

## Socio-maternal Behaviors in Response to an Infant Birth in *Colobus guereza*

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**ABSTRACT.** A number of social behaviors were observed in a captive troop of *Colobus guereza* on a regular basis for eight months. These included clasping and related behaviors, forward mounts, rear mounts, presents, troop positions during rest periods, infant transfers and attempted transfers, play, and grooming. During the observation period two significant events occurred: a re-introduction of a mother and her juvenile female, and the birth of an infant to a resident female. These events caused an increase in certain adult behaviors indicating a relationship of them with similar behaviors done between mothers and infants. This similarity seemed to indicate the co-evolution of "maternal" behaviors for use in adult social interactions and the phenomenon of infant transfer or sharing. The maternal and socio-maternal behaviors and their infantile precursors are then discussed in relation to the ontogeny of behavioral forms, the ontogeny of motivation in such behaviors, and the idea of infantile regression during development and in adult life.

### INTRODUCTION

During the rise of interest in primates, baboons because of their visibility and availability, became the first well studied primate group (ZUCKERMAN, 1932; DEVORE, 1965). Because baboon society is male dominated with socio-sexual behaviors (HANBY & BROWN, 1974; ROWELL, 1967, 1972; WICKLER, 1967), sexuality took on extended importance in discussion of primate sociality. Despite contrary evidence (LANCASTER & LEE, 1965) some writers have continued to state that sexuality forms the basis for primate social life.

In some leaf eating monkeys (Colobinae) socio-sexual behaviors play a minor role. *Colobus* society instead is oriented around infant sharing and modified "maternal" or socio-maternal behaviors. Graded variations of these behaviors as well as the motivations underlying them are reminiscent of the mother-infant relationship. This relationship is the basis for many adult social behaviors including sexual ones, and it is important for maintaining female group cohesion.

Although many primate females show interest in infants, it is only in certain Colobinae species including *Colobus guereza*, that infant transfer between troop members at birth is a normal part of the troop social activity (HORWICH & MANSKI, 1975). *The importance of the infant to all troop females with the consequent infant sharing, and the emphasis on socio-maternal behaviors have evolved together to form the basis for an alternate type of primate society.*

In *Colobus guereza* the male's accepted dominance over females is rarely reinforced with obvious aggressive behaviors, although his loud "territorial" calling probably functions to dominate. His efforts instead go into intertroop territorial displays, infant rescue, breaking up troop fights, and copulation. Females, in contrast, form

close relationships which they reinforce with subtle behaviors. Contrary to statements by JAY (1965) and ULLRICH (1961) on the lack of hierarchies, these behaviors are used in dominance interactions for maintaining a hierarchy. They increase in frequency and intensity following the infant birth and show ontogenetic similarities to mother-infant behaviors.

Although socio-maternal behaviors are of prime interest to colobus females, they also show socio-sexual behaviors. Cercopithecines also show many infantile and socio-maternal behaviors as adults (ANTHONEY, 1968; BOESE, 1973; KUMMER, 1967, 1968, 1970). There seems to be a motivational similarity between socio-maternal and socio-sexual behaviors. Spectacled langur males even use both forward mounts and sexual-like rear mounts to dominate females. Thus many adult social patterns (forward mounts, clasps, and sexual mounts) may all stem from the infant's clasp of its mother. Synchronized hand and foot grasping and lipsmacking behavior which occur commonly with these adult contact behaviors support this idea.

## MATERIALS AND METHODS

A troop of eight *Colobus guereza* monkeys was observed for two hour periods between 8 and 10 A.M. CST at Brookfield Zoo from November 10, 1972 until July 8, 1973 for 215 hours. Eighteen behaviors were observed and recorded. The initial troop was six colobus: an adult male (*M1*), two adult females (*F1*, *F2*), a sub-adult female (*F3*), a 2.5-year old male (*M2*), and a 1-year old juvenile female (*F4*) (see HORWICH & MANSKI, 1975). They were maintained in a public display cage 3.7 m × 1.8 m × 2.4 m. A shelf extended from the rear wall to the front bars 1.1 m from either side wall. The cage also contained two tree limbs and a nylon chain hammock. On February 14, 1973 the group was moved to two connected cages with molded gunite walls and shelves. These cages measured 3 m × 2.3 m × 2.4 m and 3.7 m × 1.8 m × 2.4 m and contained suspended tree branches.

On February 15, 1973, a female (*E1*) and her 1.5-year old juvenile female (*E2*) were re-introduced. Following the birth of *E2*, they had been moved to an adjacent cage separated by bars. They were introduced and re-separated once when *E2* was six months old. *E1* died of infected injuries received in fights during the second introduction. A second change occurred when *F5* was born to *F2* on April 11, 1973.

## RESULTS

### INTRODUCTION OF *E1* AND *E2*

*E1* and *E2* were successfully introduced to the adult male. Two days later when the troop was reunited, the females fought with *E1* and *M1* then chased *E2*. The females carried *E2* and *E1* held a three-month-infant of *F1*. *E1* and *E2* were again separated from the others.

During the second introduction there was a high level of aggression involving *E1* and *E2*. Most of the acts were directed by the adult and subadult females toward *E1*. *M1*'s aggressive chases of *E2* which occurred are reminiscent of infant killing in male langurs (MOHNOT, 1971; SUGIYAMA, 1967). The female aggression began with many present-like postures (see clasps below) by dominant females. *E1* responded by

