

Social Behavior of the Wild Black-capped Capuchin (*Cebus apella*)

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ABSTRACT. The author undertook a field survey of the capuchin (*Cebus apella*) lasting 60 days from December 1976 to January 1977, and determined the basic daily activity of its groups and spacing of group members in the day time. Furthermore, based on studies of various types of interactions between individuals of the groups, he was able to show that (1) decisive rank orders exist both among adults and among sub-adults of both sexes; (2) grooming at the resting time is peculiar to adult males; (3) with quite mild agonistic interactions being maintained, a high tolerance exists between the group members; (4) alpha males represent individuals which can be called leaders of groups; and (5) a strong psychological or spiritual bond exists among the adult males, which can be termed a "male-bond." Furthermore, according to comparative studies on some adjoining groups, it was found that the group structure is strongly influenced by the individuality or character of the adult males of each group. The present findings are generally in agreement with those for *C. apella* studied by the author and other researchers in other localities. It can be safely said therefore that these findings are probably common to this species of monkey. Based on a comparison with findings for three other species of *Cebus*, the author attempts to clarify the points of difference between *C. apella* and these three other species of *Cebus* from the viewpoint of behavioral science and sociology.

INTRODUCTION

Recently, many field studies have been made on New World monkeys, including *Cebus apella* which is one of the most widely ranging species of the New World monkeys (HILL, 1960). It lives in many different forest habitats (HERNANDEZ-CAMACHO & COOPER, 1976; MOYNIHAN, 1976; HILL, 1960), has various food habits (IZAWA, 1979), and exhibits highly adaptational characteristics in its feeding behavior (IZAWA & MIZUNO, 1977; IZAWA, 1978, 1979). However, little has yet been reported on the detailed social life of *Cebus apella*. In order to clarify this, the author undertook an intensive field survey of *C. apella* for the 60 days from December 3, 1976 to January 31, 1977.

The study site was located on the lower bank of the Duda River which forms the western border of La Macarena National Park, Colombia (Fig. 1). Prior to this study, from October 1975 to February 1976, A. MIZUNO and the author had investigated New World monkeys at the same site (MIZUNO, 1976; IZAWA, 1976b). At that time, habituation of the capuchin was performed to a considerable extent and observation trails extending 23.6 km were set up. As a result, the author was able to initiate his intensive survey of the capuchin immediately from the beginning of the study period.

The observation trails were extended a further 10.3 km during the course of the present study. As the study proceeded, habituation became so advanced that the author could observe the capuchin at intervals of 3 m at maximum proximity. According to the physical characteristics of each capuchin, individual identifications were effected completely.

The author could grasp the group as a social unit of capuchins and clarified the group struc-

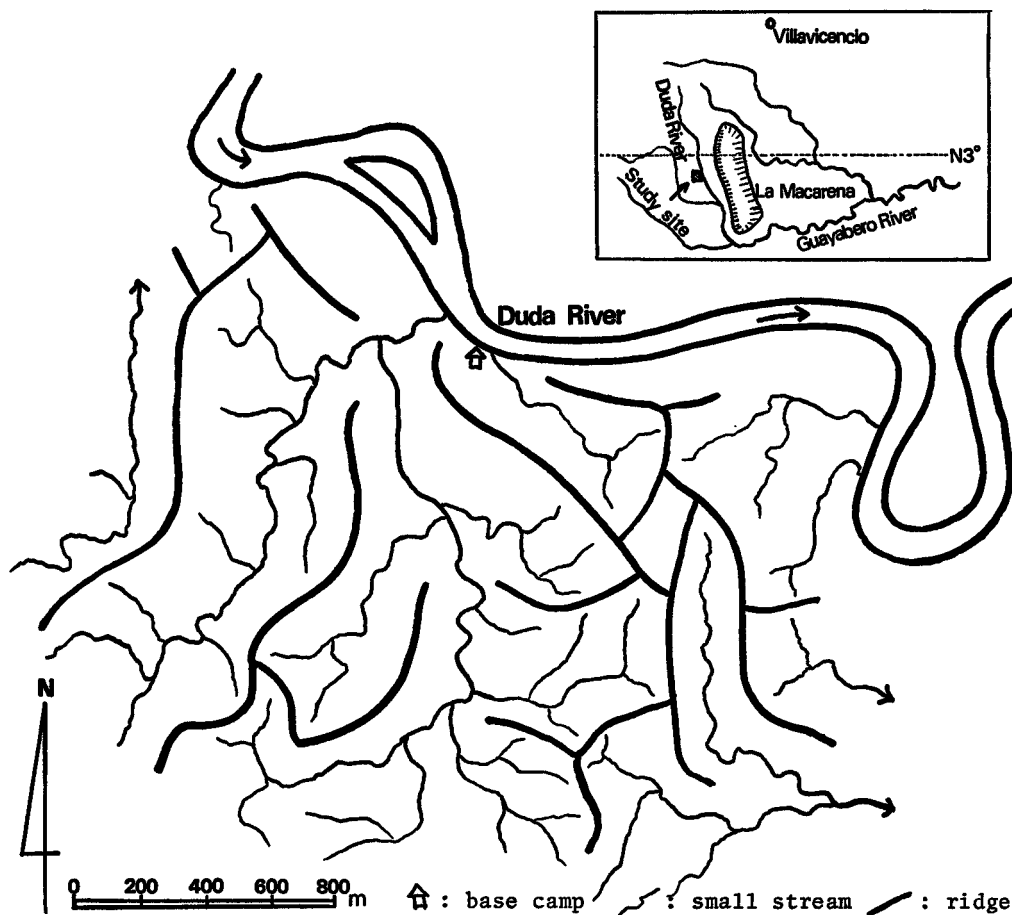


Fig. 1. Map of the study site.

ture by observing various types of interactions between the individuals forming the group. Direct observations amounted to a total of 110 hr. No nocturnal observations were made.

The author here reports and discusses the results, comparing them with observations on other New World monkeys, especially the three other species of *Cebus*.

GEOGRAPHIC FEATURES AND VEGETATION AT THE STUDY SITE

The study site is undulating, and the altitudinal difference between the surface of the Duda River and the top of the highest hill is about 140 m. The water level of the river of course rises and falls somewhat in accordance with the amount of rainfall: the difference in depth during the present study period was 3.5 m and that during the previous study period was 5.5 m. The study site covers the whole basin of a stream of width 3.5 m at the confluence with the Duda River, as well as the upper basins of some other streams surrounding this stream (Fig. 1).

The entire vegetation of the study site and its vicinity is Neo-tropical forest, in which, however, marked wet and dry seasons are seen. In the dry season extending from October or November to March or April, many tall trees such as of the Moraceae and Mimosaceae which

form the forest canopy, lose their leaves and almost all the undergrowth dies back. The forest, therefore, becomes so thin as to be light and can be seen through. Even in the wet season, the study site remained non-flooded.

The study period coincided with the dry season, with the rainy days numbering 5, and the hours of rain totaling about 19 during the 60 days. Only once did it rain continuously for more than 12 hr.

As for the characteristics of the vegetation at the study site, *Jessenia polycarpa* and *Astrocaryum chambira*, both of the Palmae, grow densely. *Bambusa guadua* and *Phenakospermum guianensis* grow thickly in patches, the former mainly on the steep slopes of the valleys and the latter on the ridges of the hills. *Heliconia* sp. and *Arundo* sp. are prolific in the lowland on the sides of the Duda River.

RESULTS

DAILY ACTIVITY

Even though habituation has progressed, it is inevitably not easy to observe the capuchin continuously for hours. One of the main reasons for this is that the monkey sometimes moves agilely without vocalization or making a noise. Another reason is that it frequently utilizes the patches of *Bambusa guadua* on the steep slopes where the observer is unable to penetrate. This is also true for the patches of *Heliconia* sp. and *Arundo* sp. on the river sides which, although not so frequently as the patches of *Bambusa guadua*, it often utilizes. The other reason is that the capuchin sometimes forms mixed groups with the squirrel monkey (*Saimiri sciureus*), which is very shy to observers, and then tends to join the rapid escapes of the squirrel monkey. Accordingly, the author has never been able to make continuous observations on the capuchin for periods exceeding 8 hr. However, he was able to grasp the group as a social unit by observing certain individually identified capuchins as continuously as possible.

