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Sense in bizarre behaviour in rhesus monkeys

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INTRODUCTION.

Monkeys which have experienced social isolation often show behavioural abnormalities, i.e., postures or movements not seen in animals reared and living in the wild. This was noticed in animals which experienced rigorous social isolation during early stages of life [1–4] as well as in animals which experienced much milder forms of isolation at later stages [5–8]. The term " abnormal " behaviour refers to activities not seen in feral animals; the morphology of the activities is often very strange and idiosyncratic. In fact, the range of both quantitative and qualitative variation is so great that accurate descriptions of one individual seem almost without validity when applied to another individual. Descriptions found in the literature therefore are often, with an occasional colourful exception, restricted to vague qualifications such as " abnormal " or " unusual ".

This paper considers the morphology of abnormal activities observed in rhesus monkeys which had experienced a certain degree of social isolation. Analysis of the morphology of the behaviour started from the hypothesis that abnormal behaviours should preferably be interpreted as distortions of normal behaviour. The aim of the study was to detect preferably simple patterns in the confusing variation in the abnormalities. The results show that patterns can be recognized at different levels of integration. As an overall pattern, it appeared that all of the abnormal activities can be tentatively interpreted as representing certain kinds of social behaviour displayed in the absence of a partner.

SUBJECTS AND METHODS.

Subjects were 19 adult female rhesus monkeys which were selected from the laboratory colony because they were known to exhibit at least one type of abnormal behaviour. The subjects had experienced social deprivation, as they were usually caged singly (cage dimensions 60 × 60 × 80 cm) for prolonged periods of time (from 6 to 10 years) and in most cases from childhood onwards. In the cage rooms, the monkeys could see and hear others (for a more detailed description of their housing conditions, see [9]). Only one or two times a year had the animals been sociayll housed for a few weeks. The personal histories of the subjects varied. Differences in abnormal behaviour between individuals might therefore be attributable to differences in experience. Each monkey was continually observed for two hours when alone in a cage (80 × 160 × 80 cm) from where other monkeys could be seen and heard. Each subject was allowed to become accustomed to the observation room for at least one day prior to observation. During observation, all activities of the subject were described. The times of onset and durations of a number of activities were recorded by use of an observer operated event recorder. Descriptions of the abnormal activities are given in Tables 1 and 3 and will be discussed below.

RESULTS.

In agreement with most literature reports, the observed abnormalities could be divided into two main categories: *A*) stereotyped locomotions and gross rythmic stereotypy; and *B*) self-directed and " bizarre " behaviour. For the sake of clarity, these two categories are discussed separately.

A) *Stereotyped locomotion and gross rhythmic stereotypy.*

1) *Description.* – Stereotyped locomotion differed from normal locomotion in the fact that, while steadily moving, the animal (*a*) did not fixate on an endpoint of the walking path; and (*b*) rigidly repeated the same locomotion pattern. The form of the locomotion stereotypies of the various monkeys was very diverse and highly idiosyncratic in comparison with their normal locomotion. The various stereotypies observed are listed in Tab. 2. Close consideration of the behavioural morphology led to the conclusion that the variations in form can be described on the basis of path length and plane of movement. In addition, nonlocomotory movements during walking added to the degree of idiosyncracy.

a) *Path length*; stereotyped locomotion often involved the walking of a closed loop which, of course, is the only possibility if cage size does not permit a straight path over longer distances. The loop's length, however, could vary in size; a single loop could be i) extended to the *whole floor* of the cage, ii) extended

Table 1. – *Stereotyped locomotion and gross rhythmic stereotypy.*

Long path length

Loop – walking over an almost elliptical path that extends to the entire oblong cage floor.

8 loop – walking in an 8–shaped loop; in two animals, the leftward turn was accompanied by a side–step.

Short path lenght

Circle – similar to loop but the path covered only half of the cage's floor.

Tilted circle – the animal raises the torso at one point of the circle and comes down on all fours at a later point, sometimes accompanied by head toss.

8 track – as 8–loop, except that the path extends to only half of the cage floor.

Somersault – the animal crouches a little, elevates torso, grasps ceiling with both hands, leans backward while lifting hindlegs and which then hold onto the ceiling, brings hands to the floor and then drops feet all in one sequence, which may be repeated over again.

Zero path length

Incomplete somersaults

Backward dangle – incomplete somersault, performed not further than lean backward.

Frontal lift – incomplete somersault, up to elevating torso.

Dangle – a somersault exerted up to hands grasping the ceiling, the animal then drops one hand, assumes a normal body orientation, turns around while unwinding the other arm still holding onto the ceiling, which is then released. It can be regarded as changing direction halfway through a somersault.

Pendulum – holds on to the ceiling, then drops one hand and moves sideways to normal body position with one hand still holding on to the ceiling; i.e., the animal maintains a position assumed briefly in dangle. In that position, the animal sways rhythmically sideways by pushing itself with the free hand away from the nearby wall.

Twirl – the animal elevates torso as in somersault, but does not hold on to the ceiling; instead, it makes a turn around the vertical axis and then lands on all fours. It is reminiscent of a dangle without holding on to the cage ceiling.

Others

Spot gallop – galloping without displacement

Flutter – walking with the arms pacing from left to right and back, while the legs are hardly or not displaced.

Back and forth – the animal crouches down and backwards, the forelegs walk forward and then it crouches again as if retreating; the whole sequence could be repeated a number of times.

Side step – mainly the arms are walking from left to right; just before changing from right to left, the animal puts out its left foot and steps over the right. No such step was made during the change in the opposite direction.

Sway – while standing up on the hindleg, the arms are walking from left to right and back along the cage wall; in other words, flutter while in a more or less upright position.

Shoulder circle – the arms walk from left to right while also going up and downward. The legs are moved very little, so that the upper chest of animal describes a circle.

"Bounce"

Side shake – a rhythmic motion of shalking the substrate as in normal bouncing, but flexion and extension of the two arms alternate.

Rock shake – the animal stands up while the arms rest somewhat apart on the wire mesh. Upper part of the body moves rhythmically up and down and a little bit sideways. The force seems to come from movement of hands and wrists.

Foot tap – the same as rock shake except that now the rhythmic movement also involves the hips, while the left foot is held in front of the right (superficial impression is that the animal is tapping to the beat of a song).

Vertical hop – stands bipedally in the corner of a cage and moves rapidly up and down on the toes and fingers supported by the cage's wire; the frequency is as high as two or more hops per second.

Side hop – position as in vertical hop except that the animal moves from left to right instead of up and down. The side hop occurred singly, as interruption of the more prolonged vertical hopping.

Soft Bounce – moves body up and down while standing quadrupedally on toes and fingers; the movement is quite rapid but not as vigorous as in normal cage shaking.

Hollow backed bounce – the animal crouches a little and then forcefully moves front part of the body upward while the hands hold on to the cage's bottom. It differs from frontal lift in that the animal holds onto the cage floor.

Hop bounce – while standing on hindlegs with hands supported by the wire, the animal jumps up and down much like in normal bouncing, while bending the one or the other knee, thus lifting one foot from the floor.

to *only half* of the cage, which was only slightly larger than the animal's home cage, iii) practically *zero* in length, e.g., when the animal walked in place or when it walked only with the arms while the hindlegs remained in place. It is important to note that locomotion stereotypies can shade off into gross rhythmic stereotypy as the path length becomes closer to zero. As indicated in Tab 1, a number of stereotypies with zero path length could be regarded as incomplete somersaults.

b) *Plane of movement* could be i) *horizontal* as in ordinary walking on the floor, ii) *vertical* as in somersault or iii) *tilted*, in which case the animal elevated its body during one half of the loop while it was on all fours during the other part. The orientation of the body axis is in principle independent of that of the path because of the fact that a monkey can walk upright bipedally. However, if the path length was not zero, the orientation of body and path were identical.

c) Other movements; i) *changing direction* consisted of animals walking along an 8–shaped track (AC, EJ), of a leftward turn which was accompanied by the left foot stepping over the right foot during the left-wards turn only. This sidestep caused an abrupt and sometimes also a rather rapid change in the direction of walking; as such, the movement was reminiscent of a monkey evading another individual. Changing of direction also occurred with zero path length. The change of direction could be lateral but also back and forth. In the latter case, the backward movement was reminiscent of a monkey's ducking in preparation for a jump. ii) *Head toss*: in one monkey (IF), this consisted of turning the snout sideways, upward and then frontally back into normal position, all performed in one quick sequence. In one other monkey (BU), the snout was turned downward rather than upward (similar patterns are also referred to by Paulk et al., [7]). The head toss often accompanied the making of a turn during stereotyped locomotion (but monkey IF also headtossed when seated). The movement resembled quickly looking away as is observed in feral monkeys when avoiding the gaze of another animal. iii) "*Bouncing*" was characterized by rapid movements performed by arms and legs resulting in up-and-down movements of the body; this occurred only during locomotion with zero path length. The movements were faster than in normal locomotion but slower and less vigorous than in normal bouncing. Bouncing or branch shaking by feral animals probably serves as a warning to other troops at a distance to stay away. The present subjects also showed the normal, vigorous (species specific) bouncing, which resulted in cage shaking; it was often elicited by hearing monkeys doing the same in other rooms. From the above results, one may conclude that the category of stereotyped locomotion and gross rhythmic stereotypy described in Tab. 1 can be tentatively interpreted as representing idiosyncratic ways of distorting and combining only a few normal activities.

2) *Amounts of locomotion*. – As an illustration of the interindividual variation, Tab. 2 gives the distribution of the various types of locomotion stereotypy over the individuals as well as the total time spent in each type. This table shows that the amount of time a subject spent in stereotyped locomotion varied from zero to about 20 per cent of observation time. Some

Table 2. – *Amounts of time spent in locomotion stereotypes and normal locomotion by the various subjects given as per cent of observation time.*

locomotion stereotypies					individual identification																		
					BU	AA	IF	AM	GU	AI	FL	AX	YY	AC	EJ	FU	AB	81	EX	12	34	64	32
loop	L	H					**6**		**8**														
8-loop	L	H	c										**12**	**9**	**10**								
circle	S	H			.5	**20**		**13**	**5**	**2**													
tilted circle	S	T					.2																
8 track	S	H	c												**5**								
somersault	S	V							**2**	**2**	**5**	**10**											
backward dangle	Z			i								.0							**5**				
frontal lift	Z		c	i						**3**	.0												
dangle	Z		c	i								.0											
pendulum	Z		c	i									**3**										
twirl	Z			i													**5**						
spot gallop	Z		c																				
flutter	Z		c										.2										
back and forth	Z		c											**3**									
side step	Z		c											**1**									
sway	Z		c													**1**							
shoulder circle	Z		c																.6				
side shake	Z			b				.2															
rock shake	Z			b														**7**					
foot tap	Z			b														**8**					
vertical hop	Z			b															**11**				
side hop	Z			b															**3**				
soft bounce	Z			b											.1				.6				
hollow backed bounce	Z			b											.2		.2						
hop bounce	Z			b											.5								
total stereotyped locomotion					.5	**20**	**6**	**13**	**15**	**8**	**5**	**10**	**15**	**13**	**16**	**1**	**5**	**15**	**20**				
total normal locomotion					.4	.6	.1	**2**	.7	.2	.5	**3**	.5	.5	.8	**4**	**1**	.5	**1**	**6**	**2**	.7	.6

Descriptions given in Table 1. L, S, Z = long, short, zero pathlength; H, T, V = horizontal, tilted, vertical plane of movement; c = changing direction; i = incomplete somersaults; b = "baunce category"; h = head toss.

Table 3. – *Contexts and " self oriented " activities.*

Agonistic

Self–aggression which may vary from a simple bite of a hand or foot to very complex often quite frantic wrestling, grabbing and biting of limbs (see also Goosen and Ribbens,[8]);

warding off in which the animal is making movements as if rapidly and frantically kicking and pushing away an opponent;

prone, a posture adopted by an animal which is attacked and cannot or does not flee. It cannot be unambiguously assessed whether it should be interpreted as the behaviour of an attacked animal. However, the posture is included as a reminder of this possible interpretation.

Sexual

mount, the animal stands up on hindlegs and firmly holds itself near the hip or thigh.

present, with head down, posture adopted by female animal prior to or during sexual intercourse. Normally the animal can also present when standing normally on all fours, but this posture when not oriented to another individual cannot be distinguished from normal standing.

clitoral stimulation by the tail or hand. In tail stimulation the tail is stiffly curved and moved up and down, a movement probably originating from tail waggling.

Groom

self–grooming is the self–directed counterpart of social grooming. The same pattern can of course also represent simply cleaning one's own fur.

chin and or a *leg* or *arm raised* are postures which can be adopted by a groomee. Prone, present or slump can also be adopted by a groomee. Normally, a gromee also looks quite fixedly ahead avoiding movements or postures which could be interpreted as hostile by the partner. The rigid position and the fixed features are also apparent in the self–directed pattern.

caress, an arm or leg is extended and the fingers or toes, are gently and slowly stroking the fur or lightly tapping the body at one point or another. Sometimes, the movement is reminiscent of scratching.

Caressing was not very rigid in form; all subjects caressed by hand or foot different body parts. This variation is of course in line with the interpretation of being groomed because this also involves different body parts.

Infantile

hug or *sitting against* a larger part of the body, possibly a self directed counterpart of sitting against another monkey which may or may not be accompanied by embracing the partner.

self–hold of a smaller part of the body, namely, holding a *hand, a foot,* holding the *hands on top of the other and on the foot* or having *closed fists.* What these activities have in common with holding another individual is that they provide a similar tactile stimulation of the palms of the hand. Grabbing and holding on to a tuft of hair could also be placed in this category.

suck, sucking digits of finger or toe, which originates from infantile sucking the mother's nipple. A complicated pattern in which the animal holds with one hand, sucks on one finger, while it wriggles other fingers of one or both hands is also placed in this category; the finger wriggling might originate from clasping and unclasping the hand while holding on to the mother.

Face press, the animal lifts one or two hands and holds them in front of or next to the face. The full hand may be against the eye, against the side of the brow, or a finger may be pressing upon the eyelid and eyeball, or the hand does not touch the face. The patterns might originate from the infantile holding onto a mother while seeking the comfort of pressing the face against her and sucking the nipple. By the face press, the animal provides itself with stimulation similar to the normally received tactile stimulation and also with visual stimulation (darkening).

crouch, a criterion used in order to distinguish this posture from just sitting was that the highest point of the head was lower that than of the back.
The posture is similar to the conservation response observed in young rhesus infants after separation from their mother [11]. Normally, this posture can be adopted by a sleeping animal and by one being groomed.

individuals showed only or mainly one pattern, while others spent considerable amounts of time in two or more. The number of patterns and the amount of time spent in stereotyped locomotion were significantly correlated (Kendall's tau $= + .50$, $p < .01$). Apparently, animals spending much time in stereotyped locomotion had, on the average, a more varied repertoire of stereotypies than did animals which spent little time in such activity. There was no indication that certain categories of stereotyped locomotion were associated with each other in their distribution over the various individuals. Most individuals showing abnormal locomotion (11 out of 15) walked in a stereotyped way over some distance (long or short path length); in the 4 remaining monkeys, the locomotion stereotypies had only a zero path length. In individuals which showed the two kinds of stereotypies (either of or not of some path length), most of the time was spent in stereotypes covering some distance. This means that, despite the occurrence of movements on the spot in the locomotion stereotypies, walking over a certain distance is still the main component. As indicated in Tab. 2, all animals also showed normal locomotion. The total time spent in normal locomotion did not exceed the 6 per cent observation. In animals with locomotion stereotypy, the amounts of normal and stereotyped locomotion were not significantly correlated (Kendall's tau $= + .11$). The amount of time spent in normal locomotion was, with one exception (FU), always less than that spent in stereotyped locomotion. The amount of normal locomotion in animals which did and those which did not show stereotyped locomotion is not significantly different. These two results support the idea that normal and stereotyped locomotion differ in causation (as suggested by Paulk et al., [7]).