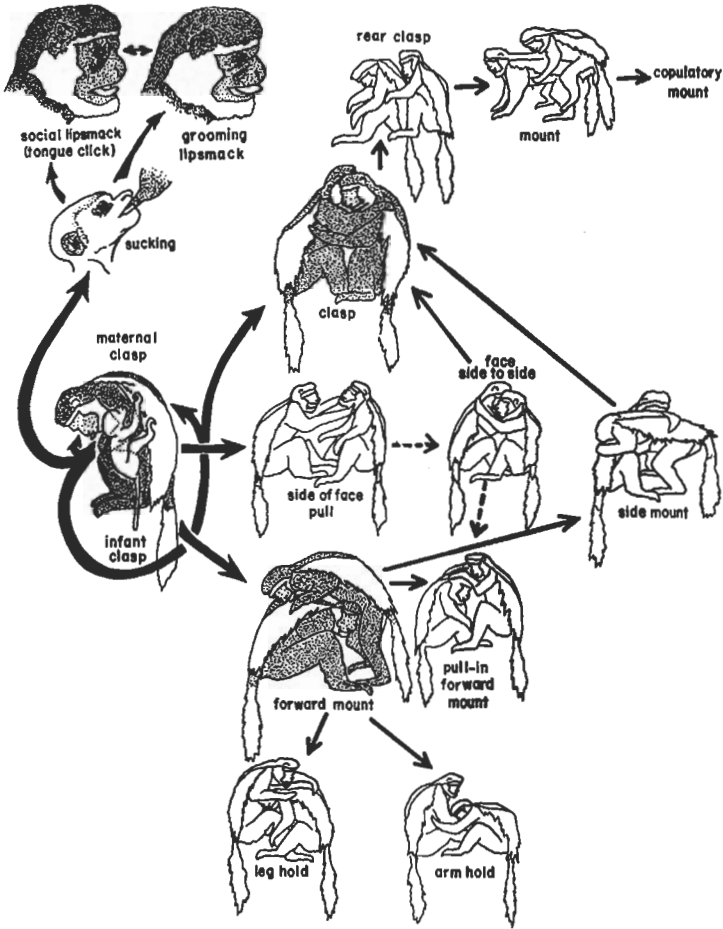


Fig. 1. A composite drawing showing the relationships of social behaviors in *Colobus guereza*. The thick solid arrows represent ontogenetic relationships. The thin solid arrows represent relationships in form and the broken arrows show temporal sequences that often occur. The four main derivations from infant clasping—sucking behavior are: (1) maternal clasp, (2) adult clasp, (3) forward mount, and (4) lipsmacks.

clasping their backs (Fig. 1) and was often pulled around the cage, which seemed to reduce overt aggression. As *E1* rebuffed females' approaches they responded with aggressive cuffs, pulls, and bites. The cuffs were a quick extension of the hand, hooking the other animal with the fingers. Pulls extended the cuff, as the aggressor held onto the recipient, sometimes directing a bite to the shoulder and neck areas. An aggressive jump display similar to that done by males jumping on all four limbs in the same spot was noted (HORWICH & LA FRANCE, 1972). The females instead, did a jump display on *E1*, sometimes ending by pulling *E1* with their hands.

SOCIO-MATERNAL FORMS OF BEHAVIOR

Clasps

The usual clasp involves two animals embracing ventro-ventrally with arms en-

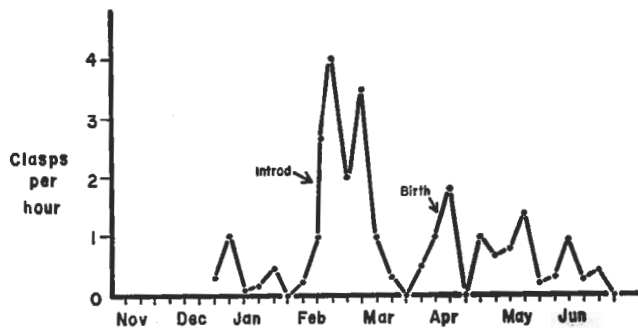


Fig. 2. The frequency of clasps per hour performed by all troop members as a function of time in weeks.

circling each other and hands grasping the side or back fur, or the neck. Their heads, adjacent and parallel, face in opposite directions, often with the chin hooked on the other's shoulder. One animal may clasp another without a response.

One variation is a rear clasp (Fig. 1) done dorso-ventrally, with the clasper's arms embracing the other's sides and her head resting on the recipient's back. This position often results from the recipient turning away prior to the clasp in a present-like posture. If the receiver is lying, she is clasped horizontally, from the front or rear.

During a clasp, two types of fur ruffling of the side or back may occur which may vary with the intensity of the motivation: (1) a modified back scratch done with one hand, similar to that seen in a spectacled langur mother to its infant (HORWICH, 1974b); (2) alternate combing with both hands, often using the mouth (intense modification of grooming).

Troop clasping (Fig. 2) increased following the introduction. During the first week most were due to *E1* with *E2*. Following this most were done by juveniles *E2* and *F4* indicating *E2*'s first group relationship. Smaller peaks occurred immediately after the birth and three to six weeks later, attributable to adult females. Most were between *F1* and *F3*, the adult non-mothers who sought possession of the infant.

#### *Forward Mounts*

In a typical intensity forward mount, a standing individual forces the other's head down with its hands, then extends its face and chest over the other's back with its pelvic area over the recipient's head (Fig. 1). The mounter's hands then grasp the side or back fur of the receiver. Fur ruffling may also be performed. Lipsmacking (tongue clicking) occurs while the mounter positions herself and also by both animals occasionally during the mount.

In one extreme variation, the mounter seems to try so hard that it removes one or both legs from the ground, draping itself over the recipient's shoulders, thus projecting its head and body way over the receiver's back with her crotch over the receiver's neck. In this less ritualized, more intense mount, loud lipsmacks (with the mouth opening wide) along with intense and exaggerated grooming and fur mouthing occur. The receiver usually sits quietly receiving the mount, but sometimes clasps the mounter's leg to its ventrum. Less frequently, the mount proceeds with both the mounter's legs

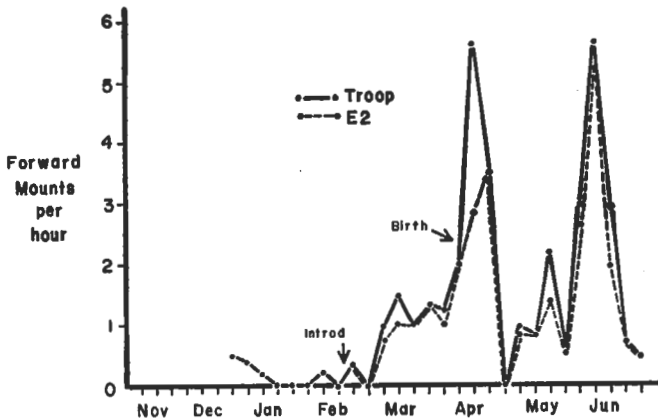


Fig. 3. The frequency of forward mounts per hour performed by all troop members and E2, the introduced member, alone, as a function of time in weeks.

on one side of the recipient's head. The receiver may then grasp the mounter's back, indicating the affinity of a forward mount to a clasp. A final variation becomes a side mount (Fig. 1) in which the mounter drapes her ventrum over the back of the recipient from the side so that their bodies are perpendicular to each other. Fur ruffling and lipsmacking may occur during any of the variations.

