

Social Hierarchy Under Different Criteria in Groups of Squirrel Monkeys, *Saimiri sciureus*

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ABSTRACT. Under different criteria the individual members of groups of squirrel monkeys show different social capacities. The ranking of the subjects was much the same for Restraining and Genital display. The hierarchies for Approaching and Following fitted well with each other, showing few similarities with the above two. Location of individual ranks for Withdrawing tended to be the opposite to that of Approaching and Following.

Restraining and Genital display showed quasi-linear hierarchies, with males on top and females at the bottom of them. For Approaching, Following, Withdrawing, and Genital inspection the results varied from quasi-linear structure to circular or even unisexual arrangement. As a rule the animals behaved towards partners close in rank to themselves.

Several individual roles could be isolated: An alpha male role, directing Restraining and Genital display to all other partners more frequently than any of them towards him, basing his ability more in adequate distribution of total performance among social partners than in high total frequency; an omega male role under the same criteria, whose function would be to connect with the hierarchy of females and a scapegoat role, a very passive female receiving all kinds of attention from most subjects.

INTRODUCTION

The early students of primate social behaviour placed a heavy emphasis on dominance or social status as a general factor in group organization. Dominance was most clearly reflected in situations in which there was some element of competition, giving rise to the view that dominance could be defined in terms of priority of access to desired objects, such as food or an estrous female.

Critics pointed out that for many species competition for incentives as tested in the laboratory had no clear counterpart in the wild. It was also emphasized that even where some element of competition was involved, a direct confrontation between two animals was only one of several ways of gaining access to incentives. In addition to the varied ways in which dominance could be achieved, it was also pointed out that the social functions of highly dominant animals were far richer than is implied by defining dominance in terms of priority of access.

Probably most students of primate group behaviour are now willing to abandon the narrow, if operationally precise, definition of dominance in favor of the following more general one: "Dominance is a complex concept assessed by observation of the frequency and the quality of several types of behaviour in various kinds of situations with reference both to other animals within the group and to external events." (HALL & DEVORE, 1965).

It seems therefore that an analysis of the various individual capacities within a group would provide the most objective view of its social structure.

For the squirrel monkey, the criterion of priority of access to incentives (food, water, or sex) has not received wide acceptance as an indicant of dominance or social status (PLOOG, BLITZ, & PLOOG, 1963; PLOTNIK, KING, & ROBERTS, 1965; BALDWIN, 1968; CASTELL & HEINRICH, 1971) and the search for behavioural correlates of social structure has tended to focus on species-typical displays (Genital display), since there is evidence of males in laboratory and semifree-ranging conditions arranging the distribution of interactions for this behaviour within the group in a linear hierarchy (PLOOG, BLITZ, & PLOOG, 1963; BALDWIN, 1968; ALVAREZ, 1973).

Restraining, a pattern of physical coercion, was also shown to be arranged in a linear hierarchy in captive groups (ALVAREZ, 1973).

When a combination of measures was scored (Pulling, Pushing, Biting, Mounting, and Genital Display) in a group of four males, a strict linear hierarchy was obtained (PLOTNIK, KING, & ROBERTS, 1965). The use of this procedure, however, defies an analysis of social organization. On the other hand, results on non linearity cannot be taken into account when dealing only with total individual frequency of performance and not the distribution of the interactions among the group members (CASTELL & HEINRICH, 1971), since an individual can possibly distribute adequately its low frequency of performance among given partners to become a high ranking group member.

Another objectionable procedure when dealing with the squirrel monkey social organization is to make statements on the hierarchical ranks of different individuals without providing the observational backing, i.e., under what criterion is a subject classified as the alpha animal, for example.

The question thus comes out whether the members of a group of squirrel monkeys show different capacities for different kinds of behaviour. To test this hypothesis we shall work out the rate of performance and network of interactions for the different patterns of the ethogram.

As some of the most recent studies have shown the squirrel monkeys tend to arrange spatially in unisexual subgroups (THORINGTON, 1967; MASON & EPPLE, 1969; BALDWIN, 1971; ALVAREZ, 1973). It is for this reason that we should expect them to arrange their interactions also in a unisexual pattern.

METHODS

SUBJECTS

Two groups of squirrel monkeys, each consisting of three adults of each sex, were observed, both of them for 20 days. No subject had previous contact with any other member of its group before it was formed.

We numbered the males of both groups from one to three and the females from four to six.

APPARATUS

The observations were conducted at the Delta Primate Center (U.S.A.). Each group of monkeys lived for the whole period of observation in a cage measuring 15 × 13 ft at the floor, 11 × 15 ft at the roof and 7 ft high. An observation compartment was

attached to them, where the observer could see the monkeys through a small one-way observation screen.

The animals would spend most of their time on a runway system, placed 3 ft above the ground and made from $3/4$ in \times $1\frac{1}{2}$ in lumber (thinner side up), forming a grid consisting of 9 foot squares, which covered the whole cage.

The cages were framed in wood, roofed, and the sides were covered with wire and thin wire net to prevent the entrance of mosquitoes. Both cages were located in the edge of a pine wood away from human traffic and every effort was made to avoid visits and noise near the cages.

Six food containers and water bottles were distributed at equal distances above the runways. The animals were fed every day after 2 p.m., the food being deposited in equal amounts in each of the food containers.

OBSERVATION PROCEDURE

Observations followed a time-sampling procedure in which the activity of each group member was recorded in written form at two-minute intervals for a total of 30 observations per period. Each group was observed for one hour once a day, and the time of the observation period was changed every other day so that in two successive days each group was observed once in the morning (from 9:00 to 10:00 a.m.), and once in the afternoon (from 1:00 to 2:00 p.m.).

The identity of the actor and the number of time units (two-minute periods) in which the individual patterns of behaviour occurred were noted. Data on social behaviour included the actor and object in cases where such discrimination could be made. From these records it was possible to calculate the total frequency of two-minute intervals in which any given behaviour occurred and was directed towards particular individuals.

From these records a rank order for each of the group members could be worked out, regarding total frequency of performance (performance rank order, PRO) and position in the hierarchy regarding the direction of the activities (direction rank order, DRO).

