

# BEHAVIOURAL REPERTOIRE OF ADULT SILVERY MARMOSETS *CALLITHRIX A. ARGENTATA* AND *CALLITHRIX A. MELANURA*

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Omedes, A., 1981 (1983). Behavioural repertoire of adult silvery marmosets *Callithrix a. argentata* and *Callithrix a. melanura*. *Misc. Zool.*, 7: 193-211. Barcelona.

Qualitative data were collected on the behaviour of adult *Callithrix a. argentata* and *C. a. melanura* marmosets. 71 behaviour patterns of locomotion, postures, facial expression, head movements, ear positions and movements, tail positions, interaction with objects, social contact, grooming and scent marking activities and display were defined.

The behavioural repertoire of both subspecies, the situations in which the behaviour patterns were present and the differences between both subspecies in these respects are described.

Silvery marmosets have an extensive behavioural repertoire of which facial expressions, postures and patterns involving piloerection are the main components. Situations can be identified by the patterns displayed. Aggressive and defensive patterns are distinctive.

The differences observed between both subspecies were mainly during sexual interactions and displays of aggression either to conspecifics or to humans.

It may be stated that *C. a. argentata* and *C. a. melanura* can be designated as subspecies on criteria based on the differences they show in their means of communication.

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## INTRODUCTION

The study of the origin and evolution of displays began with DARWIN'S book *Expression of the Emotions in Man and Animals* (1872), in which he stated that the movements features and gestures of monkeys are almost as expressive as those of man.

The term "display" was defined by SMITH (1969) as acts that animals possess in their behaviour repertoire that have specialized in the course of evolution to convey information. Display acts include postures, movements, vocalizations and other sounds and the release of volatile chemicals. The habitat in which the animals live, plays an important role in determining the kind of communication which is used. *Symphalangus syndactylus* lives in dense vegetation of the tropical forest and due to that, subtle visual signals are enough for intragroup relations, while intergroup communication requires more elaborate signals both visual and vocal.

ZIMMERMAM et al. (1980) compared

some forms of communication between some New World monkeys, and found that olfactory communication is more important in the prosimians *Galapago senegalensis* and *Nycticebus coucang* and in the marmoset *Callithrix j. jacchus*, that the visual communication is more relevant and more differentiated in Talapoin, and that the two Platyrrhini considered *Callithrix jacchus* and *Saimiri sciureus* displayed a more extensive vocal repertoire.

Marmosets (genera *Callithrix* and *Cebuella*) gnaw holes in certain trees from which gums and saps are exudated in response to injury (ROBINSON, 1963). RAMÍREZ et al. (1977) and STEVENSON & RYLANDS (in press) report that marmosets are highly dependant on this exudate as food source. Although marmosets also feed on insects, fruits, flowers, eggs and fledglings they are less dependant on fruit than tamarins (STEVENSON, 1980).

Marmosets of the genus *Callithrix* have been split into two groups (HERSHKOVITZ,

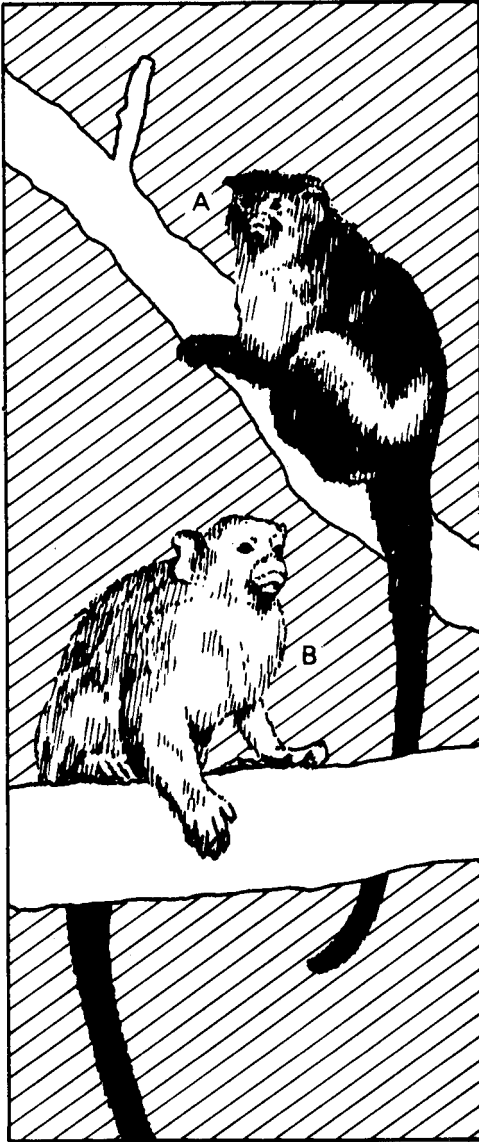


Fig. 1. A. Adult *C.a. melanura*; B. Adult *C.a. argentata*.