Troop forward mounts increased markedly three weeks following the introduction and again following the birth (Fig. 3). Another increase eight to ten weeks after the birth was related to infant transfer attempts by the juveniles. Most forward mounts are given by E2 although F1 gives a considerable amount to F2 the first week following the birth. The main receivers are the three adult females to whom E2 is submissive, showing the clear submissive nature of the forward mount. E2 shows the greatest frequency toward F1 and F2 prior to and at the birth. In contrast, E2 forward mounts F3 prior to the birth and again nine weeks later when she is participating in infant transfers. E2 was first seen to forward mount at six months when she draped her small body over M1's head as he lay on the floor. The males never showed forward mounts. However, BECK (pers. comm.) noted a male in the Stone Memorial Zoo forward mounting a female.

#### Leg and Arm Holds

These behaviors are similar to the forward mount but the target areas are displaced (Fig. 1) in that the arm or leg of the recipient is grasped and pulled toward the ventrum. The behaviors are more often given by females to males and they mainly occurred following the cage change and the introduction.

#### Chin and Side of Face Pulling

In chin pulling, one animal cups its hand under the chin as if to pull the receiver's face to make eye contact (HORWICH & MANSKI, 1975). The other animal usually resists. Pulling the recipient by its white side-of-face patches (Fig. 1) seems to serve the same communicatory function. The intensity varies from momentary grasping the

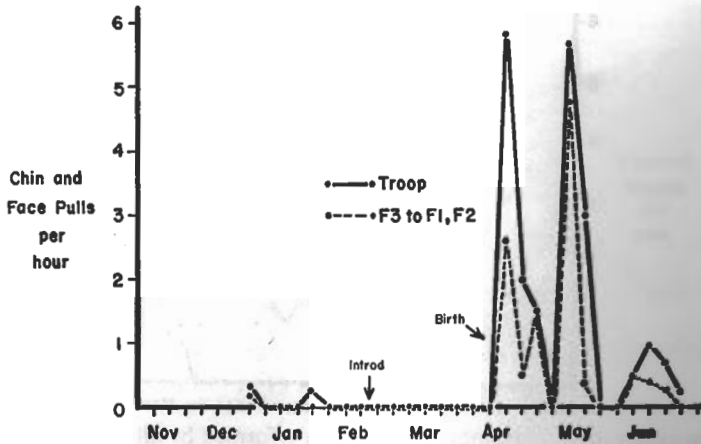


Fig. 4. The frequency of chin and face pulls per hour performed by all troop members and by *F3*, alone, toward other adult females, as a function of time in weeks.

face, to harshly pulling the receiver toward the grasper. This may lead to a face side to side behavior and clasp (Fig. 1).

These dominance behaviors were rare until the birth. A high level occurred one week and five to six weeks following the birth. Although the first peak was composed of both chin and side pulling, the second peak consisted essentially of only chin pulling (Fig. 4). Side pulling is more violent and less ritualized. The second peak occurs when transfer attempts are increasing. Most (69%) were done by *F3*, who had been gradually taking over the dominance role from her mother *F2* (Fig. 4). *F1* received most of the behaviors (68%) from *F2* and *F3*. Generally, these were dominance behaviors done between adult females. Ninety-two % were done by adult females and 81 % were done between adult females. Only 5% were done by *M2* who gave a few to *F2* two weeks after the birth.

#### Face Side to Side

In these behaviors the faces of both animals rest next to and parallel to each other, facing in opposite directions. Each had one arm along side of the other's face with the hand grasping the other's neck (Fig. 1). This posture was seen only two weeks after the birth (Fig. 5a). Most were given between *F2* and *F1* with a few by *F3* to *F2* and *F1*.

#### Pull-in Forward Mounts

These are the dominance counterpart to the submissive forward mount and incorporate aspects of the side of face pulling. The actor grasps the fur of the recipient by the back of the ears, upper sides of the face, or shoulders. While sitting she aggressively pulls the receiver, first by the white face hair and then by the shoulders or the arms so that the receiver's head is underneath her chest or stomach (Fig. 1).

All pull-in forward mounts were done by adult females to other females only in the first month following the birth. Most were done by *F2* to *F1* with a few by *F2* to *F4* (Fig. 5b). Although the final stereotyped form of forward mounts appeared similar, the pull-in forward mounts are clearly dominant and forward mounts submissive.

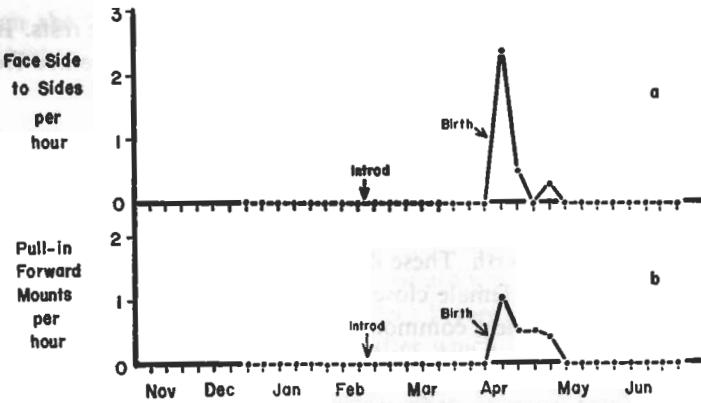


Fig. 5. The frequency of (a) face side to side behaviors and (b) pull-in forward mounts per hour as a function of time in weeks.

*Social Space during Rest Periods*

During each observation period, the troop rested once or twice. The position of each monkey was recorded on a cage map. Individuals within one foot of each other were considered part of a resting group even though a distance exceeding one foot existed between members on opposite peripheries of the group. Figure 6 exhibits the percentage that each member rested alone which is the mirror image of their sociality. Generally, adult females rested together more than the adult male rested with them.