To facilitate identification of individual animals, small patches of fur were dyed or bleached.

The following patterns of behaviour were noted by individual subject within each two-minute period (definitions are not given for those terms which are self-explanatory). A representation of some of them is shown in Figure 1.

Feeding

Drinking

Huddle posture

“When a squirrel monkey huddles, it squats with its head facing down and its rear end contacting the tree limb. Its arms are often between its knees, hands on the tree limb. Its tail comes up between its arms and the end is draped over one shoulder. There is also a semi-huddle position which is the same as the huddle except that the tail hangs down” (MAZUR & BALDWIN, 1966).

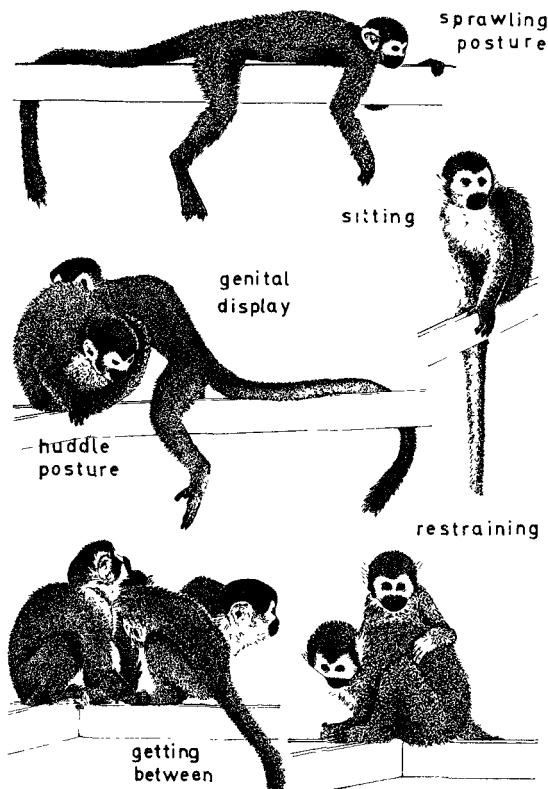


Fig. 1. Some of the patterns of behaviour of the squirrel monkeys used in this study.

Sprawling posture

“The monkey is stretched out on its stomach, straddling the limb, with one or more of its arms and legs and its tail dangling below the limb. There is also a semi-sprawl postures in which the arms are not dangling” (MAZUR & BALDWIN, 1966).

Sitting

The four limbs rest on a support while the back is kept in a more or less vertical line and the head up, the tail hanging down.

Locomotion

Locomotor movement of the limbs (walking, running, jumping, etc.).

Genital manipulation

Manual stimulation of own penis or vulva.

Urine washing

While supporting itself on one arm and one leg, the actor urinates on the palm of the free hand and rubs the urine against the sole of the free ipsilateral foot.

Chest impregnation

While a few spurts of urine are emitted...“one hind foot is thrust several times

across the ventral surface of the chest with such a force as to unbalance the animal ...” (MACLEAN, 1964), which remains in a sitting posture during the performance of this behaviour.

Social grooming

Combing or spreading the partner’s fur with fingers.

Wrestling

Playful fighting. Under this category are included running upside down toward and away from partner and playfully jumping toward him and/or gently hitting the partner with hands or feet.

Genital inspection

Placing the nose in proximity to the partner’s genitals.

Courtship dancing

“The active performance was conducted by a male and the passive partner was a female. The male made slight movements with head, arms, and trunk, while the legs moved relatively little. The movements were circular, fairly fluid but not fast, and a certain distance in front of the partner. It looked like a dance, and there was no doubt that the movements were addressed to the partner which sat quietly but watched the performance attentively. No erection was observed during this behavior and yet it is thought a part of sexual behavior.” (PLOOG, BLITZ, & PLOOG, 1963)

Mounting

“The active partner approached the passive participant from behind and mounted it in a way that its arms embraced the flanks of the passive partner while the legs were flexed. The active animal often climbed off the ground or branch and perched on the passive animal’s legs.” (PLOOG, BLITZ, & PLOOG, 1963)

Pelvic thrusting

While in a mounting posture, the actor gives pelvic thrusts on the mounted animal.

Approaching

The actor runs, walks, or jumps toward partner from a minimum distance of four feet. This category covers only the case when an animal is progressing toward a particular individual, not toward a group of individuals.

Following

Walking, jumping, or running behind and within 4 ft of a locomotory animal.

Withdrawing

A was said to withdraw from B when: (1) A was motionless and within 4 ft of B, (2) B approached A or directed a specific response toward him and A increased the distance between himself and B.

Restraining

The performer grasps hip, back, or top of head of receiver, restraining in this way his movements.

Getting between

While two animals are sitting in contact, the actor makes its way between them by pressing with hands and shoulders.

Close genital display

The actor is less than one foot away from partner toward whom he faces with "...laterally positioned leg with hip and knee bent and marked supination of the foot, abduction of the big toe, erection of penis/clitoris..." (WINTER & PLOOG, 1967).

Distant genital display

"...the monkey inclines the head to one side and abducts one thigh while the penis gradually reaches partial or full erection... at the same time there is a typically scratching of the body with a hand or foot, together with high-pitched, soft vocalization during which the corners of the mouth are retracted" (PLOOG & MACLEAN, 1963). In the present research, genital erection could not always be observed and was not considered in scoring this pattern.

Biting

"...An animal would try to seize its enemy with its hands and try to bite at any part of its body, usually the face. All movements were extremely quick, and fighting was always accompanied by loud screaming vocalization (PLOOG, BLITZ, & PLOOG, 1963).

RESULTS

In order to gain a clear insight into the distribution of interactions within each social group the results are presented separately for each of them. In both cases we shall consider the total frequency of performance of nondirective and directive activities, as well as the network of direction of interactions, considering the subjects as individuals and as males or females.

Of all activities described above only the following were frequently observed, and will be the only ones discussed: Locomotion, Sitting, Huddle posture, Feeding, Drinking, Genital manipulation, Approaching, Following, Withdrawing, Restraining, Genital display (Close), Genital inspection, and Getting between.