3) *Seeking certain kinds of social contact?* – If one attempts to interpret the above–mentioned activities presumed to be involved in the locomotion stereotypies, it seems that the monkeys behaved as if: *a*) avoiding social contact (as indicated by changing direction and head toss); or *b*) signalling other individuals to stay away (as indicated by " bouncing "). According to this hypothesis, a number of monkeys were apparently busying themselves for prolonged periods of time in an idiosyncratic way with avoiding and/or diminishing close social contact. This suggests that the stereotyped locomotion results largely from seeking specific kinds

of social contact (which however are not available) while avoiding other (available) forms. The origin of this behaviour might be related to the fact that, under normal conditions (when animals are not caged), walking is likely to bring the individual to a place where the form of social contact sought is found or where the animal's motivations are otherwise changed. Under deprived conditions then, the individual's environment hardly changes, so that some animals apparently persist in seeking. The amounts of time spent in stereotyped locomotion were greater than those for normal locomotion but in the same range as those for the longer lasting self-directed social activities (compare Tab. 2 and Tab. 5, discussed below in section B3). As a *post hoc* hypothesis, one might say that the monkeys sought certain forms of social contact for about the same amount of time as they engaged in certain types of self-directed social contact.

B) *Self-directed and " bizarre " behaviour.*

1) *Description.* – This category of abnormal behaviour included activities which can be clearly recognized as social behaviour which is redirected to the animal's own body (e.g., self-aggression, self directed sexual behaviour, digit sucking). But there was also a variety of " bizarre " activities for which such an explanation is not obvious. It was investigated whether the various bizarre activities could also be interpreted as self-directed forms of social behaviour.

Fig. 1 gives a list of a number of what one may loosely call social contexts and roles. The figure also illustrates a number of postures and movements which can be interpreted as representing the salient social activities of the context concerned as performed in the absence of a partner. Descriptions are given in Table 3. The left-hand drawings in Fig. 1 represent the activities clearly recognizable as social motor coordinations. A number of activities also show some distortion in shape due to the redirection of the motor coordinations towards the animal's own body. This redirection suggests that these activities also mimicked social stimulation; otherwise, it is difficult to account for the fact that these activities were self-directed instead of being performed *in vacuo*. The right-hand drawings in Figure 1 represent activities in which the mimicking of social stimulation occurs by motor coordinations which are not obviously of social origin. Genital stimulation by hand or tail takes place by a modified manual genital exploration or tail wagging, respectively, caress; the mimicking of stimulation received as a groomee occurs presumably through slowed down scratching movements. The various forms of self-hold all seem to mimic manual stimulation by remnants of the more complex infantile holding on to a mother. The above results suggest that a number of abnormal activities can be regarded as idiosyncratically distorted ways of maintaining certain forms of social communication when there is no partner present. As such, one might say that some individuals " interacted " with a self-invoked " ghost partner ". In other words, it might be that the abnormal activities were shaped by exteroceptive feedback from the animal's own actions insofar as the feedback resembled the normal social stimuli of which the animal had been deprived.

Table 4. – *Amounts of time spent in self-directed activities by the various subjects; numbers give percentage of observation time.*

	individual identification																		
	BU	AA	IF	AM	GU	AI	FI	AX	YY	AC	EJ	FU	AB	81	EX	12	34	64	32
A. self bite, fight			.0	.7	.4	.0	.1	.1		.3	.1	.2		.2		.1		.5	.0
ward off								.1		.3		1		.2					.0
prone					.0			.1					.0	.2	1		.0		
S. self hip grasp				.1						.1				.0	.0	.1			
genital stim.				.1		.5	.2		.2										
present	.3	.2	.0	.7	.0		.2		.3	1	.1	.1	.2	.1	.6		.1		
G. self groom	45	7	2	5	1	6	2	17	4	1	.1	.2	17	22	1	12	24	13	20
snout raised	1	.4	.0			.2	.1										.1		
leg, arm raised	2					8					.0				9		.1		1
caress	26		2	1	.4	6			.1			1	2	28	9	1	.1		6
I. self suck	.2	4		6			74	.3				.0						.1	
self face press						10				2	41				3		.4		
self hug	3		12	36	16				12				1	3	.2	.5	4	1	
self hold									7					x		6	x	8	14
crouch	.7		16	22					15	8	.0		1	19	2				10

Dascription are given in Fig. 1 and Table 3. A = agonistic; S = sexual; G = groom; I = infantile. x = close fists, although not measured, took more than 1 per cent of the observation time.

2) *Simultaneous occurrence of self-directed activities.* – The illustrations in Fig. 1 could be regarded as elementary, since they seemed to represent only one type of social activity. Almost all of the remaining abnormal patterns can be regarded as combinations of two or more of these elementary patterns. A number of striking combinations are given in Fig. 2. The figure illustrates that some of these activities were very intricate in morphology and difficult to interpret unless regarded as combinations of the patterns described above. The frequency of the various single and combined self-directed activities in the group of subjects as a whole was studied by the use of Fig. 3. In this graph, each short vertical line represents one individual showing an elementary pattern; a long or branched line represents one individual displaying simultaneous combinations of the connected elements. The graph contains more than 19 lines because some of the 19 individuals showed more than one type of self-directed activity. The graph shows that most combinations involved caress (presumed to mimic stimulation received as a groomee) and various postures which can be adopted by a groomee in a social situation. This suggests that most of the combined self-directed abnormal patterns originated from mimicking the type of stimulation which is appropriate for the context, as judged from the posture. The same phenomenon holds true for other combinations given in Fig. 3, namely, (*a*) self-aggression and warding off; (*b*) genital stimulation and self-hip-grasp; and (*c*) combinations of face press, hug and suck finger or toe. The magnitude of such " appropriate " combinations supports the earlier hypothesis based on form analysis of the activities that the abnormal activities reflect attempts to maintain certain forms of social communication when no partner is present.

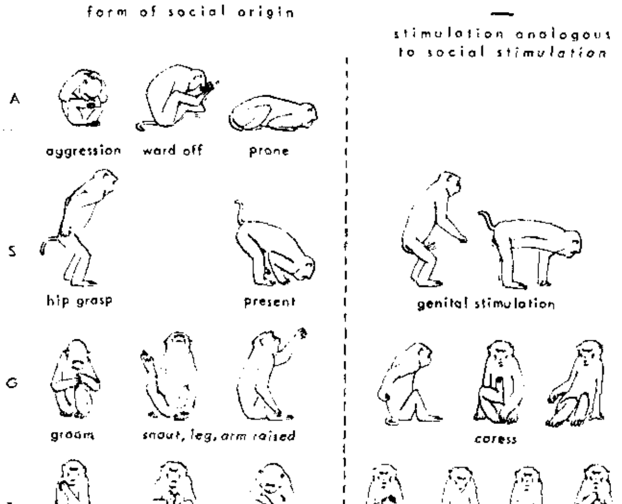

Fig. 1. – Social contexts and postulated corresponding self-oriented activities. Descriptions given in Tab. 3.

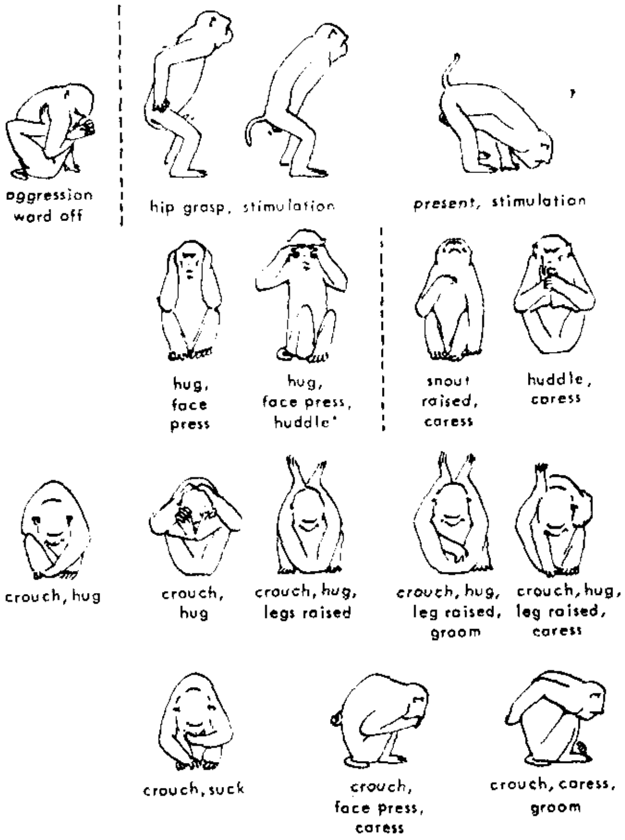

Fig. 2. – Simultaneous combinations of self-directed activities given in Fig. 1 and in Tab. 3.* The subjects presses its right knee against its belly.

3) *Amounts of self-directed behaviour.* – As an illustration of the great extent of interindividual variation, Table 4 gives the distribution of the various forms of abnormal behaviour over the individuals as well as the amount of time each individual spent in the respective activities. For the sake of simplicity, simultaneous combinations of activities (as shown in Fig. 3) have not been indicated as such; the data are given as if simultaneous activities occurred separately. Self-grooming was shown by all subjects, as is the case in feral animals. Twelve of the 19 subjects showed suck or face press; all of the remaining 6 subjects showed self-hugging and/or self-hold. This suggests that many, if not all, individuals had to some degree retained or regressed to infantile behaviour. The various types of self-directed activities showed no particular association in their distribution over the various subjects.

The amounts of time an individual spent in the various self-directed activities varied from zero up to 74 per cent of the observation time. The amounts of time spent in self-directed agonistic and sexual activities was rarely over 1 per cent, whereas much more time was often spent in self-directed activities falling under the grooming and infantile contexts. This time account is remarkarbly similar to that for the corresponding normal partner-directed activities in feral animals. Feral animals also spend relatively little time in aggressive or sexual behaviour, whereas activities such as grooming, being groomed, hugging, huddling or nursing are, on the average, consume far more time. This suggests that social deprivation gave rise to strange forms of behaviour but it did not generally

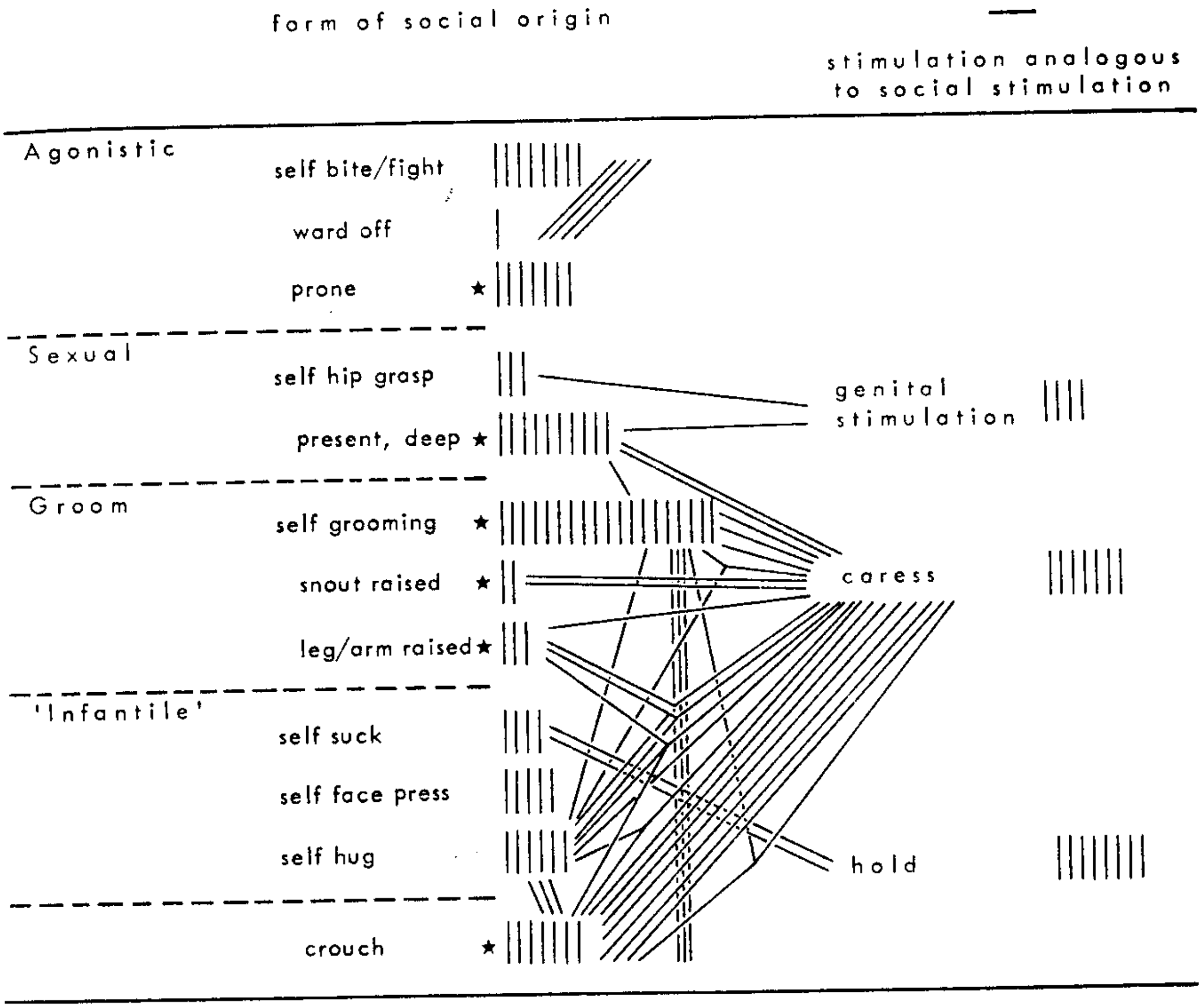

FIG. 3. – Frequency of simple and simultaneously combined self-directed activities described in Table 3.★ Each solid upright slanting or branched line represents one individual which displays the simple element or a simultaneous combination of the connected elements. The graph contains more than 19 such lines because each individual can show more than one such activity type. Denotes postures which can normally also be adopted by a groomee.

lead to major changes in the amounts of time spent in the predominant behavioural contexts. These similarities in time budget further support the hypothesis that the abnormal activities can be regarded as social communication carried on in the absence of a partner.

DISCUSSION.

The analysis presented leads to the hypothesis that all of the observed abnormal activities may be interpreted as symptoms of what may be called a *social deprivation syndrome*. The category stereotyped locomotion and gross rhythmic stereotypy was interpreted as possibly originating from the active seeking of particular kinds of social stimulation. The category of self-directed and bizarre behaviour seemed to represent combinations of social motor coordinations and simulations of stimuli normally received from a partner.

The results presented illustrate how patterns in abnormal behaviour were considered at different levels of integration: 1) the description of the abnormal activities in terms of motor coordinations; 2) the categorization of the described abnormal activities on the basis of similarities in morphology between the abnormal activities; 3) the interpretation of the different categories of abnormal activity in terms of apparent distorsions of normal behaviour, in this case as distortions of social communication; 4) the coherence between the self-directed normally social activities, as indicated by the social deprivation syndrome. By recognizing these different levels, the initially bizarre variability in abnormal activities has now been given a sensible interpretation. This permits one to concisely formulate in what particular aspects the abnormal behaviour of an individual is or is not to be regarded as deviant. A point of concern in the postulated deprivation syndrome is the question of how deprivation could have led to such a variety of idiosyncratic symptoms. A possible answer already mentioned may be that different abnormal activities emerge where individuals differ in the kind of social experience they lack or the kind of social relations they were deprived of. A second answer may be that development under standardized conditions involving highly restricted social stimulation more clearly exposes individual differences in genotypic sensory, perceptive and motor predispositions. By contrast, development under normal conditions involves a large number of social stimuli which presumably tend to average out inter-individual differences. The abnormal activities of monkeys experiencing social deprivation remain rather unchanged when the animals are again housed under social conditions (personal observation; see also [2-4]. This suggests the behavioural reactivity to normally effective social stimuli has " hypotrophied " due to disuse at a certain stage of life as a consequence of the deprivation. As a word of caution, it should be noted that the social deprivation syndrome outlined above reflects an attempt to find a coherent pattern in the abnormal behaviour. The developmental interpretations given, therefore, represent a *post hoc* hypothesis which, of course, remains to be verified by specially devised developmental studies under controlled environmental conditions. For the moment, we can only say that the hypothesis is experimentally testable and that it offers more attractive interpretations of abnormal activities than those presented thus far. For instance, Foley [10] introduced a concept " habit residual " in reference to a monkey which lifted its leg and which as an infant had sucked its toe. Under the present hypothesis, one might venture to say that, when it grew older, the monkey had weaned itself from its self-mimicked ghost mother and from then on sat close to a ghost partner that was visually and tactually mimicked by lifting a leg.

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Social grooming in *Macaca Fuscata*

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INTRODUCTION.