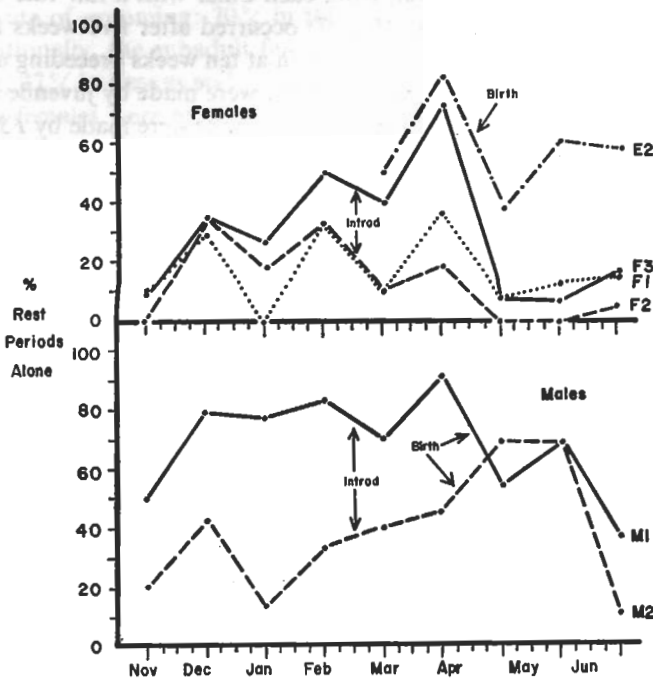


Fig. 6. The percentage of times that each troop member rested in an isolated position from other troop members as a function of time in weeks.

Following the birth, females and the males clustered more during rests. In contrast, the young male (*M2*) rested alone more at this time and was prevented from resting with the group by the adult females.

From dyadic statistics it was noted that *F1* and *F2* rested together all of the time during the first month after the birth. In contrast, *M2* did not rest with *F3* as much following the birth or the introduction. With the presence of *E1* and *E2*, *F1* and *F2* increased resting together. *F2* and *F3* decreased their mutual resting at that time, only to increase it following the birth. These data parallel field data on spacing measured by OATES (1974) who noted female closeness and the less clumped nature of males. Only the subadult male was less commonly close to others, in a peripheral role.

### Infant Transfers

Infant transfers show a peak at the second week due to adult females' interest (Fig. 7) in accordance with earlier data on this troop (HORWICH & MANSKI, 1975). A second peak at six to nine weeks, was due to immature females, *E2* and *F4*, who due to their sociality with *F3*, were able to obtain the infant at this time. This corresponds to a similar period of male interest in infants (HORWICH & MANSKI, 1975), but due to the competition from young females, the males never attempted to carry this infant.

*F2*, because she was the mother, as noted by HORWICH and MANSKI (1975) had the best success in retrieving her infant. Low ranking *F1* had less success in obtaining the infant from the more dominant *F2* and *F3*. In contrast, *F3* took the baby easily from *F2* and *F1*. Immatures, *E2* and *F4*, had good success when taking the infant from *F1* but poor success from the mother. They persisted and were able to obtain it from *F3*, reluctantly. They obtained the infant from each other with a fair rate of success.

Unsuccessful attempts at transfer (Fig. 7) occurred after five weeks following the initial peak of adult female transfers, and again at ten weeks preceding and following the two immature peaks. Most of these attempts were made by juvenile and subadult females. The main attempts during the first four weeks were made by *F3*, *F4*, and *F1*. After five weeks, *E2* made most of the attempts.

Most attempts were directed at *F3* during the first eight weeks and to *F2* from week six on when the infant had begun to establish its relationship with its mother (HORWICH & MANSKI, 1975). There was also a high rate of attempts toward *E2* at two

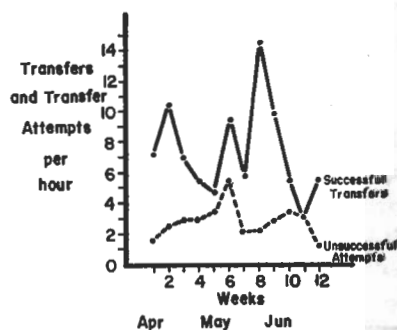


Fig. 7. The frequency of infant transfers and transfer attempts per hour for all troop members as a function of weeks following the birth of the infant.



weeks when she first got the baby. On obtaining the infant, she would run away grimacing and crying. Then as other females approached to take the infant, she would turn away. She was obviously submissive but would not relinquish the infant despite her fear.

### Social Grooming

Troop social grooming seems to follow a monthly cycle from November through February (Fig. 8), and may be related to sexual cycling (SIMONS, 1974). For six weeks following the introduction, a depressed level of grooming occurred. The frequency of social grooming increased and peaked one week before the birth. It maintained a high level for three weeks following the birth, after which it seemed to resume the four week cycle (Fig. 8).

Field data also indicate increased grooming prior to and during the birth season. OATES (1974) noted a high rate of grooming during the birth months of May and October but the data was actually taken before the births.

All troop members participated although *F3* and *F2* set the cycling. All females except the mother, showed high levels prior to and following the birth. The mother, *F2*, groomed a constant level but following the birth was lower than everyone else except *M1*. *F2* and *F3* were the main recipients of grooming following the birth. *M1* received less than usual at that time. The main increase after the birth was due to *F1* and *F3* grooming *F2*. *F3* to *F1*, *F2* to *F1*, and *E2* to *F3* and *F2* also contributed to the increase.

