

Relation of Allomothering to Infant Age in Howlers, *Alouatta pigra*, with Reference to Old World Monkeys

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Early infant transferring or allomothering is of interest in relation to the idea of genetic altruism. Possible functions vary from learning to mother, freeing the mother to feed, infant socialization, increasing troop cohesion, to adoption. Despite specific examples of functions, no main adaptive significance has been proven. Observations of transfers in two infant female howlers (*Alouatta pigra*) have indicated two periods of allomaternal interest with the later period at 6-10 weeks being the one in which infant transfer was prevalent. A comparison of the howler data with those on Old World monkey species indicates three ontogenetic profiles of early allomothering: (1) species which show initial peaks of transfer at 2-3 weeks (typified by colobines); (2) species with early interest periods but with later transfer peaks at 6-10 weeks (typified by howlers and rhesus); and (3) species or instances within species in which peaks of transfers occur in both periods (typified by patas monkeys and instances in colobines). There is some suggestion that allomothering functions differently at different ontogenetic periods, with the initial peak being associated with infant protection by experienced juveniles and adults and the later period being associated with learning to mother by inexperienced females, and contact with other troop members, including males.

INTRODUCTION

Young primates go through a series of behavioral oscillations in development, in which certain behaviors are done more frequently at certain times. This is especially true in reference to contact with the mother (Horwich, 1974a, 1974b). Allomothering of the young

infant also oscillates, showing specific age periods during which infants are more "attractive" to other troop members.

Allomothering or infant transferring is of interest in relation to the idea of genetic altruism. It has been argued to have many varied functions from learning to mother (Lancaster, 1971; Blaffer Hrdy, 1976; McKenna, 1979a; Quiatt, 1979), freeing the mother to feed (Pfeifer, 1968; Blaffer Hrdy, 1976), infant socialization (Blaffer Hrdy, 1976), increasing troop cohesion (Horwich and Manski, 1975; Struhsaker, 1975; Horwich and Wurman, 1978), to adoption (Blaffer Hrdy, 1976, McKenna, 1979b). These functions have been the subject of a number of recent review articles on primate care-giving (Blaffer Hrdy, 1976, Quiatt, 1979; McKenna, 1979a, 1979b, 1981). Quiatt (1979) takes the view that allomothering has evolved as a fortuitous part of the generalized maternal behavior of females and that it may have no function at all. However, if we look at specific primate examples, it is obvious that allomothering has functioned in many different ways in different species and in individual cases within a species. For example, infant adoption has been observed in captive rhesus (Rowell et al., 1964) and langurs (Dolhinow, 1980; McKenna, 1979), and in howlers in the field (Clarke and Glander, 1981). Group cohesion has been instigated by infant birth and consequent transferring in *Colobus guereza* (Horwich and Wurman, 1978). Learning to mother has been observed in specific individuals in which improved handling was noted in successive infants (Horwich and Manski, 1975; Horwich and Wurman, 1978). In this study we have even seen a howler mother on a number of occasions deposit her infant with an allomother so that she could participate in troop play. Thus, allomothering has had specific functions although the major adaptive significance has not been proven. McKenna (1979a) has addressed this problem.

With these examples in mind, we agree with Quiatt (1979) that allomothering has developed from generalized maternal behavior, with allomothers of many primate species showing attractions to infants (McKenna, 1979b) of specific ages. The "attractive" ages, related to the physical and psychological growth of the infant, may appear at different times during ontogeny. Infants may be attractive for different reasons and to different age and sex classes of caretakers.

We will discuss two such age periods in *Alouatta pigra* and show similar periods in Old World species. We further suggest a comparison of primate growth with animals that show metamorphic growth such as amphibians. With the major physical growth changes, from larvae to adult, there are major functional changes at different ages. We similarly suggest that the two age periods in primate development may each be more associated with different functions of allomothering. Allomothering may function to provide extra protection to the infant in early colobine allomothering. In howlers and other

species which show later peaks in allomothering, the allomothering may function to provide opportunities for learning to mother for inexperienced females, infant-male socialization, and extra protection.

METHODS AND MATERIALS

A study of infant development was carried out on a female infant in each of two troops of black howler monkeys, *Alouatta pigra*, in Bermuda Landing, Belize from April 28 to July 14, 1981. For more descriptive information on the area see Bolin (1981), Horwich, (1983b), and Horwich and Gebhard (1983). The Fig Tree troop was composed of two adult males, an adult female and her newborn female infant, and a sub-adult female. The Cashew troop was composed of two adult males, two adult females, a juvenile male, and the newborn female infant. Over 350 contact hours were spent with the howlers, of which 145 were with the Fig Tree infant, and 84 were with the Cashew troop infant. Observations were made using 7 x 35 binoculars, recording notes by hand on note pads. Observations yielded behavioral profiles of the following behaviors: frequency of transfers of infant from one troop member to another, minutes per hour on animals other than the mother, minutes per hour on the ventrum or back of the mother or distance from the mother at 1-minute intervals, presence of others within 3 feet of the infant or mother at 1-minute intervals. Other social behaviors by troop members toward the infant were recorded as well as ad lib records of general troop behaviors including grooming and play. All frequencies of behaviors were totalled per week and divided by the number of observation hours to provide an hourly mean of behaviors per week.

The age of the Fig Tree troop infant was known to be less than 2 weeks when we arrived. The age was known by local ferrymen since this troop spent much of its time in a village Fig Tree next to the ferry landing. We thus began our data collecting with the good assumption that we were collecting the second week's data. The Cashew troop infant's age was estimated to be 3 weeks based on the pelage and behavioral data which was later confirmed by the quantitative graphic changes.

RESULTS

Little mention of infant transfer was noted in older studies of howlers, although Carpenter (1934) mentioned that infants were sometimes taken from the mother and carried by other troop members until they were retrieved by the mother. Glander (1975) first systematically observed transfers in marked individuals of *Alouatta palliata* and transfers have since been studied in *howlers*, *Alouatta seniculus* (Mack, 1979). Most recently

an excellent study has been completed on infant development and non-mother interactions in *A. palliata* (Clarke, 1982). In *A. pigra*, troop size is small and individuals were all identifiable. In both of our troops, only one other female was present who acted as the allomother. Despite the larger troop sizes in *A. palliata*, usually one female acted as the main associate in infant transfer (Glander, 1975).

Infant transfer in howlers differs from transfers in Old World monkeys in generally being much more passive on the part of the allomothers. On occasion, allomothers would approach and look at or sniff an infant and might touch its head or face. As noted in *A. palliata* (Glander, 1975; Clarke, 1982) the females would approach the mother and infant and remain near, looking, sniffing, or occasionally touching it. They would then extend the neck or chest out with the chin extending over the infant. Some touching and guiding of the infant onto the allomother with her hands was noted in *A. pigra* during the first month. Although this was not seen in *A. palliata* by Glander (1975), taking of the infants by non-mothers was subsequently seen by Clarke (1982). Glander (1975) also noted a soft vocalization during the transfer which we did not or were unable to hear in *A. pigra*. Often, especially in infants over a month of age, the infant would climb onto the back of another troop member who was resting next to its mother. It seemed as though by resting next to the mothers, the troop members sought out this contact.

The following figures show the developmental profiles of the allomaternal care in *A. pigra* and how it relates to behaviors of mothers and infants.