Both in natural habitats and in captivity, it is not uncommon for one member of a group of monkeys to be seen approach another member and, once contact has been established, raise the fur of the second individual and brush it carefully with either the palm or back of the hand, picking out all sorts of detritus and ectoparasites. This behaviour, which is very common among primates, is referred to as " allo- " or " social grooming " when one individual directs its attention to another, as in the example above. When body cleansing is self-directed, the activity is referred to as " auto- " or " self grooming." These terms apply to mammals in general [1] and to primates in particular [2]. Often, after one individual has finished grooming its partner, it turns its back on the groomee who, in turn, immediately starts to groom the former groomer. On other occasions, subjects may be seen to groom each other simultaneously. Sparks [3] proposed calling the former " reciprocal social grooming", or more shortly, " reciprocal grooming", referring to the latter as " mutual grooming".

A third form of grooming also exists. In this case, several individuals jointly direct their grooming attention to a single subject or, alternatively, to each other. Either form is known as " multiple grooming."

Grooming has an obviously hygienic function and many researchers have pointed out its role in the prevention of parasite epidemics [4-8]. Simonds [9] observed how grooming in bonnet macaques (*Macaca radiata*) also had a therapeutic function. He noted that some subjects in a group of these monkeys showed a marked inclination for cleaning their own wounds as well as those of other monkeys, thereby facilitating scar formation. To a great extent, every primate is capable of satisfying its own hygienic requirements by self-grooming. However, as some parts of the body are overlooked because they are beyond reach, self grooming is not sufficient. Consequently, social grooming becomes indispensable. Furuya [4] (in *Macaca fuscata*), Hutchins and Barash [10] (in *Lemur catta*, *Macaca niger* and *Macaca silenus*) have shown that social grooming is most frequently directed precisely to these areas. The same researchers have, in fact, noted a particular preference for back, nape-of-neck, head and flank grooming.

The idea that social grooming might also have social implications, besides a hygienic function, was expressed for the first time by Watson in 1908 [11]. He considered social grooming to be the basic form by which *Macaca mulatta* related to each other. In mother-offspring relations, grooming constitutes an indispensable form of tactile communication for the correct development of affective bonds [12-15]. Mother-to-infant grooming begins shortly after parturition. In *Macaca fuscata*, mothers groom their sons and daughters of all ages without distinction [16] although mother-to-daughter grooming diminishes significantly as the daughters grow but mother-to-son grooming does not. The daughters themselves are probably partly responsible for this drop in activity because, between the ages of 3 and 5, they establish new social grooming relationships with older females from other family groups. On the other hand, males between 3 and 5 limit grooming to their mothers and relatives [17].

Notwithstanding its stereotype nature, grooming behaviour is, to a great extent, acquired [4, 18]. Social deprivation experiments have, in fact, shown that infant socially deprived monkeys grow up with an incapacity to groom correctly [19]. On the other hand, once social grooming has been learnt, it becomes part of the young monkey's behavioral repertoire and the frequency with which it grooms its mother increases in relation to its development, but also as a function of sex and age. Young females are known to spend more time grooming their mothers than young males [4, 20]. The overall time that young females dedicate to grooming increases steadily over the first six years of growth whereas mother-grooming by young males reaches its maximum when monkeys are three years old after which it diminishes rapidly to disappear when the young males are approx. 5 years old [20].

Furthermore, from age 2 onwards, young females are seen to groom their mothers to the same extent that their mothers groom them. Males, on the other hand, never exchange mother-son grooming to such an equal extent [16].

Besides grooming bouts with their mothers, both adult and young subjects also engage in grooming with other subjects in different age and sex groups. However, the frequency with which one subject grooms with other subjects indicates that the choice of grooming partners is neither random nor coincidental: preferential grooming partners exist. For example, during the mating season, social grooming in free-ranging groups of Japanese monkeys increases noticeably between heterosexual couples [21], and high ranking males appear to prefer females as grooming partners. This would seem to be strictly connected to sexual behaviour [4]. Likewise, though less markedly, " sub-leader " males dedicate more care and attention to the body surfaces of females than to other group membres and younger males pay most attention to subjects between the ages of 1 ½ and 3 ½ years old. No interactions of this type are recorded between young males and the leaders or infants: this is probably due to group social structure.

As for grooming bouts between individuals of the same age and sex class, bout frequencies vary considerably, being very frequent among females, rather high among young adult males and minimal among leaders and sub-leaders [4].

The non-random distribution of grooming is one of the main arguments in favour of the social function of grooming. Most researchers agree on attributing an important social significance to it, and several indications have emerged from the literature. It has been suggested that social grooming may reduce social tension [3, 4, 22], that it may indicate and maintain dominance [23, 24], that it may foster group cohesion [14], that it may serve to stabilize, maintain and renew pacific relations [25], that it may facilitate social integration [18], that it may contribute to hierarchy stabilization [26], that it may reinforce social bonds [4, 27, 28] or that it may be the expression of pre-existing bonds [20]. With the intent of investigating the social function of grooming in *Macaca fuscata*, we have related it with male ranking and with behavioural patterns which are usually observed to precede social grooming. In carrying out our study, we have borne in mind the need, as underlined by Furuya [4], to overcome the shortcomings attributable to data covering only limited periods of the year. Consequently, we have extended our study to include both the mating and parturition seasons.

MATERIALS AND METHODS.

Our research observations were conducted in an area inside the Rome City Zoo. The area consisted of an approximately 700 m², oval-shaped pit, 5 meters deep and with a considerable number of vertical and horizontal structures (tree trunks, ropes, swings, ledges, concrete steps and three small pools) which enriched the environment substantially (Fig. 1). Our study was conducted on *Macaca fuscata* monkeys, 27 of which constituted a natural group captured on Mount Takasaki (Japan). The captured subjects were transferred to Rome Zoo on 4 May, 1977. The monkeys may, therefore, to a great extent, be considered to have completed their adaptation process. From the time the initial group, comprising 9 males and 18 females, was introduced into the observation environment, substantial changes have occurred. Some members have died and there has been a high number of births over the last three reproduction seasons. Table 1

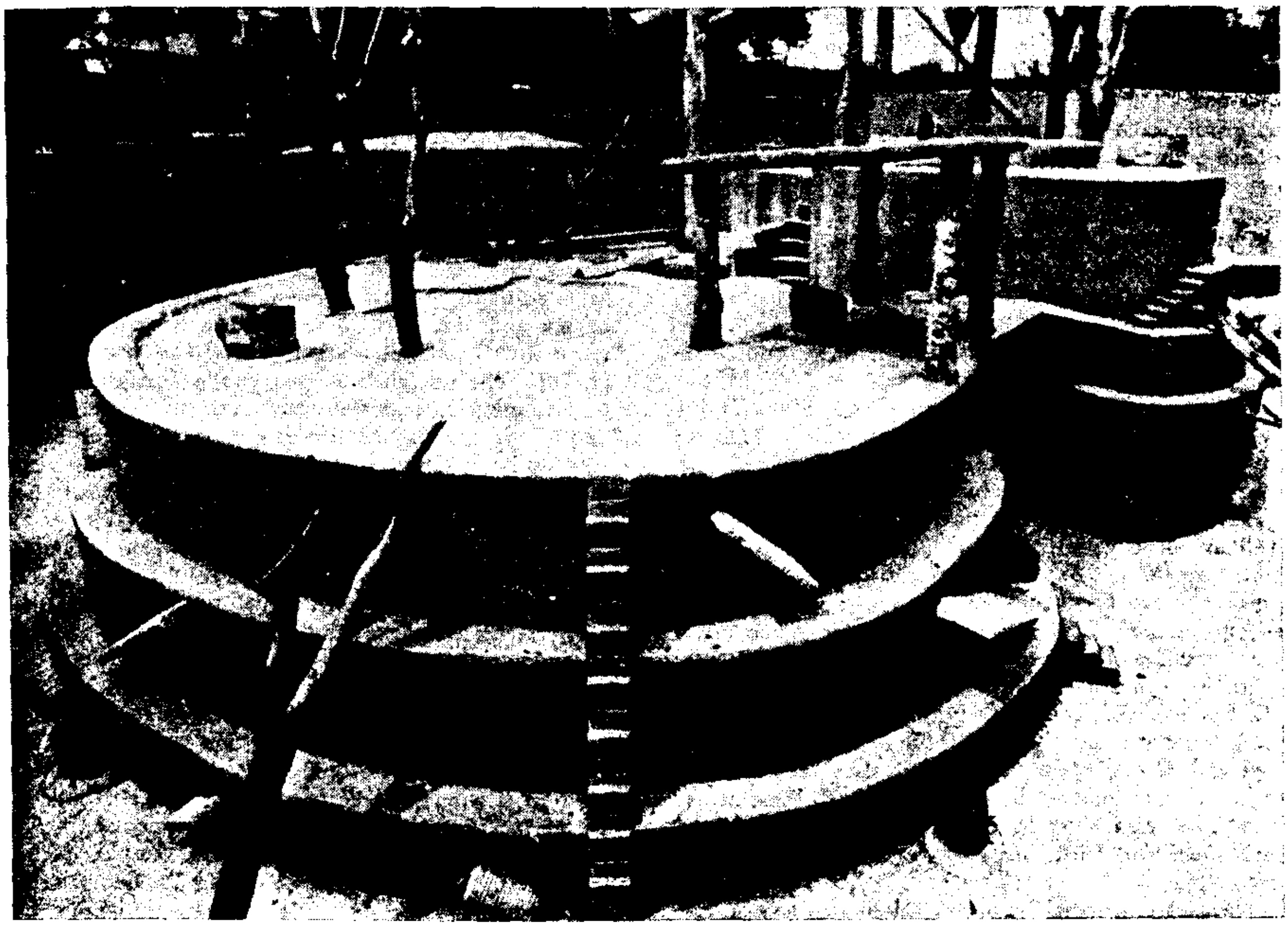

FIG. 1. - Observation environment.

Table 1. – *Group composition as of 7 January, 1980.*

Imported group				Born in captivity in		
♂♂	age	♀♀	age	1977	1978	1979
Aa	18	1a	12	Ij1	Oi1	Pi2
Ba	11	2a	10	18j2	Mj2	Qi3
Cs	7	3a	10	19j3	Ni3	Ri4
Ds	6	4a	10	Jj4	Kj4	22i6
Es	6	5a	9	20j5	Lj5	23i7
Fs	5	6a	9		21j9	Si8
Gs	5	7a	8			Ti11
Hs	5	8a	7			Ui14
		9a	7			Vi15
		10s	6			
		11s	6			
		12s	6			
		13s	5			
		14s	5			
		15s	5			
		16s	4			
		17j	3			

shows the composition of the Japanese monkey group as of 7 January, 1980, the day on which we began observations. Each subject is identified with conventional symbols: males with a capital letter and females with a number, followed by the initial of their respective age classes (a = adult, s = subadult, j = juvenile, i = infant). Age classings were according to Napier and Napier's criteria [21].

Individuals born from 1977 onwards were further identified by a number to indicate their respective mothers. Altogether, our observations covered a total of 45 subjects: 22 males and 23 females, of which there were 2 adult males, 6 subadult males, 5 juvenile males, 9 infant males and 9 adult females, 7 subadult females, 5 juvenile females and 2 infant females.

Observation Period.

Study observations were conducted in two distinct periods: one from 7 January, 1980 to 20 February, 1980 in the mating season and the other period from 21 April, 1980 to 12 June, 1980 during which time the first births occurred.

Observation Method.

The data gathered during the mating season were obtained by focal animal observations of 13 male subjects (2 adults, 6 subadults and 5 juveniles). No subjects younger than 1 $\frac{1}{2}$ years old, belonging to the class of infants, were considered because these did not exhibit grooming behaviour but were involved in non-reciprocal grooming bouts with their mothers and, to a much lesser extent, with siblings (personal observations). Furuya [4] reports similar observations for the same species in the field. Each daily observation session lasted 2 hours and each male was focussed on for one hour by one of the four observers who recorded the subjects interactions with other group members.

For each grooming bout, data on who approached whom, who initiated social grooming, who interrupted body contact by moving off to a distance further than an arm's length and grooming bout duration were all recorded. Recurrent pre-grooming behaviour patterns, such as mounting and particular postures that we have called "invitations to groom" were also recorded. "Invitations to groom" have been taken to include the following behaviour patterns 1) Subject A lies down near Subject B who begins grooming Subject A within a few seconds; 2) Subject A sits down in front of Subject B, who begins grooming Subject A within a few seconds; and 3) Subject A goes and lies down with back turned to Subject B and, more often than not, turns his head to look at B who is 4–5 meters away. If a bout of social grooming was suspended for more than 30 seconds and then continued, the interaction was counted as two distinct bouts. When bouts were suspended for less than 30 seconds, the interaction was counted as one, even if the subjects had moved in the meantime. In cases of mutual grooming, each partner's grooming activity was considered as a separate bout. The same applied for multiple grooming. At the end of February, males Gs and Cs were seriously wounded during agonistic interactions. As a result, Gs died and Cs was isolated from the group. During the same month, Op1 and Np3 graduated from the infant class into the juvenile class. Consequently, observations on males conducted during the second period focussed on 13 males, of whom 2 were adults, 4 subadults and 7 juveniles. As for the females, 3 became adults and one subadult. Consequently, female age class composition became: 12 adults, 5 subadults, 4 juveniles and 2 infants.

Furthermore, due to the drop in group allogrooming activity, data gathering focussed on behaviour patterns, i.e., each observer recorded all social grooming bouts that occurred in the pit sector assigned to him to observe. This method was found to be less accurate that the preceding one because some information concerning approaches, invitations and moving away from the partner was lost. On the other hand, the second method did enable us to record a sufficient number of grooming bouts that led to good statistical processing and to a comparison with data gathered during the first observation period.

In both observation cycles, displacements in which Subject A approached Subject B and sat, or stopped for a moment beside or on the same spot as B, who moved away either simultaneously or very shortly thereafter, were recorded. Agonistic interactions in which subjects exhibited at least one kind of threat behaviour, chasing or physical assault, as described by De Waal, Von Hoof and Netto [29] for *Macaca fascicularis*, were likewise recorded.

RESULTS.

On the basis of data gathered for dyad agonistic interactions and displacements, two linear dominance hierarchies were worked out for each observation period. When compared, these two hierarchies were found to match exactly. Though displacement matrices reveal perfectly *linear* hierarchies, matrices for agonistic interactions show some inversion. In the first cycle hierarchy, these inversions appeared in connection with Jg4 e Ig4, 9th and 10th-ranking coetaneous juveniles, respectively, and 5th-ranking male subadult Gs. It may be worth noting that Ig4 and Ig4 were both sons of high-ranking females and were often seen to interact in play, social grooming and other forms of contact. In the second cycle, only one inversion was noted and this involved the same Jg4 and third-ranking male Ds. Fig. 2 shows the dominance hierarchies for the two observation periods. The second, non-mating-season period hierarchy, exhibits some modifications due to the absence of subjects Cs and Gs and the rank shifts of Ba and Jg4. More than a promotion, Bs's rank shift should be considered as a reacquisition of the position previously occupied, as shown in an earlier study on the same group of monkeys [30]. In the case of young Jg4, son of dominant female 4a, it is interesting to note that he frequently engaged in play and social grooming with dominant males Aa and Ba.

During the mating season, an average of 39 social grooming bouts per hour were recorded. During the following observation cycle, the figure dropped to 17.5 per hour. This decrease in social grooming is to be connected with a lower incidence of male-male interactions (from 12.2 to 6.7 bouts/h) and male-female bouts (from 26.8 to 10.8 bouts/h) during the second period. Especially noticeable was the drop in social grooming between males Aa, Ba and Ds and the adult females (from 10.4 to 2.5 bouts/h) and between mothers (1a, 2a, 4a, and 5a) and their young offspring (from 7.2 to 1.1 bouts/h).

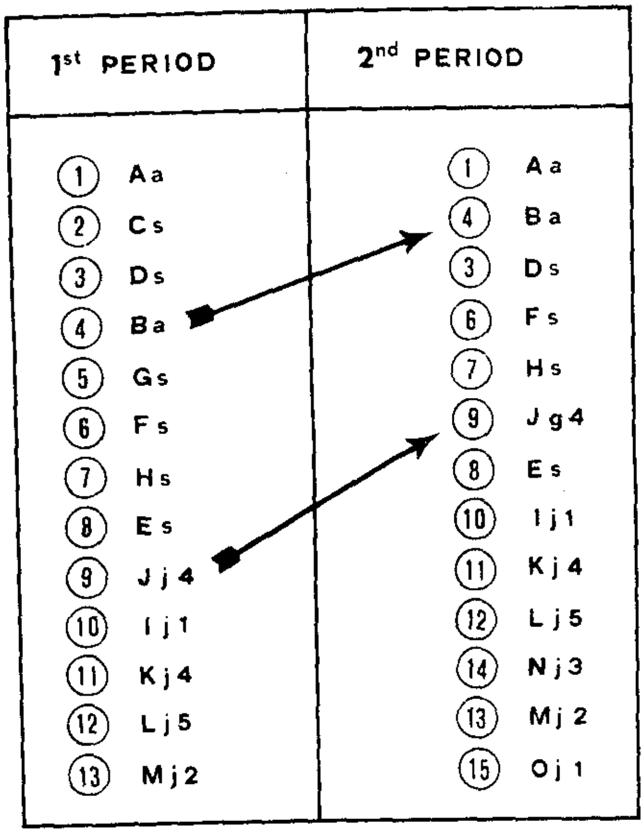

FIG. 2. - Male agonistic hierarchy. Arrows indicate rank variations between observation periods.

