Development and Mother–Infant Relations Among Captive Patas Monkeys

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*Generalizations about the rate of behavioral development and mother–infant relations in nonhuman primates are often based largely on observations of a few closely related species of macaques. Patas monkeys (*Erythrocebus patas*) are sufficiently distant phylogenetically and distinct in their social and ecological adaptations from the well-studied macaque species that observations of their patterns of infant development and mother–infant relations may indicate to what extent macaque patterns are typical of Old World monkey species. Eight patas infants living with their mothers in an established captive group were observed for 960 hr over the first year of life. These infants showed a rapid rate of behavioral development and attainment of independence from mothers. Patas also have one of the fastest rates of sexual maturation of any Old World monkey species. This pattern of rapid social and sexual development can be viewed as a response to a highly seasonal savannah environment in which there is a premium on ability to achieve nutritional, locomotor, and social self-sufficiency as quickly as possible and to reproduce as early and as often as developmental constraints will permit. Patterns of infant development and mother–infant relations may be best understood as an integral part of a species' overall life history pattern.*

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INTRODUCTION

Laboratory studies of nonhuman primates have provided information on normative behavioral development and have explored important theoretical questions concerning the nature of mother–infant relations (e.g., Harlow, 1961; Harlow *et al.,* 1963; Hansen, 1966). An understanding has emerged from these studies of the typical course of the development of independence in immature monkeys and the effects of social companions on the mother–infant dyad (e.g., Hinde *et al.,* 1964; Hinde and Spencer-Booth, 1967; Jensen *et al.,* 1967; Hinde, 1969, 1974; Kaufman and Rosenblum, 1969; Rosenblum, 1973; Kaufman, 1974, 1975). Developmental studies of Old World monkeys in the laboratory have, for the most part, concentrated on a relatively small number of species, with the most extensive data available coming from rhesus macaques, so that the question arises: to what extent are the patterns exhibited by macaques typical of other monkey species with different life history patterns and different social and ecological adaptations?

The patas monkey (*Erythrocebus patas*) is an Old World monkey species which is sufficiently distinct from the well-studied macaque species, both phylogenetically and in its social and ecological adaptations, to provide an indication of how typical macaque patterns are. Previous comparative studies (e.g., Hinde, 1971; Chalmers, 1972) were limited by problems of lack of comparability of the data themselves, small sample sizes, or insufficient information about the natural social and ecological context in which the developmental patterns occurred.

This study describes the course of behavioral development of patas monkeys over the first year of life focusing on the following three questions.

(1) What is the relationship among species-specific patterns of mother–infant relations, rate of development, social organization, and ecology?

(2) How do the behaviors of mothers and infants determine the rate of acquisition of independence in infants?

(3) What are the immediate and long-term consequences for mothers and infants of extensive allomaternal caretaking?

METHODS

The subjects of the study were eight infant patas monkeys, four males and four females, living with their mothers in an established social group at the University of California (Berkeley) Field station for Animal Behavior Research. The group was housed in a grassy 30 × 30-m outdoor enclosure with an adjoining 4 × 10-m indoor heated sleeping area. The group had access to all parts of the enclosure during the day but was confined to the in-

door area at night during the winter months (November through March). Monkey chow and water were always available, and the monkeys also ate plants, insects, and an occasional small vertebrate found in the enclosure. The group consisted of seven adult females, their offspring, and one adult male, and averaged about 15 animals; it was thus similar in size and composition to wild patas groups in Uganda (Hall, 1965) and within the size range of groups observed in Kenya (personal observation).

The mother of one infant died during the study after a brief illness. Data for this infant are included only through the month preceding its mother's death. To maintain the sample size, an infant of the same sex was chosen at random from the next cohort of infants born in the colony and its data are included in the analysis presented here.

Observations on the eight infants totaled 960 hr. Each subject was observed for 6 hr per week for the first 12 weeks of life and 6 hr per month during months 4–11. A 20-hr block of observations was collected for each infant at the age of 1 year. This schedule was adhered to with a few exceptions due to adverse weather conditions or illness. Patas typically give birth during the day (Chism *et al.*, 1978, 1983) and the births of three subjects were observed. Observations began on two other infants within 2 hr of birth and on the remaining three within 24 hr of birth.

Fourteen frequently occurring behavior patterns were defined (Table I) and their occurrence was scored every 30 sec using a one–zero sampling method (Altmann, 1974). This method gives the number of half-minute intervals in which each behavior occurs, rather than the actual frequency or duration of the behavior (Hinde, 1973), and was adopted here to achieve maximum comparability with previous developmental studies of cercopithecines. Comparisons of scores for these behaviors are expressed throughout in terms of the median percentage of half-minute periods in which they occurred.

Less frequent mother–infant behaviors, all interactions between mother–infant pairs and other group members, and significant events in the group at large were recorded as they occurred so that rates of occurrence per hour could be calculated.

Observation sessions were at least 60 min but not more than 120 min in duration, and no more than one such session was conducted on any one infant on any particular day. Approximately equal numbers of observation sessions within each weekly or monthly block were made in the morning (0800–1100 hr), midday (1100–1400 hr), and afternoon (1400–1700 hr) time periods.

The results presented here are based on data collected on the Berkeley colony between 1973 and 1976. Supplementary information based on qualitative observations of 17 infants born into the colony after 1976 and on 47 infants born into two wild patas groups in the Laikipia District of Kenya

Table I. Frequently Occurring Behaviors

On ventrum, eyes closed	The infant clings to the mother with its eyes closed.
On nipple, eyes open	The infant has the nipple in its mouth and its eyes open.
Clings	The infant clings with its hands and/or feet to its mother's ventrum and it does *not* have the nipple in its mouth.
Rests in contact	The infant is in contact with some portion of its mother's body (e.g., sitting in her lap, leaning against her) but not clinging or on the nipple.
Within arm's length	The infant is within an arm's length (0.5 m) of the mother but not in contact with her.
Within 3 m, greater than arm's length	The infant is more than an arm's length from its mother but within 3 m.
Greater than 3 m	The infant is greater than 3 m from its mother.
Wholly out of contact	The infant remains out of contact (i.e., at a distance of an arm's length or greater) throughout the entire 0.5-min period.
Mother grooms infant	The infant is groomed by its mother.
Hold/cradle	The infant is held by the mother with one or both arms while clinging to her ventrum.
Restrain	The infant is prevented from moving out of contact with its mother by being held or otherwise physically restrained.
Retrieves	The infant is approached by its mother and picked up or otherwise induced to cling.
Reject	Weaning rejection: The infant is deterred from nursing or denied access to the nipple. Other rejection or punishment: The infant is prevented from establishing or continuing contact with the mother by being pushed away, hit, threatened, or held down.
Approach/leave	The infant or the mother moves from a distance greater than an arm's length from the other dyad member to a distance less than or equal to an arm's length (approaches), or either partner moves from a distance of an arm's length or less to a distance of greater than an arm's length from the other partner (leaves).

during a 2-year field study carried out between 1979 and 1981 is included where appropriate. Inspection of the data indicated that the largest and most rapid changes in mother–infant contact behavior occur during the first 3 months of life. During this period, also, the interest and attention of other group members are important to the behavior of mothers and infants. Results for the first 3 months are therefore presented separately from those for the remainder of the first year.

RESULTS

The First 3 Months

Physical Appearance of Infants

Patas infants have a distinct natal coat of sparse, silky, dark fur and a bare, pink face. This coat is replaced between 7 and 12 weeks of age by a

fluffy, red-brown juvenile coat. At the same time the face darkens, white sideburns appear, and dark chevrons develop over the brows. The onset and duration of coat loss are consistent, varying by about 1 week between individuals. Infants less than 2 months of age thus look completely different from older infants.

Contact Behavior

Four types of mother-infant contact behavior are defined in Table I. Changes in scores for the mother-infant contact behavior over the first 12 weeks are shown in Fig. 1. Although "on mother, eyes closed" was the predominant activity during the first week, both visual and tactile exploration began at this time, including visually following objects, scanning the surroundings, and touching, rubbing, or rhythmic grasping and releasing of the mother's fur or skin. First attempts to break contact with mothers by crawling up and off the ventrum occurred in the first week also, and two of eight infants first moved away from their mothers as this time (Table II).