The main data on allomothering shows that other troop members, including males, show a main interest in infants at 6-10 weeks of age. Figures 1, 2, and 3 indicate this period of social interest. Figure 1 shows a peak in infant transfers to the other troop female at 8-10 weeks. Time spent on the allomother was also high during these weeks (Figure 2). In *A. seniculus*, an increase of time on others was also noted by the second month, with a decrease by the third month (Mack, 1979). In *A. palliata*, Clarke (1982) noted non-mother interactions with female infants to be most numerous between 8-12 weeks, the frequency of takes and transfers showing a very similar profile to Figure 1.

Males are infrequently used as alloparents although they seem to take only a passive interest in the infant, allowing it to climb onto their back without displaying such social behavior toward it. Figure 3 shows that in both troops this same period of 6-10 weeks was when these interactions took place. In the Fig Tree troop very little male-infant interactions occurred, although for a brief period during week 9 one of the males did carry the infant on its back on a few occasions. It should be noted that this was during the 2-week period when the troop was dispersed during rainy season travels and the allomother

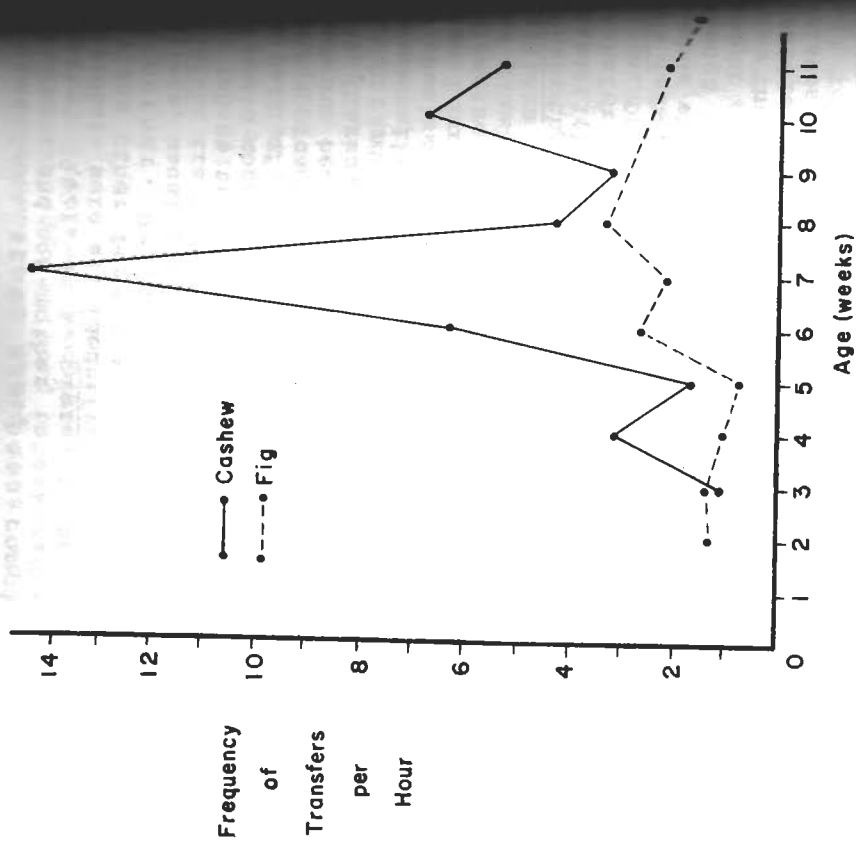


Figure 1. Frequency of transfers per hour as a function of age in weeks in two female infant howlers.

lost the troop. A major difference between the two troops involved a closer integration of the Cashew troop which seemed related to the play initiation by the young males. Supportive data on an infant born to a captive pair of black howlers, *Alouatta caraya*, indicates a peak in male carriage at 8 weeks of age (Figure 14). This male was quite attentive to the infant, and when the female moved away from the climbing infant, the male came and sat near it. Bolin (1981) similarly noted *A. pigra* females to deposit infants close to males before going off to forage as did Glander (1975) in *A. palliata*. Bolin (1981) interestingly, compares *A. pigra* to monogamous primate species. This possible tendency toward monogamous behaviors in *A. pigra* is associated with small troop sizes and low male to female ratios (Bolin, 1981; Horwich, 1983a; Horwich and Gebhard, 1983).

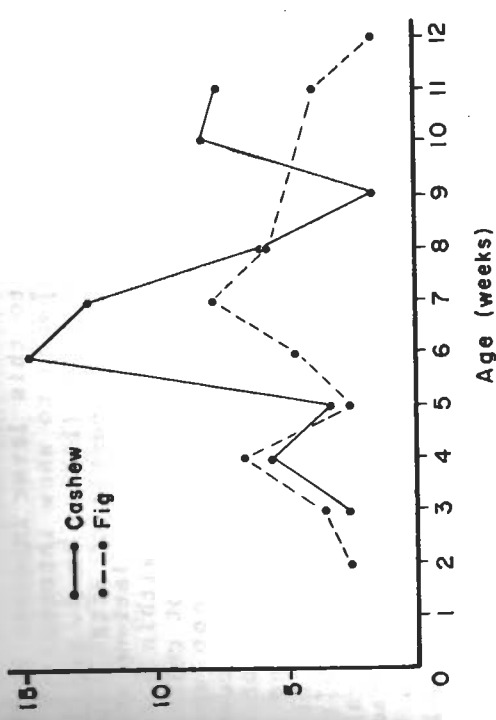


Figure 2. Time (minutes per hour) spent by two female infant howlers on their allomother as a function of their age in weeks.

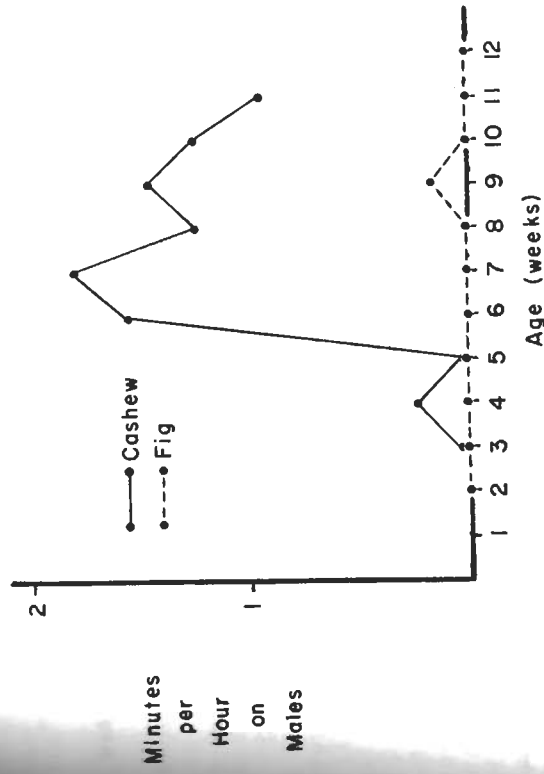


Figure 3. Time (minutes per hour) spent by two female infant howlers on troop males as a function of their age in weeks.