In the field, although the grooming rate was generally lower than our average rate, the general troop breakdown was similar. Adult and subadult females accounted for the highest rate of grooming: 70% in this study and 86% in LESKES and ACHESON (1974). Additionally, the subadult female accounted for a disproportionate amount of grooming: 37% in LESKES and ACHESON (1971) to 48% in this study. In both cases the subadult females were most frequently involved in infant transfers. LESKES and ACHESON (1971) noted a definite link between grooming and infant transfers. OATES (1974) noted, in agreement with us, that juveniles and infants were groomed at a

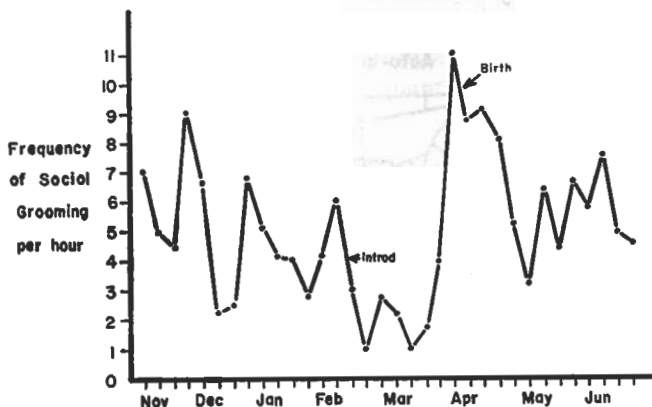


Fig. 8. The frequency of social grooming per hour for all troop members as a function of time in weeks.

higher than expected rate, the subadult male was groomed at a lower rate, and the adult male was groomed at a higher than expected rate.

In general, grooming is particularly done by females who groom not only themselves but also the dominant male and the young. Subadult females seem particularly interested in grooming. In contrast, subadult males are groomed less and have a peripheral role.

*Groom Bout Length*

Grooming bouts generally lasted under 1 minute but could last as long as 10 minutes (Fig. 9). In the field, 15-minute bouts were noted (LESKES & ACHESON, 1971). Most longer bouts were directed at lesser groomed areas, the limbs and belly. Fur mouthing during grooming was consistent despite bout length: .37 mouthings per

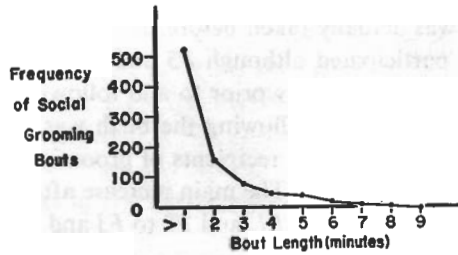


Fig. 9. The frequency of social grooming bouts as a function of bout length in minutes.

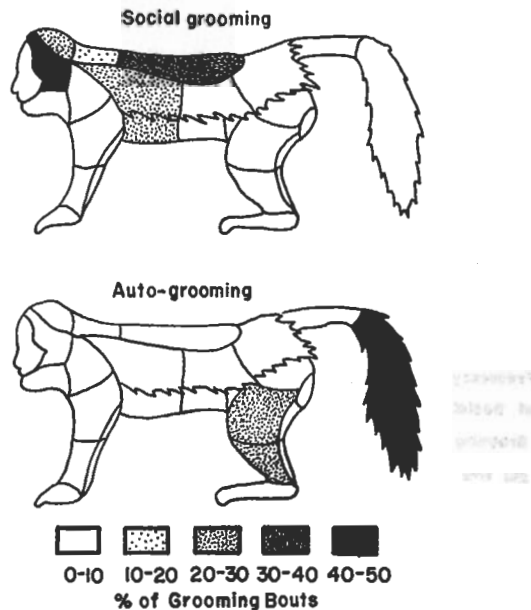


Fig. 10. Schematic drawing of a colobus body showing the percentage of social and auto-grooming bouts that each body area was groomed relative to the total number of bouts by all troop members.

grooming minute in long bouts and .32 in short bouts. Females of all ages gave more short bouts except when grooming the adult male, who received a preponderance of long bouts from all adult females. This male gave long and short bouts equally but showed longer bouts to *F1* and *F2*. *F4*, who was only beginning to groom, gave mostly short bouts.

### Areas Groomed

Most social grooming in colobus was directed to the ear and cheek, followed by the head, back, side, and chest (Fig. 10). This agrees with Japanese macaque studies (FURUYA, 1965) where most grooming was directed to the recipient's back; but the sides, rump, and neck were frequently groomed. One main difference is the high incidence of colobus grooming directed at the ear and nearby regions. In colobus infants, the pelage is white except for the ears, parts of the face, and the limbs which blacken early and in some species may be dark at birth (HORWICH & MANSKI, 1975). The infant's ear may act as a sign to direct grooming to that area. Although in adults, ears are no longer of contrasting color, frequent ear grooming is another case of parental behavior being carried into the adult interactions. Figure 10 additionally, indicates that pelage color does not seem relevant to the areas groomed.

## SOCIO-SEXUAL FORMS OF BEHAVIOR

### Presents

The presenter, faces away, turning her rump toward the receiver. The intensity of the present varies from a subtle presentation during a pause while passing the receiver, to stopping, presenting, and looking back. The tail is usually placed to the side but it may be bent upwards. The distance between animals varies but if close, the receiver may sniff the rump of the presenter.

Presenting increased three weeks after the introduction and reached a peak prior to the birth. It remained low until it increased slightly at six and nine weeks after the birth (Fig. 11). Most of these were directed at the dominant male and most were from *M2*, the juvenile male, and *E2*, the newly introduced juvenile female.

The submissive communication of this gesture is clear in that a new troop member did it to the adult male and to other individuals except the younger juvenile female. It is also clearly done by both sexes to the dominant male.

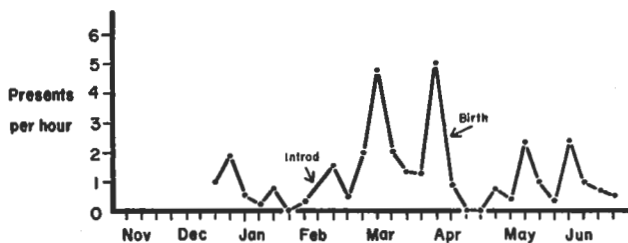


Fig. 11. The frequency of presents per hour for all troop members as a function of time in weeks.

### Mounts

The mounter places her hands on the receiver's back, and her ventrum on the receiver's back. The mounter's feet are on the ground or on the back of the receiver's lower leg. The receiver may stand or sit. Mounts were performed by subordinants more often. The general form and orientation suggest them as variations of the rear clasp. As in the rear clasp, the submissive female clasps the dominant one.