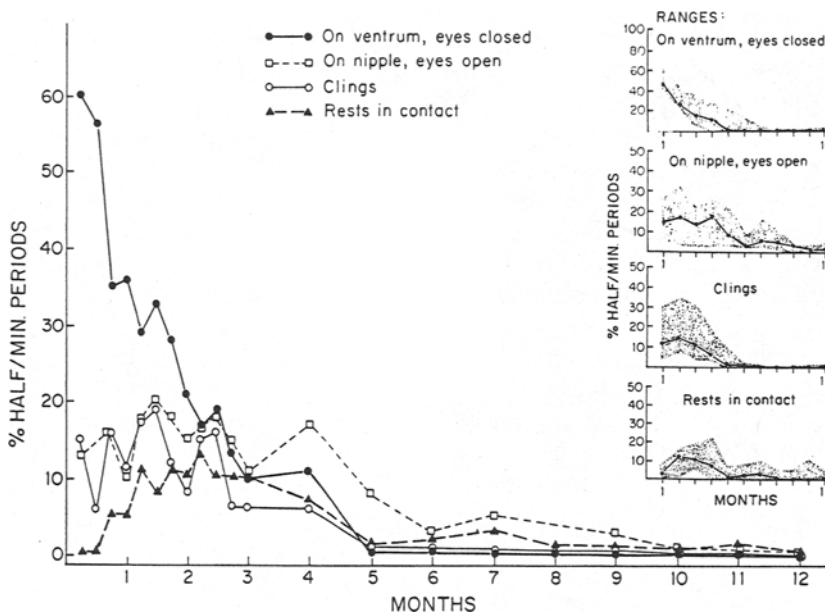In the second week, scores for "clinging to mother with eyes open"

Fig. 1. Median percentage of half-minute periods during which infants engaged in four contact behaviors. Insets indicate ranges for the four measures. For months 1-2, $N = 6$; for months 3-12, $N = 7$.

declined by more than half. This change was due to the onset of infant transfers in which infants were taken from their mothers by other group members. Since infants were most often taken (and were probably easier to take) when they were awake and clinging to their mothers but not actually nursing, such transfers did not result in a decline in scores for periods spent suckling.

In the second week scores for the measure "wholly out of contact" reached a median of 11% of all half-minute periods, due primarily to infant transfers rather than either mother- or infant-initiated breaks in contact. At this age, infants were being held or carried by other group members for about 25% of the time when they were awake. The most dramatic change in contact behavior during the first 3 months was the drop in scores for on mother, eyes closed in the second half of the first month, reflecting the increased activity and mobility of the infants at this age (Fig. 1).

Motor Behavior

Median ages at which 15 motor patterns were first recorded are given in Table II. Most infants achieved coordinated reaching (looking at an object, reaching for and grasping it) by the third week, and by the following week most were able to put objects into their mouths. Three infants ate their first solid food on the day they first put items into their mouths, but most infants did not begin to eat solid food until the seventh week. The onset of independent feeding did not coincide with any major change in scores for suckling.

The median age at which infants first moved independently more than an arm's length from their mothers and first walked steadily was 5 weeks; the median age for independent climbing was 6 weeks. Since infants were transferred before they could walk steadily, in the first month mothers had to approach and retrieve infants to reestablish contact. Once they were able to walk steadily, infants could usually escape would-be caretakers to return to their mothers.

Bipedal scanning began in the third month. Adults and juveniles scan bipedally to locate other group members, when alarmed or when presented with a novel or alarming stimulus such as a snake. Infants also scanned bipedally in such situations but they scanned more often than larger animals because their small size made it difficult to see over even moderately tall grass.

Social Behavior

The first social behavior observed was play, marked by the playface which appeared in the eighth week. Mounting appeared soon after the

Table II. First Observed Occurrences of Selected Behaviors in Patas Monkeys

Infant	Releases grip for tactile exploration	Coordinated reaching	Eye-hand mouth coordination	Eating solid food	Off mother (on own)	Off mother (taken)	More than arm's length from mother
Median Range[a] (N)	Day 11 4-20 (6)	Day 21 6-38 (6)	Day 34 21-62 (6)	Day 46 25-111 (6)	Day 25 6-39 (6)	Day 11 3-16 (5)[b]	Day 29 11-83 (6)
Infant	Steady walking	Competent climbing off mother	Mounts	First wean reject	Playface	Display	Bipedal scan
Median Range (N)	Day 29 9-59 (6)	Day 35 9-59 (6)	Day 59 58-282 (5)[c]	Day 58 4-119 (6)	Day 50 23-155 (4)[c]	Day 112 51-178 (5)[c]	Day 69 30-317 (6)

[a]All of infant AV's scores for first observed occurrences were excluded, as he was housed alone with his mother for the first 6 weeks while recovering from an injury.

[b]Infant NE's score was excluded, as she was housed alone with her mother for part of week 1 because her mother was being harassed by other group member.

[c]One or more infants were never observed to perform this behavior during the first year.

playface, in the ninth week. There was no difference in the median age at the first appearance of mounting for males and females. While mounting occurs exclusively in sexual contexts among adult patas, mounting by young infants occurred in play and exploratory contexts. Infants mounted other infants and juveniles of both sexes and attempted to mount adult females. Other animals were tolerant of infant mounting attempts.

Regulation of Mother — Infant Proximity

Infants out of contact with their mothers were scored as being in one of three proximity categories: within arm's length, within 3 m (but greater than arm's length), and greater than 3 m. Fig. 2 shows the proportion of half-minute periods infants spent in each proximity category.

During months 2 and 3 scores for periods spent close to the mother (within arm's length) or at large distances from her (greater than 3 m) increased rapidly but scores for periods spent at intermediate distances did not. This pattern was an effect of infant transfer: infants were often taken by other group members as soon as they moved out of their mother's reach and were more than 3 m from their mothers when they were playing or exploring near an allomother. No proximity category was scored for infants under the control of another group member; they were scored only as being "wholly out of contact" with their mothers.

Approaches and departures by mother and infant were scored only when either moved into or out of arm's length. Fig. 3 shows the percentages
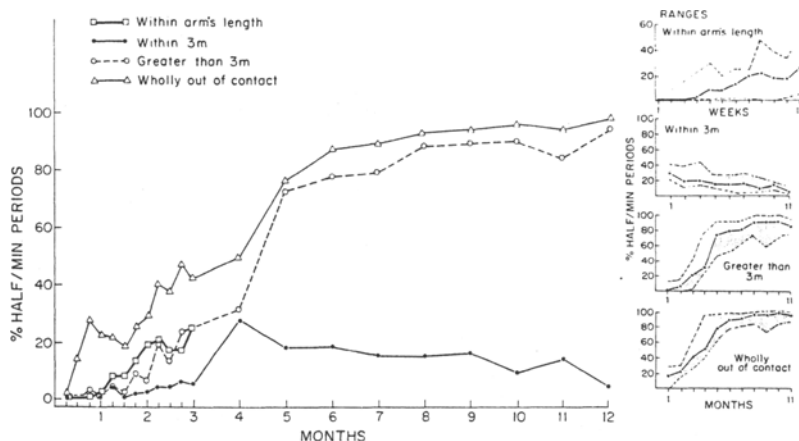

Fig. 2. Median percentage of half-minute periods during which infants were in three proximity categories or were wholly out of contact with their mothers. *N*'s and ranges as for Fig. 1.
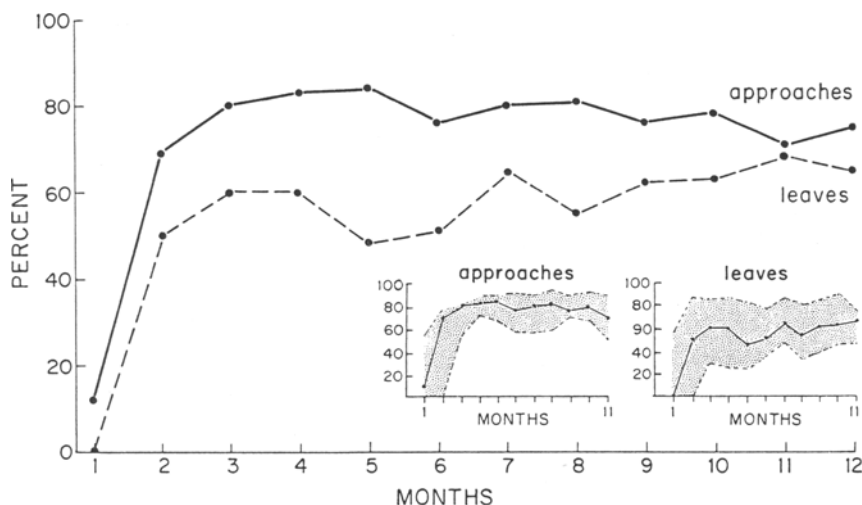
Fig. 3. Median percentage of all approaches and leaves by either member of the mother-infant dyad which were due to infants. *N*'s and ranges as for Fig. 1.

of all approaches and departures which were due to the infants' movements. In keeping with their limited locomotor abilities, infants rarely approached or left their mothers during the first month, and the mothers' approaches and departures were primarily in response to infant transfers: a mother typically moved away from her infant after it had been taken by another monkey and approached her infant to retrieve it. Only when infants began to move about independently did the question of proximity regulation arise. During the second month, infants and mothers were equally responsible for departures, but infants were primarily responsible for reestablishing proximity by approaching (for example, after transfers). By the third month, when play was an important activity, infants were responsible for most approaches and departures.