In addition to this later interest in the infants, the allomothers seemed to show interest in the young infant as well. Glander (1975), in *A. palliata*, notes that the neonate is the center of attraction for all group members. Figure 4 shows oscillations of the amount of time that allomothers remained within 3 feet of the mother and infant. Since data were not collected during the first weeks in the Cashew troop and since a separation of the two Fig Tree females occurred during weeks 9-10 due to the wet season change of range, the graph is not clear. However, the Fig Tree allomother stays close at week 4 and the Cashew troop allomother's proximity is high at week 4 and possibly earlier, fluctuates to peak again at week 7, and again in weeks 10-11. This alternates with the mother's contact with her infant (Figure 8). Troop play in the Cashew troop also peaks at times opposite from those the allomothers spend near the mother (Figure 5). Play was mainly instigated and performed by the subordinate male in the troop who played mostly with the juvenile male. The total play in Figure 5 is mainly from play bouts of these two males. The notable exception is during weeks 5-6 when the mother was enticed to play with the two males. On occasion she would play while carrying her infant, but she quite often specifically sought out the allomother who rarely played and was usually in another area from the players, and sat next to her, allowing her infant to crawl onto the allomother. Thus freed, the mother immediately proceeded

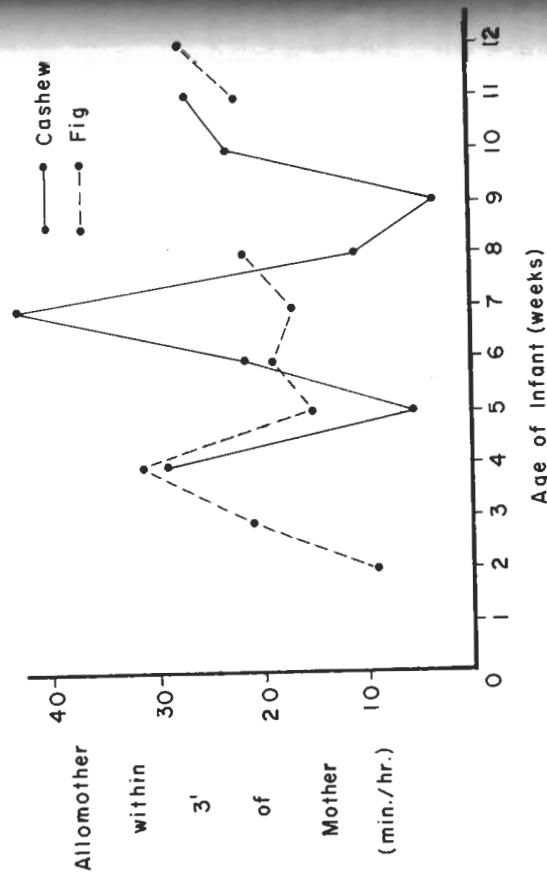


Figure 4. Number of 1-minute intervals per hour that the allomother spent within 3 feet of the mother as a function of the infant's age in weeks.

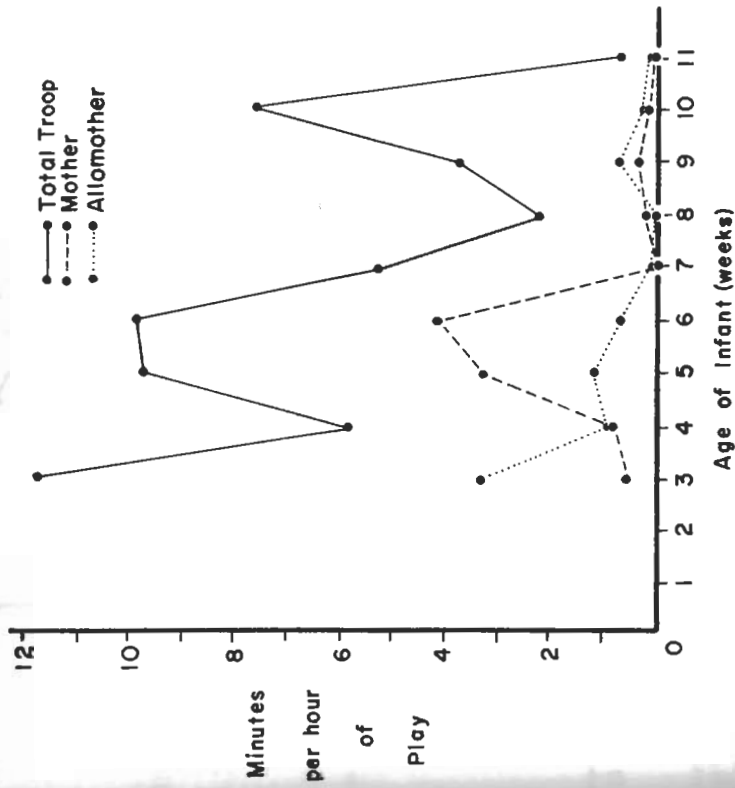


Figure 5. Minutes per hour during which members of the Cashew troop engaged in social play as a function of age of the infant in weeks.

to engage in very active, exuberant play with the young males. Her main play occurred prior to and during the main peak of transfers when she specifically used the allomother as a babysitter while she played.

Despite the occurrence of allomothering, the infants and their mothers showed typical primate contact profiles (Horwich 1974a). An infant spends its initial few weeks on its mother's ventrum, being active on its mother's more time on its mother's ventrum at 8-9 weeks, after which it begins exploring the environment on its own. Figures 6-9 show this relationship. Figure 6 exhibits the total time the infant spent on its mother in any position. There is a gradual decline until 9 weeks, after which a large dropoff occurs. This is complementary to Figure 7 which shows that after week 9 both infants spent almost one-third of their time alone, exploring branches while their mothers rest or forage nearby. Figure 8 shows that the position on the mother's ventrum is initially the exclusive position and after the early weeks it decreases. However, during weeks 8-9 both infants show a

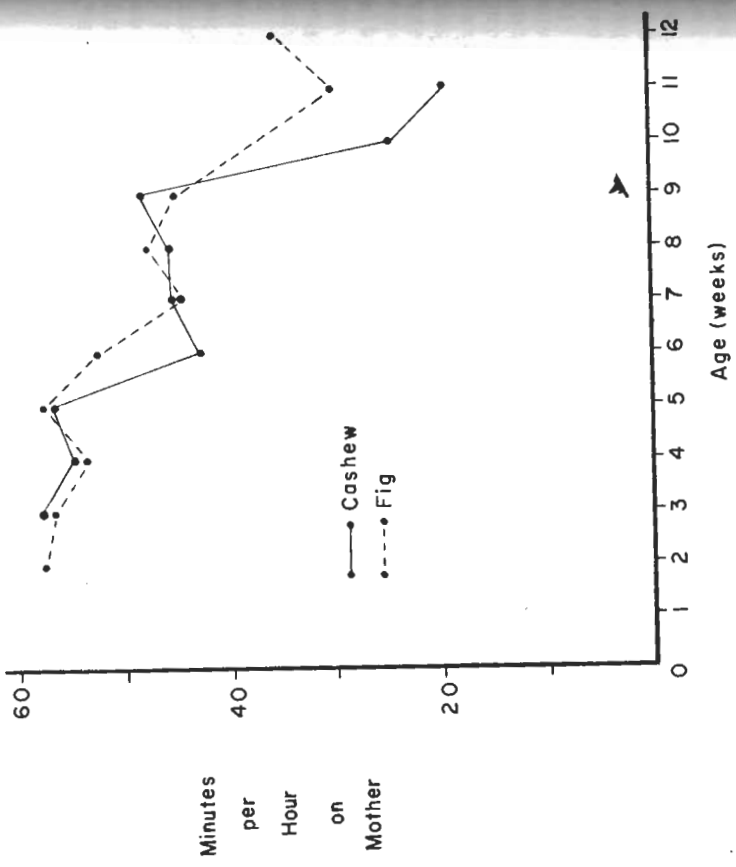


Figure 6. Time (minutes per hour) spent by two female infant howlers on their mother as a function of their age in weeks.