SOCIAL GROUP 1

When considering the total frequencies per individual subject of the behaviours most often observed, it can be seen in Table 1 that female 4 is the animal less often performing those activities involving physical activity or at least visual impact from the environment (Sitting) and precisely the one who spent more time in Huddle posture, where the animal shuts off the visual input from the environment. For the rest of the animals does not seem to be any other consistent difference except for the total frequency of social activities of male 2, who is the one most often performing active social patterns except Genital inspection and Genital display.

Significant positive correlations were found for the total performance rank order (PRO) of the group members between the patterns Following and Restraining ($p < .05$) and between Restraining and Getting Between ($p < .05$).

Table 1. Total frequency of 2-minute periods containing the most frequent activities by individual subjects (Group 1).

Animals	Non-directive activities						Directive activities						
	Locomotion	Sitting	Huddle posture	Feeding	Drinking	Genital manipulation	Approaching	Following	Withdrawing	Restraining	Genital display	Genital inspection	Getting between
♂ 1	141	57	535	41	11	2	23	0	9	22	22	0	4
♂ 2	142	101	452	51	3	0	42	13	5	54	1	1	17
♂ 3	124	94	492	54	11	3	17	0	7	23	8	7	2
♀ 4	40	25	566	12	1	0	17	0	6	4	0	0	0
♀ 5	150	59	547	75	15	0	27	0	18	5	0	0	0
♀ 6	117	59	509	20	22	0	19	1	5	31	4	0	28

The network of interindividual relations is presented in Table 2 and Figure 2, where two ways of representation were chosen: A simple hierarchical arrangement and a sociogram of the target type, specifically of the kind used by BONFENBRENNER (1945) in human choices: "To provide an appropriate and consistent scale for drawing, the radii of successive circles have been adjusted so that the area of each division is equal to one quarter that of the whole target." Symbols for individual animals are located in the sociogram; increasing proximity to the center indicates increasing frequency of receiving the behaviour in question. This technique is especially appropriate for distinguishing between peripheral animals (receivers on few occasions) and "stars" or centers of group attention (receivers on many occasions). Arrows of different thickness are used here to indicate the frequency of behaviour directed by one animal to another.

For approaching the arrangement is of a circular kind for the whole group, although males among each other and females among each other show a linear pattern of interactions. It is interesting to note that the male most often approached by the other two males (number 1) is the one most often approaching females, while these never approached him, although they did it towards the other two males.

The interactions for Following are restricted between animals of the same sex and, as would be expected, the pattern resembles very much the previous one.

The arrangement of interactions for Withdrawing is also of a circular kind. The individual males arranged in a linear hierarchy for this behaviour and the females much more often withdrawing from the males than from each other, mainly from male 1, who was the one most frequently approaching them.

Restraining flows in a linear pattern for all the animals in the group except for two of them, animals 1 and 6 (the last of the males and the first of the females), who show the same rank for this activity. The three males locate their ranks in the top of the hierarchy and the three females at the bottom. The male most often approached is also the most often restrained and he is also the one most frequently restraining females, so that as we ascend in the hierarchy the animals more and more to the bottom are receiving less attention from them, in other words, the monkeys concentrate restraining to those close in rank.

S O C I A L G R O U P 1

		ACTIVITY							RECEIVERS																			
		1	2	3	4	5	6	Σ	1	2	3	4	5	6	Σ													
P E R F O R M E R S	1	7	7	0	2	7	23	0	0	0	0	0	0	P E R F O R M E R S	2	20	20	0	0	2	42	10	3	0	0	0	13	P E R F O R M E R S
	3	11	4	2	0	0	17	0	0	0	0	0	0		P E R F O R M E R S													
	4	0	3	5	7	2	17	0	0	0	0	0	0			P E R F O R M E R S												
	5	0	1	1	18	7	27	0	0	0	0	0	0				P E R F O R M E R S											
	6	0	3	0	14	2	19	0	0	0	1	0	1					P E R F O R M E R S										
	Σ	31	18	33	34	11	18	145	10	0	2	1	0						14									
			R ₁ <.001	R ₂ <.05	P<.001	R ₃ <.001	R ₄ <.001	R ₅ <.01	N.S.	N.S.	N.S.	N.S.	N.S.						N.S.									
		APPROACHING							FOLLOWING																			
P E R F O R M E R S	1	16	3	0	0	0	19	0	0	13	5	4	22	P E R F O R M E R S														
	2	2	13	0	0	0	15	30	1	5	9	9	54		P E R F O R M E R S													
	3	1	1	4	1	0	7	6	15	0	0	2	23			P E R F O R M E R S												
	4	5	1	0	0	0	6	3	1	0	0	0	4				P E R F O R M E R S											
	5	6	5	0	6	1	18	0	0	0	3	2	5					P E R F O R M E R S										
	6	1	2	1	0	1	5	4	0	0	12	15	31						P E R F O R M E R S									
	Σ	15	25	17	10	2	1	70	43	16	1	33	29							17	139							
		R ₁ <.02	R ₂ <.01	R ₃ <.001	R ₄ <.001	P<.02	N.S.	R ₁ <.01	R ₂ <.001	N.S.	R ₃ <.001	R ₄ <.01	N.S.															
		WITHDRAWING							RESTRAINING																			
P E R F O R M E R S	1	0	0	0	11	7	4	22	0	0	0	0	0	0	P E R F O R M E R S													
	2	1	0	0	0	0	0	1	0	0	0	0	1	1		P E R F O R M E R S												
	3	4	4	0	0	0	8	0	0	5	2	0	7	P E R F O R M E R S														
	4	0	0	0	0	0	0	0	0	0	0	0	0				P E R F O R M E R S											
	5	0	0	0	0	0	0	0	0	0	0	0	0					P E R F O R M E R S										
	6	0	0	0	3	1	4	0	0	0	0	0	0						P E R F O R M E R S									
	Σ	5	4	0	14	8	4	35	0	0	5	2	1							8								
		R ₁ <.01	P<.02	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.															
		GENITAL DISPLAY							GENITAL INSPECTION																			
A C T I V I T Y	1-2								1	1	0	0	0	1	4	P E R F O R M E R S												
	1-3	6	2	3	1				2	1	2	0	2	0	17		P E R F O R M E R S											
	1-4	2	0	0	0	0	0	0	3	0	0	0	0	0	2			P E R F O R M E R S										
	1-5	0	0	0	0	0	0	0	4	0	0	0	0	0	0				P E R F O R M E R S									
	1-6	0	0	0	0	0	0	0	5	0	0	0	0	0	0					P E R F O R M E R S								
	2-3	0	0	0	0	0	0	0	6	0	0	4	2	0	0						P E R F O R M E R S							
	2-4	0	0	0	0	0	0	0	Σ	2	6	6	5	1	0							0	0	24	1	1	51	
		R ₁ <.001	P<.02	N.S.	N.S.	N.S.	N.S.	N.S.	R ₁ <.05	N.S.	N.S.	N.S.	P<.01	P<.05	P<.05													