Maternal Caretaking Behavior

Although most infants were able to cling unaided within minutes of birth, mothers supported infants with one hand while climbing, running, or jumping for 2 to 3 days after birth; some mothers supported neonates briefly whenever they began to move. The maternal response to weak or injured infants seemed to depend on the age and parity of the mother. An old multipara constantly supported her injured infant for 3 weeks, altering her movement and feeding patterns until he was able to cling unaided. A young primipara, on the other hand, made no attempt to support her weak

neonate while he clung or nursed. In a wild group this infant would probably have died; here, however, he was hand-reared and was not included in this study. When mothers with young infants were inactive, they usually cradled their infants with one or both hands around the infant's back. Such cradling may provide assistance in helping neonates, especially weak ones, to maintain a hold on the nipple and may reduce infant heat loss at night or during wet weather.

Scores for cradling are shown in Fig. 4a. Except for a sharp rise in the fifth week, cradling scores decreased steadily over the first 3 months. The rise in the fifth week coincided with the time when many infants first began to leave their mothers independently and mothers may have been using cradling as a subtle form of restraint. Mothers were rarely seen to restrict their infants' movements out of proximity in more obvious ways. Restraints occurred in less than 0.5% of the half-minute periods during each of the first 12 weeks and was not observed at all after the fourth month. Retrieval of infants was only slightly more frequent, with median scores of 1% of the half-minute periods in the fifth week and less than 0.5% during the rest of the first 3 months.
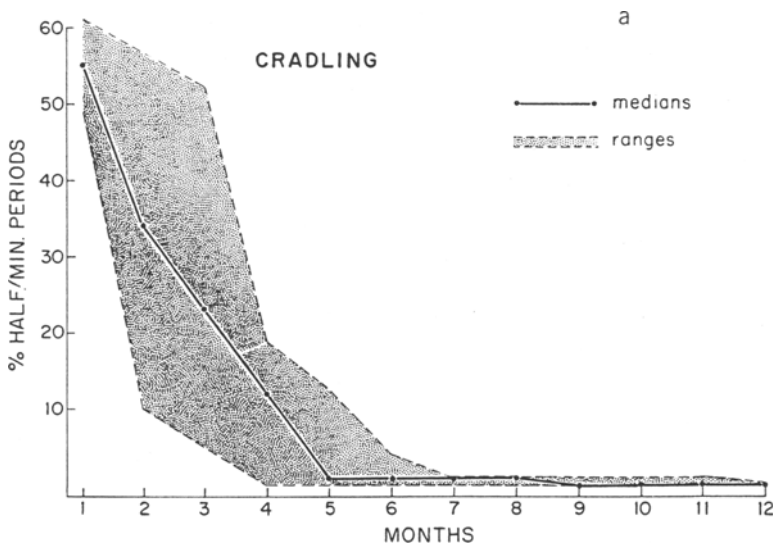

Fig. 4. (a) Median percentage of half-minute periods during which mothers cradled their infants. N's as for Fig. 1. (b) Median percentage of half-minute periods during which infants were awake and nursing compared with the mean frequency per hour of maternal weaning rejections. N's and ranges as for Fig. 1. Bars indicate standard errors of rejection scores. (c) Median percentage of half-minute periods during which mothers groomed their infants. N's as for Fig. 1.

By the twelfth week most infants had experienced maternal rejection of nursing or nursing attempts. Rejections were infrequent, however, never exceeding 1 per 5 hr of observation during the first 3 months (Fig. 4b). Rejection of other contact attempts and maternal punishment were also rare, and the combined frequency of these behaviors was never greater than 1 per 10 hr of observation during the first 3 months. Maternal punishment was always mild, usually consisting of batting at the infant or mouthing its hand or arm. This mildness contrasted with the rough, abrupt treatment infants received from other caretakers. Low frequencies of rejection and punishment did not indicate a lack of active encouragement of infant independence: a mother would move away from her infant, stop and look back at it until it began to approach, then again take a few steps and pause until it caught up. In this way infants were encouraged to follow mothers
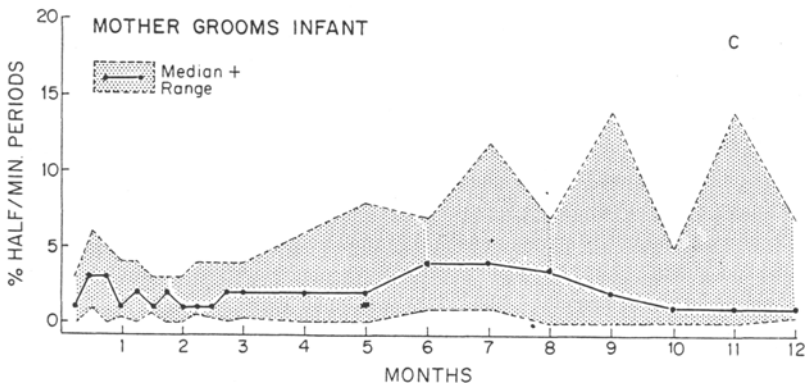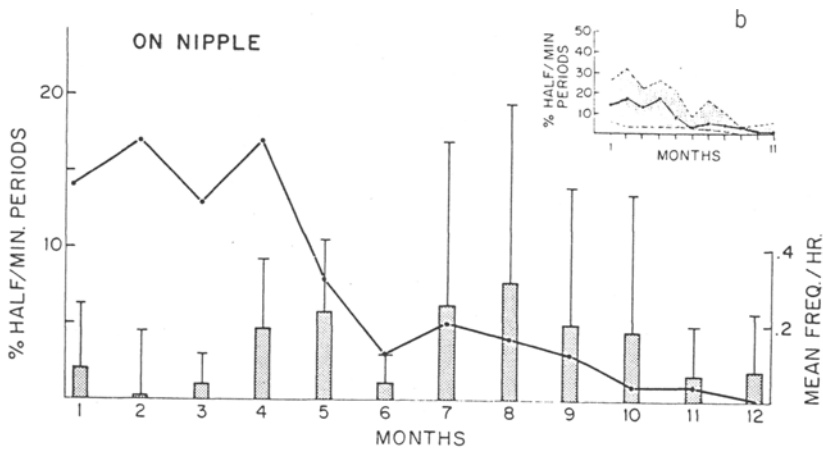
rather than being carried. Patas females in wild groups in Kenya used the same behavior pattern to encourage infants to follow them while they foraged (personal observation).

Mothers made frequent visual and olfactory inspections of their infants during their first few weeks, peering at their faces, sniffing them, and picking them up by the legs to inspect and sniff the genitals. Mothers groomed their infants infrequently (Fig. 4c); the median monthly scores for this behavior were never higher than 3% of all half-minute periods during the first 3 months.

Relations Between Infants and Other Group Members

All 25 infants born into the Berkeley colony over a period of 10 years were transferred, as were all 47 infants born during two birth seasons in two wild patas groups studied in Kenya (personal observation).

Infants in the captive group were transferred as early as 12 hr after birth, but the median age at first transfer for infants included in the study was 11 days (range, 3-16 days). Monkeys approaching a mother with a neonate gave contact calls ("moos"; Gartlan and Gartlan, 1973) and sniffed or nuzzled the back of the infant's neck. They frequently inspected the infant's genitals, lifting it by the legs and sniffing or touching the genital area while mooing repeatedly. Usually, a would-be caretaker approached the mother, grabbed the infant, and tried to pull it off the ventrum. If this direct approach failed, subterfuge was tried: for example, grooming the mother until she relaxed her grip on the infant and the infant could be pulled away. If the mother moved off, the other monkey often followed, threatened the mother, and continued to try to take the infant. To prevent infants being taken, mothers clasped them tightly or lay down on top of them and hit or threatened would-be caretakers. Protracted and noisy struggles over possession of infants resulted from this maternal resistance, but determined attempts to take infants almost invariably succeeded. Maternal rank appeared to have no influence on whether infants were transferred, but high-ranking females in this study may have had less difficulty in retrieving their infants.