The main activity of the capuchin groups in the daytime was feeding. Such activity can be categorized broadly into two types as follows: (1) capuchins feed, moving not in a mass but in a scattered formation in a certain area; and (2) although moving freely individually, they feed in groups moving in a certain direction, either slowly or busily. The former type of feeding was typically observed when they took their main food, as described previously by the author (IZAWA, 1979), whereas the latter was seen when they ate insects rather than fruit. However, the distinction between these two types of feeding was not always obvious.

In the former case, another kind of activity, resting of the group, was observed: many of the group members gathered at one or two adjoining places to rest at the same time. It is worthy of note that one or a few individuals inevitably fed apart from such congregations of resting capuchins, and there was no case where all the group members rested together at the same time. Needless to say, one or a few group members also take brief rests when other members are feeding slowly moving in a certain direction.

A very extreme case in which the capuchins feed busily moving in a certain direction is seen in the rapid moving of almost all the group members en masse, which could well be called moving activity. Such activity was observed typically in cases where they crossed the ridges shown in Figure 1. In this event also, a few group members fed apart from the other group members. While crossing the ridges, the capuchins often became scattered to feed.

In addition to the above rapid moving activity, another form of rapid movement not accompanied by feeding, i.e., rather a type of escape, was occasionally observed in cases where

large-sized raptorial birds suddenly appeared or flew off or the capuchins suddenly encountered the observer.

As indicated above, it was often rather difficult to discriminate among the three activities, i.e., feeding, resting, and moving, and also difficult to determine the capuchin's daily activity precisely. However, it became apparent that among the total hours of observation, the period for which more than half of the group members rested amounted to 258 min (3.9%), the period for which more than half of the group members rapidly moved without feeding amounted to 205 min (3.1%), and the remaining 6,130 min (93%) constituted the period for which more than half of the group members fed.

In this paper, the author thus utilizes the terms for activity, i.e., resting, rapid moving, etc., to describe situations where more than half of the group members followed the behavior concerned.

As for the moving distance per day, complete traces of the capuchins were not possible but fragmentary data suggested that the capuchin moves about 1 km at the least and more than 3 km at the longest.

AGE CLASSES

Infant: The class of infant covers capuchins at stages prior to juvenile I, i.e., from newborns to animals which are still strongly dependent on their mothers.

Juveniles: Capuchins which have no marked tufted hair on the crown and still have white hair largely on the forehead are ranked as juveniles. These are divided into three sub-classes.

Juvenile I: Members of this class are still given milk while resting with their mothers, but rarely ride on their mother's back except in rapid moving; *Juvenile II*: Members of this class never ride their mother's back. Apart from their mothers, they often play with similar aged capuchins and often stay with adult males; and *Juvenile III*: Members of this class rarely play and often stay alone at the periphery of the group expanse.

The above-mentioned discrimination of juveniles accords not only with body size but also with changes in size of the white hair from the forehead to the crown top.

Sub-adult: The sub-adult has physical characteristics which are intermediate between the adult and juvenile. Since sub-adult capuchins, especially males, tend to stay alone at the periphery of the group expanse and never play with the other group members, it is easy to discriminate sub-adults from juveniles.

Adults: Sex difference in the adult capuchin is clear. Males are larger and more robust than females, and the well-grown tufted hair on the male's crown is pointed, whereas that in the female is fringy. Also, males have squarish faces with prominent jaws and cheeks. Accordingly, it is easy to discriminate the sexes without relying on the genital organs. According to the growth of the tufted hair on the crown, the age class of adults can be separated into two sub-classes, adult I and adult II. *Adult I*: Tufted hair on the crown is developed. The hair from the crown front to the crown top is black, and traces of white hair are found on the forehead; and *Adult II*: The white hair on the forehead has completely disappeared.

There is no means of determining the absolute ages of the above age classes through the short-term study. However, based on the observations of caged capuchins at the Japan Monkey Centre, the author has estimated the juvenile I to be about 0.5 to 1 year old, juvenile II

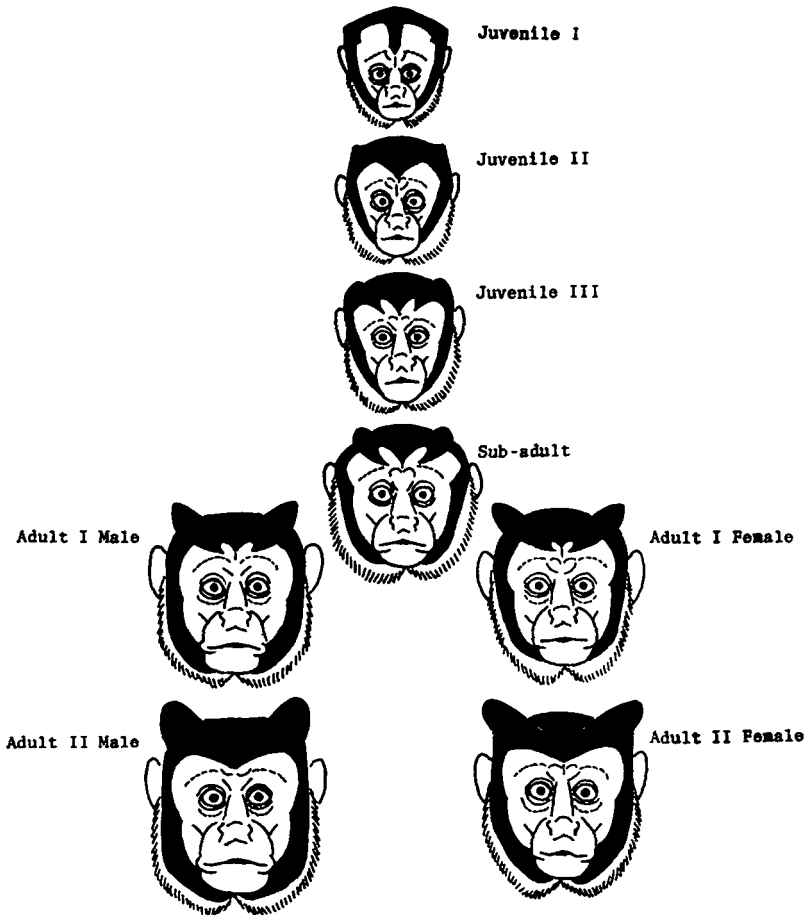


Fig. 2. Changes in forehead patterns according to growth.

to be 1 to 2 years old, juvenile III to be 2 to 3, sub-adult about 4, adult I about 5, and adult II to be 6–7 years old or over.

Figure 2 illustrates the changes in color and shape of the hair from the forehead to the crown top in juveniles I, II, III, sub-adult, and adults I and II.

SPACING OF THE GROUP MEMBERS

One of the groups whose members were individually identified, the M-group, consisted of 16 animals (Table 1).

It is generally impossible to determine how the group members are spaced with respect to each other while they are scattered to feed at a certain place in the forest. However, the author was able to study the capuchins' spacing to some extent by means of their vocalization and sounds made. While being scattered to feed, the capuchins usually exchange two types of whistling. One is low and soft in tone, and exchanged within short distances. The other is strong and high-pitched, and exchanged over long distances. The latter type of whistling facilitated the determination of the spacing of the group members to some extent. In addition

Table 1. Members of the M-group.