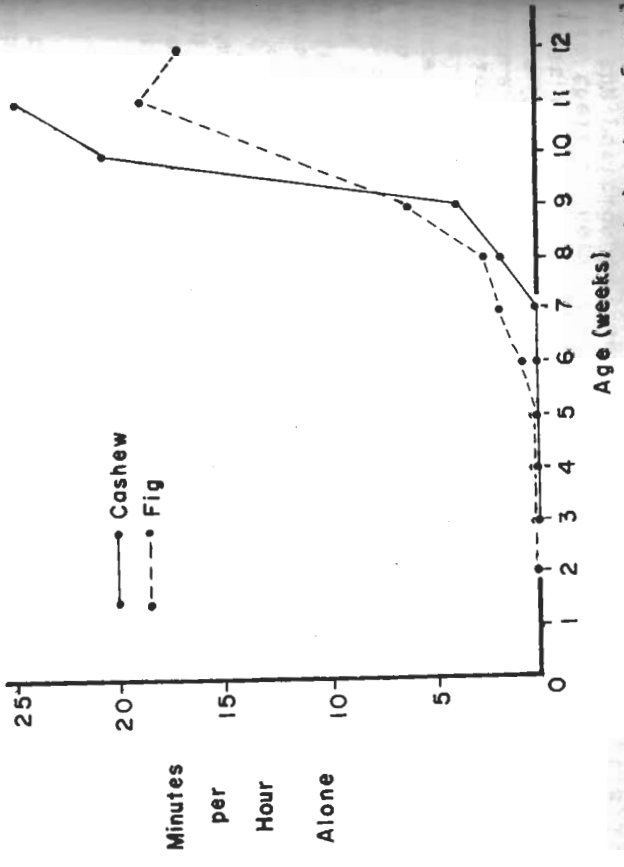


Figure 7. Time (minutes per hour) spent by two female infant howlers out of contact with other troop members as a function of their age in weeks.

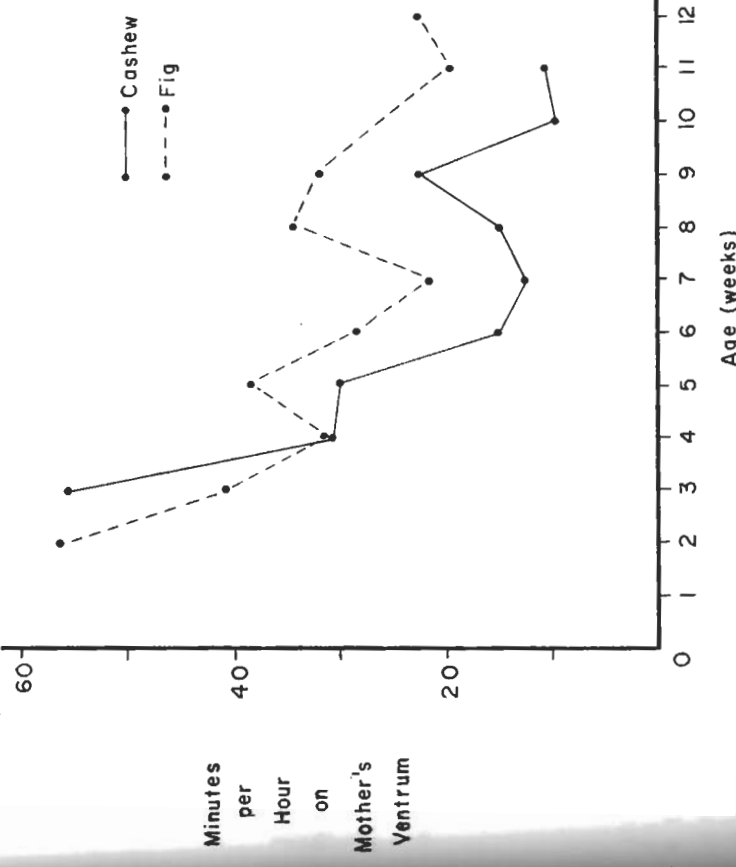


Figure 8. Time (minutes per hour) spent by two female infant howlers on their mothers' ventrum as a function of their age in weeks.

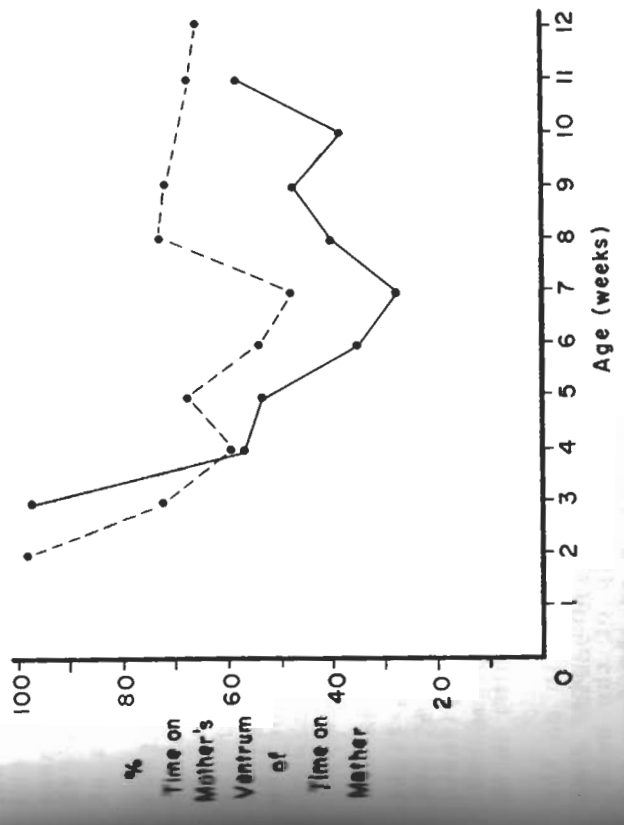


Figure 9. Percent of time spent on the mothers' ventrum of total time on the mother by two female infant howlers as a function of their age in weeks.

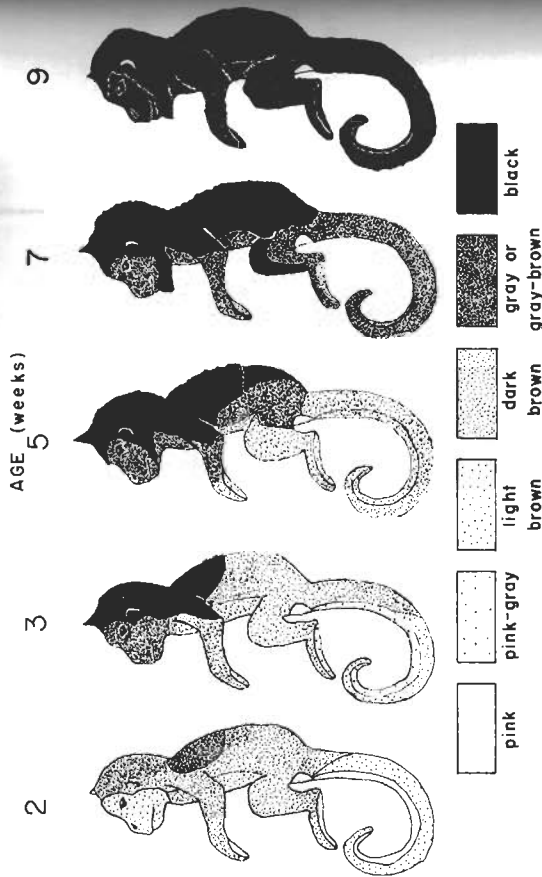


Figure 10. A composite of pelage changes in infant howlers showing physical appearance at 2, 3, 5, 7, and 9 weeks of age.

reversal and spend more time in the ventrum position. A dip in the numbers of transfers and time on the allomother also occurs during these weeks (Figures 1 and 2). Figure 9 further supports this, showing that the percent of time spent on the mother's ventrum increases after 7 weeks of age. This oscillation of infantile regressive contact has been noted in many species of primates and other mammals (Horwich, 1974a).