Mounting is greatest the week following the introduction (Fig. 12). A second peak occurred three weeks after the birth coincident with the peak in transfers. The most frequent mounters were *E2*, *F1*, and *F4*. Most mounting was done by *E2* to *F3*, *F4* to *E2*, and *F1* to *F2*. The second peak was due to *F1* mounting *F2*.

### INDEPENDENT BEHAVIOR PATTERNS

#### Auto-grooming

In contrast to social grooming, auto-grooming was directed mainly at the tail, outer leg, and thigh (Fig. 13). During the introduction and in other intense social interactions, displacement auto-grooming of the leg by subordinants was often seen.

Troop auto-grooming shows a possible monthly cycling similar to social grooming (Figs. 8 & 13). Only *F4* did no auto-grooming.

#### Play

Any of three behavior patterns were recorded as an instance of play: (1) chase—one animal runs from another often stopping to look behind at the chaser; (2) wrestle—(a) two animals grasp each other's neck or shoulders, directing gentle, mouthing bites at each other's back, hands, and feet. While the hands grasp the players close, the feet

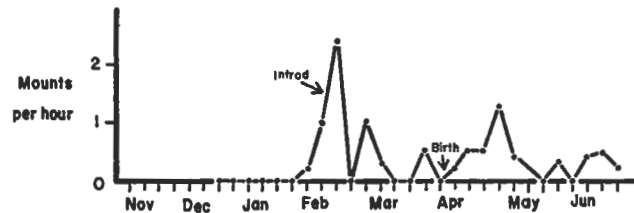


Fig. 12. The frequency of mounts per hour for all troop members as a function of time in weeks.

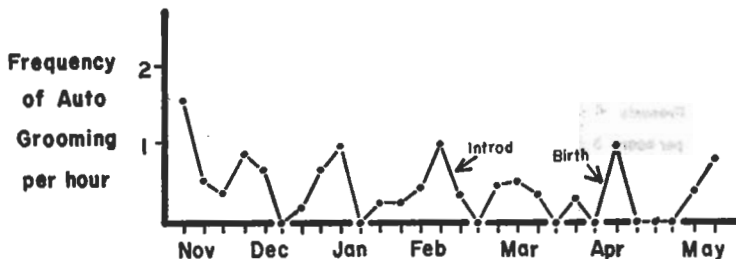


Fig. 13. The frequency of auto-grooming per hour for all troop members as a function of time in weeks.

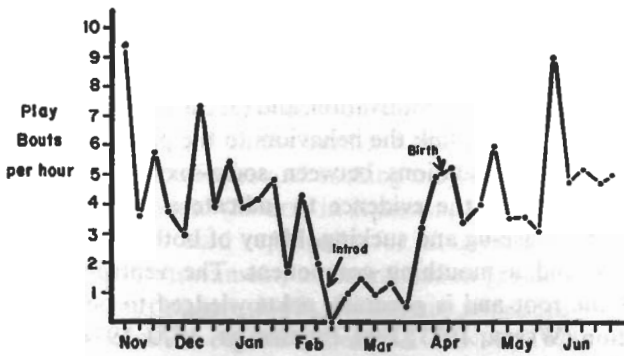


Fig. 14. The frequency of play bouts per hour for all troop members as a function of time in weeks.

push the other away. This mainly occurred between juveniles; (b) two animals, usually adults, sit with mouths wide open and teeth showing, synchronously swinging their forearms and hands at each other. In long bouts, both wrestlings were mixed with chases.

The frequency of play for the troop was profoundly affected by the introduction. A high level of four to five bouts per hour decreased for six weeks following the introduction (Fig. 14). The birth seemed to cause only a slight decrease in play (Fig. 14). *M2* and *F4* showed this clearly whereas the new juvenile, *E2*, began extensive play only after the birth. All adults indicated higher levels before the introduction. However, a decrease began before the introduction suggesting seasonality in play: a high period occurring in November, decreasing during the winter, only to increase again in spring. Since most play was elicited by *M2*, the trend could have been an ontogenetic fluctuation as noted in other species (HORWICH, 1972, 1974b). However, the main players, *M2* and *F4*, radically reduced play after the introduction. *F1* and *F4* also seemed to show a monthly cycle in play.

Although primarily a juvenile behavior, play was seen in all adults in this group but was not seen in adults in the field (OATES, 1974). In the zoo, the adult male seemed to establish dominance over the young male during play. The juvenile would initiate play by poking at the adult but would then grimace and cry during the bout. In baboons, one commonly sees play sequences where smaller juveniles grimace, cry, and return to their mothers when play gets too rough.

## DISCUSSION

### SOCIO-MATERNAL BEHAVIORS AND THEIR ONTOGENETIC PRECURSORS

Although earlier believed that sexuality was a central force in primate social life, it is no longer the dominant thought. Data have shown that in baboons, the existence of socio-sexual behaviors led to the erroneous conclusion, and sexuality as restricted to mating behavior, plays a reduced role in sociality. In colobus as well, almost no sexual behavior and rare socio-sexual behaviors were observed. In contrast to baboons, colobus accentuate socio-maternal behaviors between females instead. They

have been termed socio-maternal because of the following evidence of their evolutionary derivation from maternal behaviors: (1) the descriptive forms of the behaviors are similar to those done by a mother to her infant, (2) mother-infant behaviors and socio-maternal behaviors show similar motivation, and (3) the increase of the socio-maternal behaviors following the birth, link the behaviors to the presence of the new infant.

Since similarities and gradations between socio-sexual and socio-maternal behaviors occur, we consider the evidence to indicate a common evolutionary precursor from infantile clasping and sucking. Many of both types retain infantile hand and foot clasping and a mouthing component. The ventro-ventral embrace best exhibits its infantile root and is generally acknowledged to be a ritualized infantile "clinging" reaction (WEBER, 1973; EIBL-EIBESFELDT, 1970, 1971).

*Evidence for Similarity in Form of Socio-maternal Behaviors to Maternal and Infantile Behaviors*

Figure 1 visually demonstrates the wide variety of similar behavior patterns displayed by *Colobus guereza*. Gradations between the related behaviors were also occasionally seen. The thick arrows represent possible ontogenetic trends, the thinner solid arrows represent behaviors which show a relationship in form, and the dotted line arrows indicate a temporal sequential continuity.