Mothers whose infants had been taken alternated bouts of feeding or foraging with attempts to retrieve infants. They followed, sat next to, or groomed animals which had taken their infants, sometimes using the same type of subterfuge to retrieve the infants as other animals employed to take them away. Nearby monkeys often chased or threatened a mother attempting to retrieve her infant. A female whose own infant had been taken frequently took another infant from its mother, and occasionally mothers took other infants while they had possession of their own, carrying both infants ventrally.

All group members except the adult male held and carried infants, but infants in the captive group were taken from their mother primarily by adult females. Immature females aged 6 months to 2.5 years were enthusiastic caretakers of infants and frequently tried to take them. Immature males occasionally got possession of infants, usually (although not exclusively) using them in a specific interaction pattern described below. Adult females limited the access of immatures to infants by threatening them or attacking them when they approached infants.

When adult females took infants, behavior such as holding, carrying, and grooming predominated. Females also bit or hit infants, held them to the ground with a hand or foot, or, occasionally, played with them. Immature females held, carried, cuddled, groomed, and played with infants but rarely were aggressive toward them. Immature and adult females, including females that were themselves experienced mothers, were often awkward in handling infants, carrying them upside down or clutched to the ventrum facing outward or dragging them by an arm or a leg. Mothers never treated their own infants in such ways.

Immature males occasionally held, carried, and cuddled young infants. A more typical form of immature male–infant contact, however, was one in which a young male approached an infant from behind as if attempting to mount, picked it up, and held it to his ventrum. The immature male then ran bipedally toward the adult male, holding the infant and squealing. As the infants treated this way were usually squealing also, these occurrences were highly conspicuous, yet other group members rarely intervened. The adult male responded by yawning and moving away or by visually threatening the perpetrator. Since access to very young infants was limited for immature males, infants taken by them in this way were usually capable of rapid independent locomotion; and this, combined with the inherent awkwardness of trying to run bipedally while carrying a squirming baby, meant that the episodes were usually brief, ending with the infant escaping and returning to its mother.

Infant response to transfers changed with age. Neonates responded to transfer attempts by screaming, giving distress calls (coos), and clinging tightly to their mothers. Removing such an infant from its mother was difficult; as soon as one limb was pulled free, the infant would cling tightly with another. Once removed, the infant continued to call and struggle, and even very young infants sometimes refused to cling to nonmaternal caretakers. If the monkey which took the infant cradled it or allowed it to take the nipple, the infant usually quieted and clung or went to sleep. If infants were handled roughly by caretakers, however, they continued to cry and struggle, sometimes for an hour or longer.

Once infants achieved independent locomotion they struggled free from animals which treated them roughly and returned to their mothers but would sit or explore in the vicinity of a caretaker so long as no attempt was
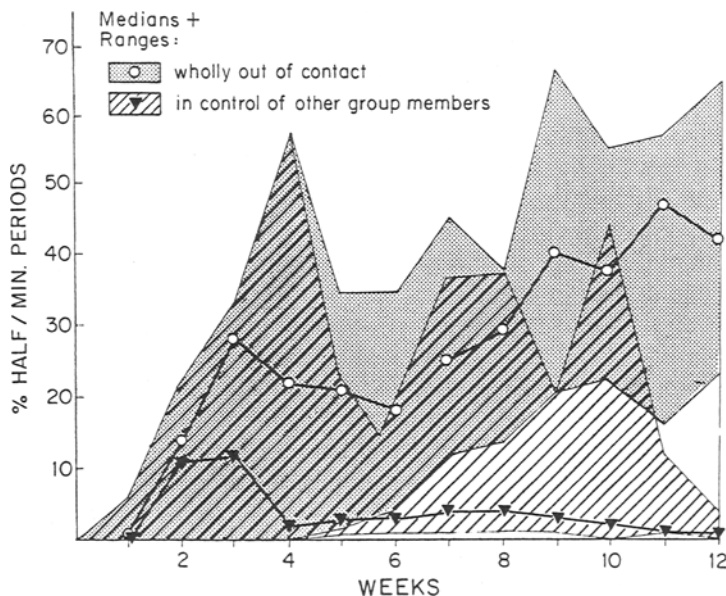
Fig. 5. Median percentage of half-minute periods during which infants were wholly out of contact with their mothers or were in the control of other group members. *N*'s as for Fig. 1.

made to restrain them. Caretakers used a variety of methods to keep mobile infants near them, ranging from the subtle, such as initiating play or grooming the infant, to the not so subtle, such as holding the infant by the tail.

The median number of half-minutes in which infants were held, carried, or otherwise controlled by nonmaternal caretakers rose to a peak in the third week and remained above 5% until the tenth week (Fig. 5). By the end of the third month, infant transfers by adult females had virtually ceased. At this age infants became more accessible to immatures, but as infants were now spending a large proportion of time playing, they were more likely to play with immatures than to be held or carried by them.

Although transfers often appeared to be traumatic events for infants, by the end of the third month some infants had established close associations with particular adult females which were their frequent caretakers, and these associations continued up to and beyond the end of the first year.

Relations Between Mothers and Other Group Members

The disruptive nature of infant transfers suggests that they had the potential to influence relationships between mothers and other adult
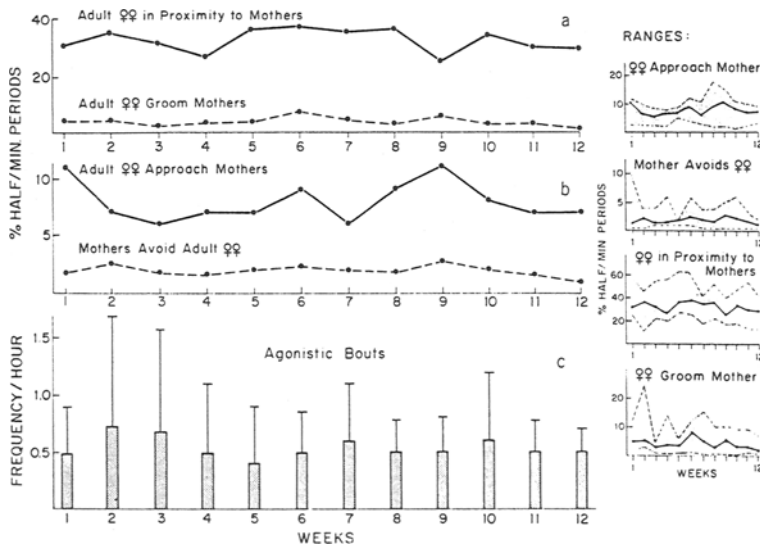
Fig. 6. (a) Median percentage of half-minute periods during which adult females were in proximity to mothers or groomed mothers. (b) Median percentage of half-minute periods during which mothers were approached by or avoided adult females. (c) Mean rates of agonistic bouts in which mothers were recipients (bars indicate standard errors). Ranges (shown in insets, right) and N's as for Fig. 1.

females in the group as described by Hinde *et al.* (1964) for macaques. Over the first 3 months there was little change in the pattern of affiliative interaction between mothers and other adult females as measured by the number of half-minute periods in which mothers were approached, groomed, or sat with (Figs. 6a and b). There was thus no evidence that mother–infant pairs or mothers were most attractive to adult females during the period when infant transfers were most prevalent. Rather, it was the new infant which attracted the attention of the adult females; and their interest focused on removing the infant and handling it, not on grooming or sitting with its mother. Typically, an allomother did not remain near the mother once she had possession of the infant. Avoidance of other females by mothers also showed little change over the first 3 months, occurring in about 2% of the half-minute periods throughout (Fig. 6b). Aggression toward mothers, although highest during the second week, just prior to the peak in infant transfer in week 3, never exceeded 1 bout/hr of observation (Fig. 6c).

One possible effect of harassment by other group members is increased maternal restraint of infants (Hinde *et al.,* 1964). In this study, restraint was always infrequent and no such effect was apparent.