1977): the species of *C. jacchus* and the Argentata group, which includes *C. argentata* (Silvery marmoset) and *C. humeralifer*. It has been suggested that *C. argentata* has intermediate characteristics between *C. jacchus* and tamarins. STEVENSON (1978) suggests that since both *C. jacchus* and *C.*

*argentata* show the same gnawing behaviour and have similar dentition they occupy a similar ecological niche in different geographical regions.

Very little is known of the communication of two subspecies of Silvery marmosets (*C.a. argentata* and *C.a. melanura*) in captivity and no information is available from studies in the wild, nor is anything known about the third subspecies *C.a. leucippe*. Some observations have been published by EPPLE (1967, 1970a, 1975), OMEDES & CARROLL (1980) and STEVENSON (1976) on *C.a. argentata*, by STEVENSON (1978) on *C.a. melanura* and by OMEDES (1979, 1981) on both subspecies of Silvery marmosets.

The aims of this paper are to give a detailed description of the behaviour patterns that form the behaviour repertoire of Silvery marmosets and also to study the contexts in which they are used, the associations between patterns and the differences between two of the three subspecies.

## MATERIALS AND METHODS

### 1. Introductory information on Silvery Marmosets

#### 1.1. Taxonomy

The name Silvery Marmosets is commonly used to describe any of the three subspecies of the marmoset *Callithrix argentata* (family *Callithricidae*). Marmosets are Primates of the suborder *Haplorrhini* and infraorder *Platyrrhini*, the latter known as New World Monkeys.

There are three subspecies of Bare-ear or Silvery Marmosets (HERSHKOVITZ, 1977):

a) Golden-white bare-ear marmoset, *Callithrix a. leucippe*-Tomas. Tail dominantly pale buff or golden.

b) Silvery marmoset, *Callithrix a. argentata* - Linnaeus. Tail black or dark brown. Forehead, cheeks, sides of crown silvery white; centre of crown, back and outer sides

of limbs silvery white, greyish, drab or brown, whitish hip and thigh patch obsolete or absent. Ears unpigmented or mottled (fig. 1b).

c) Black-tailed marmoset, *Callithrix a. melanura* – E. Geoffroy. Tail black or dark brown. Forehead, entire crown, back and outer sides of limbs brown. Whitish hip and thigh patch sharply defined (Fig. 1a).

## 1.2. Distribution

The three races of this species are Brazilian and only *Callithrix a. melanura* extends into Bolivia and Paraguay. Fig. 2 shows their distribution.

## 1.3. Ecology

There is very little known of the ecology and social structure of Silvery marmosets in the wild and only scattered observations are available. MILLER (1916) and KRIEG (1930) detected the presence of troops of three to twelve individuals. This marmoset uses nests in tree hollows for sleeping, keeping warm and giving birth (KRIEG, 1930). Silvery marmosets are mainly insectivorous, but also eat small birds and mammals, eggs and large quantities of fruit (HILL, 1957; HERSHKOVITZ, 1972). ENDERS (1930) and NAPIER & NAPIER (1967) examined the stomach contents of wild specimen and found only fruit and vegetables.

## 2. Husbandry

The specimens of *Callitrix a. melanura* used in this study were kept in the Zoology Department of the University College of Wales, Aberystwyth and those of *Callithrix a. argentata* were in the Jersey Wildlife Preservation Trust, Jersey, Channel Islands. No specimens of *Callithrix a. leucippe* were available for this research project.

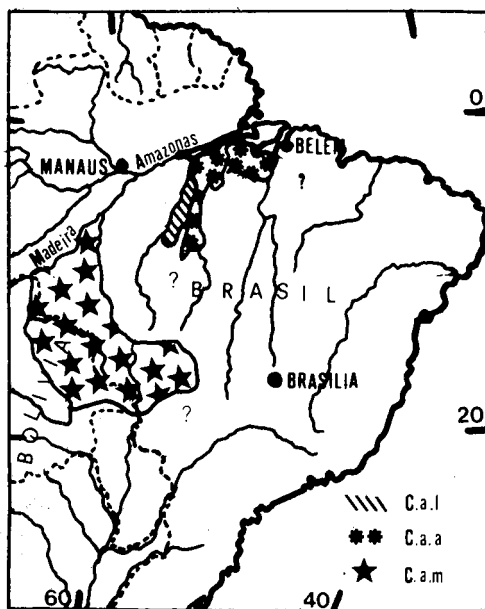


Fig. 2. Distribution of *Callithrix argentata* (from HERSHKOVITZ, 1977).