Animal	Age/sex class		Remarks
<i>Chamusa</i>	Adult II	Male	Alpha male
<i>Leo</i>	Adult II	Male	Beta male
<i>Gustavo</i>	Adult I	Male	Gamma male
<i>Carafea</i>	Adult II	Female	
<i>Marca</i>	Adult II	Female	
<i>Oreja</i>	Adult I	Female	
<i>Coneja</i>	Adult I	Female	
<i>Moso</i>	Subadult	Male	Peripheral male
<i>Blanca</i>	Subadult	Female	
<i>Negro</i>	Juvenile III	Male	
<i>Abel</i>	Juvenile II	Male	
<i>Henry</i>	Juvenile II	Male	Probably <i>Carafea</i> 's offspring
<i>Fredi</i>	Juvenile II	Male	Probably <i>Marca</i> 's offspring
<i>Orejito</i>	Juvenile I	Male	<i>Oreja</i> 's offspring
<i>Rosa</i>	Juvenile III	Female	
<i>Conejita</i>	Juvenile I	Female	<i>Coneja</i> 's offspring

to the whistling, large sounds made by capuchins while striking to crack fruit of *Astrocaryum chambira* (IZAWA & MIZUNO, 1977; IZAWA, 1979) were helpful in estimating the capuchins' spacing. As a result, it was shown that in many cases capuchin groups were scattered within a radius of more than 50 m. In three cases, they were scattered beyond a radius of 200 m.

While resting and moving rapidly, the group members usually form a compact mass. Such an occasion is an opportunity to determine the presence of group members in the compact mass. Table 2 shows the number of individuals present in the M-group during resting and rapid moving times after December 19, when individual identification of the group members was completed. The compact mass formed during resting time is an assembly of individuals who remain within about 20 m around the alpha male, and that formed during rapid moving time is all individuals that were observed passing a certain spot within 10 min while rapidly moving in places which afforded an unobstructed view. The cases shown in Table 2 represent only those in which the author was able to follow the group continuously for more than 2 hr a day. On the other hand, some group members were found in the group expanse during each observation day at any time, i.e., moving, resting, and feeding, although they were not seen in the compact mass. Table 2 shows such cases also and cases in which the author was unable to find group members on a given observation day at any time.

From the table, it can be said that a high cohesiveness exists among the group members except two animals, *Leo* and *Moso*. In the case of *Leo*, the beta male, the percent of presence in the resting and rapid moving mass was 22.5%, which was considerably less than in the other individuals, whereas that of staying in the group expanse was 70.6%, which was rather high. Furthermore, the beta male was never confirmed to be in any adjoining groups. *Moso* will be considered in detail in a later section.

The size of the moving area of the M-group during the study period was estimated to be 2.6 km², including the inaccurate areas on the eastern to southeastern verge of the study site, where the author failed to trace the group continuously (Fig. 3).

RANKING

Decisive ranks existed among the individuals of both sexes in the age classes of juvenile III, sub-adult, and adults I and II.

Table 2. Checksheet of individuals of the M-group.

Animal	Dec. 19		Dec. 20		Dec. 23		Dec. 26		Dec. 27		Dec. 30		Jan. 1		Jan. 4		Jan. 5			
	M	A	M	A	M	A	M	A	M	A	M	A	M	R	A	M	A	M	R	A
Chamusa	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Leo	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Gustavo	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Moso	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Negro	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Carafea	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Marca	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Oreja	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Coneja	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Blanca	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Rosa	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Abel	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Henry	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Fredi	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Orejito	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Conejita	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△

(continued)

Table 2. (continued)

Animal	Jan. 7		Jan. 8		Jan. 14		Jan. 17		Jan. 23		Jan. 25		Jan. 26		Jan. 29	
	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A
Chamusa	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Leo	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Gustavo	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Moso	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Negro	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Carafea	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Marca	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Oreja	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Coneja	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Blanca	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Rosa	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Abel	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Henry	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Fredi	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Orejito	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△
Conejita	○	△	○	△	○	△	○	△	○	△	○	△	○	△	○	△

M: during rapid moving time (○: present, —: absent); R: during resting time (○: present, —: absent);
A: within the group expense at least once during each observation day (△: present, —: absent).

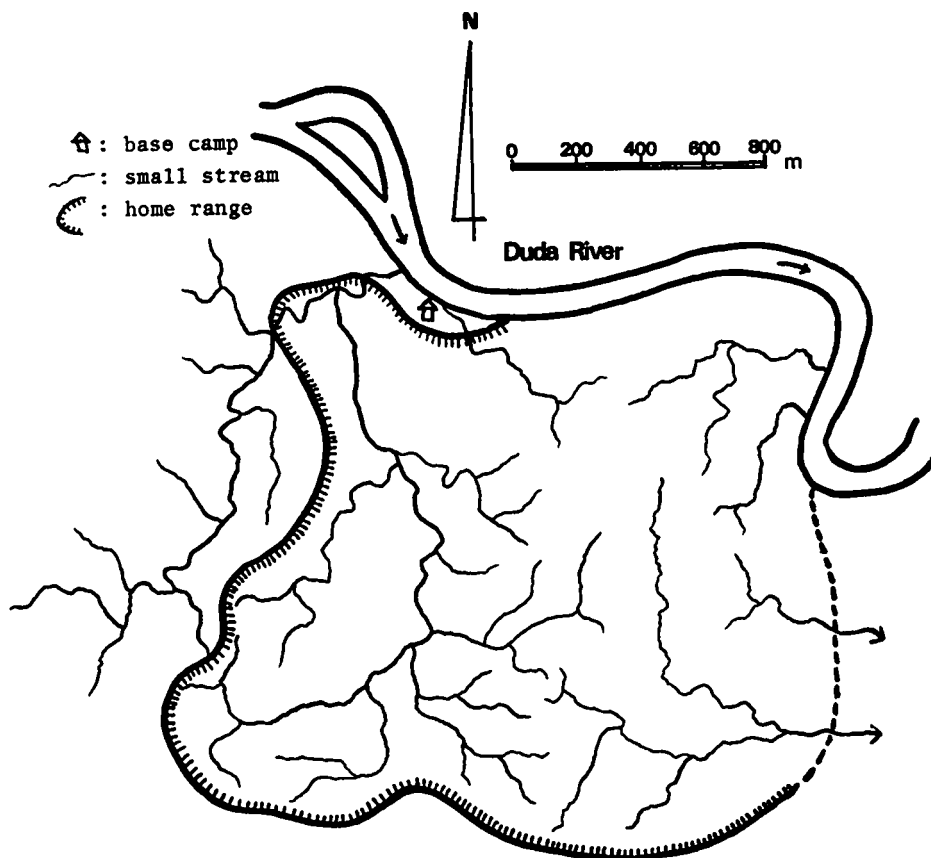


Fig. 3. Home range of the M-group during the study period.

Ranking is actualized in connection with food, especially (1) the large fruit of *Grias haughtii* (IZAWA, 1979); (2) joints of bamboo suited for cracking the fruit of *Astrocarium chambira* (IZAWA & MIZUNO, 1977); and (3) internodes in which frogs or grasshoppers lurk (IZAWA, 1978). In addition, dominance relations became apparent in connection with the fruit of *Pourouma lawrencei* and *Pseudolmedia leavis* (IZAWA, 1979). While feeding on the fruit of these species, one capuchin avoided another's approach: this was also the case with clusters of *Jessenia polycarpa* (IZAWA, 1979).

In males, clear ranking existed among five individuals. These were, from high ranking to low: *Chamusa*, *Leo*, *Gustavo*, *Moso*, and *Negro*. This ranking accords with the order of estimated ages. *Chamusa* seemed to be the oldest of the five. Reversed ranking was observed once each between *Leo* and *Gustavo*, and between *Moso* and *Negro*. It is believed that the former was caused by the presence of *Chamusa* and an adult female *Carafea*, who often stayed with *Chamusa*, as well as *Gustavo* with them. The latter was caused by the presence of *Chamusa* and three other juveniles with them.

In females also, decisive ranking was apparent if none of the three adult males remained near. The order was, from high ranking to low: *Carafea*, *Marca*, *Oreja*, *Coneja*, *Blanca*, and *Rosa*. As in the males, this ranking accords with the order of estimated ages based on physical development.



Fig. 4. Grooming by the alpha male during resting time. When *Chamusa* began to rest, juveniles came to him one by one and begged for grooming. *Chamusa* groomed them all thoroughly; never did he reject the juveniles. *Orejito* (juvenile I male) is being groomed on his belly (right) and *Fredi* (juvenile II male) is crouching to await his turn (left).