Figs. 3, 4 and 5 show various social grooming pair configurations. Groomers and groomees are listed in lefthand columns and headings, respectively. For grooming interactions to be considered " reciprocal ", it was sufficient for just one bout between a particular pair to be of this sort.

Social grooming among males.

During the mating season, 51 out of a possible 78 grooming pairs were formed among the males. Of these, 34 pairs exhibited exclusively non-reciprocal grooming activity, 12 engaged in some reciprocal sessions and 5 pairs reciprocated grooming but *not* during the same session. During the second period, 44 male-male pairs were noted; of these, 24 exhibited non-reciprocal behaviour, 18 engaged in reciprocal grooming and 2 pairs alternated grooming at least once, but in different sessions.

Fig. 3 shows the male-male allogrooming pairs that were formed in both data-gathering periods. Because subjects are ordered from top to bottom and from left to right in decreasing rank, the diagonal line highlights the direction of grooming interactions, showing, to the right of the diagonal, social grooming by a dominant subject on a subordinate one and, on the left of the line, grooming interactions performed by subordinates on more dominant subjects.

Non-reciprocal grooming interactions. - Fig. 3 shows that non-reciprocal grooming was exhibited mostly by low-ranking subjects who acted as the groomers of higher-ranking subjects. If we consider bands to the right and left of the diagonal, so as to comprise all possible male pairs of groomers and groomees no more than 3 rank position either side of the band, it may be noted that not only are most non-reciprocal interactions distributed to the left of the diagonal but that they occur most frequently outside the aforesaid band left of the diagonal. This distribution pattern was recorded in both observation periods but appeared most distinctly in the first period.

Reciprocal grooming interactions. - Unlike the pattern for non-reciprocal grooming, bouts of male reciprocal grooming occurred mostly between near-ranking subjects. This appears graphically in the form of an obviously symmetric distribution of dyads clustered around the main diagonal and within the aforementioned lateral bands (Fig. 3). Fig. 3 also reveals the rare cases of high-ranking groomer - lowranking groomee interactions. Another relevant aspect to be noted from Fig. 3 is that, during the first period of observation, dominant male Aa engaged in no social grooming with the other males of the group. This fact appears to be a major confirmation of our observations made in a previous study and would seem to be connected with a characteristic sexual activity which induced the alpha male into establishing a succession of consort relationships with adult and subadult females during the mating season, each relation lasting for a few days.

To conclude, reciprocal grooming bouts were observed to occur almost exclusively between near-ranking males, whereas non-reciprocal grooming was

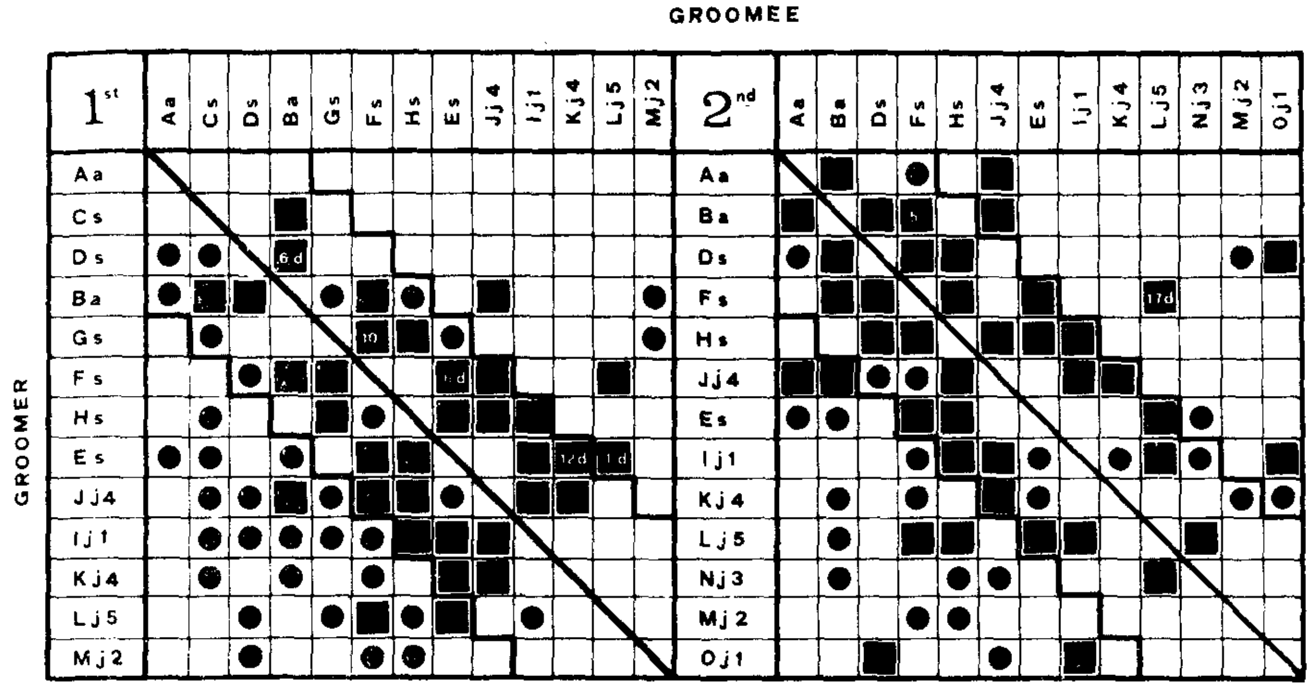

FIG. 3. – Social grooming interactions between males during the two observation periods:

● non-reciprocal interactions;

■ – reciprocal interactions;

5 – non-immediate reciprocal interaction. The number indicates the minimum time lapse (minutes or days) in which grooming was reciprocated.

exhibited mostly by lower-ranking males acting as groomers of higher-ranking members. This was noticed in particular during the first observation period.

Male-to-female social grooming.

Of the 50 male-female dyads which formed during the first period out of the 273 possible combinations, only 17 pairs exhibited interactions in which grooming was performed exclusively by the male. During the second period, 16 of the 43 social grooming pairs never exhibited any form of reciprocal grooming (Fig. 4).

Non-reciprocal interactions. – The number of non-reciprocal male-female social grooming pairs did not vary from one observation period to the next although partners did change in all but two cases. As for the distribution of this type of interaction, it may be noted that male adults and subadults, and female subadults and juveniles never interacted according to this pattern in either of the two data gathering periods. Male subadult Gs, absent in the second period, exhibited a particular case in that he engaged in exclusively non-reciprocal behaviour and only with female 3a.

Reciprocal interactions. – During the mating season, the four highest-ranking males showed particular care and attention in their exclusive grooming of adult females. These females were also very thorough in caring for their infant and juvenile offspring, the offspring frequently returning similar grooming attention to the mother. Juvenile females were often seen to interact with juvenile males and especially with their brothers. It seems particularly interesting to note that adult males never engaged in reciprocal or non-reciprocal grooming with either subadult or juvenile females in either period of our study. Another point is that, apart from during the mating season, males Hs and Es had no grooming interactions at all with any of their potential partners.

Female-to-male social grooming.

Of the 273 possible female-male pairs in the first period of observation, only 72 combinations were observed in grooming sessions. In 39 cases, the females exhibited exclusively non-reciprocal grooming behaviour. In 25 pairs, males groomed at least once and in 8 cases reciprocation was not immediate because grooming roles were exchanged in subsequent social grooming sessions. During the second period, the number of couples dropped to 50. This was attributed mostly to the considerably lower number of non-reciprocal grooming dyads (only 23). In 24 dyads, on the other hand, partners switched grooming roles as already described.

Non-reciprocal interactions. – During the mating season, subadult and juvenile females interacted with higher-ranking males via non-reciprocal grooming (Fig. 5). Even the young sons of the high-ranking females tended not to reciprocate the grooming attention received from the younger adult and subadult females. Although difficult to interpret, it is nonetheless interesting to note that subject Ds, third-ranking in the hierarchy, formed a considerable num-

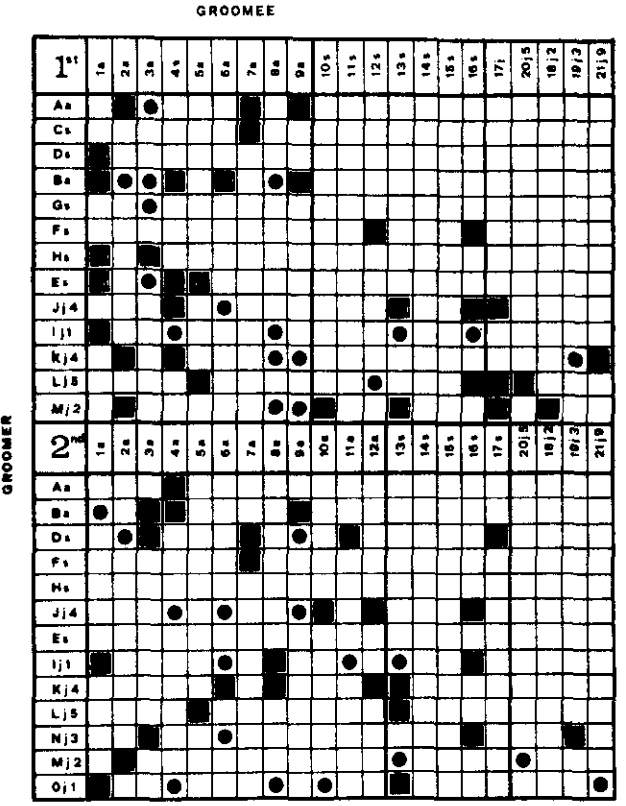

FIG. 4. - Male-to-female social grooming during the two observation periods:

● = non-reciprocal interactions;

■ = reciprocal interactions;

■ = non-immediate reciprocal interaction. The number indicates the minimum time lapse (minutes or days in which grooming was reciprocated.

ber of social grooming pairs with females of the group in which grooming was exhibited exclusively by the latter.

Reciprocal interactions. - Obviously, the comments reported above for male-to-female social grooming interactions still hold true. Furthermore, during the second period of observation, some reciprocal grooming relationships disappeared, particularly those between adult females and the highest ranking males.

One item of considerable interest was the nearly total absence of social grooming between females and male Gs during the first period. As mentioned above, Gs was found dead in February. Outside the mating period, the formation of allogrooming dyads was seen to cut across different age and sex classes in a remarkably different way, there being a more uniform distribution of reciprocal and non reciprocal interactions.

Behaviours prior to social grooming interactions.

For grooming to occur, the space between one subject and the other must become zero. In other words, if grooming partners are not already in physical contact, they must make contact. The approaching of one subject towards another may, therefore, be considered as the initial pattern for each social grooming sequence. Diminishing the distance between subjects until one touches the other may be an apparently freely chosen act or the behavioural response to a request from the other partner, said request being expressed by peculiar behaviour patterns such as invitations or, in the case of male-interactions, mounts. Analysis and evaluation of approaches, invitations and mounts supply important information for the understanding of social grooming and its social function; the information becomes particularly important if related to sex, age and status of subject.

Approaches.

Male-to-male. - 161 male-to-male approaches were recorded in the first period and 118 in the second. 128 out of 161 approaches in the first period showed that the subject approached was also the one to initiate grooming whereas in only 33 interactions was he the groomee. Corresponding figures for the second period were 84 and 34, respectively. During the first cycle, the approach-and-groom sequence was exhibited much more by subordinate subjects than by dominant ones (95 vs 33). On the other hand, dominant subjects were the most active approach-and-be groomed subjects (25 vs 33). Likewise, during the second cycle, subordinates seemed to have the prerogative on approach-and-groom sequences (65 subordinates vs 19 dominant subjects) but the greater tendency of dominant subjects to approach lower-ranking subjects and be groomed was not confirmed (18 vs 16). Fig. 6 refers to male-male dyads. Approachers are listed in the left hand column. Arrows indicate whether the approacher was most frequently (>66% of approaches) the groomer or the groomee. The equal sign indicates pairs that did not exhibit such a net difference (>66%) in groomer: groomee roles. The figure shows that it was far more common for a subject to approach and groom rather than be groomed in both periods. This was particularly true where lower-ranking subjects were the ones to approach. The tendency to approach

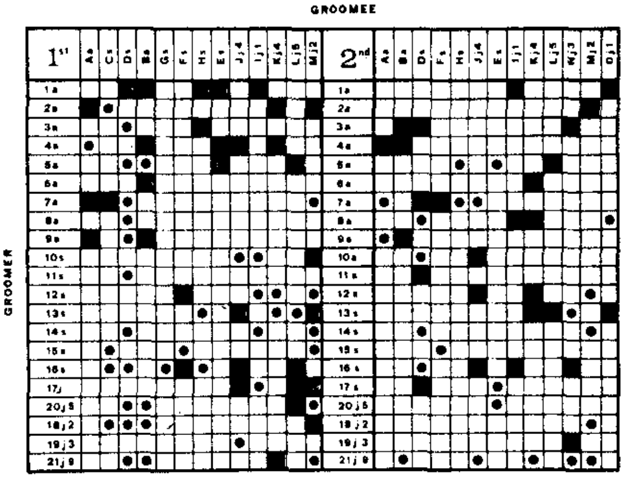

FIG. 5. - Female-to-male social grooming in the two observation periods:

● = non-reciprocal interactions;

■ = reciprocal interactions;

■ = non-immediate reciprocal interaction. The number indicates the minimum time lapse (minutes or days) in which grooming was reciprocated.

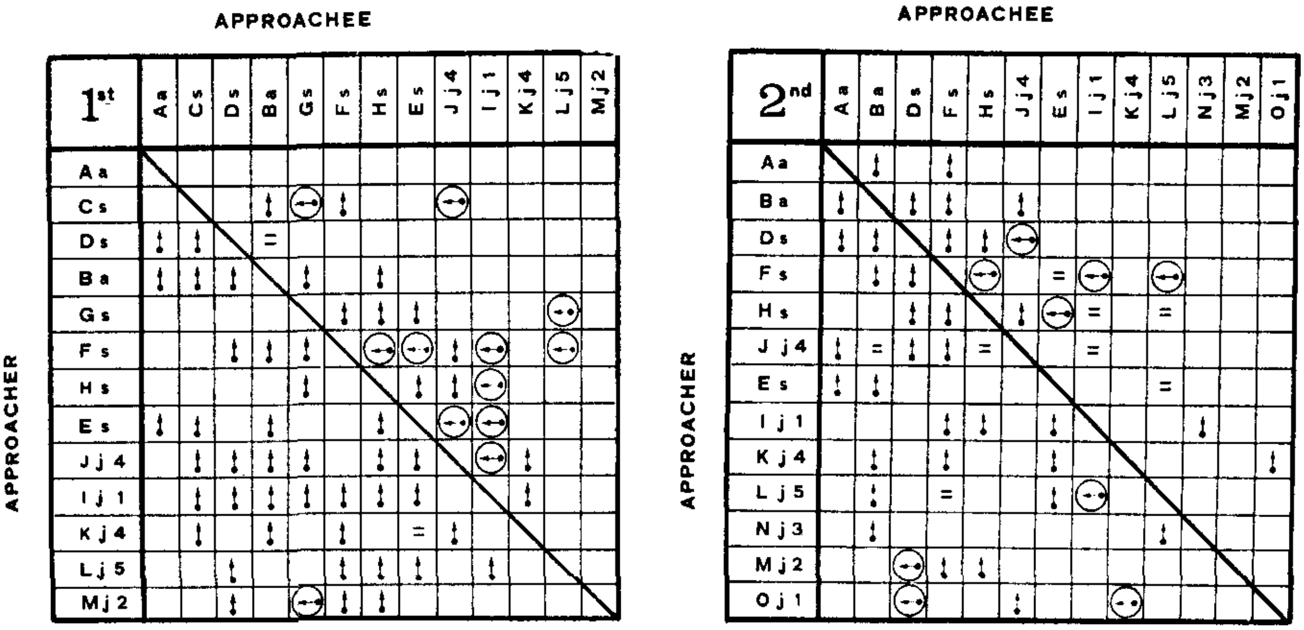

Fig. 6. – Approaches that preceded social grooming between males in the two observation periods. Arrow direction indicates the recipient of grooming (groomee) for at least 66 % of approaches. Symbol = indicates cases in which this percentage was not reached.

and groom seemed to be reversed only when the approacher was a dominant subject or, more rarely, when the approacher was a juvenile subordinate of very low rank.