Adult males rarely interacted with mothers of young infants and appeared to avoid them. At the beginning of this study there were few im-

matures in the group so that their behavior toward mothers could not be compared meaningfully with that of adult females. More recent data on the behavior of juveniles toward mothers and infants will be presented elsehwere (Rowell, T., and Chism, J., in preparation).

Month 4 Through Month 12

Contact Behavior

In the fourth month, infants spent approximately half of all observation periods in some form of contact behavior with their mothers. By the eighth month, median monthly scores for this measure had declined to about 5% and scores remained at this level for the rest of the first year (Fig. 1). After the fourth month, infants rarely slept clinging to their mothers during the day, although they continued to do so at night throughout the first year. Mothers had stopped carrying their infants except during group alarms by the seventh month, when scores for clinging reached zero. Suckling and resting in contact with the mother continued throughout the first year at low levels, with median monthly scores of 5% or less after month 5 for both measures.

Infants continued to increase the number of half-minutes spent wholly out of contact. This pattern, which began in the first 3 months, reached an asymptote at 6 months, with a median score of 88%.

Regulation of Mother–Infant Proximity

To take into account the increasing size and activity of infants, mother–infant proximity categories were reduced after month 3 to contact, within 3 m of the mother, and greater than 3 m from the mother (Fig. 2). In the fourth month, infants were within 3 m of their mothers about as often as they were at a greater distance, in those half-minutes in which they were out of contact at all, while by the fifth month infants were four times as likely to be at distances of more than 3 m from their mothers as to be within 3 m. Between month 4 and month 5 median scores for being within 3 m of mothers declined from 28 to 18%, while median scores for being more than 3 m from mothers more than doubled (from 31 to 73%). After month 5 there was little change in median scores for within 3 m but periods spent more than 3 m from mothers continued to increase, reaching 90% by month 9.

After the first month of life, infants consistently approached their mothers more often than their mothers approached them (Fig. 3). Throughout the 4- to 12-month period, infants were responsible for 75% or

more of all approaches by a member of the mother–infant dyad. Thus, after the first 2 months of life, patas infants were overwhelmingly responsible for reestablishing proximity to mothers. Breaks in proximity, as determined by the percentage of infant departures of all departures, were due about equally to infants and mothers during months 4–8, while during the final quarter of the first year infants were initiators of 65% of the breaks in proximity. In general, then, infants rather than mothers were primarily responsible for regulating proximity through approaches and departures during the 4- to 12-month period.

Weaning and the Development of Infant Independence

Weaning is the control of, decline in, and eventual elimination of nursing and, as such, bears a complex and often distant relationship to the production of a "weaned" infant (Rosenblum and Kaufman, 1967). Nursing by patas infants ceased completely only when their next sibling was born, usually at the end of the first year. If an infant's mother did not give birth, or if the new sibling died, the infant continued to nurse at least through the end of the second year. The only infant observed trying to nurse after its next sibling was born was promptly rejected. Mothers employed a variety of behaviors to prevent or discourage nursing. They pushed infants off the nipple, wiped infants off the ventrum by moving an arm across the chest, pulled the nipple out of the infant's mouth by raising an arm, or leaned on their elbows to effectively deny access to the nipples. An infant which persisted in its efforts to gain the nipple might be bitten or hit, but usually the mother gave in and allowed it to nurse after a brief struggle. Infants screamed or cried when rejected by mothers but did not exhibit prolonged tantrums such as have been described for langurs (Jay, 1965) and baboons (Ransom and Rowell, 1972; Nash, 1978). Mothers sometimes appeared to try to distract infants from attempting to nurse by initiating play or by grooming them. When mothers allowed nipple contact after an initial rejection, they usually terminated it after a brief period by gently disengaging the infant from the nipple. This rarely elicited further protest from the infant and the two often remained in proximity for some time afterward. In general, weaning was neither very traumatic for the infant nor particularly striking to the observer and can best be described as low-keyed.

Besides weaning rejections, mothers continued to reject other, nonnipple contacts and to punish infants by biting or hitting, as described for the first 3 months. The combined frequency for all rejections never exceeded 0.4 bout/hr during the first year. The frequency of rejections rose from the fourth month to the eighth month. After the eighth month, weaning rejections consistently declined, while the frequency of other rejections fluctuated between 0.05 and 0.10 bout/hr.

Table III. Spearman Rank Correlation Coefficients for Measures Associated with Weaning

	Wholly out of contact	Frequency of all rejections	Frequency of weaning rejections	Play
% approach		0.579*		
% leave		0.229		0.594*
% approach – % leave	– 0.670*	0.434		– 0.050
Maternal rank		– 0.109		
Maternal age		0.109		
Wholly out of contact		– 0.072		0.850**
Eyes open/on nipple			– 0.261	

*$p \leq 0.05$.
**$p \leq 0.01$.

Nursing scores declined rapidly between the third and the sixth month of life, considerably before the peak of weaning rejections was reached in the eighth month (Fig. 4b). While these results do not support the idea that there is a quantitative causal relationship between rejection and the decrease in nursing scores, maternal rejection might have had a delayed effect. For example, increased rejections in one month might have resulted in declining nursing scores in the following month. Such a relationship was found for patas infants in months 4–5 and months 7–8, but the reverse pattern was seen in months 6–7. In months 9 –10, a decrease in the rate of rejection was followed by a decrease in nursing. Thus, no consistent delayed effect of rejection on nursing was apparent.

Spearman rank correlation coefficients were calculated for pairs of measures implicated by Hinde (1974) in the development of independence in infant monkeys (Table III). Not surprisingly, the number of periods spent in play and the proportion of departures due to infants were positively correlated, as were play and the number of periods spent wholly out of contact with mothers. Two other coefficients reached significance: the number of periods spent wholly out of contact was negatively correlated with the difference between the percentage of approaches and the percentage of departures due to infants, and the frequency of maternal rejection was positively correlated with the percentage of approaches due to infants.

Patas infants increased their share of both approaches and departures between 4 and 12 months of age, but the infants' share of approaches increased more than their share departures and this resulted in the negative correlation. The positive correlation between maternal rejections and the proportion of infant approaches was examined in more detail by analyzing all recorded rejections ($N = 133$, including 80 weaning rejections). For each rejection, the following information was extracted from notes: (i) whether the infant or the mother approached during the preceding minute or

whether the pair was already together; (ii) whether one or the other partner left following the rejection or, if they remained together, whether the infant persisted in trying to nurse or gain contact; and (iii) the activity of each partner 1 min before the rejection and 1 min after.

Eighty-two percent of all rejections occurred when the mother and infant were already together, while only 13% of the rejections immediately followed the approach of an infant to its mother. It does not appear, therefore, that it was the approach itself which elicited the rejection as might be inferred from the positive correlation between approaches and rejections. When individual infants were ranked for each month on the proportion of approaches and the frequency with which they were rejected, no consistent relationship was found between the two ranks (correlation coefficients were not calculated because of the large number of zero scores for rejection). Thus, approaches themselves do not increase the likelihood of rejection, nor do rejections reduce the infant's tendency to approach. The relationship between rejections and approaches remains unclear and the correlation may be fortuitous.

After 82 (62%) of the rejections, infants remained with their mothers; infants persisted in trying to nurse or to remain in contact after 38% of all rejections. Infants were usually successful when they persisted; for example, infants persisted in trying to nurse after 32 of 80 weaning rejections and were successful in doing so in 30 (94%) of these. Of 51 instances in which the mother–infant pair separated after a rejection, it was most often the mother which left (33 times, or 65%). Overall, maternal rejection seemed an ineffective way of preventing or terminating nursing or contact by infants, if that was its object.

Infants fed or foraged within the minute preceding or following a rejection in just 3% of all cases, indicating that there was little direct relationship between seeking nipple contact and an infant's immediate nutritional needs. Maternal rejection in patas monkeys appeared to have only a small role in the proximate coordination of nursing with maternal activities, as had been previously suggested for this and other species (Hinde and Spencer-Booth, 1967; Altmann, 1980; Chism, 1980). Only two rejections occurred while the mother was feeding or foraging, and infants were rejected about as frequently when their mothers were engaged in social activity (47%) as when their mothers were alone and inactive (43%). Sixteen percent of all rejections, however, occurred immediately after an agonistic interaction between the mother and another monkey, suggesting that many maternal rejections were actually redirected aggression.