Table 2. Distribution of directive interactions among members of group 1.

The female most frequently approached by the other females is also the most often restrained by them.

When comparing the individual total performance rank order (PRO) for this behaviour with the direction rank order (DRO), where not the total frequency of

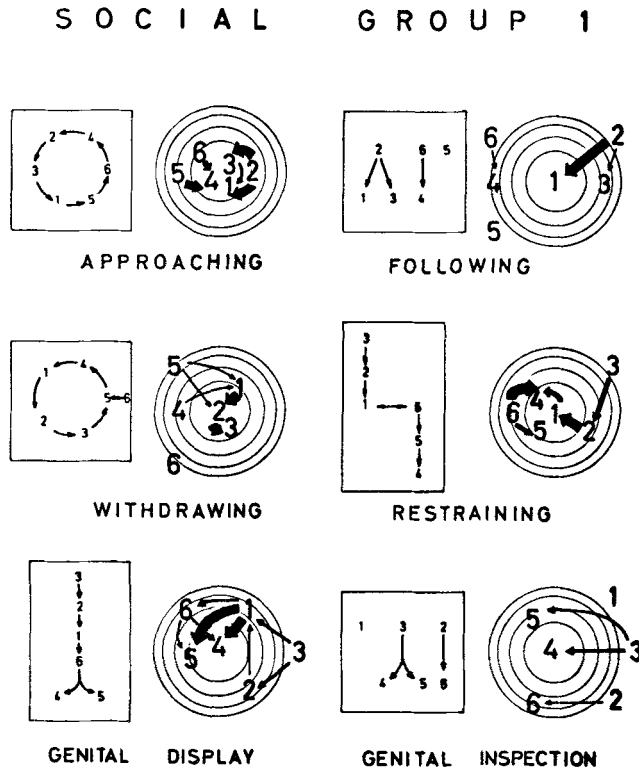


Fig. 2. Networks of interindividual interactions within group 1. For each pattern of behaviour a simple hierarchical arrangement of the individuals within the group and a socio-gram of their interactions are presented.

performance is considered but the distribution among group members, the low correlation obtained between both series of ranks shows that not only frequently performing Restraining locates one animal high in the hierarchy for this activity, so that to be the alpha animal male 3 does not need a high rate of performance. The situation of the bottom of the hierarchy does seem to be related with a low level of performance (animals 4 and 5).

A linear pattern is also showed for Genital display, again with the males at the top and the females at the bottom of the hierarchy, the location of individual status (DRO) being very much the same as for Restraining ($\rho=0.97, p<.01$).

Again for this behaviour the male at the bottom of the hierarchy of males is the one displaying toward the females, the two other males never doing so.

The correlation between PRO and DRO for this activity was also low, again male 3 did not need a high rate of performance to be the alpha male; but rather to direct his displays conveniently. Actually animal 1, occupying the lowest position among the males was the one showing the highest frequency of performance.

No hierarchy could be discernible for Genital inspection. It is interesting to note, however, that the male who paid the females least attention for Restraining and Genital display was the one most frequently inspecting their genitals, followed by