Male-to-female approaches. – During the mating season observations, a total of 181 male-to-female approaches were noted. In 106 cases, the male also became the groomer whereas the female groomed in the remaining 75 cases. This latter pattern occurred most frequently whenever a male juvenile was seen to approach his mother. During the second data-gathering cycle, 61 out of 84 male-to-female approaches also resulted in male-to-female grooming whereas, in the remaining 23 interactions the males were the groomees. During the first period the general tendency to approach-and-groom was reversed in a high number of dyads (21 out of 56) whereas the second period showed a return to the approach-and-groom tendency, the approach-and-be groomed sequence being recorded for only five pairs of a total 27.

Female-to-male approaches. – During the first period of observation, females approached males to interact with them for a total of 157 times. In almost all cases, i.e. 141, the female proceeded to groom, the other 16 interactions showed the male to be the groomer. During the second period, approaches by females dropped to 113; of these, 90 resulted in female groomer interactions and 23 female groomee interactions. In considering grooming pairs, females were seen to exhibit a strong tendency to approach-and-groom. In only 7 out of 55 grooming pairs did the female receive grooming once contact had been made. Likewise, during the second cycle, in only 10 out of 36 dyads was the male the groomer.

Invitations to groom.

The approach-and-be groomed sequence occurred 33 times during the first observation period, thereby outnumbering the approach-and-groom sequence. It is interesting to note that in most, of these cases (21/33), one subject would approach another and would then assume an inviting posture, soliciting an immediate response from the approachee. During the second period, in only 8 out of 34 cases did the males, before being groomed, exhibit invitation behaviour. This variation may possibly have been due to the different method used in collecting data. Invitation-to-groom behaviour was seen not to be limited to the interval between approach and grooming but was also seen to be exhibited to induce the grooming partner to approach and then groom the inviter. Fig. 7 indicates all dyads in which one male invited another to groom him according to both possible sequences of approach-invite-be groomed or invite-be approached-be groomed. The figure shows the dominant subject to be the one to usually exhibit invitation behaviour. During the first period, this pattern occurred 16 times out of 21; during the second period, 9 times out of 13.

Male-to-female and female-to-male invitations. – During the mating season period of observation, heterosexual social grooming interactions were seen to be generally initiated by males (32 times out of 41), and in particular, it appeared that high-ranking males were the ones to induce the females to groom them by exhibiting invitation behaviour. During the second cycle, no substantial difference in invitation-to-groom behaviour was noted between the two sexes (15 invitations by males and 19 by females).

Male-to-male mounts.

During our study, we often observed a male subject exhibit mount behaviour to another male partner and then, immediately thereafter, engage in social grooming with the same partner. 20 and 22 mounts were recorded during the first and second observation periods, respectively. Most mounts were performed

INVITEE

INVITER

1st	Aa	Cs	Ds	Ba	Gs	Fs	Hs	Es	Jj4	Ij1	Kj4	Lj5	Mj2
Aa													
Cs				*	*			*					
Ds									*				
Ba			*						*				
Gs							*					*	
Fs				*			*	*				*	
Hs									*	*			
Es						*	*		*	*			
Jj4										*			
Ij1											*		
Kj4													
Lj5													
Mj2					*								

INVITEE

INVITER

2nd	Aa	Ba	Ds	Fs	Hs	Jj4	Es	Ij1	Kj4	Lj5	Nj3	Mj2	Oj1
Aa						*							
Ba			*	*									
Ds													
Fs							*	*					
Hs							*	*		*			
Jj4					*								
Es										*			
Ij1													
Kj4													
Lj5				*			*	*					
Nj3													
Mj2													
Oj1													

Fig. 7. – Male-to-male pairs, formed in the two observation periods, in which at least one event of allogrooming was preceded by an invitation.

by dominant males on lower-ranking males, i.e., 13 times in the first period and 20 times in the second.

Fig. 8 reports the pairs in which mounts occurred. Arrows indicate whether the mounter then went on to groom or to be groomed. An equal sign indicates the only dyad in which both cases were recorded. It may be seen from the figure that, with only a few exceptions, of the two it was always the dominant subject to be groomed after mount interaction, independently of whether he had been mounted or, as was much more frequent, he had mounted. The only subjects to groom lower-ranking subjects after having mounted them were, in both periods, subadult male Hs who groomed juvenile male Jg4 (son of the dominant female) and, outside the mating season and for 5 times, alpha male Aa who groomed adult male Ba, second in the hierarchy.

Discussion and Conclusions.

During our observations, we had occasion to notice the care and attention with which the Japanese monkeys studied perform grooming. The *Macaca fuscata* group of the Rome zoo exhibited a marked readiness to perform social grooming, engaging in this activity especially during the early afternoon and on sunny days. This is not particularly surprising seeing that "preferential grooming hours," corresponding to the middle hours of the day, seem to be fairly common among primates (viz. *Macaca fuscata* [4], *Presbytis johnii* [18], *Macaca radiata* [31], *Hylobates lar* [32], *Macaca arctoides* [33]).

Most social grooming bouts began with the grooming of the back, proceeding to the nape of the neck, the head and then the flanks. On some occasions, particular grooming behaviour, which was of considerable importance for its undoubtedly hygienic significance, was also exhibited. One of these behaviour patterns consisted in delicately raising the eyelids of the grooming partner and cleaning the eye socket area. Another particular pattern was directed to the mouth area where a careful and through cleaning of the gums and teeth was performed. In general, partners appeared to be calm and relaxed during grooming interactions, the groomee particularly so. On several occasions we did note, however, that subordinate males or females would approach adult males very carefully, ensuring first that their prospective partner was in the mood to be groomed. To be certain, however, the lower-ranking subject would brush the dominant one's fur very delicately with a forepaw and, if the more dominant male appeared to accept the initiative, the lower-ranking subject would then slowly and cautiously begin cleaning the fur.

In the group of monkeys we studied, choice of social grooming partner was found not to be random, unlike the observations on *Macaca radiata* by Simonds [9]. Grooming partner selection was found to be influenced by various factors, such as age, sex and parental relations, as already seen among Japanese macaques by Furuya [4] and Kurland [16]. Sade [25], Kaufman [34], Rosenblum [35] and others have found that consanguineous subjects, and females in particular, spend long periods in physical contact, exhibiting considerable social grooming activity. This pattern was borne out in our study by the observation of frequent social grooming sessions between mothers and their sons and between these sons and their older sisters. Outside the mating season, these interactions diminished noticeably. In our opinion, the drop observed was attributable to the progressive detachment of young males from their mothers, to the mothers' particular physiological state as they approached parturition and, above all, to the birth of offspring of adult females 2a and 5a. Arrival of the newly born is always an important event in a group of monkeys and the females are intensely engaged in the relationships to be established with their offspring. As a result, the juvenile males tend to move away from their mothers with increasing frequency and spend much of their time playing with other monkeys of their same age, interspersing games with bouts of social grooming. Notwithstanding the fact that the ties between mother and juvenile male weaken, the mother always tries to maintain visual contact with the son as far as possible and to intervene readily in case of necessity. During our observations, we frequently saw one juvenile male be attacked by other members of the group and solicit his mother's intervention by emitting high-pitched vocalizations. The mother would rush to the scene immediately, take his defense and, after a brief hug, would begin to groom him. On the strength of these observations, we had the impression that grooming diminished a state of general tension and excitement in the male juvenile.

During the mating season, adult males and females of *Macaca fuscata* form consort pairs that stabilise for a few days. During this time consorts appear to support each other in cases of agonistic interactions with other members of the group [36]. During the same time, copulation occurs repeatedly but, for ejaculation to occur, the male must cover the female repeatedly and, between one copulation bout and the next, various minutes may pass, each bout being limited to just a few pelvic thrusts. Between one copulation bout and the next, consort pairs were frequently observed to engage in reciprocal grooming sessions. This fact induces us to consider this pattern of social grooming as a ritualised strategy to maintain and prolong contact with the sexual partner. We therefore agree with Goosen [37], who demonstrated a direct correlation between proximity and social grooming in *Macaca arctoides*. The noticeable, second-period drop in intense social grooming activity between high-ranking males and adult females observed during the mating season shows the close correlation between social grooming and consort behaviour, thereby reinforceing the idea that consort grooming may be considered as a strategy to prolong proximity. In our opinion, the mating season allogrooming has the primary function of preventing the accumulation of tension that may derive from prolonged consort contact. Michael and Herbert [38], Kaufman [34], Chalmers [39], Bernstein [40], Rhine [41], Lindburg [14] and Drickamer [42] have also revealed the existence of a characteristic increase in heterosexual grooming during menstrual cycle fertility periods. Carpenter [27], on the other hand, suggested that the female might recur to grooming to deviate male aggression and elude his attacks. From a quantitative analysis of the social grooming interactions between males, there was seen to be a high number of social grooming interactions during the mating season and that, during the following period, social grooming diminished considerably. A similar pattern was also noticed for the frequency of agonistic interactions and this would tend to support those that suggest the existence of a correlation between aggressive behaviour and social grooming activity [22, 43–45], and contradict those that contend that the evidence in favour of such a hypothesis is inadequate [14, 23, 34, 41, 46–49].

On the other hand, grooming among females in many species of primates is generally quantitatively greater than among males [3], though the same tendency does not appear to apply to aggressive behaviour. Goosen [50] notes that a positive correlation could exist between social grooming and agonistic behaviour, by which grooming would increase with the increasing of aggressive attacks. A negative correlation is also feasible, because, as grooming interactions increase, aggressive interaction frequency would appear to drop. Consequently, Goosen seems to be right in stating that the search for a relationship between the two activities is rather difficult, because, so far, no one has been able to state how much agonistic behaviour a subject could exhibit: likewise, it is even more difficult for us to determine how much grooming is necessary to inhibit the onset of aggressive behav-

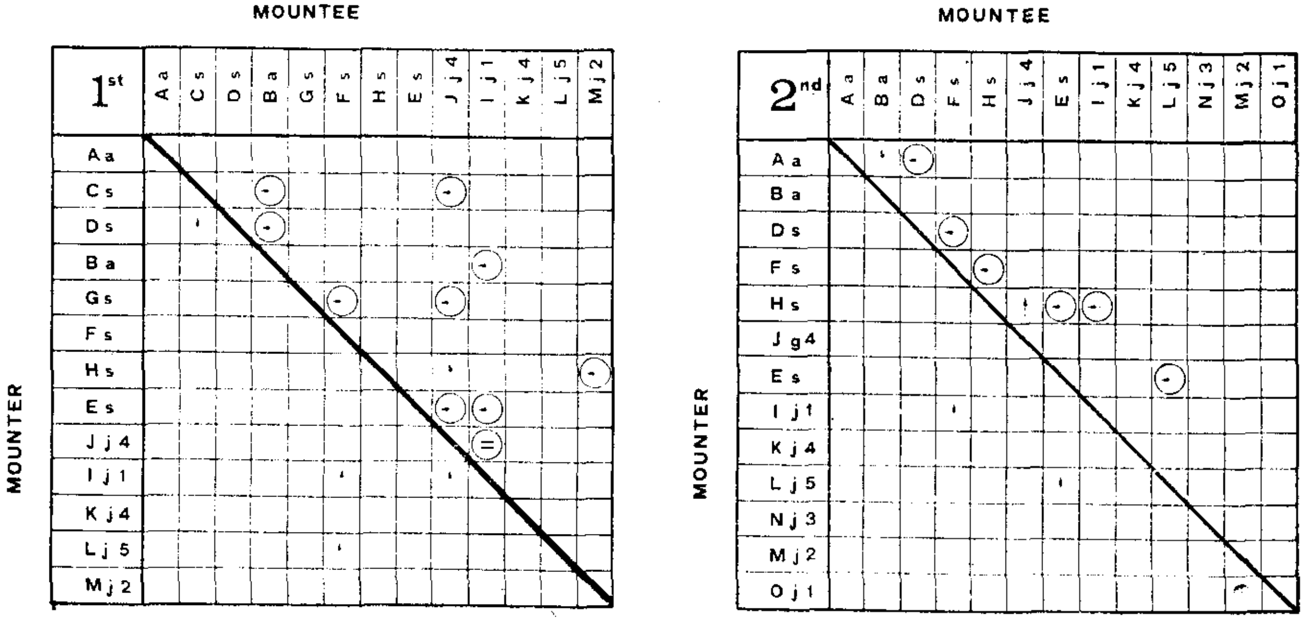

FIG. 8. – Male-to-male pairs, formed in the two observation periods, in which at least one event of social grooming was preceded by a mount interaction. Arrow direction indicates groomee for at least 66 % of mounts. Symbol = indicates cases in which this percentage was not reached.

our. We do not exclude that social grooming may influence the frequency of aggressive interactions but we do sustain that this influence cannot occur as a direct and immediate effect but rather as a secondary consequence. Much of our data also appears to be in contrast with the idea that grooming is inhibitory of aggressive attacks. Near-ranking subjects engage in reciprocal grooming but, according to the hypothesis mentioned, it would seem logical to expect both partners of a reciprocal grooming bout to exhibit a marked tendency to exhibit aggressive patterns. Yet this supposition seems rather implausible because, were this the case, each subject, and the lower-ranking one in particular, would do everything possible to avoid the grooming partner. Our observations, on the other hand, do not bear out this case because we noted that it was usually the subordinate monkey which approached the higher-ranking one to groom him. When a dominating subject approached a lower-ranking one, in order to be groomed, more often than not, it would communicate its peaceful intentions by exhibiting invitation behaviour. This is, however, hardly surprising if we consider that primate partners appears to be relaxed during grooming bouts [2, 18]. For a more satisfactory explanation of social grooming, an alternative hypothesis to that of correlating grooming activity and aggressive behaviour might be that of hypothesizing the existence of an interdependent relationship between social allogrooming pattern and tension levels. Mason [51] suggests that social grooming may act as a arousal reducer. In our opinion, social grooming not only reduces an overall state of excitement, it also acts as a stabilising effect on low level tension. Consequently, an approach between males of similar social status may be viewed as an approach between low tension subjects, and reciprocal grooming may be seen as the activity which prevents tension from increasing, thereby enabling partners to maintain prolonged contact. Analysis of non-reciprocal interactions reinforces the hypothesis of a correlation between social grooming and tension levels and contrasts with the idea of a presumed correlation between grooming and aggressive behaviour. The idea that a male juvenile could approach an adult without the latter's having expressed an explicit request to the former by means of invitation behaviour or mounting, and risk the possibility of being attacked would not seem very logical. Our studies show that lower-ranking subjects tend to approach high-ranking males just in moments of great relaxation, if necessary taking care to ascertain that the higher-ranking males are receptive to being groomed as described above.

Grooming also appeared to have a soothing effect, as was borne out by our above-mentioned observations of a subject which had just been involved in a agonistic bout, and was therefore in a state of evident excitement, being groomed and soothed. Mother-son grooming interactions are examples of such a soothing function of grooming that the mother performs on her son and viceversa. Clearly, these cases do not conctradict our hypothesis because, thanks to the particular nature of their relationships, the subjects in question do not risk being attacked when they approach. As for prolonged proximity, it must provide some advantages, otherwise, what explanation could there be for some individuals that are prepared to risk being attacked or obliged to submit to conditioning by responding to invitations and interactions. Trivers [52] suggests that a possible consequence of grooming may be that of coalition formation. Poirier [18] underlines how he never once observed acts of aggression on *Nilgiri langur* subjects that were involved in social grooming. Likewise, the attacks occurred very rarely in our group of Japanese macaques.

Lastly, the prolonged grooming of, or proximity with, a dominant subject may be occasion for a juvenile to acquire higher rank in the dominance hierarchy. This was observed with male Jg4 in the group we studied. In fact, during the second period of observation Jg4, who achieved a fair promotion in rank, was seen to interact in reciprocal and non-reciprocal grooming sessions with dominant males.