The period of social interest in the infant parallels its physical changes. Figure 10 shows the pelage changes in the developing infant. By 5 weeks of age the infant begins major changes toward the juvenile-adult pelage, and by 7 weeks the change is mainly achieved except for slower fur growth on the ventrum, limbs, and tail which grow in by 9 weeks when the full juvenile-adult pelage is exhibited. Specific changes are enumerated below:

Week 2 - The infant is mostly dark brown with a light brown tail, face, and forearms due to the slight skin pigmentation under the hair. The hands, feet, genitals, and tail ventrum are pink and unpigmented. The beginning of the juvenile hair is coming in on the shoulders and back.

Week 3 - Juvenile short black hair is coming in on the back of the head, shoulders, back, and upper arms with a definite hair peak on the top of the head. Short gray black hair is coming in on the face and tail ventrum, and pigmentation is beginning on the palms, soles, and tail ventrum.

Week 5 - Black juvenile hair now extends along the shoulders, upper arms, and back, thickening, with a ridge extending onto the forehead and along the sides of the face. A longer peak occurs on the top of the head. The under tail is now pigmented gray with an orange tinge with short gray hair coming in. The palms and soles are more pigmented, but the hind legs and belly are not yet fully pigmented.

Week 7 - Black hair extends along the top ridge and into the beginnings of a beard and is noticeably longer on the whole ventral surface. The palms and soles are still pinkish gray. The face due to short gray hair still has a "bald" appearance.

Week 9 - The infant has almost the full juvenile pelage with all the skin, including palms and soles, fully pigmented. The hair is also longer though not as long as a juvenile's hair; the infant still displays a small head peak, and the longer head fur is demarked from the face fur.

DISCUSSION

Within the numerous primate species which have been studied, three ontogenetic profiles of early allomothering have emerged: (1) species which show initial neonatal peaks; (2) species with later peaks at about 8 weeks; and (3) species or instances within a species in which both peaks occurred.

Early infant transfer

This situation is typified by many colobine species. The infants are born with very clearly differentiated natal coats, quite different from the parental pelage. It is thought that the coat color plays some part in the infant transfer phenomenon or at least in advertising the neonate to troop members (Alley, 1980; Blaffer Hrdy, 1976). Clear examples of early transfer peaks were noted in *Colobus guereza* (Horwich and Manski, 1975), the common langur, *Presbytis entellus* (Dolhinow, 1982; McKenna, 1981; Scofield and DeBoid, 1980; Sugiyama, 1965), and in the Nilgiri langur, *Presbytis johnii* (Poirier, 1968). Figure 11 shows examples of field data adapted from Sugiyama (1965) and Poirier (1968) by Horwich and Manski (1975), indicating an early peaking of transfers at 2-3 weeks of age, with most transfers occurring during the first months.

Late infant transfer

Examples in cercopithecines in which a later peaking of allomothering occurs at about 8-10 weeks are represented by data on rhesus macaques (Rowell et al.,

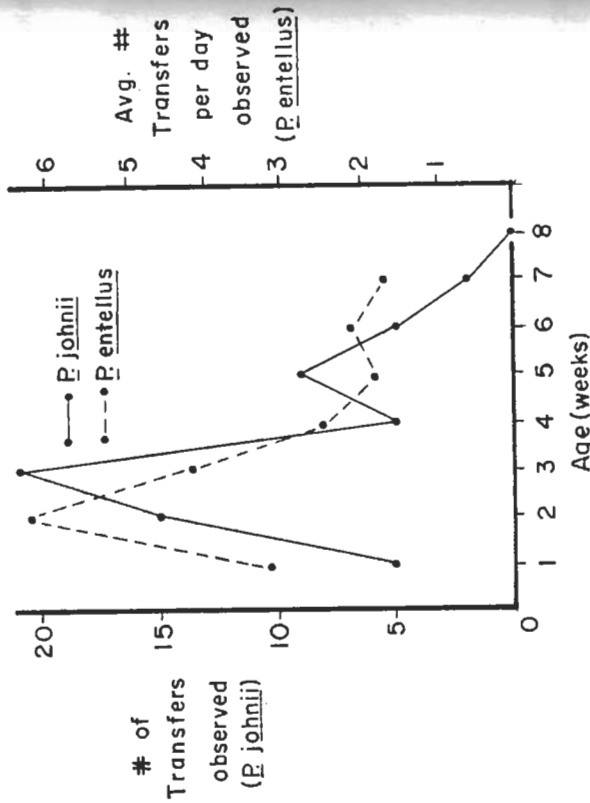


Figure 11. Frequency of transfers in two species of langurs in the field: frequency of transfers observed as a function of age in weeks in *presbytis johnii* (adapted from Poirier, 1968); average frequency of transfers per day per infant for six *Presbytis entellus* infants as a function of age in weeks (adapted from Sugiyama, 1965).

1964) and in the howlers of this study. Figure 12 shows rhesus cuddling-carrying peaking at 8-10 weeks and additionally shows that rhesus mothers show a bimodal peaking of interest in the infants at the neonatal stage as well as at 8-10 weeks. However, due to the more protective nature of rhesus mothers, the transfers of cuddling does not peak until the second period. This early maternal possessiveness is a general characteristic of many cercopithecine mothers (McKenna, 1979b) but is absent in most colobines. Our howlers (Figures 1 and 4) and those of Clarke (1982) show similar profiles, perhaps due as much to the more passive transfers in howler allomothers. Male *A. palliata*, however, showed an earlier peak of transfers at 4-6 weeks (Clarke, 1982). In the second period of interest, infants generally are more available to the non-mothers at about 6-10 weeks when the infant begins to move out on its own, yet is still not very competent in its movements. The howler passive transfers at this time occur when the infant crawls onto other troop members. At this time as well, infants in many species show a real social interest in other troop members and display tonguing behaviors which are precursory to and similar to adult lipsmacking or tonguing behaviors (Horwich and Wurman, 1978; Horwich 1983b). A captive *Alouatta caraya* infant showed a male

