but since that characteristic is presumably shared by all adolescent females of all species, many of which do not exhibit such aggressiveness, that explanation cannot be sufficient to explain all such behavior.

Juvenile female patas monkeys have a young-adult pattern of social behavior early in their third year, which is accentuated as the year continues. The rapid establishment of an adult pattern of interaction with females and infants may help to maintain the coherence and continuity of the female group, as Loy and Loy (1986) suggested.

Juvenile male patas monkeys effectively make a sudden transition into subadulthood by leaving their natal group. The scrotum begins to change color from gray to blue in early adolescence (at about age 3 years), and at about the same time the testes first become visible. We suspect that the blue color of the scrotum may act as a visual cue to the harassment behavior juvenile males direct to adult males and to the onset of attacks by adult males on adolescent males. It should be noted, however, that in the wild and in captivity, mature patas males can live together without overt fighting as long as no females (receptive or otherwise) are present, so the blue scrotum may be a necessary but not sufficient condition to provoke male aggression. In the wild, although young males left their natal groups at the time when their scrota were just becoming visible and changing color, the timing of this step must be to some extent under the individual's control. The increasing solitariness of the young males in their third year was very striking and the withdrawn, mother-attached older juvenile male is very different from the boisterous testing juvenile male baboon or macaque of a comparable age (Ransom and Rowell, 1972). In wild groups, resident adult males were not aggressive to juveniles, so other factors must cause young males to leave their natal groups. Small groups of 3-year-old males sometimes leave wild groups together, and dispersing juveniles may join other, older males. There is an attraction between males, which is perhaps evident in the behavior of young males toward their resident adult male but which is extremely difficult to investigate within the limitations of captivity.

In sum, the sex differences in juvenile patas monkey behavior reported here show a mixture of patterns, of which some appear to be "predictive" of the patterns of differences in adult behavior and some appear to be specific to the particular circumstances of the patas juvenile period. Among these later patterns, a contributing factor is the very different social circumstances in which male and female patas juveniles find themselves, with females rapidly establishing themselves in the social fabric of their natal groups during the same period when young males are preparing to leave their groups and live for several years either alone or in a shifting series of all-male associations.

ACKNOWLEDGMENTS

REFERENCES

Baldwin, J. D. (1968). The social behavior of the adult male squirrel monkey in a semi-natural environment. *Folia primatol.* 9: 281-314.

Blurton-Jones, N. G., and Konner, M. J. (1973). Sex differences in behaviour of London and Bushman children. In Michael, R. P., and Crook, J. H. (Eds.), *Comparative Ecology and Behaviour of Primates,* Academic Press, London, pp. 689-750.

Bramblett, C. A., Pejaver, L. D., and Drickman, D. J. (1975). Reproduction in captive vervet and sykes monkeys. *J. Mammal.* 56: 940-946.

Brindley, C., Clark, P., Hutt, C., Robinson, I., and Wethli, E. (1973). Sex differences in the activities and social interactions of nursery school children. In Michael, R. P., and Crook, J. H. (eds.), *Comparative Ecology and Behaviour of Primates,* Academic Press, London, pp. 690-750.

Burton, F. D. (1977). Ethology and the development of sex and gender identity in non-human primates. *Acta Biotheoret.* 26: 1-18.

Chamove, A., Harlow, H. F., and Mitchell, G. D. (1967). Sex differences in the infant-directed behavior of preadolescent rhesus monkeys. *Child Dev.* 38: 329-335.

Cheney, D. L. (1978). The play partners of immature baboons. *Anim. Behav.* 26: 1038-1050.

Chism, J. B. (1978). Relationships between patas infants and group members other than the mother. In Chivers, D. and Herbert, J. (eds.), *Recent Advances in Primatology, Vol. 1.* Academic Press, London, pp. 173-176.

Chism, J. B. (1986). Development and mother-infant relations among captive patas monkeys. *Int. J. Primatol.* 7: 49-81.

Chism, J. B., Rowell, T. E., and Olson, D. K. (1984). Life history patterns of female patas monkeys. In Small, M. (ed.), *Female Primates: Studies by Women Primatologists,* Alan R. Liss, New York, pp. 175-190.

Clarke, M. R. (1978). Social interactions of juvenile female bonnet monkeys, *Macaca radiata. Primates* 19: 517-524.

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes,* University of Chicago Press, Chicago.

Coe, C. L., and Rosenblum, L. A. (1974). Sexual segregation and its ontogeny in squirrel monkey social structure. *J. hum. Evol.* 3: 551-561.

Dittus, W. P. J. (1977). The social regulation of pupulation density and age-sex distribution in the toque monkey. *Behaviour* 63: 281-322.

Dixson, A. F., Scruton, D. M., and Herbert, J. (1975). Behaviour of the talapoin monkey (*Miopithecus talapoin*) studied in groups in the laboratory. *J. Zool.* (London) 176: 177-210.

Dolhinow, P. J., and Bishop, N. (1970). The development of motor skills and social relationships among primates through play. *Minn. Symp. Child Psychol.* 4: 141-198.

Ehrhardt, A. A. (1974). Androgens in prenatal development: Behavioral changes in non-human primates and man. *Adv. Biosci.* 13: 154-162.

Gartlan, J. S., and Gartlan, S. C. (1973). Quelques observations sur les groupes exclusivement males chez *Erythrocebus patas. Ann. Fac. Sci. Cameroun* 12: 121-144.