To conclude, the tension-reducing and tension-stabilising function hypothesised for social grooming would seem to underlie an overall reduction in group tension, as stated by Terry [26]. By prolonging subject proximity [50], social grooming would therefore seem to facilitate group cohesion [28] and foster conditions that seem to diminish the chances of agonistic bouts occurring.

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Primate socialization variables

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INTRODUCTION.

This paper attempts to isolate some early variables affecting primate behavioral development in the hope of eventually constructing an evolutionary framework. Until recently, potential contributions of biologically oriented explanations of social development and social behavior were largely ignored or misunderstood. However, as Simmel [1] has noted, as an interest in the biological aspects of socialization has increased and its importance been recognized, there has been an acceleration of interdisciplinary research and communication. Field investigators have spent considerably more time viewing the end results of the socialization process rather than concentrating on the process itself. Some investigators have attempted to systematize the rapidly accumulating data by relating ecology to social behavior and social organization. However, to understand the variables contributing to the diversity of nonhuman primate societies and social behavior, a wider framework is needed. Since most primates live in stable, complex, bisexual, year-around social groups, one fruitful avenue of research would attempt to discern how the socialization process affects behavior, and through this behavior, the social order. Because of problems inherent in the field situation, studies in the laboratory, whereby constant conditions can be maintained and elaborate testing procedures can occur, are requisite. The total web of social learning, sensorimotor coordination, and the reflex system can only be tentatively described in the field. Therefore, if the complex factors determining the behavior of mature animals living in social groups are to be evaluated, detailed experimental analysis is necessary. Laboratory and field studies must supplement one another and, wherever possible, hypotheses about social learning generated from field observations of socialization must be tested under controlled laboratory conditions.

More specifically, this paper attempts to provide a definition of the socialization process; reviews those biological factors influencing socialization; discusses the relationship between the learning and socialization processes, the interaction between socialization and the social structure, the affect of kinship ties on socialization, the infant-adult male interactive relationship, the role of play in the socialization process, the mother-infant dyad, and the weaning process.

SOCIALIZATION DEFINED.

It is often harder to define socialization than it is to isolate consequences. A key problem with nonhuman primate studies, especially field studies, is the lack of longitudinal behavioral data. For example, most field studies last from twelve to twenty-four months, hardly enough time to comprehend socialization and learning processes. Therefore, much of the theoretical framework was originally drawn from studies of *humans* [2-6] *dogs* [7-9] and *cats* [10]. This is a highly diverse group; however, that there are similarities in the mammalian socialization process is apparent [11]. One result of the lack of data from primate behavior led to borrowing concepts from other works; early socialization studies were strongly influenced by the critical periods hypothesis. However, this scheme cannot be completely superimposed upon the nonhuman primates. Primates live in highly complex, bisexual, year-round social groups, and through an animal's learned social relationships with group members, individuals learn how to interact and behave within their social group. Socialization refers to the sum total of an animal's past social experiences which, in turn, may be expected to shape future social behavior. " Socialization is that process linking an ongoing society to a new individual. Through socialization, a group passes its social traditions and life-ways to succeeding generations " [12]. The socialization process ensures that adaptive behavior will not have to be discovered anew each generation [13]. This definition has its critics [14]. The definition suggests a unitary socialization process when, in fact, the development of social behavior is multidimensional, consisting of a large number of processes that are temporally separated by continuously changing sets of determining variables.

The socialization process simultaneously refers to the external stimuli received by an organism, the individual nature of the process, and to the end product or consequences [12, 13, 15-18]. Each individual is the outcome, the result, of a given socialization process and we must look at the variables influencing this output both vertically (through time) and horizontally (in terms of social interactions). The results, or consequences, of socialization not only depend upon the original genetic material of the individual [19, 20] and the degree to which many other factors permit realization of that potential; they are also influenced by the behavior of the adults and peers with whom the individual is or has been in regular contact [21–26]. Socialization variables have a differential effect depending on the time and level of the socialization process [17]. We must investigate how an animal adapts to different developmental situations. A nonhuman primate must learn to adapt to three conditions: (1) it must learn to become a member of its species, (2) it must learn to become a member of a particular social group and we must remember that social groups exhibit great variability, even intraspecifically, and (3) it must adapt to its environment [27]. These adaptations can be accomplished in many ways and we should be looking into more specific adaptive pressures at different points in an animal's life. At any one point in time animals may be unable to meet all these pressures.

Primate learning and socialization.

Among other features, the nonhuman primate socialization process is influenced by the facts that these are social living animals, that they have a prolonged period of immaturity, and that the mother nurses the young. These traits are characteristic of mammals generally. Bekoff [11] emphasizes the idea that many, if not all, aspects of primate social behavior and organization are not unique, but also occur in nonprimate species. There is a need for detailed, naturalistic, descriptive information at all mammalian levels. Such comparative studies are essential for generating valid concepts and explanations of socialization processes.

The fact that most primates are social animals residing in highly complex, bisexual, year–around social groups of varying size and composition is crucial. The social group has long been the primate niche, indeed, the social group has long been the mammalian niche. Group characteristics vary interspecifically, however, most primates spend part of their life in close association with conspecifics. Within the social group an animal learns to express its biology and adapt to its surroundings. Differences among primate societies depend upon the species' biology and, to a great extent, upon the circumstances in which animals live and learn. The composition of the social group, the particular balance of interanimal relationships, constitutes the social environment within which youngsters learn and mature. Because of the highly social nature of nonhuman primates we must view groups, as well as individuals, as the adaptive units of the species [12]. Social living places a premium upon learning. Although many animals have social behaviors, many behaviors are largely dependent upon fixed and innate cues. On the other hand, primates respond not only to fixed cues but to learned behaviors. Since there is considerable individual and behavioral variability within the social environment, primates must be flexible and discriminating in their social responses [28]. One highly important and adaptive trait common to nonhuman primates is the degree of behavioral flexibility and adaptability [29–31]. Since most primates live a rather complex social life, they must learn to adjust to one another. Compared to most of the animal world, primate societies may have the greatest differentiation of learned social roles. Social living is requisite for the younger primate to perform effectively as an adult. Animals with restricted social experiences, those raised in isolation or in unnatural conditions, exhibit some degree of social maladjustment, most especially in mothering, sexual, grooming, and aggressive behaviors [32–35]. Laboratory studies suggest that the full development of an animal's biological potentialities requires stimulus and direction from social forces such as are usually supplied from the social group [35–38]. While troop, or social life is important, it must be cautioned that not all primates have the " same degree " of social life (i.e., orang–utans [39] and Nilgiri langurs [12,40]. Why then do some nonhuman primates still live in a social group if the animals do not take advantage of the opportunities of group life in the form of protection, grooming, and play? Washburn and Hamburg [41] suggest that a primary reason for group existence is learning, the group being the center of knowledge and experience far exceeding that of its individual constituents. Within the group experience is pooled and generations linked–troop traditions are more advantageous then individual learning in many situations [12, 16, 28, 42]. Tradition pools individual experiences and is superior to individual learning if the new behavior is difficult to acquire individually in direct interaction with the environment [12]. Troop tradition is based upon a long life expectancy (a primate biological trait) and a leading role for older animals (in fact, primate societies may be loosely viewed as gerontocracies). Within the social context the animal is socialized, learns what foods to eat, who are existing predators, and the correct mode of behavioral interaction. Primates learn their mode of survival by living in a troop where they benefit from the shared knowledge and experience of the species [15, 43]. The primary reinforcement for all normal primate learning is the social context, the group in which the infant is born and nurtured. Even independent sensorimotor activities like observing, manipulating, and exploring receive some facilitation, or inhibition, from the group setting [44, 45]. Contrasting social structures impose differences in learning patterns leading to individualized behavior formation. This implies that group modification will alter the socialization process yielding individuals with different behaviors [12, 26, 43, 46, 47]. Flexibility and adaptability, learning to coexist within the social context and learning one's role in the social order, is at an optimum for primates. Primates inherit an ease of learning. Primates learn to be social, and under normal circumstances individual learning almost always occurs [41]. The development of social transactions between members of primate groups is dependent upon the development of cognitive abilities in early infancy. Cognitive skills, rather than strictly physical attributes and motor abilities, are of great importance in the integration of infants into primate societies [19, 20]. Presumably, in most higher mammalian social systems, and, particularly in primate social systems, individual behaviors are controlled by a continuous process of social learning arising from group interactional patterns. Learning to act according to social modes is extremely important, for animals whose behavioral traits do not conform sufficiently to group norms are less likely to reproduce and may be ejected. Social selection of this type apparently has a strong stabilizing influence upon the genetic bases of temperamental traits and motivational thresholds [48]. There are various social learning processes involved in these conformities and although learning processes vary interspecifically, there are consistencies. Social facilitation and observational learning seem to be the most important [49].

BIOLOGICAL FACTORS INFLUENCING SOCIALIZATION.

Prolonged Immaturity. Primate socialization is influenced by certain primate biological characteristics. Washburn and Hamburg [41] suggest that group life is the sociological response to the primate biological adaptation of prolonged immaturity (it is, of course, possible that the situation is reversed, e.g., prolonged immaturity may be a biological response to group life). Prolongation of preadult life is biologically expensive, but a major compensation is learning. Despite restraints imposed upon the social order, the long infancy period is advantageous; " ... it provides the species with the capacity to learn the behavioral requirements for adapting to a wide variety of environmental conditions " [41]. One result of prolongation of youth is an extention of time available for learning and socialization. With retardation of growth and a longer period of immaturity, there is a clear tendency for individual experiences to play a more subtle role in shaping behavior into effective patterns (see i.e., [11]). An extended period of infant dependency enhances the amount and complexity of learning possible, while increasing opportunities to shape behavior to meet local environmental conditions. Flexibility of behavioral patterns may be one of the principal benefits of the longer dependency period [12, 13, 16, 30, 40, 43]. There appears to be a positive correlation between prolonged postnatal dependency and increasing complexities of adult behavior and social relationships. Prolonged youthfulness allows more time for contact with peers in the form of play and more time for adult contact which probably promotes the socialization process and helps integrate youngsters into the social group [50]. Prolonged nursing is related to prolonged immaturity. The fact that a primate mother normally bears one infant per parturition, and the fact that this infant is relatively helpless for varying lengths of time, promotes strong mother–infant contact. Furthermore, since the infant is relatively helpless, the mother is responsible for much of the early locomotion, carrying it about on her back or stomach (or in the mouth, as in some New World monkeys and prosimians). Many of the infant's early perceptions of the world are from the mother's back and stomach, serving to channel sensory input and setting the first stage in molding the infant's relations with other animals. Infants riding on the back or ventrum of dominant mothers witness different interanimal relations than infants riding on the back or ventrum of subordinate mothers.

Postpartum Activities. Certain immediate postpartum activities may help bind the mother and infant and vice versa. Perceptual data (i.e., [51]) suggest that infants relate to their mothers via visual and olfactory channels. Harlow's [36, 52] and Mason's [32, 38] work, among others, clearly shows that tactual senses are important in this early contact. However, there may be other factors " binding " the pair, i.e., the mother's cleaning of the infant. Among some mammals like sheep, rabbits and cats, a mother's postpartum licking and cleaning of her infant leads to proper maternal-infant attachment and to activities like proper bowel evacuation. Material on immediate postpartum primate activity is limited by the scant number of births witnessed; however, there are suggestions that a similar condition is found among nonhuman primates [53, 54].

Consumption of the afterbirth can serve a number of functions, i.e., the afterbirth might satisfy the mother's appetite for a few days which would allow her to give her full attention and energy to the infant. Consumption would also prevent an odorous source from possibly attracting predators. Such consumption may also help a mother recognize and relate to her infant and vice versa. Among prosimians and monkeys there is a rather consistent pattern in which the mother licks both herself and her infant clean soon after birth. Many primate mothers also consume the placenta and umbilical cord soon after expulsion. Loris [55], lemur [56], and galago mothers generally consume the afterbirth before directly attending to the infant. Similar patterns have been observed in some New World monkeys, i.e., Takeshita [57] notes that the third phase of squirrel monkey (*Saimiri sciureus*) delivery behavior involves consumption of the placenta. Hopf [58] notes that squirrel monkeys also consume the umbilical cord and Williams [59] reported that a woolly monkey may nibble the umbilical cord. Similar patterns emerge in Old World monkeys. Brandt and Mitchell [53] report that a guenon (*Cercopithecus erythrotis*) mother licked the infant and afterwards consumed the placenta. A similar pattern has been noted for a mona monkey (*Cercopithecus mona*) [57]. A patas mother has been observed to lick her infant and eat the umbilical cord and placenta [49]. Gillman and Gilbert [60] reported that a baboon mother licked the infant clean and consumed the placenta. Rhesus (*Macaca mulatta*) mothers have been reported to consume both umbilical cord and placenta [61, 62] and presumably stumptail macaques eat the placenta [63]. Fedigan and Fedigan [19] report that Japanese macaque mother's lick the infant clean. Because few pongid births are recorded, the situation is less clear. However, gorilla infants born at the Columbus Zoo have been licked clean and mothers have been reported to consume the placenta and afterbirth. Chimpanzee mothers may consume the afterbirth, and an orangutan mother has been seen to suck the fetal membranes [64].

Physical maturation. Social influences have varying effects depending upon the developmental state of the receptor. The developmental state may be defined in a number of ways, but few definitions will probably be more exact than studies of postnatal myelinization. There is little concretely known about the role of brain myelinization; the relationship between myelinization and onset of function in ontogeny is still incompletely understood, and there is considerable disagreement. Although more is known about brain functions and development of social behavior among rhesus than in any other primate, little is known about the subject linking the two, e.g., the interaction of neurological and behavioral maturation. Myelinization studies can lend supporting information to neurophsiological sudies of maturation, and their major advantage lies in the realm of comparative neuroanatomy. Furthermore, there is a wealth of data on the myelinization process for many animals. Although the data is not well understood, especially concerning the relationship to the onset of behavioral patterns, brain myelinization has a role in developmental rates [65]. The role of myelinization in species with short and prolonged periods of immaturity is speculative. Development of social behavior is inextricably tied to C N S maturation involving the ontogeny of sensory and motor patterns [11, 66–69]. Although the interaction of all the variables is not clearly understood, Parker's [69] application of Piaget's work suggests that such research would further clarify the interacting principles. Because we can understand the organization of behavior better by studying how it changes over time, Piaget's emphasis on developmental sequences is significant. Piaget's approach can be valuable towards establishing an evolutionary perspective for the socialization process, for his methodology shows how natural selection has evolved different behavioral programs in different lineages. Although Piaget's model deals with the organization of human intelligent behavior, Parker [69] proposes its utilitarian value as a framework for analyzing the organization of behavior generally. Piaget's emphasis is on the continuity of motor and mental operations making the model suitable for comparing the intelligence of human and nonhuman primates; however, the model has limited value as cross-specific intelligence test.

Endocrine Data. Increasingly, endocrinology is playing a major role in helping interpret and define behavioral ontogeny. The work of Goy and others has shown clearly the impact of hormonal bases upon behavioral expression. Much of the endocrine data is currently applied to the development of sexual behaviors [70, 71]. As Wallen et al. [70] note, little attention has been paid to the interaction between social experience and the prenatal endocrine environment, although both have a profound influence on behavioral development. Attempting to fill this void, Wallen et al. [70] have examined how an individual's response within a social environment is determined by its hormonal history by testing the effects of prenatal androgen administration or testicular activity on the subsequent display of prepubescent sexual behavior. Goy and Goldfoot [72] state that the basic psychosexual orientation is not determined by social experience as much as it is related to prenatal exposure to specific hormones.

Vom Saal and Bronson [73] have recently demonstrated that rodents, which produce litters containing many pups, show considerable variability among adult females in terms of reproductive characteristics, and that part of that variability can be traced to the former intrauterine proximity of female to male fetuses during prenatal development. Female fetuses that develop between male fetuses have significantly higher concentrations of the male sex steroid testosterone in their blood and amniotic fluid than do females that develop between other female fetuses. Individual variation in sexual characteristics of adult female mice may be traceable to differential exposure to testosterone during prenatal development because of intrauterine proximity to male fetuses. Whether this phenomenon has any bearing for nonhuman primates is questionable. However, among the nonhuman species with short birth–spacing, i.e. the prosimians and some New World monkeys, this phenomenon may be operative.

Endocrine and maturation data add the needed dimension to help interpret behaviors normally witnessed by the naturalistic observer. Results currently appearing from endocrine and neurological studies strongly support the assumption that socialization can only be understood when field and laboratory workers cooperate. The naturalistic observer is at a grave disadvantage, being able only to observe outward manifestations (e.g., behavior) of inner processes.