Ranking between males and females was not observed so noticeably as that in males only or in females only, since particularly familiar relationships are sometimes established between certain males and females, and adult males and females staying with females often exerted an influence on the females.

GROOMING

The start and end of resting activity (i.e., the state in which more than half of the group members rested) usually began with the alpha male. When the alpha male commenced resting, juveniles and adult females gathered to join him, and when the alpha male stopped resting to move, the juveniles and adult females followed him (Fig. 4). It was occasionally found that although the alpha male had begun to rest, no more than one or two individuals joined him; then, more than half of the group members did not rest together at the same time.

The behavior that is typically observed during the resting time includes allogrooming and sleeping. Table 3 shows the number of allogroomings observed during the resting time. Allogrooming was often observed as one series of groomer and groomee between two individuals, but in this table the author prefers to count the groomer and groomee as one each: When two capuchins were allogrooming, they both sometimes groomed by turn. Each time the grooming partners switched roles was counted as one case of allogrooming.

As seen from Table 3, one-sided grooming from the alpha and gamma males to juveniles I and II was observed during the resting time at a noticeably high frequency. When being groomed, the juveniles I and II were almost always sleeping.

Grooming is thus a typical behavior of the resting time, but allogrooming was also observed when the capuchins fed at one place en masse and when they fed moving slowly. Table 4 shows the number of allogroomings observed during such feeding time. The method of counting the numbers was the same as in Table 3.

It can be seen from Table 4 that during the feeding time, besides one-sided grooming from the gamma male to juveniles II, that from adult females to juveniles I and II was frequently observed, whereas that from adult males to other juveniles was rarely observed. The high frequency of grooming from adult females to juveniles I must reflect the fact that they are mothers and offspring and often move together.

Table 3. Allogrooming during resting time.

Groomer	Groomee											Total	
	Chamusa	Leo	Gustavo	Moso	Carafea	Marca	Oreja	Coneja	Blanca	Juvenile III	Juvenile II		Juvenile I
Chamusa	—	0	0	0	4	2	1	2	0	2	31	17	59
Leo	0	—	0	0	0	0	0	0	0	0	0	0	0
Gustavo	2	0	—	0	2	1	0	0	0	1	28	1	35
Moso	0	0	0	—	0	0	0	0	0	0	0	0	0
Carafea	4	0	1	0	—	1	0	0	0	0	4	0	10
Marca	4	0	0	0	3	—	0	1	0	0	3	0	11
Oreja	2	0	0	0	1	2	—	2	1	0	1	5	14
Coneja	3	0	1	0	2	2	3	—	0	0	2	6	17
Blanca	1	0	0	0	2	1	1	2	—	2	0	0	9
Juvenile III	1	0	0	0	0	0	0	1	3	0	1	0	6
Juvenile II	4	0	3	0	1	0	0	0	0	0	0	0	8
Juvenile I	0	0	0	0	0	0	1	1	0	0	0	0	2
Total	21	0	5	0	13	9	6	9	4	5	70	29	171

Table 4. Allogrooming during feeding time.

Groomer	Groomee											Total	
	Chamusa	Leo	Gustavo	Moso	Carafea	Marca	Oreja	Coneja	Blanca	Juvenile III	Juvenile II		Juvenile I
Chamusa	—	0	0	0	1	0	0	0	0	0	1	0	2
Leo	1	—	0	0	0	3	0	0	0	0	2	0	6
Gustavo	3	1	—	0	2	0	0	0	0	0	7	0	13
Moso	0	1	1	—	0	0	0	0	1	0	1	0	4
Carafea	2	0	1	0	—	1	0	0	0	0	4	0	8
Marca	0	4	0	0	1	—	0	0	0	0	5	0	10
Oreja	0	0	0	0	0	0	—	1	0	0	0	14	15
Coneja	0	0	0	0	0	0	2	—	0	0	0	17	19
Blanca	0	1	0	1	1	2	0	0	—	1	0	0	6
Juvenile III	0	0	0	1	0	0	0	0	0	0	0	0	1
Juvenile II	0	0	2	0	0	0	0	0	0	0	0	0	2
Juvenile I	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	6	7	4	2	5	6	2	1	1	1	20	31	86

AGONISTIC BEHAVIOR

Agonistic interactions within the group were mild. Fighting accompanied by physical contact such as biting was never observed between any individuals.

Threatening between adult males, and from adult males to individuals of other age/sex classes, was almost always effected by means of facial expression, and was made only with a stare. The threatened individuals only assumed a submissive facial expression, turned their faces away, or just changed their positions a little. Only three times was chasing of adult males observed, and it happened in a moment.

Carafea was the only adult female who threatened the adult males *Leo* and *Gustavo* by facial expression. Whenever that happened, *Chamusa* remained close to her. On the other hand, the sub-adult male *Moso* was threatened by all the adult females. Threatening between adult females was observed more frequently than that between adult males, and it tended to be exaggerated, including open-mouthed threats. Chasing of adult females was observed seven times, and was accompanied by threatening vocalization. Table 5 summarizes the agonistic interactions within the M-group.

Based on the fact that the agonistic interactions within the group were so mild and observed rather infrequently, whereas grooming was often observed (Tables 3 & 4), and that plural capuchins often remained very peacefully in close proximity to each other without grooming, it can safely be said that a very high tolerance prevails within the capuchin group. This is also indicated by the fact that the author never found capuchins with any kind of wound or scarring on any parts of their face, even the ears. Furthermore, no digital disorders were observed in any animals except *Marca* who once had a distorted index finger on the left forelimb, but this recovered in two weeks. The reasons for this distortion is unknown.

PLAY

Social play always occurs among juvenile I and II capuchins. Juvenile III capuchins were observed to join them six times, but sub-adults and adults never did.

The main play activities of juveniles include chasing and being chased in trees, hugging with an open-mouthed face display, and gentle wrestling. Chasing and wrestling on the ground were observed four times each. During, or at the end of play, one capuchin often approached the other and threw itself into the latter's arms, with its face buried in its chest. While maintaining this posture, both rested for a while.

WARNING BEHAVIOR

Inhabitants of the Guayabero River area informed the author on three occasions that a dog which barked at capuchins entering a field was counterattacked by the full adult males and received a serious wound. However, it remains unknown as to whether any particular group members follow any positive group defense behavior against invasions, since such a situation was never encountered by the author during the study period.

On four occasions, it was observed that a capuchin emitted a keen warning vocalization one or a few times on hearing a loud flapping sound probably made by raptorial birds. All the group members then rushed into bush near the ground and hid themselves. The warning vocalization was emitted by an adult female in one case, and probably by adults, based on the vocal characteristics, in the remaining three cases. In all of these four cases, the capuchins were feeding with the squirrel monkey in a mixed group. In response to the capuchin's warning vocalization, the squirrel monkey behaved similarly to the capuchin.

Table 5. Agonistic interactions.

Actor	Receiver										Total		
	Chamusa	Leo	Gustavo	Moso	Carafea	Marca	Oreja	Coneja	Blanca	Juvenile III		Juvenile II	Juvenile I
Chamusa	—	2	1	0	2	0	0	0	0	0	0	0	6
Leo	0	—	3	1	1	0	0	0	0	1	0	0	6
Gustavo	0	1	—	0	0	2	1	0	0	1	0	0	5
Moso	0	0	0	—	0	0	0	1	0	0	1	0	2
Carafea	0	2	2	1	—	4	2	3	1	2	5	0	22
Marca	0	0	0	2	0	—	3	3	1	1	2	1	13
Oreja	0	0	0	3	0	1	—	2	0	1	1	0	8
Coneja	0	0	0	2	0	0	0	—	1	0	1	0	4
Blanca	0	0	0	0	0	0	0	0	—	1	0	0	1
Juvenile III	0	0	0	1	0	0	0	0	0	1	0	0	2
Juvenile II	0	0	0	0	0	0	0	0	0	1	3	1	5
Juvenile I	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	0	5	6	10	3	7	6	9	3	8	15	2	74

Table 6. Warning vocalizations emitted to the observer.