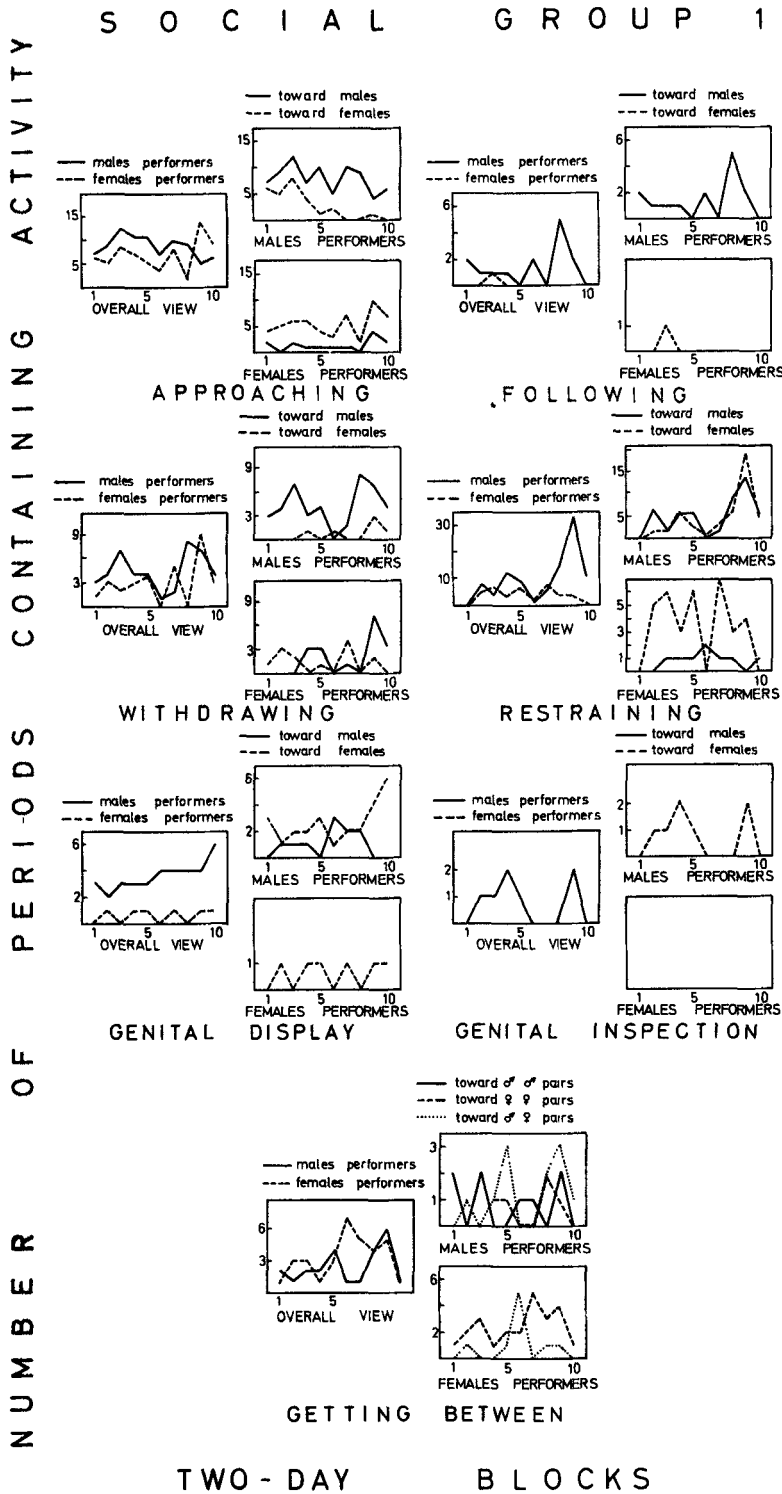


Fig. 3. Overall frequency of performance and direction of social patterns of behaviour when considering only the sex of the subjects for group 1.

the next animal in the hierarchy for these activities (male 2), and the male who most frequently interacted with them in other respects (male 1) never did inspect them.

Of the females, number 4 is the most often approached, followed, withdrew from, restrained, displayed, and inspected, the first three activities being directed to her mainly by the other two females, the last three by the males.

Among the males, number 1 is in the lowest position for all behaviours but Withdrawing, being the one who withdraws from the other two males.

Males number 2 and 3 alternate in the highest rank, the former most often seeking proximity towards 3 and 1 and number 3 most often restraining and displaying towards them.

Getting between is, according to our definition, directed towards two animals at the same time, thus we cannot work out an interaction hierarchy for this behaviour. As can be seen in Table 2, however, it is female 6 the one most frequently performing this activity, precisely towards pairs where one of the members is a female.

Among the males, number 2 shows the highest frequency for this pattern, interfering both between unisexual and heterosexual pairs, male 2 also interfered, although to a lesser degree, between males and females, whereas male 3 got between the other two males, paying no attention to the females.

Considering not the identity of the subjects but their classification as males and females it can be seen in Figure 3 that males are in general more active than females for Approaching, Following, Genital display, and Genital inspection (not statistically significant difference for the first and the last activities, statistically significant for the second and third, $p < .05$ and $p < .01$, respectively, Wilcoxon test).

Concerning the direction of the social activities towards males and females there is a unisexual distribution with respect to Approaching (statistically significant, $p < .01$), Following (not statistically significant), Withdrawing by males (statistically significant, $p < .01$), Restraining by females (statistically significant, $p < .05$), and Genital display by females (statistically significant, $p < .05$). With respect to Withdrawing by females, Restraining by males, Genital display by males and Getting between for actors of both sexes there was no unisexual separation in direction of activities. Concerning Genital inspection, a pattern performed in this group only by males, in all cases females were the receptors, the difference was not, however, statistically significant.

SOCIAL GROUP 2

For the total frequency of performance of the most frequent behaviours there are no evident interindividual differences for the nonsocial activities; for the social ones female 4 appears the most active for Approaching, Following, Restraining, and Getting between (see Table 3).

The correlations between total performance rank order (PRO) for the six animals show much higher values for this group than for the other one and for a wider array of activities: a significant positive correlation was found between Locomotion and Feeding ($p < .05$), Locomotion and Genital display ($p < .05$), Sitting and Feeding ($p < .01$), Sitting and Withdrawing ($p < .05$), Feeding and Drinking ($p < .05$), Feeding and Genital manipulation ($p < .05$), Feeding and Genital display ($p < .01$), Genital

manipulation and Genital display ($p < .05$), Approaching and Following ($p < .05$), Approaching and Genital inspection ($p < .05$), and between Restraining and Getting between ($p < .05$).

The distribution of interindividual interactions can be seen in Table 4 and Figure 4 for this group.

The arrangement of the flow of interactions for Approaching is linear for the whole group except for the two highest positions in the hierarchy, which are at the same level.

The correlation of the PRO and DRO for this behaviour was significant ($\rho = 0.93$; $p < .05$), suggesting that the position of each subject in the hierarchy was a result of the total frequency of performance.

For Following the pattern of interactions is circular, although the direction of this activity usually goes towards animals of the same sex as the performer, the hierarchical structure within each sex class being linear.

The pattern for Withdrawing is also circular, made up of two linear within same sex hierarchies connected at the ends. Hierarchies completely different from that of Approaching with respect to location of individual status.

Restraining is directed among the group members mainly toward animals of the same sex (only male 2 restrained female 5 once). The male hierarchy is linear, that of females presents two positions at the same level, both animals with this rank engaging in the restrain of the third one.

The distribution of interactions for Genital display shows the males connected in a triangular pattern, with all the females below them, arranging themselves in a linear hierarchy.

No hierarchy was recognized for Genital inspection, pattern only directed from males towards females and by the latter to each other. It is of interest that male 3, the alpha animal for Restraining and of high status for Genital display, did not ever inspect the females' genitals.

Although in general the hierarchies for the different behaviours are less well defined in this group than in the other, the positions of the individual status for the various activities are in this group more constant, for example, animal 6 is of the females the one most often approached, followed, restrained, displayed, and inspected, being the one most often withdrawing from the other females.