Infant sucking and clasping is considered the ontogenetic root of four major behavior patterns (Fig. 1): **maternal clasp**, **adult clasp**, **forward mount**, and **lipsmacks**. The maternal patterns of infant transfer (see HORWICH & MANSKI, 1975) and clasps show similarity to the side of face pull which sequentially leads to the side of head clasp and the full body clasp. Adult clasps show a relationship to the rear clasp, mounts, and the copulatory position. The forward mount shows affinities to the maternal clasp, leg holds, arm holds, pull-in forward mounts, and the side mount. In turn, the side mount shows the gradation between forward mounts and clasps.

Finally, infant sucking shows ontogenetic roots for the development of maternal kissing (see HORWICH & MANSKI, 1975), and grooming and greeting lipsmacking (tongue clicking). Tonguing, anticipatory to nipple contact and seen in mildly anxious situations, is probably the intermediate step from which the ritualization of the other two behaviors occurred. The ontogenetic basis of lipsmacking from sucking has been noted in baboons (ANTHONEY, 1968), macaques (CHEVALIER-SKOLNIKOFF, 1974; BURTON, 1972), and perhaps in capuchins (OPPENHEIMER, 1972). ANTHONY (1968) actually noted brown infants to embrace the female then lipsmack on her nipple for a few seconds.

Sucking and grasping components are strongly interrelated in the infant and the association seems to persist in modified forms at later stages of development (MASON, 1965a). This was commonly seen in colobus where embraces of all types were often accompanied by slow clucking lipsmacks or by mouthing of the fur. Guinea baboons often give rapid lipsmacks in varied embracing situations. Likewise, bonnet macaques often combine embracing with neck chewing (SIMONDS, 1965).

*Evidence for Similarity in Behavioral Motivation*

Socio-maternal behaviors seem motivationally linked to a state of anxiety or ex-

citation. The performance of these behaviors leads to a behavioral completion; a reduction in the insecure feeling which restores the animal to a motivational steady state. Similarly, the infant uses clinging-sucking to reduce its own excited state during stress periods (see MASON, 1972). As development proceeds, the individual responds differently to a similar problem. In the mother's absence the older infant may accept other troop members as substitutes and sucking may be transposed to its own limbs or to areas of the other animal (MASON in KUMMER, 1967; BOESE, 1973).

Since any object that is used repeatedly for clinging can become the focus of emotional dependence or attachment, a generalization gradient will develop around the object of attachment (MASON, 1972). In extreme situations very different substitutes will become attachment objects (MASON & KENNY, 1974). Thus a sharp distinction cannot be drawn between mothers, siblings, other adults, and peers, as sources of important psycho-social qualities (MASON, 1972). For the developing young, these social beings have overlapping attributes and "object functions". Thus, *the modifying of the infantile response to other troop members or things, although regressive in nature, shows a growth away from the specificity of the mother-infant bond.* This is important in the survival of infants of species which exhibit aunting and infant transfer (HORWICH & MANSKI, 1975; LANCASTER, 1971) since it appears to ease the weaning process (ROSENBLUM, 1971; BOULIÉRE, HUNKELER, & BERTRAND, 1970).

Additionally, in female infants, rejection frustration may be eased by their being permitted to play an aunt role to the newborn. This mixed role after the sibling birth, of being both an infant and mother-aunt, exhibits a similar motivation whereby the sibling can generalize her response and get comfort from clasping the new infant instead of her mother. HARLOW (1971) noted this in macaques. We noted a similar pattern in a five-year old captive female orangutan who showed a regressive clasping and remaining near her mother after the birth of her brother. After a few months when she was permitted to carry the infant she mouthed his hand as a substitute while she clasped him.

Another case of maternal generalization occurs in Hamadryas baboons (KUMMER, 1967), where a year old female may transfer the mother's protectorate role onto a subadult male who she forms a consortship with. He responds in a typical "maternal" role, which may have a similar affect in reducing his stress as well. These males are more strongly motivated toward maternal behavior than males of other species (KUMMER, 1967). Subadults reduce their infant cuddling when they have females in their group (KUMMER, 1967). In contrast, *Papio cynocephalus*, shows neither single male groups nor such maternal behavior in males (KUMMER, 1968). Colobus males rarely exhibit much infant contact except when rescuing infants, and females may exclude them from such contact (HORWICH & MANSKI, 1975; WOOLDRIDGE, 1971). Thus although different species may have the same stereotyped postures, other genetic variables may guide different species toward varied uses of these patterns to form different social structures (ANTHONEY, 1975).

There are many other examples where adults derive security by embracing. Baboon group leaders in stress from troop fights embrace their females (KUMMER, 1967). Nilgiri langur subordinates embrace and groom the dominant during threat sequences (POIRIER, 1974). A mature chimpanzee may embrace, touch, or mount another animal

under stressful circumstances similar to a frightened infant (VAN LAWICK-GOODALL, 1968).

In Guinea baboons infant grasping contains core elements for embracing and mounting (ANTHONEY, 1975). A six-month old baboon mounted a female (because of her estrus condition), in situations where clasping would ordinarily occur. This showed that the embrace and mount are closely related patterns probably caused by similar motivation in the performer. The recipient's posture seems to determine which behavior appears (ANTHONEY, 1968). Thus variations of similar patterns may account for mounting, posterior grasping, and mutual embracing in baboons (ANTHONEY, 1975).

#### *Evidence from the Social Effect of Infant Birth*

When the change in social behaviors following the birth and introduction is compared to the baseline situation, a clear pattern emerges. Following the introduction which was a more intense situation, the main socio-sexual behaviors (mounting and presenting) showed increases and only one of the socio-maternal behaviors showed an increase. Following the birth, socio-maternal behaviors, especially forward mounts increased dramatically and they showed a startling correlation with infant transfers indicating a very strong association of these two behaviors. The exception was clasping, which is both a maternal and infantile response. It increased following both situations but was more intense following the introduction. Another important distinction is that following the introduction, the male was a participant in the social interactions whereas after the birth he did not involve himself except as a protector of the infant and to occasionally break up fights between females involved in transfers.