There was no correlation between the frequency of rejection and the maternal age or rank (Table III). Experienced multiparous and inexperienced primiparous mothers showed almost identical frequencies of rejection, 0.18 and 0.17/hr, respectively. Male infants were rejected significantly

more often than female infants in months 6 and 7 (Mann–Whitney U test, $U = 0$ and $P = 0.028$ for both months). Males were also rejected more often in months 8 and 9, but the results just missed significance ($U = 1$ and $P = 0.057$ for both months). The highest frequency of rejection recorded during the study was by an old female to what proved to be her last infant; this female remained alive and healthy 7 years after the birth of this infant.

Relations Between Infants and Other Group Members

Mothers rarely restrained infants after the third month, so maternal control over which individuals their infants interacted with and what form these interactions took diminished. Some mothers threatened, chased, or hit other adults and immatures which were aggressive to their infants or which were simply nearby when the infant showed distress. Other mothers looked away or ran away when their infants were threatened. This occasionally led to a mother fleeing from her screaming infant, which was in turn fleeing from an aggressor. The mother's response appeared to be determined largely by her current social relationship with the animal threatening her infant and by which other animals happened to be nearby at the time.

Relationships established between infants and their frequent non-maternal caretakers in the first 3 months had effects on later affiliative and agonistic interactions. Two female infants, TP and NE, each had mothers that often avoided agonistic interactions involving their infants. Each of these infants established a close relationship with a high-ranking female who aggressively defended the infants throughout their first year. A male infant, AV, had a particularly strong association with a high-ranked female, BB. BB was an effective and active defender of AV, whose own mother avoided all agonistic interactions involving her offspring. In his eleventh month, AV was in proximity to BB in 38% of all half-minute periods, while he spent only 14% of such periods in proximity to his mother.

Grooming by infants was rare during the first year, occurring at the rate of 1 grooming bout in 6 hr of observation. Grooming performed by infants was typically cursory and abrupt. Up to month 9, infants were groomed in about as many half-minute periods by their mothers as by all other monkeys together. Thereafter, grooming of infants by all others increased to about twice that of mothers alone. Comparing the amount of grooming received by infants with that received by other age–sex classes, infants were groomed about one and a half times as much as older immatures (aged 1–3 years) but only half as much as adult females [comparisons based on data from Rowell and Hartwell (1978)].

As infants aged 4 months and older increased their contacts with juveniles, mounting of juveniles by infants was observed. Such mounts oc-

curred both during play sequences, particularly at the beginning of a play bout, and during bouts of adult sexual activity. Infants also continued to mount adult females throughout this period. Adult females were tolerant of infant mounting attempts and adult males ignored them. Infants of this age were mounted by other infants and juveniles but not by adults of either sex. The sexual solicitation posture of adult female patas consists of a distinctive crouch combined with puffing out the cheeks and blowing through pursed lips. This posture was not observed in infants of either sex during the first year. When mounted, infants stood still or collapsed.

After the ninth month, a new behavior pattern emerged in male infants which was related to adult sexual activity: harassment of adult males. Infant males approached and followed the adult male, squealing, cooing, and hitting or grabbing at the adult male's face and conspicuous blue scrotum. During these episodes, infant males carried their tails arched up and over the body in a characteristic posture. Since female infants did not use this tail-carriage posture, it had the effect of announcing the sex of the infant to all observers including the adult male. Loy and Loy (1977) observed an immature male patas in a captive group showing the full adult female solicitation posture when harassing the adult male. Young males often crouched while harassing in the Berkeley colony, but although observation conditions were excellent, the cheek inflation and blowing characteristic of receptive adult females were not seen. On the other hand, young males typically sucked or chewed on their fingers between hitting or grabbing at the male. This behavior also was never seen in a female of any age, but it was so characteristic of the immature males that it was later used to help identify sex in the field.

During 570 hr of observation of male patas aged 4 to 12 months, 22 episodes of harassment were observed, beginning as early as 8 months of age. In the Berkeley colony, harassment occurred only when females in the group were receptive. One third of the harassment episodes occurred during copulations and an equal proportion occurred when the adult male was alone, inactive, or feeding or when he walked near the infant. In a quarter of the episodes the infant joined other immature males that were already harassing the male. The adult male responded with open-mouth threats directed at the harassers, and if they persisted, he usually moved away. Infant and juvenile males combined to harass every observed copulation attempt during this study. In contrast, infant females watched their mothers' copulations from a distance.

Adult male patas frequently display using a sideways bounce off any available vertical surface. Adult females also use this display during agonistic encounters and, in the wild, when initiating group movement (personal observation). Two female infants showed the display in their second month, while it was observed in male infants no earlier than the fourth month. Displaying

first appeared in solitary play, with the infant kicking its feet against the fence, bushes, or other animals and then bounding away. Displaying was later incorporated into sequences of chasing or wrestling, and after 6 months it frequently occurred in play bouts.

After 6 months of age, infants began to participate in agonistic bouts, particularly those which involved their relatives. Infants joined their mothers and siblings in attacks on other monkeys, usually bringing up the rear but occasionally running up to bite the victim (unless the animal under attack was the adult male). Infants often continued to follow or hit the victim for some time after the older animals had lost interest and moved away. At this age, infants also began to defend their mothers, threatening, biting, hitting, and chasing her attackers. Such defense often deflected or terminated the attack. The infant daughters of TT and NN were particularly effective in the defense of their mothers, both of which were often the subjects of aggression. The daughters had each formed close associations during infancy with high-ranking females, and although these females did not support the infants' mothers directly, the effect of their support of the daughters was to deflect attacks away from their mothers.

Play was an important social activity from 6 months onward. For the purpose of this analysis, play was divided into three types:

   social play, including activities such as wrestling, chasing, batting, and grappling, performed with one or more partners;

   parallel play, including synchronous exploratory or locomotor activities such as climbing, tumbling, and handling of objects, performed in parallel with one or more animals; and

   solitary play, including exploratory or locomotor activities such as leaping, galloping, and object manipulation, performed alone.

Infants spent between 12 and 19% of all half-minute periods engaged in play in the second half of the first year. This represented a large proportion of the periods spent in all social activity. Solitary play and parallel play were the first types of play to appear, but social play was the most common type during most of the first year (Fig. 7). Parallel play was always rare, occurring in less than 1% of all half-minute periods throughout the first year.

The 1-Year-Old

By the end of its first year, a patas infant was a functionally independent member of its social group. Infants moved about on their own, even during group alarms, and ate an adult diet which they obtained for themselves.
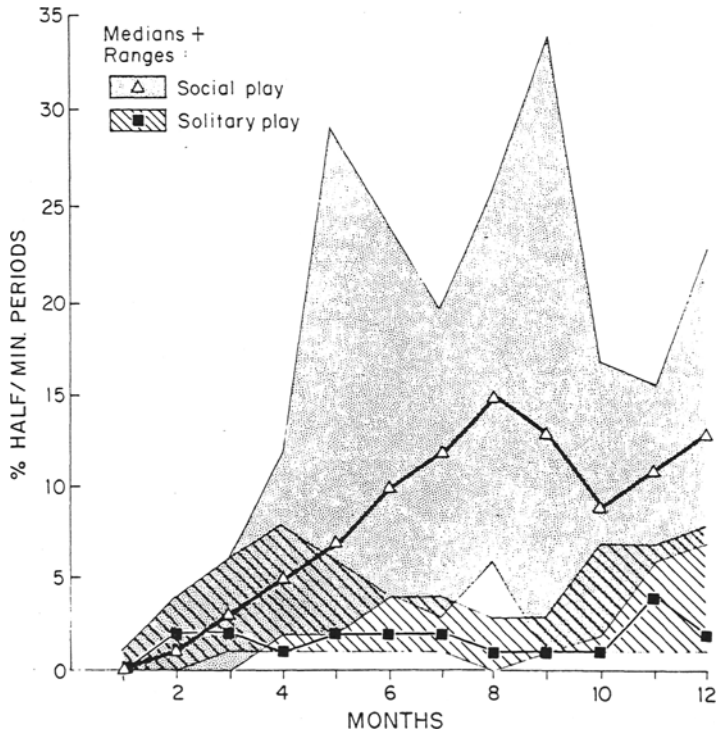
Fig. 7. Median percentage of half-minute periods during which infants engaged in social or solitary play. *N*'s as for Fig. 1.

One-year-olds had well-established social relationships with other group members, and with the exception of female sexual behavior patterns, all adult behaviors had appeared at least in a rudimentary form by this time.