Chronological Age. Certain key areas of social development are completed early in life. Over 85 % of the communicative behaviors witnessed among adult rhesus are found in twenty-month–old juveniles [27]. Some of the few behaviors not shown by the juveniles were attributed to physical immaturity. Sade [74] suggested that the rhesus behavioral repertoire is virtually complete by twelve months. Young juveniles learn their roles and status within the group by an early age; the process normally termed " socialization " thus appears virtually completed by the end of the juvenile period. Adult socialization (which has been termed modification) is characterized not so much by developing new behavioral patterns and relationships, as by modifying and specifying existing patterns [27].

Laboratory studies on nonhuman primates [38, 52, 75–79], canids [9, 80, 81], and the work by Schneirla and Rosenblatt [82], among others, suggest that the growth cycle can be conveniently divided into specific periods. Harlow and Harlow [83], for example, divide the primate growth cycle into four periods, during each of which different developmental processes are operative. Because socialization is a continuous process occurring at all developmental stages, why is it valid to specify age as a variable? It is becoming clear that the specific or average age of an individual may be a significant antecedent variable in the socialization process in the following ways: (1) there may be a simple causal relationship between age and some dependent variable and (2) there may be a more complex effect of age, not to be expressed in simple quantitative terms. The socialization process may have qualitatively different kinds of effects at various periods in the life cycle. While Harlow's suggestion that the primate growth cycle can be divided into four stages is most useful, socialization is a life–long process. Loy's [27] suggestion that the primate socialization process is actually composed of two interacting processes–the developmental stage of socialization and the social modifiability stage– calls for some revision of Harlow's scheme. While we must be wary of establishing concrete stages in the socialization process, it is clear that at different ages qualitatively and quantitatively different things are happening. Perhaps dependent upon such variables as species, habitat and phylogenetic position, the stages of primate socialization are sliding stages and not strictly cross–specifically comparable [17]. Such an interpretation is indicated by Parker's [69, 84] data on stumptail macaques.

It is becoming incumbant upon researchers of primate socialization to define the adaptational process operative at different life stages, i.e. with studies of specific events like weaning [45, 85] they vary and play different roles. At different times in the life cycle qualitatively and quantitatively different things occur, and unless we isolate behaviors at an early age, we may be unable to understand later social development (see, for example, [86]). By the same token, because a behavior is important during one life stage, does not necessarily imply that it will be important during another life stage.

Gender. Gender is a most important variable influencing socialization. There is a relationship between the socialization and learning processes of infant males and females and their subsequent adult roles [12, 13, 15–17, 31, 87–89]. Gender is rather immediately determined by conspecifics at birth by direct observation. Many observers report that group members may pay close attention to the newborn's genitals by peering at, touching, sniffing, or mouthing them. This seems to be the first basic step towards classifying the gender of the new group member. The manner in which an individual learns its role, including the male and female roles, may be heavily influenced by the immediate environment, as well as by its original genetic component [23]. Arnold [90] discusses the influence of sexual differences in the brain upon behavior. Goy ([91], for example) and his associates (see also [92]) have studied hormonal influences on the development of sexual differences in rhesus; an up date of this work is found in Testa and Mack, [71] and Wallen *et al.* [70]).

The high hormonal levels circulating in the blood of newborns suggest that during fetal or neonatal life, hormones act in an inductive way on the undifferentiated brain to organize certain circuits into male and female patterns. Early hormonal influences may affect the ease of learning and expression of behavior later in life, even though the hormonal level is low during the period of infancy and early adolescence. Gender differences in behavior are also tied to the dynamics of group social interaction, i.e., by learning role patterns. Social roles are not strictly inherited in animal societies [93]; laboratory studies indicate that primates without social experiences lack marked sexual behavioral differences [94]. Studies of the mother–infant interactional dyad in pigtail [95] and rhesus macaques [96] clearly show that there are sexual differences in the development of maternal independence. The effects of such early behavioral trends are apparent later in life [12, 13].

Differential treatment occurs soon after birth due, perhaps, to the mother's reactions to dissimilar behavior in male and female young. Developmental studies of laboratory-reared rhesus [96, 97] and of the provisioned Cayo Santiago colony [98] show that mothers threaten and punish male infants at an earlier age, and more frequently, than female infants. Another early behavioral difference between males and females was described by Jensen et al. [77, 78] on pigtail macaques. They found that in a deprived laboratory environment, where an adult male was missing, the behavior of the male infant was more adversely affected than was the female's behavior. Male and female differences are seen in such social activities as play [12, 13, 15–17, 21, 43, 44, 50, 89, 99–103], aggressiveness [87, 104], development of independence from the mother [25, 47, 85, 95, 96, 98, 105], tool manipulation [28] and demonstrativeness of role playing [11], among others. A major feature differentiating male and female primates is the expression of aggression, both by them, and directed at them. Males are more aggressive than females and mothers of male infants are more punishing than mothers of female infants. A rhesus mother, for example, threatens and punishes her male infant at an earlier age and at more frequent intervals than her female infant whom she restrains, protects, and retrieves [96, 97]. Developmental studies of laboratory-reared rhesus infants elucidate some interesting points regarding male aggression; for example, even isolate-reared laboratory "motherless mothers" are more brutal towards male than female infants. Since exposure to excessive punishment has been correlated with later hostile behavior [106, 107], the infant male's predisposition towards rougher play and rougher infant-directed activity appears to be subtly supported by its mother's behavior and through his observations of other mothers with their infants [98]. Infant male macaques on Cayo Santiago began receiving aggression from their mothers in the second month, with a peak in months nine to eleven [98]. Male infants received significantly more aggressive behavior than female infants.

The amount and frequency of affiliative and supportive mother–infant interaction is undoubtedly related to the amount of aggression. Studies of feral baboons [25, 108] show that there are consistent differences in the development of the mother–infant relationship and peer interactions as early as two months. Female infants are more consistently involved in close associative behaviors such as grooming, and are usually in closer proximity to other animals than are males. Males begin the process of peripheralization earlier [108] as the mother's earlier rejection of the male infant forces it into earlier contact with other male infants, usually in the form of peer play group interactions. Males are often found in age-graded play groups which range farther from the mothers as they mature. Young females, however, usually remain with the adults. Sociographic analyses show that male juveniles interact in larger groups than females, who mostly associate with only one partner. Preliminary data based on the same methods reveal a similar pattern in human children [42, 109, 110]. While young females maintain close ties with adult females, males also remain in proximity to one another. It may be important for males (especially those destined to a subordinate position) to have a stable relationship with one another, especially older, more dominant males than with females who can be rather easily avoided. Juvenile females seem to develop their social relationships during long grooming sessions with other females and while holding or exchanging infants. Peer group play seems more important for males than females [47]. These gender differences vary among species. Among bonnet macaques neither males nor females showed a strong and significant preference for the mother until after twelve weeks. Females however showed an earlier preference for the mother than did males throughout the entire first year. Pigtail macaques, on the other hand, showed significantly less preference for their mother than did bonnet macaques, and pigtail males after twenty-four weeks showed no preference for their mothers. The strong and enduring bond of a bonnet macaque female infant to the mother may provide the basis for incorporating female infants into the adult female core of the group [47]. The females' strong avoidance of strangers may reflect their hesitancy to establish new relationships, strengthening the cohesiveness of the female subgroup. Rosenblum and Alpert [47] feel that this mechanism helps explain why females in the wild only rarely leave their natal groups. Males, on the other hand, while showing a strong preference for the mother early in life are eventually forced from, and leave, the mother and show a greater readiness to move towards strange conspecifics. For males, the tendency towards establishing relatively less intense bonds with the mother, and a greater responsiveness to strangers, may interact to produce a greater inclination towards their peripheralization and facilitate a readiness to transfer troop allegiance.

An interesting behavioral difference related to gender is discussed by McGrew [28, 111]. Male chimpanzees apparently do more overall general manipulation than females; however, females are better in manipulatory skills, and at Gombe they exhibit more frequent tool use in obtaining insects by fishing and dipping. McGrew's findings are supported by other accounts suggesting female superiority in manipulatory skills (i.e., catching of thrown objects by Japanese macaques [112]). Among humans, females are superior to males in manual dexterity from early childhood onwards [113]. McGrew's data show that males focus their object manipulation more often on growing vegetation, taking the form of vigorous locomotory play, either alone or socially. Females, however, show a greater tendency to manipulate movable detached objects rather than growing vegetation. How these activities relate to later adult behavior is unclear; however, the fact that females are more adept at termite fishing and dipping suggests that females are purveyors of this social tradition. Quite possibly females are more adept at these patterns because females spend more time with their mothers and have more opportunity for observational learning and actual experimentation.

Much has been written about primate play behavior. Males play harder, begin play at an earlier age and cease play at a later age, and play for longer periods of time than do females. There are qualitative and quantitative differences in the play of young male and female primates; however, Hinde and Spencer-Booth [114] note that gender differences arise not so much in time of onset of play as in its expression. Harlow and Harlow [83] distinguish the play of male and female laboratory rhesus at about two months. This dichotomy also appears in the field. Male baboons play rougher and more frequently; female baboons groom more frequently and spend more time with newborn infants [115–117]. Similar data is found in studies of vervets [118] and human children [109, 110, 119]. Among humans, for example, the frequency of rough-and-tumble play for boys is significantly higher than for girls.

Dolhinow and Bishop [120] suggest that a powerful endocrine effect influences sexual differentiation in play behavior. Females exposed to androgens during a critical period of early development become masculinized as pseudo-hermaphrodites [121–123]. These masculinized animals tend to develop play patterns approximately halfway between typical male and typical female patterns. Baldwin and Baldwin [50] suggest that, a number of other factors affect the differential expression of play according to gender. Males are usually physically larger and stronger than females; this alone may explain some differences between the frequency and duration of play. This, plus the endocrine influence, increases the likelihood that females experience less novelty and more aversive contact during exploration or social play than do males. This may be partly responsible for "... shaping the quiet, withdrawn, gentle activities of females and the tendency for females to orient to object manipulation play rather than the social contact play typical of males" [50]. This agrees with McGrew's observations, and confirms Tsumori's [124] observation that females learn to attend to lower but safer arousal levels afforded by manipulatory play and by exploration. As young females withdraw from rowdy play bouts, they may discover "play mothering," a pattern reported by Jay [29] and Poirier [40, 43] for langurs, by van Lawick-Goodall [125] for chimpanzees, by Lancaster [23, 126] for vervets, and by Baldwin [127] for squirrel monkeys. Play mothering reinforces quiet, low arousal activities in adolescent females and accentuates gender differences in play behavior. A fourth variable that must be considered is the fact that females of many species reach social-sexual maturity prior to males, quickening the termination of female play behavior. We might continue to list differences in the development of male and female primates, but the important point is that these differences are related to adult social roles and experiences (cf. [12, 13, 43, 87–89]). In most species adult males and females play different roles, and their early social experiences seem to "condition" them for this. Early in their development males are forced from their mothers out to the peer group where they mature and become less dependent upon the females and they learn to be assertive, aggressive animals. Females, on the other hand, remain with their mothers and other females–they learn to interact with other females, and most importantly they learn how to provide proper infant care. The major role which a nonhuman primate female must learn is that of being a mother. The socialization and learning process of female nonhuman primates seems to be geared towards producing a healthy, effective mother. Learning plays an important role in the development of skill in performing maternal behaviors. The fact that young females soon drop out of play groups, that they have strong affiliative associations with adult females, and that they are in continual contact (visual or tactile) with infants is important. Many studies note that young juvenile females are inept at handling infants, but by adulthood they can carry and handle infants with ease and expertise [23, 128, 129]. The dynamics of the maternal learning process occur under the mother's watchful eye; instances of carelessness, clumsiness, or real abuse are soon dissuaded. Through a simple conditioning process juvenile females learn appropriate behavior patterns with their reward being the continued presence of the infant. Laboratory studies support the contention that early experience practicing the mothering role may be preparation for adult maternal behavior [131].

SOCIALIZATION AND THE SOCIAL STRUCTURE.

Because nonhuman primates are group living social animals, the socialization process must be viewed and understood *within the social structure.* If the development of nonhuman primate behaviors involves the interaction of a genetically determined base with a set of environmental conditions, then we must remember that the environmental context of most primate infants is largely social. Group structure (and probably kin–structure) reflects and influences individual behavior [31, 40, 46]; not only the form of group organization, but group life itself, is dependent upon the early environment of individual animals.

The reciprocal relationship between socialization and the social structure is not necessarily one of discrete interactions, but may take the form of cycles or other sequences prolonged over substantial time periods. Primate social groups differ according to many variables, but with few exceptions animals learn to use their biology effectively and adapt to their habitat *while living within the group* [41]. Differences in primate societies are due not only to biology, but to the circumstances in which an individual lives and learns. The character of a social group is related to the strength of interanimal affinities and to the degree to which relationships are tolerated by other group members. Kummer [131] suggests that differences in primate groups may be rooted *in age–sex class affinities.* The species-specific group structure determines with which animals an infant will interact.

Rosenblum and Alpert [47] discuss the relationship between the socialization process and social structure among bonnet and pigtail macaques. Bonnet mothers are more passive and pigtail mothers are more coercive in regulating their infants' behaviors. Bonnet macaque infants, therefore, exhibit more initiative than pigtail infants in promoting and maintaining proximity and contact. This is especially true early in life. " This different demand on infants of the two species correlates with the differences between bonnet and pigtail social structures within which the infants must assume their developing role " (page 475). The bonnet macaque group structure is less clearly hierarchical than the pigtail group structure, and the bonnet group allows *a relatively fluid pattern of interanimal interactions.* In the pigtail group, however, interactions are more restricted and individual roles are more rigidly defined. Pigtail macaque individual behavior is thus more completely dictated by group structure; in bonnets, however, behavioral regulation appears to reside to a greater degree with the individual animal. Because of this difference, bonnet infants ultimately engage *in a relatively looser social organization requiring greater social initiative on the part of its constituents.* Pigtail macaques, in contrast, must be socialized to respond in a relatively fixed social structure requiring a greater adherence to predefined roles by the newly maturing animals.

KINSHIP TIES.

Long–term studies on Cayo Santiago [133–137] and at the Japan Monkey Centre [138] have clearly shown that a youngster's adult behavior is influenced by animals with whom it has consanguineal relationships, especially members of the matriline. Studies at the Japan Monkey Centre have shown that not only a mother's rank, but also the number of siblings on whom one can depend for support, influence one's development [138–144]. A similar situation is found among the Cayo Santiago rhesus [135, 136]. Sade's data show that different mechanisms within the kinship network affect males and females differently. Japanese macaque studies have shown that matrilineal ties affect the transmission and learning of new behavioral patterns [124, 138, 145–147]. Pathways of *habit formation follow preestablished networks of* group affinities, in the Koshima, Ohiryama, and Takasakiyama troops, habit propagation was strongly influenced by kinship. Animals of different kinship lines have different socialization and learning experiences; entire lineages consisting of a mother and her descendants tend to acquire or reject new behavioral components as a unit [42]. Since animals of different groups exhibit different behavioral patterns it seems reasonable to expect that animals within a kinship group will act more alike than animals in nonkin groups. Loy [148] has demonstrated that the matriline remains stable during food shortages. The effects of the matriline are much in evidence by the juvenile stage of development [149]. Months after separation from the natal group, rhesus monkeys 20–30 months old could act in an orderly and predictable manner because of *geneologically determined relationships* forming the core of their interactions. " With the development of mother–infant specificity, the infant monkey is linked to its matriline and, to a large extent, its future behavior is determined. The infant develops close relationships with mother, siblings and other matrilineal kin, and its kin ties then serve as the basis for its integration into the remainder of *the social group* " [149, p. 94].

Loy and Loy [151] discuss the relationship between kinship ties and the behavior of juvenile rhesus monkeys in grooming and play. Grooming between matrilineally related monkeys (comprising 6.6 % of the study group) accounted for 34.4 % of the total recorded. Related monkeys were involved in grooming over five times more frequently than expected from random selection of grooming partners. Sade [133] reported *that grooming* among related animals (15 % of the total possible grooming combinations) accounted for 62–64 % of the observed grooming sequences. The Loys found that play behavior among related animals comprised 26.5 % of the total sequences, a figure slightly more than four times greater than expected from random partner selection.

INFANT–ADULT MALE RELATIONSHIP.

Most socialization studies focus on the mother–infant or peer relationship, and the possible socializing role of adult males is largely overlooked. One reason for this is perhaps the fact that the male's socializing role is likely to be the most variable relationship, in terms of the amount and kind of contact, an infant has during its earlier years (review of this subject is found in [12, 24, 97, 150]).