Table 3. Total frequency of 2-minute periods containing the most frequent activities by individual subjects. (Group 2)

Animals	Non-directive activities						Directive activities						
	Locomotion	Sitting	Huddle posture	Feeding	Drinking	Genital manipulation	Approaching	Following	Withdrawing	Restraining	Genital display	Genital inspection	Getting between
♂ 1	224	166	442	54	27	16	77	3	64	0	15	4	1
♂ 2	183	131	513	42	17	4	89	11	30	2	9	12	2
♂ 3	193	158	481	45	11	3	25	2	62	11	10	0	8
♀ 4	145	138	487	29	13	0	90	16	39	34	2	9	22
♀ 5	187	116	479	28	9	0	48	11	19	14	2	2	3
♀ 6	140	108	498	26	1	0	22	1	37	0	0	0	0

S O C I A L G R O U P 2

P E R F O R M E R S	ACTIVITY							RECEIVERS																														
		1	2	3	4	5	6	Σ		1	2	3	4	5	6	Σ																						
	1		26	34	0	11	6	77	1		0	0	0	1	0	1																						
	2	43		29	1	13	5	91	2	7		3	0	0	0	10																						
	3	7	16		0	0	2	25	3	2	0		0	0	0	2																						
	4	4	1	9		26	50	90	4	0	0	1		3	12	16																						
	5	4	4	11	6		23	48	5	0	0	0	4		7	11																						
	6	0	2	7	9	4		22	6	0	0	0	1	0		1																						
	M	58	49	90	16	54	86	353	M	9	0	4	5	4	19	41																						
		P<.001	P<.001	P<.001	P<.001	P<.001	P<.001			P<.001	N.S.	N.S.	N.S.	P<.01	P<.05	P<.05																						
P E R F O R M E R S	APPROACHING							FOLLOWING																														
		1	2	3	4	5	6	Σ		1	2	3	4	5	6	Σ																						
	1		32	19	7	3	4	65	1		0	0	0	0	0	0																						
	2	6		5	6	9	4	30	2	1		0	0	1	0	2																						
	3	5	17		10	22	8	62	3	10	1		0	0	0	11																						
	4	0	2	0		25	12	39	4	0	0	0		3	26	29																						
	5	4	11	0	2		2	19	5	0	0	0	3		16	19																						
	6	0	0	0	1	20	21	42	6	0	0	0	0	0		0																						
	M	15	62	25	45	80	30	257	M	11	1	0	3	4	42	61																						
		P<.001	P<.001	P<.001	P<.001	P<.01				P<.001	N.S.	N.S.	N.S.	P<.02	N.S.	P<.001																						
P E R F O R M E R S	WITHDRAWING							RESTRAINING																														
		1	2	3	4	5	6	Σ		1	2	3	4	5	6	Σ																						
	1		1	1	0	10	3	15	1		0	0	0	4	0	4																						
	2	0		2	1	4	3	10	2	0		0	2	9	1	12																						
	3	7	2		0	0	1	10	3	0	0		0	0	0	0																						
	4	0	0	0		0	2	2	4	0	0	0		0	9	9																						
	5	0	0	0	1		1	2	5	0	0	0	0		2	2																						
	6	0	0	0	0	0		0	6	0	0	0	0	0		0																						
	M	7	3	3	2	14	10	39	M	0	0	0	2	13	12	27																						
		P<.01	P<.02	P<.02	N.S.	N.S.	N.S.			N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	P<.02																						
A C T I V I T Y	GENITAL DISPLAY														GENITAL INSPECTION																							
			1-2	1-3	1-4	1-5	1-6	2-3	2-4	2-5	2-6	3-4	3-5	3-6	4-5	4-6	5-6	M			1-2	1-3	1-4	1-5	1-6	2-3	2-4	2-5	2-6	3-4	3-5	3-6	4-5	4-6	5-6	M		
	1							1	0	0	0	0	0	0	0	0	0	1	1																		1	
	2																	2	2	2																	2	
	3	10																10	3	10																	10	
	4	0	0															0	4	0	0																	0
	5	0	0	0														0	5	0	0	0																0
	6	0	0	0	0													0	6	0	0	0	0															0
	M	10	2	0	0	0	1	0	0	1	0	0	0	0	0	3	21	38	M	10	2	0	0	0	1	0	0	1	0	0	0	0	3	21	38			
		P<.001	P<.001	N.S.	N.S.	N.S.	P<.001	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	P<.001	P<.01		P<.001	P<.001	N.S.	N.S.	N.S.	P<.001	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.			
GETTING BETWEEN														GETTING BETWEEN																								

Table 4. Distribution of directive interactions among members of group 2.

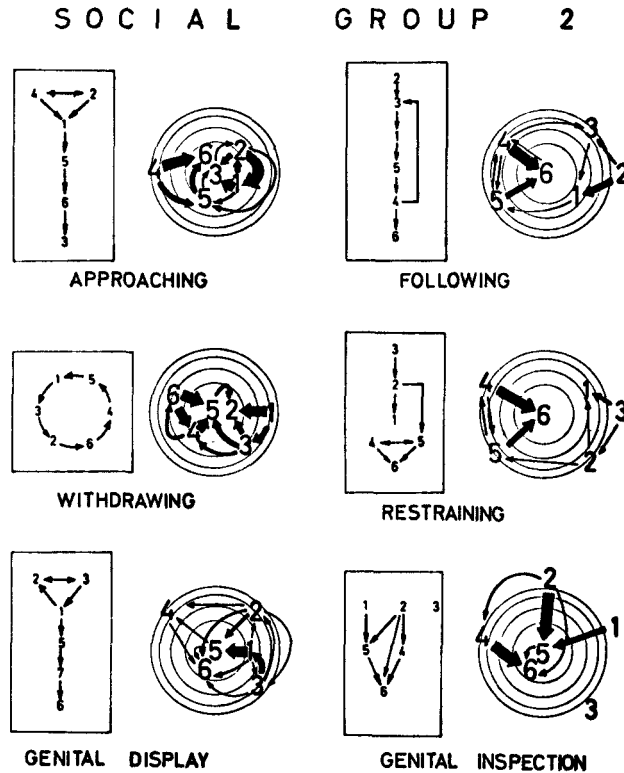


Fig. 4. Networks of interindividual interactions within group 2. For each pattern of behaviour a simple hierarchical arrangement of the individuals within the group and a sociogram of their interactions are presented.