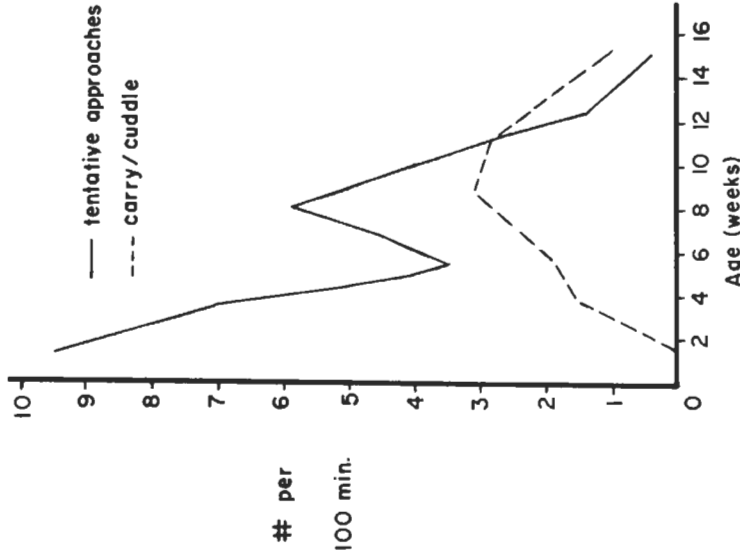


Figure 12. Frequency of records of tentative approaches and carry/cuddles per 100 minutes observation directed by "aunts" toward five normal young rhesus as a function of age in weeks (adapted from Rowell et al., 1964).

transfer profile similar to that of *A. pigra* in this study (Figures 3 and 14). Closer observation allowed by the zoo situation at Lincoln Park Zoo in Chicago showed an increase of a tonguing behavior in the infant at this time also (Figure 14). This behavior seemed to be the precursor of a social tonguing behavior used by howlers during courtship (Horwich, 1983b). *Colobus guereza* infants at about this same time develop the clucking lipsmacks used in later social interactions. This early sociality and precocial activity in the infants, with a decreased maternal protectiveness at this later period, allows for other troop members, including males and younger juveniles, to handle the infants.

Bimodality in infant transfers

Bimodality in the two main examples suggest that the second peak is linked with specific infant and troop situations, as noted in patas monkeys (Chism, 1978;

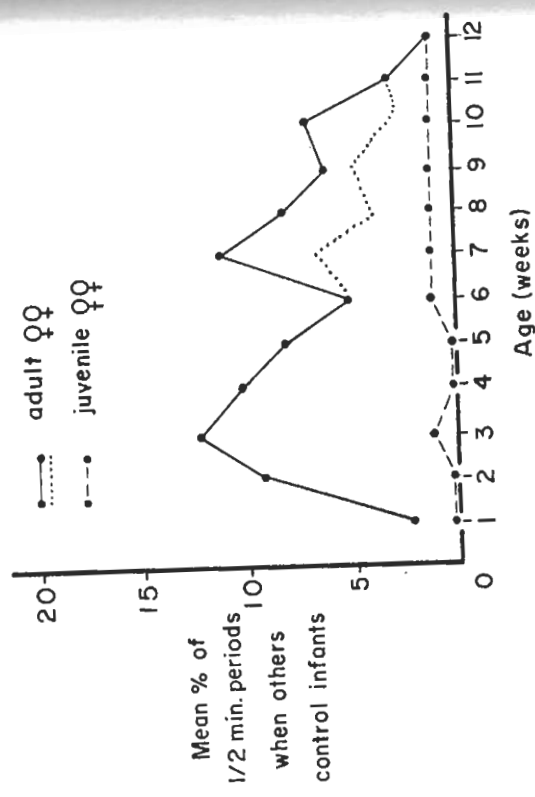


Figure 13. Mean percent of 1/2-minute periods in which infants were controlled by other group members as a function of infant age in weeks (adapted from Chism, 1978). The dotted line omits data from one infant which was inept at escaping allomothers (Chism, personal communication).

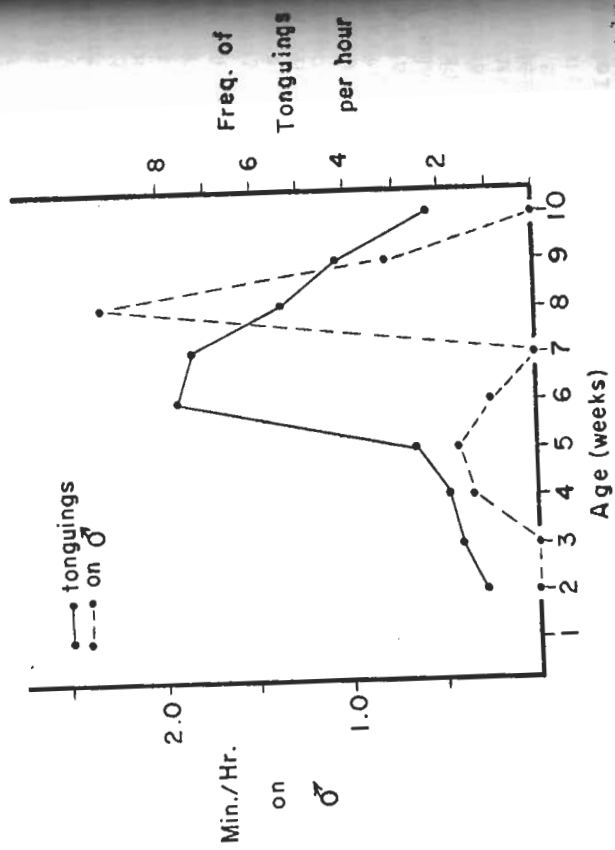


Figure 14. Time (minutes per hour) spent by a captive female infant *Alouatta caraya* on its father, and the frequency of tonguing per hour as a function of its age in weeks.

personal communication; Figure 13) and in *Colobus guereza* (Figure 15). Patas are the only cercopithecines that we have found to display the early allomothering peak of transfers. Chism (1978; Figure 13) observed a bimodal peaking. However, the second peak was mainly due to an infant (of a low-ranked mother) who was inept at escaping the allomothers (Chism, personal communication). The dotted line in Figure 13 shows the adult female data without one infant. The graph shows a gradual decline similar to most colobine transfer profiles. In her study, Chiam (1978); personal communication) noted intense interest by the juvenile females in the young infants. Due to the adults' monopolizing access to the infants, the juveniles had little opportunity to take them. However, Figure 13 (Chism, 1978) does show a low level but consistent carrying of the infants by the juvenile females after the infant is 5 weeks of age.

Colobus guereza and *Colobus polykomos* (Horwich and Wurman, 1978; Horwich and Manski, 1975) have both shown a

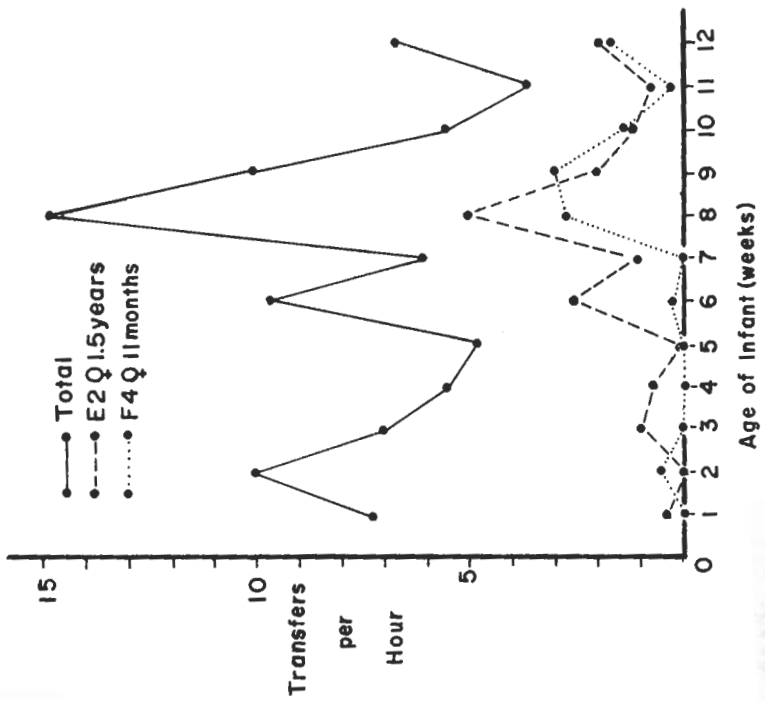


Figure 15. Frequency of infant transfers per hour for all *Colobus guereza* troop members and two juvenile females as a function of the infant's age in weeks (adapted from data from Horwich and Wurman, 1978).