The proportion of time spent in each of the six most frequent behavior categories at this age is shown in Fig. 8. Contact with mothers was rare and 1-year-olds spent about as many periods in proximity to all other adult females as to their own mothers. Play and feeding or foraging were the predominant activities at this age. Yearlings groomed infrequently and most grooming was of their own mothers, which they groomed more than twice as frequently as all other group members combined.

The presence of a new sibling was an important determinant of the amount of contact between mothers and 1-year-olds. Mothers of neonates threatened and hit their 1-year-olds when the latter approached and tried to sit nearby or to groom the new infant. Thus, the immediate effect of the birth was to decrease the time the 1-year-old spent in proximity to its mother. For example, female infants TP and BK's proximity scores decreased by 33
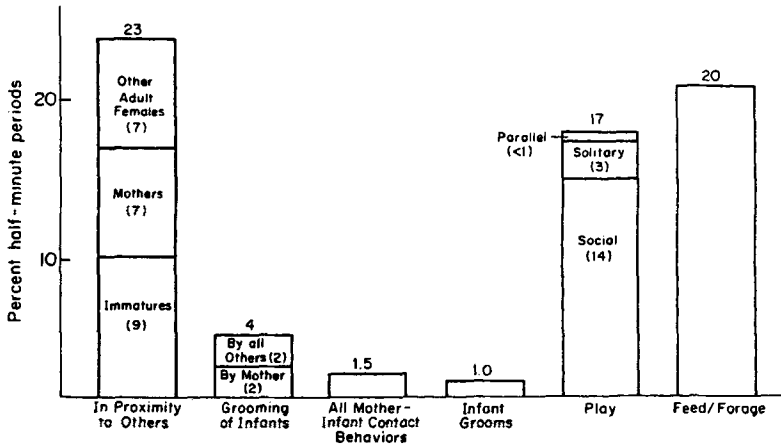
Fig. 8. Behavioral profile of 1-year-olds. Median percentage of half-minute periods during which 1-year-olds engaged in six activities. $N = 7$.

and 56%, respectively, in the month in which their next siblings were born over scores for the preceding month. After this initial repulsion, however, 1-year-olds were tolerated in proximity, and daughters were used as "babysitters" while mothers foraged or engaged in social interactions. Daughters were often responsible for returning transferred siblings to their mothers. Mothers were not observed to use 1-year-old sons as babysitters, although older juvenile males occasionally exhibited allomaternal behavior toward infant siblings. Associations between mothers and sons persisted through the third year and through adulthood for mothers and daughters.

Infants were rarely in proximity to adult males (about 0.1% of the half-minute periods). One-year-olds were groomed by adult females about twice as often as by immatures. Infants were groomed by adult females three times as often as they groomed adult females and by immatures eight times as often as they groomed immatures. One-year-olds did not groom adult males.

One-year-olds continued to maintain close relationships with group members that had acted as frequent caretakers during their early months of life, and former caretakers continued to support 1-year-olds in agonistic encounters and to sit with and groom them. One-year-olds both attempted to take infants themselves and joined in attacks by their mothers or former caretakers on other animals that took infants, and former caretakers permitted year-old females to handle infants in their possession.

DISCUSSION

Rate of Development

Mother–infant contact behaviors decreased rapidly over the first 3 months of life, so that by 4–5 months infants had achieved almost complete locomotor independence and were rarely seen to nurse during the day. This is a more rapid rate of development of independence than is seen in rhesus monkeys (Hinde and Spencer-Booth, 1967) and is equaled only by that in vervets (Struhsaker, 1971; Whitten, 1982) among Old World monkey species for which comparable data are available. An earlier study compared the rate of development of some behaviors of patas and *Macaca fascicularis* infants housed with mothers in a playpen apparatus and given access to peers for brief daily periods (Seay *et al.*, 1970). This study reported similar mother–infant contact scores for *M. fascicularis* and rhesus infants but found that patas were slower to decrease contact with mothers over the first few months of life. The authors characterized patas mothers as being more permissive in some respects and perhaps more protective in others than were macaque mothers. In the Berkeley colony also, the absence of other group members resulted in higher scores for maternal restraint of infants, as was the case for a mother which was housed alone with her injured infant for several weeks (see footnote *a*, Table II). It may be that the housing conditions and the absence of potential allomothers were responsible for the slower rates of development and increased maternal protectiveness of the patas in the earlier study.

In two wild patas groups studied in Kenya, development proceeded at a rate similar to that observed in the Berkeley group (personal observation). In Kenya, patas births were distinctly seasonal, so that with few exceptions, infants were 4–5 months old when the main rainy period began and foods, including those which could be easily obtained and processed by infants ["weaning foods" of Altmann (1980)], became more readily available. This was also the time of year when females in wild groups began to mate, although the peak of conceptions occurred several weeks later (Chism *et al.*, 1984). Thus, captive patas infants had reduced scores for nursing and mother–infant contact to a low level by the age at which infants in the wild groups were largely independent in feeding and locomotion and when their mothers were mating.

Although patas infants achieved locomotor independence early in the first year, they were slow to develop motor skills over the first few weeks of life, during which motor criteria were achieved later than in macaques, baboons, and vervets (Rowell *et al.*, 1968; Hinde, 1971). These differences

may reflect patas infants' relatively few opportunities to practice motor skills. In wild patas groups, day ranging patterns result in little time during the day when a group is stationary (Chism *et al.,* 1983). Young infants thus have little chance to explore or move off their mothers, and what opportunity exists is limited further by the intense interest of (and consequent handling by) allomothers.

Early locomotor and nutritional independence appeared to facilitate infant survival in wild patas groups. Two infants in the Kenya study groups, orphaned at 7 and 9 months of age, survived without being adopted or receiving allomaternal care (Chism *et al.,* 1984). Infants of no other species of Old World monkeys have been observed to survive being orphaned at such an early age in the absence of adoption or caretaking (cf. Altmann, 1980; Hamiton *et al.,* 1982).

Acquisition of Independence

Weaning and proximity-regulating behavior provide an indication of the relative contribution of mothers and infants to the acquisition of independence by infants. With regard to the regulation of mother–infant proximity, Hinde (1974) identified two relevant variables: (1) Who maintains proximity? and (2) changes in whose behavior are responsible for age-related changes in the time spent in proximity? Hinde and Spencer-Booth (1967) predicted a positive correlation between the percentage of approaches (minus the percentage of departures) due to the infant and the number of periods spent wholly out of contact with the mother, if mothers were primarily responsible for regulating proximity by leaving infants. A negative correlation was predicted if infants regulated proximity by leaving mothers more often. In patas, a negative correlation was obtained between percentage approach–percentage leave and periods spent wholly out of contact, and indeed, it appeared that infants were primarily responsible for maintaining proximity. They did so, however, by both leaving and approaching more. Patas mothers were largely passive partners in proximity relations after their infants were 5 months old. Patas thus appear to differ from rhesus monkeys in their patterns of proximity regulation.

Hinde and Spence-Booth also predicted that a positive correlation between periods spent wholly out of contact and the frequency of maternal rejection would indicate that age changes in proximity scores were due primarily to changes in the mother's behavior, such as was found in rhesus (Hinde and Spencer-Booth, 1967). For patas infants these two measures were positively correlated only during the first 4 months and the correlation was significant only in months 1 and 4. According to Hinde's prediction, this suggests that patas mothers are initially responsible for changes in proximity, but after the

fourth month it is the behavior of infants that results in changes in proximity scores. This prediction, however, appeared to include the assumption that the mother forces the infant to move away by rejecting it. Other studies indicated, however, that maternal rejection may decrease the infant's tendency to leave the mother (Rosenblum and Harlow, 1963; Kaufman, 1974). Patas infants did not often respond to rejection by moving out of proximity. On the other hand, since a substantial proportion of maternal rejections actually appeared to be redirected aggression, infants which spent more time near their mothers were more likely to receive such redirected attacks. Another possibility is that infants may annoy their mothers by trying to nurse or gain contact so that rejection functions to stop the annoyance rather than to drive the infant out of proximity. Thus, the negative correlation between rejection and the percentage of periods spent wholly out of contact may result from the simple absence of opportunity: if the infant is not nearby it cannot be either annoying or rejected.