#### THE CHANGE IN TROOP RELATIONSHIP AS A SOCIAL REGRESSION

*In colobus there has been a coordinated evolution of two major aspects of sociality: infant transfer and the use of infantile and socio-maternal behaviors in adult interactions.* Infant transfer has meant a loosening up of the mother-infant bond but the infantile and socio-maternal behaviors are instead redirected toward other adult females. These contact behaviors following the introduction and birth helped females regain their social equilibrium and group cohesion, as an infant regains security from its mother.

In howler monkeys an adult social behavior has similarly emerged from infant transfers. Two adults greet by sniffing axillary regions and sniffing or licking genitals. During a transfer, when the infant climbs on its non-mother's head, its perianal region is in contact with the receiver's mouth and its head is in the axillary region. As the infant seeks the nipple, the captor licks its genitalia (GLANDER, 1975). Similarly in baboons, ano-genital investigation apparently derives from maternal patterns of care and cleaning of the infant (RANSOM & ROWELL, 1972). This behavior is then included in social patterns of presenting, mounting, and handling the genitals.

One aspect of all these behavior patterns is the potential for using the same patterns for different functions. Although intensity varies, dominant and submissive animals appear to have similar emotions preceding an interaction. Anxiety is involved. The



final behavior pattern and how it is directed depends on who is doing it to whom. For example, both forward mounts and socio-sexual mounts may be done as a dominant or submissive behavior.

### *Sociality and Regression*

There are five interrelated aspects to the phenomenon of social regression or the adult use of infantile responses: (1) recurring high and low periods of maternal contact in the infant which occur at specific periods in development (dictated genetically) (HORWICH, 1974a, b); (2) regression of mother-infant contact elicited by environmental stimuli; (3) seasonal phenomena or changes which cause group regressive contacts in adults and infants; (4) ritualized adult social behaviors which have emerged and become emancipated from the infantile behaviors; and (5) abnormal cases where fixation on some aberrant behavior or developmental period occurs (i.e., Freud's regressions).

(1) The infantile cycle of maternal contact during normal development results in regressive periods of two to four weeks in monkeys. These periods have the survival function of all cyclic life functions: an organism and its parts must renew itself constantly to live. These periods contribute to the individual's rest prior to a growth spurt. Linked with this is the phenomenon of extending and contracting movements in development observed by GESELL (1939) and AMES and ILG (1964) which have their basis in the neuromuscular development of the infant. Thus certain behaviors are more frequent during certain developmental periods and they alternate with other behaviors (HORWICH, 1974b). A second function is in learning and maturation of behaviors. During periods of close mother-infant contact cerebral growth may be occurring and the infant may be learning about things which are to come and he may be reflecting and synthesizing what was learned in the active progressive periods. During this time he may also be learning through imitation. During the progressive growth phase, the infant is undergoing experiential learning. He practices activities on his own and improves his techniques. These cyclic periods are probably directed by underlying age levels of arousal, perhaps set chemically by periods of greater or lesser levels of hormones. Then certain behaviors occur and supercede others. Thus as MASON (1965b) notes, low or moderate levels of arousal predispose a primate infant to play while high levels produce avoidance of play and strengthen the tendency to cling. BOWLBY's control system also implies there are two behavior systems which have species survival and these operate ontogenetically in a dynamic equilibrium (AINSWORTH, BELL, & STAYTUS, 1971).

(2) The second aspect of regression is the response to an insecure situation. The infant returns to its mother just as a social group clump together in flight from an enemy. At this time infantile clasping in primates often occurs.

In addition to short term environmental effects which induce cohesion, there may be longer term affects. Literature dealing with extended regressive affects following infant separation from its mother is related to this. Similarly, major changes in the environment such as a cage change may have an extended effect as it did on a young lemur (KLOPFER & KLOPFER, 1970). Physical injury or illness may also be a cause of

regressions. GLANDER (1975) noted a case of a juvenile howler monkey which after a debilitating fall was allowed to ride on its mother though she had not permitted this for seven months prior to the fall.

(3) The cycling of social behaviors in infants probably grades into seasonal sociality and reproductive behavior. In gray squirrels sexual play and aggression followed cycles which became temporally coincident with adult reproductive cycles (HORWICH, 1972). Social nesting which is reminiscent of the infantile situation, alternated periods with the social behaviors during development and later seasonally. In Siberian ibex development, patterns of mother-infant contact alternate with locomotory activity. The periods of fluctuating contact eventually grade into seasonal fluctuations so that periods of high contact in yearlings and older females occur during rut and calving seasons. This is a mechanism by which young animals maintain their attachment to their mother despite these periods which stress the mother-juvenile bond (HORWICH, VAN DYKE, & COGSWELL, 1977).

(4) The occurrence of ritualized infantile behaviors in adults in response to the colobus birth shows a synchrony between the troop and the infant. It reflects the group cohesive function of regressive cycling in infants. The species then utilizes these behaviors in adult social interactions. In some species the final emancipation has not been reached and considering the similarity in motivation between mother-infant and adult interactions perhaps it may never be reached. This can be seen in the following examples. With the birth of her first infant, a female patas mother appeared very nervous and showed numerous occasions of infantile behavior. She would lower her head and stereotypically project it under her mother's arm (even if the mother's arm was not in the way), putting her nose and lips close to the nipple without mouthing it. In another case, an adult female spectacled langur achieved nipple contact with a female in late stages of pregnancy. She showed lipsmacking-like mouth movements before mouthing the breast. Additionally, two cases of a male *Colobus badius* suckling in the field for 1.5 and 3-5 minutes were observed associated with grooming (STRUHSAKER, 1975).

(5) In extended environmental stimuli which have even longer term results, such as deprivation experiments, the infants often remain fixed at a particular point in their early development in regard to some behaviors. FREUD observed this in humans. These infants may give abnormal frequencies of behaviors in an abnormal context. For example, an infantile behavior such as digit sucking may be performed beyond the appropriate age (MITCHELL, 1970).

In conclusion, developmental cycling of mother-infant contact, as well as other behaviors probably has the function of being a consistent reservoir for social contact and group structure in mammals. It may later grade into seasonal reproduction and seasonality in other behaviors. Secondly, the birth of infants may in some cases like in colobus, permit a synchrony of the troop's behavior with the infant's developmental periods. It may also stimulate restructuring of the troop hierarchy.

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