Male 3, the alpha animal for Restraining and Genital display, is the most frequently approached although not the most frequently followed. He does not, however, occupy the highest position for Approaching and Following, being number 2 the male most often seeking the proximity of the other two.

Getting between is performed in this group most often by female 4, who directs this activity mainly towards the other two females. Female 5 also behaves only towards the females in this respect, whereas female 6 never performed this pattern.

The three males direct the whole frequency for this behaviour only towards males.

Considering not the identity of the subjects, but only their sex, it is shown in Figure 5 the total frequency of performance and direction of social activities, where it can be seen that males were more active than females only for Genital display (statistically significant, $p < .01$).

With respect to the direction of the social activities towards males and females it is evident in Figure 5 a unisexual segregation in direction of activities in Approaching (statistically significant, $p < .01$), Following by females (statistically significant, $p < .01$), Withdrawing by females (statistically significant, $p < .01$), Restraining (statistically significant, $p < .05$ and $p < .01$).

The females were the only receivers of the behaviour Genital inspection.

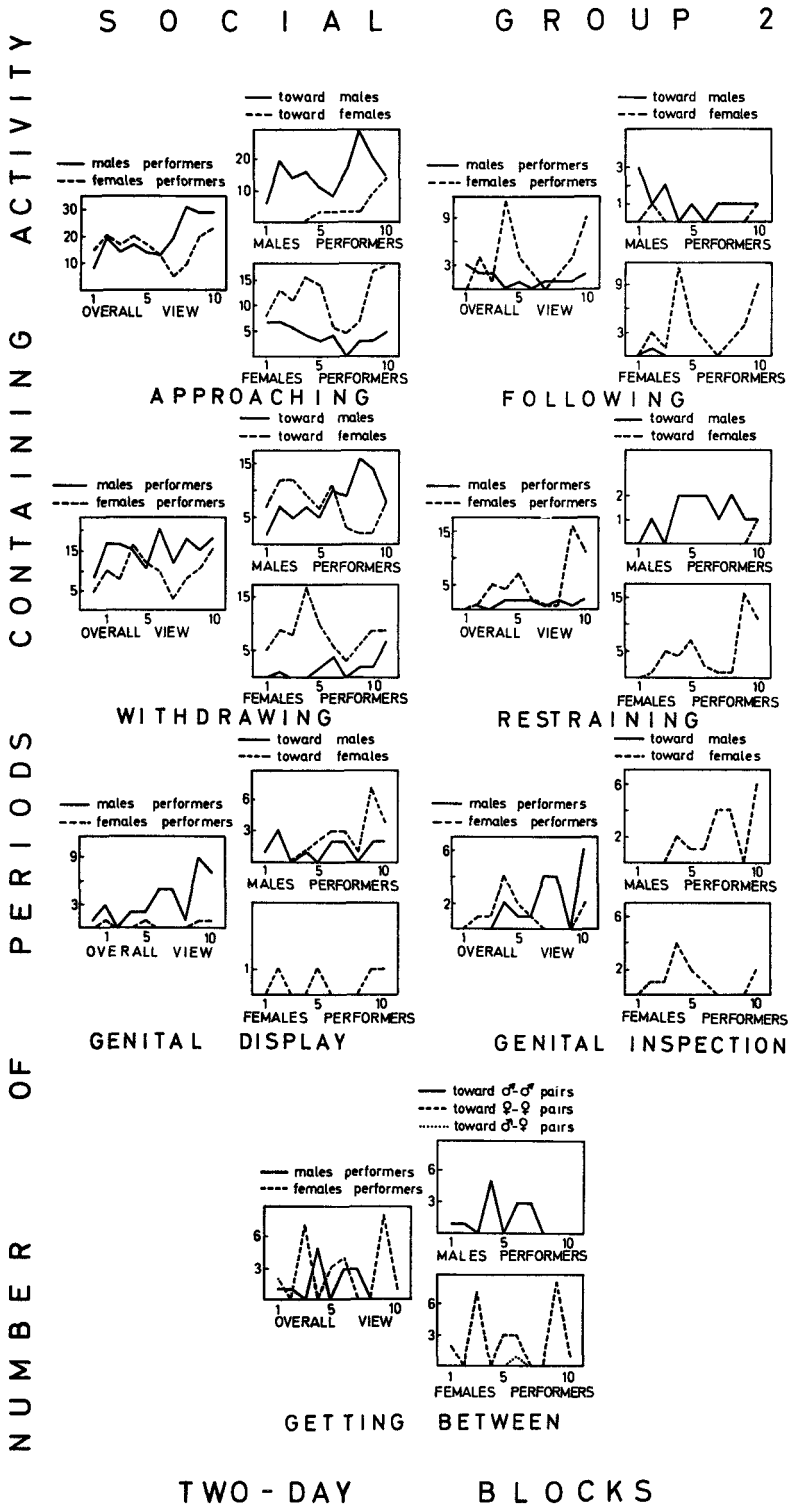


Fig. 5. Overall frequency of performance and direction of social patterns of behaviour when considering only the sex of the subjects for group 2.

The pattern Getting between was directed mainly towards pairs of animals of the same sex as the actors (the difference was not statistically significant, however).

OVERALL VIEW

In the first place, the wide array of positive correlations found between the ranks occupied by the individual subjects in the PRO for the different activities within group 2 is very suggestive. The only behaviours showing this kind of correlation in both groups were, however, only Restraining and Getting between.

There was also a tendency in both groups to behave mainly toward animals of the same sex as the actor for the activities Approaching, Following, Withdrawing, and Getting between.

When the interactions flowed between animals of different sex they tended to arrange the direction of the activities in a linear pattern, sometimes becoming circular through behaviour directed from the last animal in the hierarchy to the ones on top. In any case even when the distribution of the interactions presented a circular design, considered males and females apart their unisexual hierarchy was usually linear.

The analysis of the quantity of interactions within each hierarchy showed that each animal distributed its behaviour mainly to those animals close to itself in rank, the ones farther apart being seldom addressed or not at all.