Animal	Number of warning vocalizations	Number of rapid escapes in group thereby
<i>Chamusa</i>	4	4
<i>Leo</i>	5	3
<i>Gustavo</i>	2	0
<i>Moso</i>	4	0
<i>Carafea</i>	7	2
<i>Marca</i>	5	0
<i>Oreja</i>	10	0
<i>Coneja</i>	5	0
<i>Blanca</i>	2	0
<i>Negro</i>	2	0
<i>Rosa</i>	1	0
Juvenile II	12	0
Juvenile I	7	0
Unknown	14	1
Total	80	10

It was also observed on four occasions that when large-sized birds *Mitris salvoni* and *Psophia crepitans* flew away in surprise with the observer's approach, the capuchins escaped all at once. A warning vocalization similar to that in the above cases was again heard in these four cases. It was emitted once each by *Gustavo* and *Moso*.

In the previous year, when habituation was not satisfactorily established, the capuchin, on noticing the observer's approach, always emitted a warning vocalization, moved away rapidly or hid itself in a thicket. Table 6 shows the number of warning vocalizations emitted against the observer and their outcome. A sequence of vocalizations emitted by one individual was counted as one, and vocalizations emitted simultaneously by two individuals were counted as one each for the individuals. On ten occasions early in the study period, following the response of all the group members to a warning vocalization, the observer lost sight of them. In four of these ten cases, it was the alpha male who emitted the warning vocalization, in three cases the beta male, in two cases the adult female *Carafea*, and in one case the author was unable to determine who emitted. Occasionally, particular adult females responded to warning vocalizations of juveniles—the females were probably the mothers of the juveniles—but never did the response extend to the whole group.

Being quite different from threatening vocalization, warning vocalizations were never emitted at particular individual capuchins. Threatening vocalization was often exchanged between adult females. During the latter half of the study period, adult females, sub-adult females, and juveniles often emitted threatening vocalizations at the observer when he approached too close to the capuchins (Fig. 5).

ALPHA MALE

The alpha male is not only the highest ranking animal in his group but also the central figure of group unity. In other words, he is always the focus of group members' attention.

As can be seen from Table 2, no compact mass lacking participation of the alpha male was observed. In addition, as mentioned above, the start and end of feeding and resting activities were always initiated by the alpha male. As soon as the alpha male stopped resting and began to move for feeding, the group unity in resting became loose and almost all the group members commenced feeding. When the alpha male began to rest, almost all the juveniles and one or a few females gathered to rest and commenced grooming with each other.



Fig. 5. Threatening to the observer. Adult I male (left) of the E-group is threatening the observer as he approached, a sub-adult male (center) is feeding nonchalantly, while an adult I female (right) is cooperating with the adult I male by staring at the observer during her feeding.

There were some cases while rapidly crossing ridges that when the alpha male remained on the near-side of the ridge, one or a few males and females which had already crossed the ridge then retraced their steps. However, no case was observed in which the group stopped moving in spite of movement by the alpha male. On the other hand, it was often found that in response to vocalizations by individuals who had crossed a ridge, the alpha male then proceeded to cross the ridge and was followed by the remaining group members along the same course.

The above findings were true for capuchins which moved slowly, feeding in the group expanse. It is by no means certain that the alpha male always takes a strong initiative when his group moves, but it is quite likely that a relationship of leader to followers exists between the alpha male and other group members. This is also supported by the observed effects of warning vocalizations emitted towards the observer (see Table 6): all of the group members always responded to the alpha male's warning vocalizations.

RELATIONSHIPS BETWEEN ADULT MALES (1)

As seen from Tables 3 and 4, grooming between adult males occurred to only a limited extent. When the group was compactly united, the beta male *Leo* was often observed to stay at the periphery of the group expanse, and was sometimes missing from the group mass (see Table 2). Only on three occasions was it observed that the beta male and the alpha male fed in the same tree, and then they kept a distance of more than 5 m.

While group members were moving slowly feeding, an individual or a temporarily-formed sub-group could often be seen moving separately at a time lag of about 30 min to 1 hr. Three temporarily-formed sub-groups observed by the author were rather large in size (7-8 individuals) and contained the beta male. In all these sub-groups, a leader-to-follower relationship was found between the beta male and other individuals which was similar to that between the alpha male and other group members. It can be said therefore that the beta male is not a peripheral male even though he tends to remain alone at the periphery of the group expanse.

The gamma male *Gustavo* often stayed relatively close to the alpha male. Nevertheless, grooming between them was short, rather stereotyped, and numbered only five times. Apart from such grooming, no particular behavior suggesting affinity was observed between them.

As regards the relationships between adult males, it became clear therefore that lower ranking animals tended to avoid contact or close approaches to higher ranking animals in their daily lives.

The sub-adult male *Moso* was never found to be close to the alpha male. As can be seen from Table 2, he was confirmed within the group expanse far less frequently than the other individuals. He was twice confirmed to be with the beta male, but never with the gamma male. On the basis of these findings, *Moso* can be considered as a peripheral male, although it is possible of course that he just happened to stay near another group. Clear evidence against that however was not obtained.

RELATIONSHIPS BETWEEN ADULT MALES (2)

As described above, decisive rank orders exist among adult males. Lower ranking animals avoid contact or close approaches to higher ranking ones and both are able to maintain their daily lives peacefully.

Why then do males which maintain such relationships live together in a group? Based on the relationships between males and females—affinitive relationships were found between particular males and females (see below)—it may be possible for individual males to mate with females in the group without being disturbed by any other males. It may be significant that through interactions with the females plural adult males tend to constitute a single group.

On the other hand, based on observations made on January 29, the author was able to determine a strong psychological or spiritual bond among the adult males. The details are as follows:

Example:

January 29, 09:21. Observations started. Capuchins of the M-group had formed a mixed group with about 25 squirrel monkeys. 09:25. *Leo* was confirmed within the expanse of the feeding M-group. 10:25. A bird (*Mitris salvoni*) suddenly flew away. Surprised at this, the M-group started rapid moving activity with the squirrel monkeys. *Leo* was confirmed to participate in the rapid moving. However, he was not found from then on while the author was following the group. Neither were any quarrels or access of other groups observed. 14:15. The group including the squirrel monkeys had moved 1.4 km since the start of observations. Whistling was just heard twice in succession from a place about 200 m to the rear of the direction of the group movement. *Carafea* replied with strong, full whistling, and three other individuals joined her. Again, whistling was heard twice at distance. 14:21. The adult male *Gustavo* alone began to move towards the place where the whistling had occurred. 14:26. Whistling was exchanged at three places; i.e., within the group, near the group (probably emitted by *Gustavo*), and far from the group. The whistling far from the group seemed to emanate from the same place as that heard about 10 min earlier. 14:30. *Chamusa* also left the group to go to the place of whistling far from the group. Whistling was frequently exchanged at the three places. The observer followed *Chamusa*. 14:33. *Chamusa* stopped moving. Whistling emitted at two places to the rear was still heard frequently. Whistling within the group stopped. 14:34. *Chamusa* climbed a nearby tree (*Jessenia polycarpa*) and began to look for insects. 14:37. *Gustavo* began to return towards the group. On his way, he rested twice by lying on his belly with his limbs hung down on a tree bough. He was observed twice to walk with dragging feet. He was once suspected to have a wound on his hindlimb but soon walked normally. 14:43. Passing by about 30 m from *Chamusa*, *Gustavo* returned to the group. The whistling which had been heard far from the group approached nearer and nearer. 14:45. *Leo*, who was identified as the whistler far from the group, appeared. Dragging his right hindlimb, which seemed to be completely disabled, *Leo* was walking wearily. 14:46. *Chamusa* proceeded towards *Leo* about 20 m. *Leo* also proceeded towards *Chamusa*. 14:47. *Chamusa* and *Leo* climbed adjoining

trees. *Leo* was so weary as not give the usual threatening expression to the observer standing just beneath the tree. 14:48. *Leo* laboriously moved onto the tree which *Chamusa* occupied. They sat about 2 m apart. Quivering, *Chamusa* gave *Leo* a submissive expression and emitted the voice [qué-qué] which was an unfamiliar type of vocalization to the observer. Only once was it observed during the study period when *Chamusa* showed the submissive expression. 14:49. The observer moved underneath the tree which *Chamusa* and *Leo* occupied. Grinning his teeth, perking up his shoulders, and bending and stretching his forelimbs, *Chamusa* threatened the observer severely. Such threatening of *Chamusa* was also observed only once. In the meantime, *Leo* returned to the adjoining tree. 14:50. Taking a quick look at *Leo*, *Chamusa* slowly began to move towards the group. *Leo* followed him heavily dragging his right hindlimb. No wound was visible on the limb. 14:54. *Chamusa* returned to the place where all the members of the M-group and the squirrel monkeys still stayed. As *Chamusa* moved slowly on without resting, all the animals followed him. 14:56. *Leo* followed them desperately at a distance of about 20 m.