second peak of interest in the infant. Rearranged data on *C. guereza* (Horwich and Wurman, 1978) show that this is specifically due to immature females who had never any experience in holding infants, and who were both very low ranking, yet who were able to handle the infant frequently at this time (Figure 15). Additional field data on *C. guereza* (Oates, 1977) shows evidence of probable bimodality as well (Figure 16). Additionally, *C. guereza* as in *A. pigra* the adult males' interest peaks at this age period and an equivalent period of interest occurs in *Presbytis obscurus*, which seems to have a slower developmental rate (Horwich, 1974b). A bimodality in infant transfers was also noted in *polykomos* in which one other adult female was present (Horwich and Manski, 1975).

Finally, evidence in *C. guereza* suggests that allomaternal learning may occur at an early age well before sexual maturity. The development of allomothering in one very aggressive young female indicates that she had limited access to an infant when she was 13 months of age with a peak in her carrying infants within her troop when she was 2.5 years old, thus indicating perhaps that accomplished mothering already exists by 2-2.5 years during the juvenile period (Figure 17). This is supported in the common langur which may begin carrying infants as early as 3 months of age and attain sufficient skill

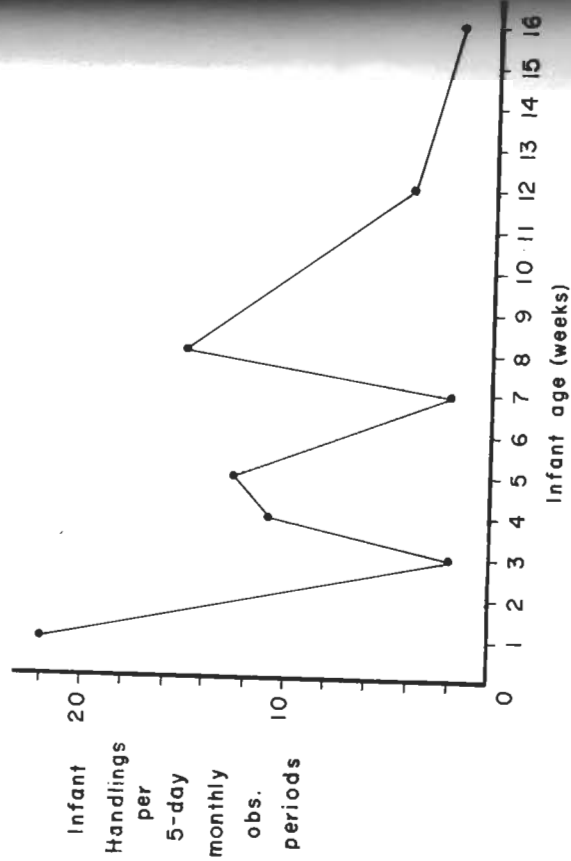


Figure 16. Number of infant handlings per 5-day monthly observation periods in wild *Colobus guereza* troops as a function of age in weeks (adapted from Oates, 1977).

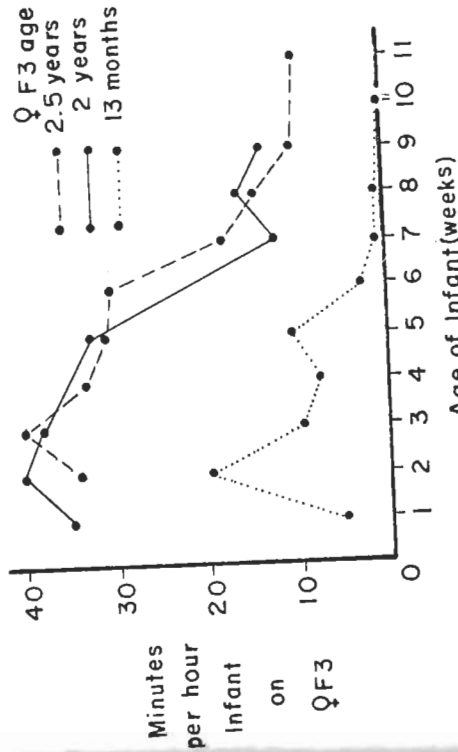


Figure 17. Minutes per hour that a female *Colobus guereza* carried troop infants when she was 13 months, 2 years, and 2-1/2 years old as a function of the infant's age in weeks (compiled and adapted from data of Horwich and Manski, 1975; Horwich and Wurman, 1978).

in providing comfort to their charges by 7-8 months (Scollay and DeBold, 1980). Scollay and DeBold (1980) noted that juvenile females allomothered most, but yearling females were the most skillful allomothers. However, Blaiffer Hrdy (1978) noted that most transfers were by nulliparae over 15 months, while those under 15 months were less competent caretakers and less successful in attaining and keeping infants. Scollay and DeBold (1980) maintain that the correlation between maternal experience and allomothering was negative, despite that their data show skillful learning taking place between 3 months and the yearling stage. Older females may then choose to disregard their earlier training and show less care to the infants. In howlers Clarke (1982) found some indication of juvenile females learning to interact with infants in an adult manner at 15-18 months of age, although it had no effect on the survival of their first infant.

Thus, what seems to be one possibility for the safeguard of the neonate's wellbeing is that during the early transfer peak, adults or experienced juveniles and sub-adults are more likely to hold the infant during the first few weeks. Later, during the second attractive period, inexperienced animals or those who have not had much contact with the infant, including males, may have a turn at interacting with the infant when it is less vulnerable, before and during its reattachment period with its mother.

Infant transfer and regressive periods

The second peak of infant transfer occurs prior to and at the same time as the regressive peaks in which the infant is reestablishing contact with its mother, spending more time on her breast and ventrum (Horwich, 1974a). The coincidence of these two peaks occurs in *C. polykomos* (Horwich and Manski, 1975), *C. guereza* (Horwich and Manski, 1975; Horwich and Wurman, 1978), and *A. pigra* (present study). Similarly, in *P. obscurus*, male interest and carriage occurred during the regressive period which was later in this species (Horwich, 1974b). This coincidence of these two phenomena, increased time on the mother and increased infant transfers, indicates another possible function. As in other functions of babysitting, attentions by other troop members may reduce stress on the mother and infant during this time of conflict, thus easing the infant into its next progressive growth phase. It is interesting to note that of the above species discussed where allomothering occurred, the infant's regressive period was less intense whereas for the infant *P. obscurus* where no allomother was present, regression was very intense, with mother-infant contact levels reaching as high as neonatal levels.