Gorski, R. A., and Barraclough, C. A. (1961). Indifferential effectiveness of small doses of testosterone propionate in the induction of sterility in the female rat. *Anat. Rec.* 139: 304.

Goy, R. W., and Phoenix, C. H. (1972). The effects of testosterone propionate administered before birth on the development of behavior in genetic female rhesus monkeys. In Sawyer, C., and Gorski, R. (eds.), *Steroid Hormones and Behavior*, University of California Press, Berkeley, pp. 193-201.

Gutstein, J. (1983). *Social Development in One to Four Year Old Patas Monkeys*, Unpublished Ph.D. thesis, University of California, Berkeley.

Hall, K. R. L., Boelkins, R. C., and Goswell, M. J. (1965). Behaviour of patas monkeys, *Erythrocebus patas*, in captivity, with notes on the natural habitat. *Folia primatol.* 3: 22-49.

Hansen, E. W. (1962). *The Development of Maternal and Infant Behavior in the Rhesus Monkey*, Unpublished Ph.D. thesis, University of Wisconsin, Madison.

Hansen, E. W. (1966). The development of maternal and infant behaviour in the rhesus monkey. *Behaviour* 30: 107-149.

Harlow, H. F. (1965). Sexual behavior in the rhesus monkey. In Beach, F. A. (ed.), *Sex and Behavior*, John Wiley, New York, pp. 234-265.

Harlow, H. R., and Lauersdorf, H. E. (1974). Sex differences in play and passion. *Perspect. Biol. Med.* 17: 348-360.

Hrdy, S. B., and Hrdy, D. B. (1976). Hierarchical relations among female langurs (Primates: Colobinae, *Presbytis entellus*). *Science* 193: 913-915.

Kummer, H. (1974). Distribution of individual distance in patas monkeys and gelada baboons. *Folia primatol. 21: 153-160.*

Lancaster, J. (1971). Play-mothering: The relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia primatol.* 15: 161-182.

Lehrman, D. S. (1974). Can psychiatrists use ethology? In White, N. F. (ed.), *Ethology and Psychiatry*, University of Toronto Press, Toronto, pp. 187-196.

Loy, K. M., and Loy, J. (1986). Sexual differences in early social development among captive patas monkeys. In Zucker, E. (ed.), *The Comparative Behavior of African Monkeys*, Alan R. Liss, New York (in press).

Maccoby, E. E. (1966). *The Development of Sex Differences*, Stanford University Press, Stanford, Calif.

Mead, M. (1949). *Male and Female*, William Morrow, New York.

Mead, M. (1935). *Sex and Temperament in Three Primitive Societies*, William Morrow, New York.

Mitchell, G. (1968). Attachment differences in male and female infant monkeys. *Child Dev.* 39: 611-620.

Moore, J. (1984). Female transfer in primates. *Int. J. Primatol.* 5: 537-589.

Moss, H. A. (1967). Sex, age and state as determinants of mother-infant interactions. *Merril-Palmer Q. Behav. Dev.* 13: 19-36.

Nash, L. T. (1978). Development of the mother-infant relationship in wild baboons (*Papio anubis*). *Anim. Behav.* 26: 745-759.

Owens, N. N. (1975). Social play behaviour in free-ranging baboons, *Papio anubis. Anim. Behav.* 23: 387-408.

Pfaff, D. W., and Zigmund, R. E. (1971). Neonatal androgen effects on sexual and nonsexual behavior of adult rats tested under various hormone regimes. *Neuroendocrinology* 7: 129-145.

Phoenix, C. H., Goy, R. W., Gerall, A. A., and Young, W. Y. (1959). Organizational action of prenatally administered testosterone propionate on the tissues mediating behavior in the female guinea pig. *Endocrinology* 65: 369-382.

Raleigh, M. J., Flannery, J. W., and Ervin, F. R. (1979). Sex differences in behavior among juvenile vervet monkeys (*Cercopithecus aethiops sabaeus*). *Behav. Neural Biol.* 26: 455-465.

Reiter, J., Panken, K. J., and LeBoeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Anim. Behav.* 29: 670-687.

Rowell, T. E., and Hartwell, K. M. (1978). The interaction of behavior and reproductive cycles in patas monkeys. *Behav. Biol.* 24: 141-167.

Rowell, T. E., and Richards, S. M. (1979). Reproductive strategies of some African monkeys. *J. Mammal.* 60: 58-69.

Seay, B. (1966). Maternal behavior in primiparous and multiparous rhesus monkeys. *Folia primatol.* 4: 146-168.

Seay, B., Schlottmann, R. S., and Gandolfo, R. (1972). Early social interactions in two monkey species. *J. Gen. Psychol.* 87: 37-43.

Wolfheim, J. H. (1977a). A quantitative analysis of the social organization of a group of captive talapoin monkeys. *Folia primatol.* 27: 1-27.

Wolfheim, J. H. (1977b). Sex differences in behaviour in a group of captive juvenile talapoin monkeys (*Miopithecus talapoin*). *Behaviour* 63: 110-128.

Young, G. H., and Bramblett, C. A. (1977). Gender and environment as determinants of behavior in infant common baboons (*Papio cynocephalus*). *Arch. Sex. Behav.* 6: 365-385.