In the above events, it is not known what sign by *Chamusa* caused not only all the capuchins but also the squirrel monkeys to remain at the same place for no less than 24 min, or why *Gustavo* on his way back to the group displayed such theatrical behavior near *Chamusa* as lying on his belly with his limbs hung down on a bough and dragging his feet like *Leo*. However, it is speculated, as the above example shows, that a particular strong bond exist among *Chamusa*, *Leo*, and *Gustavo*, which could rarely be discerned from their daily lives. Such a bond is discussed later in the section on relationships between adult males of adjoining groups.

On January 31, two days after the above observations, *Leo* was again found within the group expanse. He was a little awkward in his managing his right hindlimb, but walked almost normally.

RELATIONSHIPS BETWEEN ADULT MALES AND FEMALES

Rather affinitive relationships existed between particular adult males and females. This is apparent from the grooming behavior shown in Tables 3 and 4, and from the fact that they rested on a tree branch close to (within 1 m) or touching each other, and moved together.

The alpha male was affinitive to all females, but more so to *Carafea* and *Marca* than any of the other females. The beta male was often observed with *Marca*, while the gamma male was with *Carafea*. The latter association may reflect the relationship between the gamma male and *Henry* (see below), who was considered to be *Carafea*'s offspring. *Moso* was observed once with *Carafea* and three times with *Marca*.

No sexual behavior was observed between the males and females during the study period.

RELATIONSHIPS BETWEEN ADULT FEMALES

As shown in Table 5, threatening behavior among adult females was observed far more frequently than that among adult males. This indicates that in contrast to the situation among adult males, lower ranking females do not inevitably avoid higher ranking ones. Grooming between adult females was by no means more frequent than that between the other age/sex classes, but all the adult females were often observed resting and moving together. Among them, *Oreja* and *Coneja*, both of whom had juvenile I offspring, tended to stay with each other.

The author obtained no data suggesting that sub-adult females kept affinitive relationships with particular adult females. Also, movements of the sub-adult females with the adult females were less frequent than the movements of all the four adult females together.

RELATIONSHIPS BETWEEN ADULT MALES AND JUVENILES

The tolerance of adult males towards juveniles was quite high. Even when disturbed by one or a few juveniles while hunting and eating frogs, cracking and eating fruit of *Astrocaryum chambira*, or eating large fruit of *Grias haughtii*, the adult males rarely rejected the juveniles. In fact, when adult males were involved in such activities, one or a few juveniles almost always dangled freely about the adult males to obtain remnants, and sometimes showed submissive behavior to beg for their share. However, the adult males were never seen to give a share to the juveniles. The latter always succeeded eventually in obtaining some remnants themselves (Fig. 6).

In addition to this, one or a few juveniles were always found near the alpha male during feeding time. Only on three occasions were adult males seen to display agonistic behavior towards juveniles (see Table 5).

In the resting time, juveniles gathered around the alpha male (see Table 3) and the alpha male groomed them thoroughly. Being groomed, a juvenile slept, while others also slept clinging to or leaning on the alpha male's back. The alpha male sometimes stopped grooming a juvenile and sat still for a while with the juvenile in his arms.

The beta male groomed juveniles less frequently (see Tables 3 & 4). The reason for this is unknown, although it may be because the juveniles often stayed near the alpha male, because the beta male tended to stay alone at the periphery of the group, or simply because of an idiosyncrasy (e.g., he did not like juveniles).

The gamma male tended to be with the juvenile *Henry*, and both of them often groomed together (see Tables 3 & 4). On four occasions among the total episodes involving *Henry*, he was observed to move alternately between the alpha male and gamma male to be groomed concurrently by them. Apart from *Henry*, only *Fredi* (once) was groomed concurrently in this way by two different males, and this happened when he accompanied *Henry*. The gamma male sometimes took a brief rest sitting on a bough holding *Henry* or *Fredi* in his arms.

When juveniles gathered around the alpha male during resting time, *Oreja* (five times) and *Coneja* (four times) went up to the alpha male carrying the *Orejito* and *Conejita*, respectively, on their backs. After leaving the offspring near the alpha male, the adult females began to feed in a nearby tree. Such actions gave the impression that the adult females requested the alpha male to babysit for their own offspring. The alpha male naturally groomed the juveniles.



Fig. 6. Adult male and juvenile. *Gustavo* (adult I male) cracks a fruit of *Astrocaryum chambira* against an internode of *Bambusa guadua*. *Gustavo* (right) is examining the cracks on the fruit as *Henry* (juvenile II male) looks on.

Adult males were observed five times to carry juveniles on their backs as they moved. Once, the alpha male carried a juvenile I. Three times the gamma male carried a juvenile III, and once a juvenile I. In all cases, they moved within a distance of 30 m.

"HUGGING BEHAVIOR"

This behavior was observed six times between juveniles and individuals of both sexes and other age classes and once between juveniles. In all cases, those who were hugged at the back were juvenile II males. Five cases in which the circumstances were clarified were as follows:

Case 1: After threatening the observer a little by facial expressions from a cluster of fruit of *Jessenia polycarpa*, *Fredi* (juvenile II male) began to eat the fruit without paying further attention to the observer. *Gustavo* and *Carafea* then appeared. On noticing the observer who was standing beneath the tree, *Gustavo* hid himself at the back of the cluster and *Carafea* suddenly hugged *Fredi*, who was feeding, at the back, and showed the observer threatening facial expression. *Fredi* appeared nonchalant. After a while, the three capuchins began to eat the fruit without further attention to the observer (Fig. 7).

Case 2: While *Chamusa* and *Carafea* were cracking fruit of *Astrocarium chambira* against a joint of bamboo, *Fredi*, *Henry* (juvenile II male), and *Oreja* (juvenile I male) dangled about the adults. *Oreja* appeared, seemingly without noticing *Chamusa*. On exchanging a glance with *Chamusa*, she hugged a nearby juvenile, *Henry*, at the back and thrust three times. *Chamusa* paid no attention to *Oreja's* actions.

Case 3: *Carafea* chased *Oreja* in adjacent bushes. *Gustavo* and *Henry* were sitting side by side. *Gustavo* rapidly moved about 15 m carrying *Henry* on his back. Setting *Henry* down, *Gustavo* suddenly turned and hugged *Henry* tightly at the side. *Henry* appeared nonchalant.

Case 4: *Gustavo* was grooming *Henry*. Behind them, *Conejita* (juvenile I female), *Coneja*, and *Chamusa* came briskly in succession. Looking back to see them, *Gustavo* moved onto an adjoining tree carrying *Henry* on his back. As soon as he put *Henry* down on a bough, *Gustavo* hugged *Henry* tightly at the back and thrust once. *Henry* erected his penis.

Case 5: *Chamusa* was grooming *Henry* in a tree. *Abel* (juvenile II male) and *Fredi* rushed towards them. On noticing the observer who was standing just below, *Abel* hugged *Fredi* under his arms.