The location of individual status within the hierarchies for Approaching and Following was very much the same, and close to the opposite pattern was shown for Withdrawing.

The male most often seeking the proximity of the other two males was not the alpha animal for Restraining and Genital display, the alpha position for these two activities (which otherwise showed a close similarity in position of individual status) was occupied by another male who did not distinguish himself specially in total frequency of performance but rather in the distribution of his behaviour, appearing sometimes very passive, but behaving very adequately to maintain the hierarchy.

The bottom position in the hierarchies for most behaviours was occupied by a certain female and for those behaviours where the interactions were restricted within the same sex, there was also one particular male occupying the third position, being precisely this male the one who made the connection with the female hierarchy for those activities where all the group members were engaged in mutual interactions.

It is interesting to note that the female in the bottom position for the various activities showed a low total frequency of performance for most of them except for Huddle posture, the passive posture *per excellence*, where the animal hides its face shutting off the input from the environment.

The animal in the lowest position in the hierarchy of males behaved quite differently, not being passive at all but behaving almost continuously towards the females.

The tendency to interfere with certain pairs of animals, as expressed by the activity Getting between, is shown to the highest degree among females by the one occupying the highest position among them for Restraining and Genital display in one group and by the next one and the most often seeking contact (Approaching) in the other group; being this interference directed only towards females.

Among males, Getting between is directed mainly towards males.

The correlation between total performance rank order (PRO) showed positive correlation for both groups between this behaviour and Restraining.

DISCUSSION

The picture emerging from the results is that of a society where the individual members show different capacities for the various behaviours.

For example, the alpha position for Restraining and Genital display was occupied by a male whose rank was attained not by a high frequency of performance for these activities but by a distribution of them mainly toward the closest subjects in rank. This male, however, was not the one most often seeking the proximity of other individuals (Approaching and Following), the animal doing so occupying the second position for Restraining and Genital display.

The last position in the male hierarchy for these two activities was occupied by a subject showing the highest frequency of these behaviours directed toward females.

Our results differ in this respect with those of CASTELL and PLOOG (1967), where it was the alpha male the one most often displaying towards females. Thus the integration of individual tendencies into groups of different composition may be of upmost importance.

The females appeared very constant in the arrangements of their interactions, one of them being the focus of most attentions, the role of this individual was obviously as scapegoat, the female with this rank would be the most sought, restrained, displayed, and inspected.

The tendency showed by our subjects to interact mainly with animals of the own sex for certain activities was to be expected from previous results of semifree-ranging and captive studies (MASON & EPPLE, 1969; BALDWIN, 1971; ALVAREZ, 1973), where squirrel monkeys were observed to arrange distance and interactions in a unisexual pattern, in fact if it were not for the behaviour of the lowest ranking animal among the males of our groups most of the hierarchies would have been also unisexual.

When sufficient interactions between animals of both sexes occurred, they showed a tendency to rank themselves in a circular hierarchy, the behaviour also flowing from what would have been the bottom of the hierarchy to the top of it, transforming the linear order into a circular one.

It is of interest the widening of the concept of linearity to include other activity than Genital display, namely Restraining, with positions of individuals ranking very much in the same way for both of them.

Within the unisexual subgroups the individual ranked in a still more strict linear order, which would be expected to come out of a higher contact and greater familiarity with subjects of own sex.

These findings on linearity of social hierarchies for *Saimiri* are consistent with other evidences of linearity in seminatural and laboratory conditions. BALDWIN (1968) and DU MOND (1968) observed a linear hierarchy for Genital display between semifree ranging males during the mating seasons, and PLOTNIK, KING, and ROBERTS (1965) also reported a linear hierarchy among four captive males based on a combination of measures, including pulling, pushing, biting, mounting, and genital display. Linearity

in the hierarchy was specially clear and the hierarchy was more stable when the animals were competing for positive reinforcement; when they competed to escape a negative reinforcement, the hierarchy, although very similar to the previous one, was slightly less stable and linearity was not as strict as in the positive situation.

PLOOG, BLITZ, and PLOOG (1963) have suggested that Genital display might be correlated with social status or dominance. Our findings support this hypothesis and suggest that Restraining may be a more useful index of social status than Genital display since it occurs frequently in both sexes and provides a better quantitative basis for the description of dominance structure. Moreover, Restraining represents a form of physical coercion that is intuitively more closely related than Genital display to the conventional concept of social dominance.

In none of the reports on semifree or free ranging animals was found any indication of a hierarchy among females. The disagreement with our results are then probably related to the conditions of observations, perhaps the more simple social and physical environment of our subjects had an effect increasing familiarity among the different individuals and thus each subject prediction on the behaviour of its partners, with its effect making the hierarchy more rigid, provided that ample space is available for the monkeys to avoid interactions with those not of its choice.

The relationship between Restraining and Genital display probably arises from the fact that both activities are used by *Saimiri* in a competitive or agonistic context. It would be a mistake, however, to conclude that both behaviours have precisely the same function in social interaction. Genital display is primarily a male response and is directed from males toward females when almost no other interaction exists. The response is performed infrequently by females and is never directed toward males, which suggests that Genital display has a sexual as well as a dominance connotation. Restraining, on the other hand, is a less specialized response that is used by both males and females as a form of social restraint and has, at best, a slight sexual connotation.

One might ask why the correlation exists between the two responses. In this connection we can formulate the hypothesis that if Genital display arose in evolution from a process of ritualization of sexual patterns and if some elements of the sexual motivation are still associated with it (as it seems to be the case), the correlation between Restraining and other forms of physical coercion and Genital display may express a more general trait, which might be described as "self-assertion," or the tendency to act directly on the social environment in response to individual needs or motivations.

Finally it was apparent in our subjects a preference to behave mainly towards animals of similar rank, the tendency being most apparent for subjects rankig high, so that the alpha male for a hierarchy hardly ever behaved towards the one in the lowest position.

The tendency to distribute hierarchical signals among animals close in rank is probably widespread in birds and mammals and we can think of it as an adaptation to maintain effectively a rank position by distributing adequately a given amount of performance.

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