In howlers also the peak in transfers seems to occur coincident to a slight increase in mother-infant contact and the infant's spending time on its mother's ventrum (Figures 6 and 8). This is supported by a similar profile of mother-infant contact and non-mother infant transfers in *A. palliata* (Clarke, 1982). Although inconclusive, she mentions that high interactions with non-mothers at an early age may reduce weaning stress. Her data on female infant-maternal contact shows the clearest case of developmental regressive periods in a field situation. The data show a slight increase of mother-infant contact at 11-13 weeks and very clear increases at about 6 months and a year of age.

A second relationship of transfer and regressive periods may be related to regressive periods in young allomothers. Data in colobus suggests that learning to handle infants occurs at an early age. It may be that later regressive periods in juveniles or sub-adults may coincide with an infant birth. In such a case, the need for contact by the young female may be eased by her allomaternal role to the infant. The mixed role of infant and allomother may have similar underlying functions and obvious in the male *A. caraya*. Although only the two early periods of alloparental care were discussed, other later, periods may occur as well, which may accentuate other adaptive functions. Our study suggests that the adaptive significance of alloparental care is very complex with specific functions being accentuated at specific periods, thus expanding many of the earlier explanations of the behavior pattern.

TABLE 1. Ages at which certain functions of allomothering may be most adaptive

Age During Life Cycle	1	2-3 months	4-6 months	0.5-1 year	1 year	1-3 years	3-4 years	Adult
Extra protection	X							
Adoption (physical)	X							
Increase independence		X						
Socialization		X	X					
Adoption (psychological)		X	X	X				
Maternal learning				X				
Babysitting for feeding, Troop cohesion						X		X

Conclusions

1. Howlers, as well as cercopithecine and colobin mothers show bimodal peak interest in young infants at about 2-3 weeks and again at 6-10 weeks.
2. Colobines show peak transfers primarily on neonates while howlers and some cercopithecines transfer more during the second period at 6-10 weeks.
3. There are some species of Old World monkeys which show bimodal peaking as a species characteristic at specific times related to the current social structure.
4. Learning to mother seems to occur earlier than is usually thought. Therefore, when studying infant transfers, juvenile females as a class should be broken into smaller age classes for consideration.
5. There is a tendency for experienced females (adults and juveniles) to carry infants during the first period and inexperienced females and males to carry and show interest in the older infant during the second period.
6. Infant transfer during the later period coincides with the regressive or maternal reattachment period and may function in babysitting to reduce maternal and infant stress at this time.

ACKNOWLEDGMENTS

We wish to thank Vallen Pope, Fallett Young, Mr. Baptiste, and other residents of Bermuda Landing for their help, information, and use of their lands for this study. Special thanks go to Drs. Janice Chism and Phyllis Dolhinow for comments on the manuscript. I am also indebted to Richard Foster for directing me to the study site.

REFERENCES

- Alley, T. R.: Infantile colouration as an elicitor of caretaking behaviour in Old World primates. *Primates* 21:416-429. (1980).
- Blaffer Hrdy, S.: Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In Rosenblatt, Hinde, Beer and Shaw (Eds.), *Advances in the Study of Behavior*, Vol. 2. Academic Press, New York, pp. 101-158. (1976).
- Blaffer Hrdy, S.: Allomaternal care and abuse of infants among hanuman langurs. In Chivers and Herbert. Recent advances in *Primateology*, Vol. 1. Academic Press, New York, pp. 169-172. (1978).
- Bolin, I.: Male parental behavior in black howler monkeys (*Alouatta palliata pigra*) in Belize and Guatemala. *Primates* 22:349-360. (1981).
- Carpenter, C. R.: A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psych. Monog.* 10:1-168. (1934).
- Chism, J.: Relationships between patas infants and group members other than the mother. In Chivers and Herbert. *Recent Advances in Primatology*, Vol. 1, pp. 173-176. Academic Press, New York. (1978).
- Clarke, M. R.: Socialization, infant mortality, and infant non-mother interactions in howling monkeys (*Alouatta palliata*) in Costa Rica; PhD thesis, University of California-Davis. (1982).
- Clarke, M. R., and Glander, K. E.: Adoption of infant howling monkeys (*Alouatta palliata*). *Amer. J. Primatol.* 1:469-472. (1981).
- Dolhinow, P.: An experimental study of mother loss in the Indian langur monkey (*Presbytis entellus*). *Folia Primatol.* 33:77-128. (1980).
- Dolhinow, P.: Primate strategies of early attachment to caregivers: A case study. *Int. J. Primatol.* 3:277. (1982).
- Glander, K. E.: Habitat and resource utilization: An ecological view of social organization in mantled howling monkeys; PhD thesis, University of Chicago. (1975).
- Horwich, R. H.: Regressive periods in primate behavioral development, with reference to other mammals. *Primates* 15:141-149. (1974a).
- Horwich, R. H.: Development of behaviors in a male spectaclled langur (*Presbytis obscurus*). *Primates* 15:151-178. (1974b).
- Horwich, R. H.: Species status of the black howler monkey (*Alouatta pigra*) of Belize. *Primates* 24:288-289. (1983a).
- Horwich, R. H.: Breeding behaviors in the black howler monkey (*Alouatta pigra*) of Belize. *Primates* 24:222-230. (1983b).
- Horwich, R. H., and Manski, D.: Maternal care and infant transfer in two species of Colobus monkeys. *Primates* 16:49-73. (1975).
- Horwich, R. H., and Wurman, C.: Socio-maternal behaviors in response to an infant birth in *Colobus guereza*. *Primates* 19:693-713. (1978).
- Horwich, R. H., and Gebhard, K.: Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. *Primates* 24:290-296. (1983).
- Lancaster, J. B.: Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys. *Folia Primatol.* 15:161-183. (1971).
- Mack, D.: Growth and development of infant red howling monkeys (*Alouatta seniculus*) in a free ranging population; in Eisenberg. *Vertebrate Ecology in the Northern Neotropics*, pp. 127-136. Smithsonian Institution Press, Washington. (1979).
- McKenna, J. J.: Aspects of infant socialization, attachment, and maternal caregiving patterns among

- primates: A cross-disciplinary review. *Yrbk. Phys. Anthropol.* 27: 250-286. (1979a).
- McKenna, J. J.: The evolution of allomothering behavior among colobine monkeys: function and opportunism in evolution. *Amer. Anthrop.* 81:818-840. (1979b).
- McKenna, J. J.: Primate infant caregiving behavior. In Gubernick and Klopfer. *Parental Care in Mammals*. pp. 389-416. Plenum Press, New York. (1981).
- Oates, J. F.: The social life of a black-and-white colobus monkey Colobus guereza. *Z. Tierpsychol.* 45:1-60. (1977).
- Poirier, F.: The Nilgiri langur (Presbytis johnii) mother-infant dyad. *Primates* 9:45-68. (1968).
- Quiatt, D.: Aunts and mothers: adaptive implications of allomaternal behavior of nonhuman primates. *Amer. Anthropol.* 81:310-319. (1979).
- Rowell, T. E., Hinde, R. A., and Spencer-Booth, Y.: "Aunt"-infant interaction in captive rhesus monkeys. *Anim. Behav.* 12:219-226. (1964).
- Scollay, P. A., and DeBold, P.: Allomothering in a captive colony of hanuman langurs (Presbytis entellus). *Ethol. Sociobiol.* 1:291-299. (1980).
- Struhsaker, T. T.: The Red Colobus. University of Chicago Press, Chicago. (1975).
- Sugiyama, Y.: Behavioral development and social structure in two troops of hanuman langurs (Presbytis entellus). *Primates* 6:213-247. (1965).