The adult male's contact with the infant is minimal in some species and extensive in others; in some species males play the role of group protector, in others they play an important role in socialization. In some species the male's role is active, in others it is passive. The adult male's role in the socialization process is influenced by such factors as social structure [12, 40], habitat [22], one male versus multiple male groups, the phylogenetic position of the species [12, 13, 24], as well as the male's idiocracies.

The adult male role most often assumed is a protective response towards youngsters, but this is variable in pattern and extent [97, 151–153]. Males of a number of mammalian forms perform various " maternal " tasks and paternal care is not uncommon in rodents and some carnivores as well as in primates [11, 154]. Among nonhuman primates, most paternal care is directed towards infants once they acquire the adult coat color. A male assuming a nurturing or protective role is likely to be a subadult or sometimes an adult of fairly high rank. Paternal roles have not been reported for young, low-ranking males except when a young male is protective of his young sibling [99, 133, 134, 155, 156].

Perhaps one reason we know so little about the male's socializing role, and therefore assume it is minimal, is because it may be subtle and we simply do not look for it. It has been noted, for example, that the presence of an adult male can affect the physical development of female mice [157]. Females reared in the male's presence (though not necessarily in physical contact) gained weight more rapidly and showed earlier onset of eye and ear opening and eruption of lower incisors. Mice reared with males until weaning were more aggressive than those reared in the absence of a male [158].

INTERACTIONS WITH ONE'S PEERS AND PLAY BEHAVIOR.

That play behavior has an important role in socialization is without question; however, its precise function is debatable. Washburn [61] noted that if the field observer listed the kinds of daily behaviors witnessed among non human primates according to the amount of time consumed, the usual order would be: sleeping, obtaining food, eating, playing, resting, and other social contacts. Judging from the occurrences of play recorded in various studies, there is no question that play was a major adaptive behavioral trait during primate and mammalian phylogenetic histories. A multitude of variables, such as age, gender, group structure and dynamics, and habitat, affect the expression of play behavior [12, 18, 40, 43, 50, 80, 89, 152].

Harlow demonstrated five developmental stages in rhesus play behavior; these stages may have some cross-specific applicability. The more complicated aspects of play behavior appear with neuromuscular maturation, as Sade [159] has shown to be true for rhesus macaques. As each play pattern integrates into the next successive one during various phases of the life cycle, it undoubtedly assumes varying degrees of importance at any particular point in the life cycle. Not only do different patterns appear at different times, but they may be functionally different during the developmental sequence [18, 89].

The socializing functions of play behavior are debated; however, among the many possibilities the following are most often noted: play functions as a mechanism for social development; for establishing the dominance hierarchy; as a means of achieving social integration; and as an experimental arena for learning the communication matrix. Play behavior is essential for development of future skills requisite for survival, especially for meeting unexpected contingencies. Key elements of social life such as grooming, components of sexual behavior, and aggression are to some degree learned and rehearsed in the play group. Deprivation studies indicate that social peer group play interaction may be more important for the development of normal social behaviors than maternal interaction [19, 160–162].

The basis of the adult dominance hierarchy may be formed in the play group; e.g. play behavior may help youngsters find their place in the existent social order [163]. During play, youngsters compete for many " valued items " such as food, sleeping places, and pathways. Through trial and error, through the constant repetition of play behaviors, infants learn the limits of their self-assertive capabilities and become familiar with both the dominant and subordinate positions [120]. During play youngsters learn their place in the social group and perhaps develop group identity, e.g., play facilitates troop integration. During play, animals learn patterns of social cooperation without exceeding certain limits of aggression [164]. The successful initiation of social or interactive play is critical to the appearance of the age mate affectional system [37, 83]. Youngsters lacking the opportunity to play may be faced with the options of being maladjusted or of being excluded from the social group [165]. The play group is a major context for learning social and physical skills, and as such, is an important factor in social integration.

Play may also be an important vehicle whereby youngsters learn social communication skills [166, 167]. As an integral part of the practice of adult social roles, play serves to fully acquaint an animal with its species-specific, and perhaps group-specific, communication matrix. Socially deprived animals have problems with response integration and communication; although such animals exhibit most components of social behavior, these are not combined into an integrated pattern and effectively applied in social interaction. Mason [35], believes this is due to a deficiency in sensory-motor learning or " shaping." Although all basic postures, gestures, and vocalizations are probably unlearned, their effectiveness in social interaction is dependent upon experience as social deprivation studies demonstrate. This applies to the sending as well as the reception of messages.

A useful approach to understanding the socializing role of play behavior is to consider play a kind of " grammatical structure " [168]. During ontogeny the players learn the behavioral syntax as a mathematical game [169]. Considering play as a mathematical game allows us to look at the two components of such a game: (1) a finite number of rules or positions and (2) the rules governing the outcome. There are undoubtedly precise rules which a youngster learns in play and the acquisition of an adequate performance and competence in rules of play (following Kalmus) is a developmental process. The rules a young primate learns are not lacking some sort of logical connection or structure; Altmann's [170] stochastic approach to rhesus communication clearly shows that there is considerable predictability within the communication system of properly socialized animals. Berkson's [20] and Fedigan and Fedigan's [19] data on physically and socially handicapped infants clearly demonstrate what happens when an animal is incapable of learning these rules.

Conceptualization of play as having a behavioral syntax may allow us to appreciate more fully the interrelationship of the various behavioral patterns comprising play. As a primate develops more elaborate and intense play behavior, it may order the rules of the game into the correct sequence for proper functioning in a social unit ([167, 171, 172], however, raise doubts about this). The key to the acquisition of these rules is in the sequencing of playful interactions and the association of relatively disjunctive units of behavior into larger functional categories. The behavioral syntax for certain adult behaviors may be learned through repetition in the play context, making an understanding of the complex repertoire of signals employed in the playful interactions an area of fruitful research [89, 173].

Although we assume the primacy of play behavior for normal socialization, Baldwin and Baldwin's data [50, 174] question the relative importance of play for later social development. If their study of the Barqueta squirrel monkey population is cross-specifically applicable, then it suggests that the adaptive significance of play is more complex than ordinarily assumed. Play may function more in simply bringing animals together than in developing certain adult behaviors [18]. The Barqueta data show that, at least for squirrel monkeys, an adaptive modicum of competence develops even in the absence of play. Play may be important, however, in developing the full potential of an animal's behavioral repertoire beyond that point; e.g. play may be important in developing " complex " social behaviors, however they may be defined.

MOTHER-INFANT DYAD.

The best recent attempt to deal with variables in the mother–infant relationship is found in Altmann [175]. Many primatologists have suggested that all major social roles and classes of bonds (i.e. male–female, dominant–subordinate) may ultimately have their roots in the initial socialization of the infant by its mother [12, 13, 43, 176–178]. The maternal relationship is a youngster's first affectional bond [36, 52] and, at least in some species, is perhaps the prototype for all later such bonds [95]. With formation of a maternal attachment, favorable conditions exist for social learning; for social learning commences with the mother. Occasions for learning multiply as the growing youngster extends its social relationships beyond the mother. However, investigators have paid little attention to specifying how this accomplished. One of the primary functions of contacts with other animals may be to sharpen, strengthen, or generalize the learned behavior originating in the mother–infant bond.

A newborn's ties to the mother are the earliest, become the strongest, and seem to last the longest. For varying lengths of time, depending upon neuromuscular development [19, 20], a mother serves as the infant's locomotor organ and neocortex and determines the nature of the basic socialization environment. The neonatal infant, clinging to a mobile mother, forms an attachment to her and through her, to virtually her whole ecological–social setting. Physiological and morphological states influence the nature and extent of the early dyad, but psychological states and social habits formed during infancy influence the nature and extent of social relationships which persevere later in life [178]. Later attachments may be differentiations and specializations of this early and relatively amorphous monolithic state [12, 13, 177].

In mammalian neonates, behavior is typified by reciprocal stimulation between parent (especially mother) and offspring. The infant attracts the mother's attention; the mother then presents the newborn with a variety of tactile, thermal, and other stimuli, typically of low intensity and primarily approach–provoking. Socialization commences on this basis, and behavioral development is essentially social from the onset. The dependent nature of the bond demands that participants arrive at a mutually satisfying interactional pattern whose consistency and flexibility allow the physical and emotional maturation of both parties. The interactional pattern derives its original form and later permutations from characteristics inherent to the pair itself and to social and physical surroundings of which they are a part. For example, the mother's age and parity (e.g., previous experience, or lack thereof) affect her behavior from the onset, including her degree of " restrictiveness " or " permissiveness," as well as the success with which she satisfies her own and her infant's needs with ease and economy of effort.

There are notable differences in how nonhuman primate mothers handle their infants and in the amount of time they spend with them. Most field studies report that the mother and her newborn form the center of a cluster of interested group members, especially other females. Among baboons [152] and Japanese macaques [179], this interest may be limited to peering at or trying to touch the infant. In other species, such as langurs [128, 177, 179], vervets [129, 180], some lemurs [181], and chimpanzees [125], the mother permits other group members to hold and carry her youngster. Similar interest in infants has been reported in laboratory rhesus colonies [114, 182, 183].

Certain stimuli seem to elicit a female's solicitous reactions to her infant. Many newborns look different from the adult; for the first few months (depending upon the species) infants possess a natal coat which may be an essential element eliciting the female's maternal behavior [128, 184]. The natal coat is generally present when an infant most requires its mother's protection and nourishment. It is almost certainly more than mere coincidence that the duration of the natal coat coincides with a period of great dependency when it is essential that the infant be sheltered and protected [177]. Gartlan [180] suggests that in species with a natal coat the infant has a special vulnerability to environmental dangers.

Besides the natal coat, other factors affect the mother's initial attachment to the infant. Kaplan [51] notes a number of visual, tactile, and olfactory properties affecting the mother–infant attachment. Early olfactory experience is involved in the development of emotional attachment, and the properties affecting attachment may change, or vary, with age. For example, squirrel monkey data show that sight alone of familiar conditions (mother or environment) provided some degree of emotional comfort. Fedigan and Fedigan [19] provide evidence that infants (even their severely handicapped Japanese macaque youngster) can recognize their mother's and vice versa on the basis of vocal patterns. Nevertheless, Rosenblum and Alpert [47] note that neither pigtail nor bonnet macaque infants showed an unequivocal preference for the mother until the third month of life. They conclude that the inability to discriminate the mother, as seen in their test situation, could be a potentially maladaptive social behavior under free-ranging conditions.

A multitude of variables affect the mothering experience. Some variability within the mother–infant relationship is phylogenetically related; the relationship tends to be more complex and longer lasting (probably as a function of maturation rates) in higher primates.

That previous mothering experience affects the degree and quality of infant care is obvious. Work with primiparous and multiparous mothers showed that at least for the first three months of an infant's life, a primiparous mother is consistently more anxious; she restrains her infant more and reacts more violently to a novel or slightly threatening situation [185]. Harlow *et al.* [186] found that social experience with an infant, no matter how minimal, affected maternal behavior. The same laboratory mothers who rejected their first infants often accepted the second. As noted for both human and nonhuman primates, there are consistent differences in the behavior of first–, second–, and last–born infants, due, in part, to differential maternal treatment. The number of instances of " aunting " or " babysitting " behavior reported for colobines, rhesus, and vervets, among others, suggests that maternal experience, even prior to giving birth, is important in developing the ability to care for youngsters.

There is a considerable amount of literature suggesting that a female's status affects her mothering behavior and eventually her infant's status. Data from feral baboon studies [152] suggest that the socialization process differs for youngsters (primarily males) at opposite ends of the dominance continuum. De Vore notes that infants of lower ranking mothers exhibited considerable insecurity in the form of a greater frequency of alarm cries and more demands on the mother, leading to an intensification of the mother–infant bond. Offspring of dominant females, however, acted more secure and exhibited more freedom from mother. A study on rhesus living in a corral generated similar data–higher ranking mothers allowed their infants more freedom sooner, and were less prone to retrieve the infants as they ventured from the mother's " protective shadow." (Poirier, unpub. ms).

Behaviors expressing social ranking seem to be learned by the infant from the mother; Bekoff [11] notes a correlation in various mammals between a mother's rank and the social relationships which her infant develops. Loy and Loy's [149] data on a group of thirty–three juvenile rhesus show that juvenile dominance rankings are 95 % predictable from prior knowledge of the mother's rank. Longitudinal studies of macaques indicate that infants mimic their mother's social interactions with other adults. Furthermore, infants of high status mothers (and infants of large matrilines) can count on their mother's support in case of trouble.

The concept of identification has been introduced into nonhuman primate studies to explain the fact that Japanese macaque infants with dominant mothers tend themselves towards dominance [187]. Infants of high-ranking mothers had substantial contact with troop leaders and identified with them; offspring of low–ranking mothers had minimal contact with troop leaders and were unable to identify with them. In the Takasakiyama troop, low–ranking infants were likely to become peripheral or desert the troop [138]. Japanese primatologists speak of " acquired " or " derived " status to explain the fact that some infants " inherit " their mother's dominance status. Infants of high–ranking mothers have more contact with adult males and attain choice foods [139–141]. Because the Japanese macaque troop is comprised of a central and a peripheral part, infants born in the central part of the troop (infants of dominant mothers) associate with, and more importantly identify with, troop leaders. These infants can " look to " dominant males in times of stress, in their turn they are more likely to become leaders.

Koford's [156] and Sade's [133, 134, 159] reports on the Cayo Santiago rhesus indicate that adolescent sons of the highest ranking females hold a high rank in the adult male hierarchy. Koford [156] suggests this is apparently due to the protection given by the mother during adolescence. Sons of high–ranking females attain top status in the troop without becoming peripheralized or subdominant males. Ransom and Rowell's [25] study of feral baboons suggest that one factor determining an infant baboon's rank is the relative rank of its mother.

WEANING.

Weaning entails the physical and emotional rejection of the infant by its mother, who, although she was once the major source of comfort, warmth, and food, is now hostile and denying [188]. As Clark [85] notes in her study of chimpanzee weaning behavior, " Weaning from the nipple is the first serious break in the bond with the mother, and all the infant's behavior is affected when he is denied suckling and is supplanted by a younger sibling at his mother's breast. A period of depression sets in varying in intensity among individuals. Some infants come out of it within a few months whereas others remain depressed for a year or longer " (page 235).

A number of variables affect the weaning process, its onset, tenor, and long term effects. Some mothers reject their infants more vigorously than others, and some infants are more persistent in their attempts to resist rejection [128]. Dominant mothers seem to have less trouble weaning their infants, who seem less reluctant to leave the mother, than do subordinate infants. Variations in weaning are also related to gender [31, 87, 95, 177, 189] and habitat [22, 25, 45, 114, 190]. Jensen *et al.* [78] note that in a laboratory colony of pigtailed macaques male infants left the mother to form peer groups at an age when young females remained with the mother reports on feral Japanese macaques agree [189]. On the other hand, a feral study of Nilgiri langurs suggested no gender differences in weaning [177]. This lack of gender differences in weaning, contrasted with the Japanese situation, may somehow be related to the greater behavioral variation noted for Japanese macaque males and females compared to Nilgiri langur males and females.

Investigation of the weaning process can reveal tantalizing leads; for example, Poirier [12, 13, 15, 16, 87, 88] suggested a relationship between the method and duration of weaning and adult aggression. There may be a relationship between adult aggression and the severity of rejection with which an infant is weaned [106]. Heath (quoted in [106]) found a significantly higher degree of aggressiveness in nine early weaned rats compared with a similar sample which remained with the mother.

Anthoney [191] suggests an ontogenetic development of grooming from nursing and weaning behavior. Grooming first becomes important for the infant when it is weaned; although the mother disallows nursing, she usually tolerates the infant's attempts to groom her. Whenever the weaned infant is frightened or otherwise needs security, it comes to groom rather than nurse. There may be some link between the amount of grooming and the lenth of the nursing period.

Conclusion.

The task of discovering those factors, singly or in combination, that direct the form and development of social behavior is still in its infancy. While laboratory studies have made major strides towards understanding the socialization process, field studies are only now reaching a level of sophistication where such details can be gleaned from the material. A major outcome of primate socialization research has been the recognition that more longitudinal studies, experimental manipulation, and analysis of behavior and group structure will be rewarding. There are still many problems to be researched, for example, recent unpublished research by Poirier suggests that old females without infants may play an important role in comforting yearlings as they are weaned and their mothers turn their attention to the new infant.

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