The above five cases have several points in common. That is to say, those who hugged were inevitably older than those who were hugged, the hugging behavior was taken one-sidedly by those who hugged, and it occurred when they appeared to be tense for some reason. Further details of the hugging behavior remain unknown, but it may only be an expression of the tension of those who hug, or used for the purpose of easing their own psychological tension. It is unknown whether such behavior has any other significance for capuchins.

The two other cases of hugging behavior not described in detail, occurred between adult

Table 7. Group composition of the three groups the author observed.

Group	Adult		I		Sub-adult	
	II		Male	Female	Male	Female
M	2	4	1	0	1	1
S	1	3	1	1	1	0
E	3	5	0	1	1	2

(continued)



Fig. 7. Hugging behavior. *Carafea* (adult II female) appeared to feed on the fruit of *Jessenia polycarpa*. On noticing the observer just beneath the tree, she suddenly hugged the back of *Abel* (juvenile II male), who continued to feed.

females and juveniles II. In all of the above cases of hugging by adult females (four of seven), the juveniles II who were hugged were considered not to be offspring of the adult females who hugged.

COMPARISONS WITH ADJOINING GROUPS

Besides the M-group, four or five other groups of capuchins lived in the study site. Two of these, the S-group and the E-group were followed continuously for 6 hr and 25 min and 3 hr and 48 min, on January 28 and 30, respectively, to determine whether or not the various types of behavior daily shown by the M-group were also observed in these two groups.

Table 7 shows the group composition of the S- and E-groups, although it is possible of course that in the limited time available, the author may have missed one or a few animals in the count of peripheral males (such as *Moso* of the M-group). It is feasible also that there were one or a few individuals like *Leo* or the adult female *Marca* who often accompanied *Leo* in the M-group, who happened to be moving separately from the other group members. However, judging from several previous observations of each group during rapid moving, by the author and his assistants, the number of group members in the S- and E-groups had never amounted to more than 12 and 21, respectively (Table 7).

Table 7. (continued)

Juvenile							
III		II		I		Infant	Total
Male	Female	Male	Female	Male	Female		
1	1	3	0	1	1	0	16
0	1	3	1	0	0	0	12
1	0	2	3	3	0	0	21

Concerning the behaviors, the results for adult males of the S- and E-groups were different from those of the M-group. In the case of the S-group, an adult II male was ranked highest, equivalent to *Chamusa* of the M-group. However, this adult II male was not so affiliative to juveniles as *Chamusa*: only twice was he observed resting with juveniles, and he did not groom them so thoroughly as *Chamusa*; neither was he dangled about by plural juveniles during feeding time. On the other hand, he was twice observed grooming adult females, and three times observed to be groomed by adult females.

One adult I male behaved quite similarly to those of *Gustavo* of the M-group. He was twice observed thoroughly grooming two juveniles each. Also, one or a few juveniles always dangled about him during feeding time.

Among the three adult II males of the E-group, the two higher ranking ones (despite the fact that both were definitively ranked) always moved together. Both were apparently comparable to *Chamusa* of the M-group. Grooming between them was observed five times. On two occasions, some juveniles gathered around these males during resting time, but it was only three times that the males were observed to groom juveniles. The males were once observed grooming adult females and three times seen to be groomed by adult females.

The third adult II male, who was somewhat younger than the other two, seemed to occupy a position like *Gustavo* of the M-group. This male moved with a juvenile I male for almost all the period of observation.

Based on the above findings, it can be said that although the social unit of the capuchin is basically a multi-male/multi-female group with a rather strong cohesiveness, its group structure is influenced largely by the individuality of each of the adult males, including the alpha male, and by a male-bond which may be formed through such individuality.

SOLITARIES

It was twice observed that a capuchin moved alone independently of its group. However, since it was difficult to follow for hours a capuchin that moved agilely alone in the deep forest, the age/sex class was not determined satisfactorily in either case.

As described above, the capuchins feed in the rather large expanse of the group, but there are also individuals who sometimes tend to move alone (like *Leo* of the M-group), the sub-groups, and peripheral males (like *Moso*). The tolerance which is peculiar to male capuchins has also been described. Based on such findings and the fact that the home ranges of the M-, S-, and E-groups overlapped each other, it was difficult to hypothesize the existence of adult males who might move alone for months independently of their groups, i.e., solitaries.

Nevertheless, in view of the sex ratio in adults and in adults plus sub-adults—the number of females are larger than those of males in both adults and adults plus sub-adults—the possibility of the existence of solitaries could remain.

The question of whether solitaries do in fact exist or not is closely related to how the peripheral males develop and behave in the future and how male-bonds are formed.

DISCUSSION

COMPARISON WITH *C. apella* FROM OTHER LOCALITIES

Prior to the present survey, the author undertook surveys at two localities on the Peneya River, Colombia, between 1971 and 1974. He found that "the capuchins have a nomadic life

in which they form several small temporary groups when staying in a certain area. But when moving a considerable distance, almost all the monkeys from the temporary groups form one large group. That is the social unit of the capuchin." (IZAWA, 1976a).

One of the major reasons why the author had difficulty in determining the social unit of the capuchin in the Peneya area despite the long study period, was that the capuchin, which the author could not habituate to the end of the study period, rapidly escaped as soon as it noticed the observer. Another reason was related to the geographic features of the study sites. These were located in typical Amazonian lowland plain, which is rather flat and has continuous forest canopies. The capuchins in the Peneya area, therefore, unlike those in the area where the present study was made, did not move rapidly several times a day forming a compact mass, but tended to feed slowly or busily in temporarily-formed sub-groups. The capuchins in the Peneya area repeated such activity in a certain area throughout the day.

It is interesting that the spacing of the capuchins' daily nomadic life should be so influenced by the geographic features and vegetation of their habitat. However, concerning group sizes, composition, and social behavior, no results different from those obtained in the present study were reported. The only point which should be corrected here is the conclusion based on the previous studies that the group coherence of the capuchin tends to be loose as that of the spider monkey (IZAWA, 1976a). The present study clearly indicates that the capuchin maintains a strongly cohesive group in sharp contrast to the spider monkey (KLEIN, 1972; IZAWA, KIMURA, & SAMPER NIETO, 1979).

Some results for *Cebus apella* in the wild have been reported previously by others. Concerning group size, KÜHLHORN (1939), who undertook surveys in the Paraná River basin in southern Mato Grosso, Brazil, stated that the group members numbered between 8 and 18. THORINGTON (1967), who made surveys in the Monte Seco area of Hacienda Barbascal, east of San Martin, Colombia, reported that the two capuchin groups which he studied consisted of five and seven animals, respectively, and commented that such small numbers of group members might be affected by some artificial influence, such as hunting by human beings. According to KLEIN and KLEIN (1976), who surveyed in the east of Macarena National Park, Colombia, there were four to six groups within their study area (3 sq. miles), one group consisting of 6–12 capuchins. However, according to the detailed descriptions of KLEIN (1972), contacts which were maintained for 15 min or longer numbered 63, and "the number of independently locomoting *C. apella* counted ranged from 1 to 12 plus one infant, the median number being 8." In addition, "contacts with what appeared to be isolated *C. apella* occurred twice." However, the strong possibility must remain that he observed only part of the group expanse, if one considers the fact that the *C. apella* group usually feeds with a large expanse, as has been described above, and his study site was not located in a hilly area like that of the present study but in lowland plain like the present author's previous study site in the Peneya area, so that such short observation periods as more than 15 min, and only 2 hr at maximum may be insufficient to determine the group size actually as a unit. Accordingly, although KLEIN reported two observations of isolated individuals, it is uncertain whether they should be regarded as solitaires or not.

Similar comments also apply to the results for group size obtained by KÜHLHORN (1939) and THORINGTON (1967). The present results, with rather larger group sizes, may thus still be consistent with those of the other studies conducted in other localities.

As for the grouping of *C. apella*, THORINGTON (1967) reported that even a small group which he studied "may be spread out so that the animals are 50 to 100 yards apart," and KLEIN and

KLEIN (1976) stated that the "estimated distances between individual *C. apella* considered part of the same group ranged from a few feet to 150–200 yards." The latter authors also indicated that "considerable separation between feeding adults was the rule rather than the exception." All these findings are in agreement with those obtained by the present author.