Weaning has been cited as an example of mother–infant conflict (Trivers, 1974). Among patas, maternal rejection was infrequent and ineffective and reached a peak after nursing scores had declined to a low level, so that rejection appeared to have little influence on nursing behavior. Weaning tantrums were not observed among patas and may be maladaptive in a species that relies on crypticity to evade predators (Hall, 1965; Chism et al., 1983). It was rarely possible to locate a wild patas group by its vocalizations. When young infants were present in the group and infant transfers were occurring, however, infants engaged in prolonged bouts of squealing, which could be heard up to 300 m away. This suggests that selection against loud noises by infants cannot be the only explanation for the absence of weaning tantrums in this species.

Infant patas apparently learn very early not to interrupt their mothers' feeding or progressing and usually nursed when mothers were grooming or resting. Thus, suckling interfered very little with maternal activities. Since wild patas infants are capable of independent foraging well before the peak of maternal rejections occurred in captivity, it seems unlikely that, in patas, rejection functions primarily to force infants to shift from dependence on milk to independent foraging.

The implication that, if mothers did not force infants to become independent, they would remain dependent more or less indefinitely is at the heart of the discussions of parent–offspring conflict (Trivers, 1974). As Altmann (1980) pointed out, the conflict may sometimes be more theoretical than real. Rapid attainment of independence is often necessary for survival of patas infants. In 1 year, 6 of 25 (24%) of the patas infants in two wild study groups were orphaned at between 7 and 14 months of age, and all of these infants survived. Thus, it is not surprising that maternal rejection appears to play such a minor role in the development of independence among patas infants.

It is in the best interests of the infants themselves to become self-sufficient as soon as possible, and early independence frees mothers to begin their next reproductive efforts as soon as possible. Apparently, the low level of mother–infant contact behavior maintained after the fifth month represents little cost to the mother. Infants continue to nurse at night and they may receive enough extra calories to provide a nutritional "cushion" while their own food acquisition skills improve. At he end of the first year the birth of the next sibling forces complete independence. If, however, the mother fails to produce a live infant, or if the infant dies soon after birth, the previous infant will continue to associate with the mother in the second year at a level similar to that which characterized the end of the first year. In sum, these factors may mean that there is little evidence for conflict of interest between patas mothers and patas infants.

Allomaternal Behavior

On the basis of observations by Hall (1965), patas females have been characterized as being among the most possessive of cercopithecine mothers (Blaffer-Hrdy, 1976), although Hall himself felt that this possessiveness was probably not typical of patas living in natural social groups (Hall and Mayer, 1967). Studies of patas in captive and wild groups have now shown that extensive allomaternal caretaking of infants beginning in the first week of life is a normal part of the species' mother–infant relations (Chism, 1978; Zucker and Kaplan, 1981; Chism et al., 1984). Infant caretaking patterns of patas are most similar to those of the closely related vervet monkeys (Cercopithecus aethiops) (Gartlan, 1969; Lancaster, 1971; Struhsaker, 1971; Krige and Lucas, 1974) and also resemble those of many colobine species which permit extensive handling of neonates by conspecifics other than the mother (Jay, 1962; Sugiyama, 1965; Poirier, 1968; Hill, 1972; Horwich and Manski, 1975).

Mothers of several species in the genus Cercopithecus and its allies (Miopithecus and Erythrocebus) permit more extensive contact with young infants by other group members than is typical of baboons and some species of macaques. Among forest guenons, observations of talapoins (Miopithecus talapoin) (Gautier-Hion, 1971; Chism, 1980), diana monkeys (Cercopithecus diana) (Hunt-Curtin, personal communication), redtails (C. ascanius), and blue monkeys (C. mitis) (Cords, personal communication) indicate that mothers permit considerable contact between young infants and other group members, although other animals do not carry infants until the infants begin to move away from mothers on their own. Thus, cercopithecines show considerable interspecific variability in the degree of contact with infants which mothers tolerate, ranging from the extensive allomaternal caretaking of neonates among patas and vervets to the restrictiveness of baboons and rhesus macaques.

Several potential benefits to mothers, infants, and other group members of distributing infant caretaking widely within the social group have been suggested (Blaffer-Hrdy, 1976; McKenna, 1979; Quiatt, 1979), including (1) facilitation of adoption of orphaned infants; (2) protection of infants (e.g., from predators, injury, or intragroup aggression) beyond what the mother alone can provide; (3) increased foraging efficiency for mothers; (4) status benefits which accrue to mothers, infants, or both from associations between infants and caretakers of high rank; and (5) opportunities for immature females to acquire or practice maternal skills. This discussion is restricted to the likelihood that any or all of these benefits have contributed to the occurrence of allomaternal caretaking among patas monkeys.

The highly synchronized nature of patas reproduction means that an infant which survived its mother's death might have a lactating caretaker available to it only if its mother's death coincided with the loss of an infant by another adult female in the group. In such circumstances adoption of an infant less than 6 months of age might occur. Willingness on the part of the potential adoptee may be as important as the availability of an appropriate caretaker, however. A 4-month-old patas infant orphaned in the Berkeley colony refused all attempts by adult females to adopt it, even though these same females had acted as its caretakers before its mother's death. Dolhinow (1980) has similarly stressed the importance of infant acceptance of adoption among hanuman langurs. Thus, the occurrence of allomaternal caretaking in a species may not, in itself, ensure the adoption of dependent infants. The only successful adoption observed in the colony or wild study groups occurred in the Berkeley group when a female adopted her own mother's 3-week-old daughter when her own infant died within 24 hr of its birth (Moorhouse, personal communication). The mother of the adopted infant made no attempt to prevent the adoption.

Wild and captive patas infants are frequently retrieved by their allomothers from situations potentially dangerous to the infants (for example, when infants get themselves into precarious positions in trees). In all observed instances, however, the rescue or retrieval involved little or no risk to the caretaker. Such low-cost behavior may be an example of reciprocal altruism (Trivers, 1971) and would thus require no additional explanation.

Infant patas in the Berkeley colony derived some direct benefits from their associations with high-ranked caretakers in the form of intervention on the infant's behalf during agonistic bouts. Mothers derived at least temporary benefits from such associations also when attacks on them were deflected by caretakers interceding on the infants' behalf. Whether similar effects derive from allomaternal caretaking among wild patas can be determined only by further analysis of field data.

There have been many suggestions that primiparas are less competent or confident in their handling of infants than multiparas, although most evidence to support these suggestions has come from animals which were

captive-reared in circumstances contributing to a general lack of social skills, not just those related to mothering. Seay (1966) found few significant differences in the behavior of primiparous and multiparous rhesus mothers toward infants and no differences that were directly related to the survival of infants. Ultimately, even if primiparas and multiparas differ in maternal style, these differences will be meaningful only if they result in differential survival of infants (see also Hooley and Simpson, 1981). Drickamer (1979) found that rhesus infants of multiparas were more likely to survive than infants of primiparas. Among patas monkeys, however, there was no difference in the survival of infants born to primiparas and multiparas (Chism *et al.*, 1984). It is possible, therefore, that the experience immature female patas gain in handling neonates may contribute to their success in rearing first infants. Despite their opportunities to practice, however, primiparous females in both wild and captive patas groups were often awkward in handling their infants over the first 24−48 hr of life.

Potential risks associated with allomaternal care of neonates derive from the vulnerability of young infants to injury as a result of careless or inept handling or from being retained for long periods by nonlactating caretakers. In species where dominance hierarchies among females are rigidly defined or where intragroup aggression is frequent, neonates (and ultimately their mothers) are likely to incur costs as a result of allomaternal caretaking − either from injury during aggressive encounters or when mothers are unable to retrieve infants from nonlactating females of a higher rank. In species with relaxed dominance relations among females, neonates are still liable to injury due to inept handling.

Patas mothers in both wild and captive groups were usually able to retrieve infants from other group members regardless of rank. Aggressive episodes in patas groups are infrequent and serious wounding of immatures during such episodes is rare. Although clumsy, careless, and outright incompetent handling was a conspicuous component of allomaternal caretaking among patas, on only one occasion in several thousands of hours of observation of captive and wild patas did such handling result in serious injury to an infant. One is forced to conclude that any costs associated with allomaternal care in patas are too small to select effectively against the behavior.

Observations of patas mothers and infants indicate that infant caretaking patterns and the rate of behavioral development characteristic of a particular species are integral parts of the life-history pattern of that species. For patas, the rapid attainment of social and sexual maturity is best understood as a response to a highly seasonal savannah environment in which there is a premium on the ability to reach nutritional, locomotor, and social self-sufficiency as rapidly as possible and to reproduce as early and as often as developmental constraints will permit.

ACKNOWLEDGMENTS

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