Concerning the relationships between adults in *C. apella*, KLEIN and KLEIN (1975) reported that "rigid spacing was sometimes apparent" and added that "more than one adult capuchin feeding simultaneously from a single palm tree was never observed." The author has several times observed that pairs of particular adult males and particular adult females, e.g., *Chamusa* and *Carafea*, *Leo* and *Marca*, were feeding simultaneously on the cluster of a palm tree, but such cases were by no means common. Other results obtained by KLEIN and KLEIN agree with those mentioned here in the section on ranking.

In his observations of group procession, KÜHLHORN (1939) found that young individuals and females proceeded first and an adult male, generally only one adult male per group, was at the rear. Also, in the event that the group members escaped from predators, the adult male left last after confirming that all members had escaped. The adult male he described might correspond to the alpha male distinguished by the present author.

Besides the above reports, there are no other reports available for comparison and discussion on the social behavior of *C. apella*, the main subject of the present study.

COMPARISON WITH THREE OTHER SPECIES OF *Cebus*

Morphologically, *Cebus apella* and the three other species of *Cebus* (*C. capucinus*, *C. nigrivittatus*, and *C. albifrons*), differ from each other (HERSHKOVITZ, 1955; HILL, 1960; CHIARELLI, 1972). Regarding their areas of distribution, it appears that the distribution of *C. apella* largely overlaps with those of the other three species (HILL, 1960).

Among the various studies on these three other species of *Cebus*, their behavior in the wild was intensively dealt with in the literature by OPPENHEIMER (1968) and OPPENHEIMER and OPPENHEIMER (1973b) for *C. capucinus*, by OPPENHEIMER and OPPENHEIMER (1973a) for *C. nigrivittatus*, and by DEFLER (1979a, b) for *C. albifrons*. Making some preliminary surveys of *C. apella* at the same time, all of the above authors pointed out the similarities of the three species of *Cebus*, i.e., *C. capucinus*, *C. nigrivittatus*, and *C. albifrons*, and made comparisons with *C. apella*.

Following his field studies on *C. capucinus* and *C. nigrivittatus*, OPPENHEIMER and OPPENHEIMER (1973a) reported that these species resembled each other in behavior. Furthermore, from their brief observations of *C. apella*, they said that "the behavior of both these species is very different from that of *C. apella*, which is also quite different morphologically," and forecast that studies on the behavior of *C. albifrons* would also reveal it to be similar to *C. nigrivittatus* and *C. capucinus*.

As anticipated by OPPENHEIMER and OPPENHEIMER (1973a), DEFLER (1979b) reported in his study of *C. albifrons* that the behavioral characteristics of this species resembled those of the *C. capucinus* and *C. nigrivittatus* studied by OPPENHEIMER and OPPENHEIMER. DEFLER also pointed out from the data in his preliminary study on *C. apella* that the features of *C. apella* "suggest much more tolerance among adult males as well as between different groups than observed in *C. albifrons*, as well as a lack of the territorial behavior so prominent in *C. albifrons*."

Both *C. apella* and *C. albifrons* have been found sympatrically at the two localities in the Pencya River basin, Colombia, where the author previously made surveys. He has further

pointed out that the grouping of these two respective species was apparently different. Also, being different from that of other genera of New World monkeys, he suggested that the behavior and social structure of *C. apella* should be discussed individually and separately from the three other species of *Cebus* (IZAWA, 1976a).

By comparing the results of the above studies of OPPENHEIMER (1968), OPPENHEIMER and OPPENHEIMER (1973a, b), and DEFLER (1979a, b) with those of the present study, the author will now attempt to clarify the similarities and differences in social behavior among the four species of *Cebus*.

Concerning the daily activity, it was common to all four species of monkeys that they spent almost all of the daytime feeding and foraging. They also had in common several short resting periods during the daytime. As to the length of the resting time, a simple comparison among the four species cannot be made since the period varies from dry season to wet season and is closely related to seasonal changes in the monkeys' food. However, it may be conjectured that the length of the resting period of *C. albifrons* is the longest, being several hours (1-3 hr), and those of *C. capucinus* and *C. nigrivittatus* are longer than that of *C. apella*.

Temporary sub-groups and peripheral males were observed apart from the assembly of group members in each species of *Cebus*. It was common to the four species of *Cebus* that the group members were often dispersed, especially at times of feeding and foraging, whereas they united compactly during rapid movement. The only difference in spacing of the group members might be that *C. apella* tends to be dispersed more widely than the three other species of *Cebus*.

A dominance hierarchy in the group and alpha males exist in all four species. However, *C. capucinus* and *C. nigrivittatus*, it must be said, appear to lack rigid dominance structuring in the group. It cannot be asserted positively at the present that *C. albifrons* lacks this, but the dominance structuring of *C. albifrons* may not be so rigid as that of *C. apella*. Neither is it certain whether the male bond observed among adult males of *C. apella*, that is, the strong psychological or spiritual bond which is formed through the individuality of each adult male, exists in the three other species of *Cebus*.

It was common to *C. capucinus*, *C. nigrivittatus*, and *C. albifrons* that adult females performed grooming most frequently. In *C. apella*, the adult females performed grooming most frequently during the feeding and foraging period and adult males did it most frequently during the resting period. Grooming was received most frequently by young individuals (juveniles and infants) in *C. nigrivittatus*, *C. albifrons*, and *C. apella*, whereas it was received most frequently by the dominant males in *C. capucinus*.

Examinations of grooming behavior reveal that relationships between adult females (groomers) and young individuals (groomees), mother-offspring relationships, are emphasized commonly in all other species of primates. The fact that relationships between adult females (groomers) and dominant males (groomees) are noted in *C. capucinus*, however, might indicate a directional trend for adult females of *C. capucinus* to form a bond with adult males more positively than in the case of the three other species of *Cebus*. However, it cannot be concluded simply on the basis of these relationships in grooming behavior that the bond between adult males and adult females of *C. capucinus* is stronger than that in the three other species of *Cebus* since the social unit of all four species is basically the multi-male/multi-female group and various relationships including sexual relationships, naturally exist between the adult males and adult females. In fact, in *C. capucinus*, cases were observed in which females left their groups.

Such frequent grooming of young individuals by adult males as observed in *C. apella* has not been reported in the three other species. This suggests that in the three other species, the group unit is based on linear relationships, that is, bonds between adult males and adult females and between adult females and young individuals, whereas in *C. apella* it is based on triangular relationships, that is, bonds between adult males and females, between adult females and young individuals, and between young individuals and adult males.

It was common to the four species of *Cebus* that the agonistic interactions within the group were usually mild, a high tolerance prevailed among the individuals, and agonistic behavior was frequently observed in adult females. However, it must be noted that wounds were quite commonly seen within the group of *C. albifrons* and wounds by canine slashes were seen in *C. capucinus*, although no wounds were observed in *C. apella*. This might be due to the fact that, in addition to the high tolerance among the individuals which is common to the four species, the spacing among individuals in *C. apella* is larger than that of the three other species, and rank orders in *C. apella* are more decisive than those in the other species.

It was also common to the four species of *Cebus* that social play frequently occurred among young individuals, especially during the resting period, and that it occurred most frequently between two individuals. This could be related to the small numbers of same-aged young individuals which result from the relatively small group size of 10–30 individuals common to the four species.

In addition to the above discussion on similarities and differences in the social behavior of the four species of *Cebus*, mention must be made of the individualities of the monkeys which were noted in the present study. In *C. apella*, the individualities of adult males, especially the alpha male, may exert a considerable influence on the social behavior of the group. There are no reports on individualities in the three other species of *Cebus*. However, if the same is true for them, it will not be possible to discuss the behavioral similarities and differences adequately without paying due regard to the individualities. Comparative studies on individualities are thus anticipated in the near future. Even so, it can be said that definite differences in social behavior do exist between *C. apella* and the three other species, as well as strong similarities among all four species.

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