The animals in Aberystwyth were housed in indoor cages equipped with wooden nest boxes, branches and platforms and rubber and wooden objects hanging from the roof as described with the husbandry by STEVENSON & POOLE (1976). The cages in Jersey had an outside area furnished with branches and bushes, and an indoor area with wooden nest boxes, platforms and branches, as described by MALLINSON (1975). The husbandry was as described by MALLINSON (1975) and CARROLL (1977).

All the animals were kept in pairs of family groups composed of an adult breeding pair and up to three successive sets of their offspring.

## 3. Details of the animals used

Data presented in this paper are based on the qualitative observations carried out on adult pairs and offspring over 12 months old that were housed with the family group. This is the earliest age of sexual maturity recorded

from marmosets. The animals used were 19 *C.a. melanura* (8 ♂♂ and 11 ♀♀), and 16 *C.a. argentata* (9 ♂♂ and 7 ♀♀). A complete description and history of these marmosets is given by OMEDES (1981).

Data were collected from newly paired animals as well as established pairs, both with and without offspring.

#### 4. Collection and analysis of data

Qualitative data were collected over a period of 29 months (*Callithrix a. melanura*, 24 and *C.a. argentata* 5), in form of continuous timed observations. Data were collected for approximately 150 hours in a diary, these data include observations made during feeding and cleaning periods. Opportunistic sampling took place whenever unusual or new situations arose, for example fights, displays, matings etc. Photographs were taken in sessions of one to two hours between 9.00 a.m. and 5.00 p.m. with and electric flash, to increase the accuracy of the description of the behaviour patterns.

A comprehensive list of behaviours was compiled and a detailed description of them is presented.

Differences between the two subspecies of Silvery Marmosets were noted and have been organised into two categories, one composed of behaviour patterns that were only observed to occur in one subspecies and the other of behaviours seen frequently in one subspecies but rarely in the other.

Whenever possible the terms described by STEVENSON & POOLE (1976) were used, and whenever two or more patterns were not completely distinct they were described under a single heading.

## RESULTS

### 1. Description of behaviour patterns

Some of the following behaviour patterns have been previously described for *Callithrix*

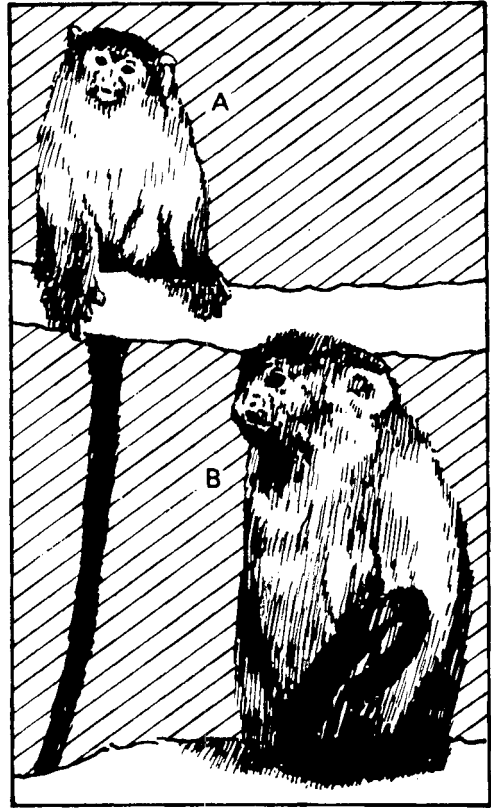


Fig. 3. A. Sit position (*C.a. melanura*); B. Rest position (*C.a. melanura*).

*jacchus* by STEVENSON & POOLE (1976) and this is shown by +/-.

#### 1.1. Locomotory patterns

“Walk”, “Run”, “Flee”, “Climb” and “Jump” gaps between objects: these behaviour patterns are used in the normal colloquial sense. “Bouncing gait”: run with exaggerated vertical jerky movements +/-.  
 “Stalk”: hide behind an object, while intermittently stare at another animal +/-.  
 “Slide”: move along, lying on side or on back, propelled by arms and legs +/-.  
 “Roll”: turn over while lying on substrate +/-.  
 “Side to side”: sway body, head raised, while staring forward.  
 “Hop over”: jump

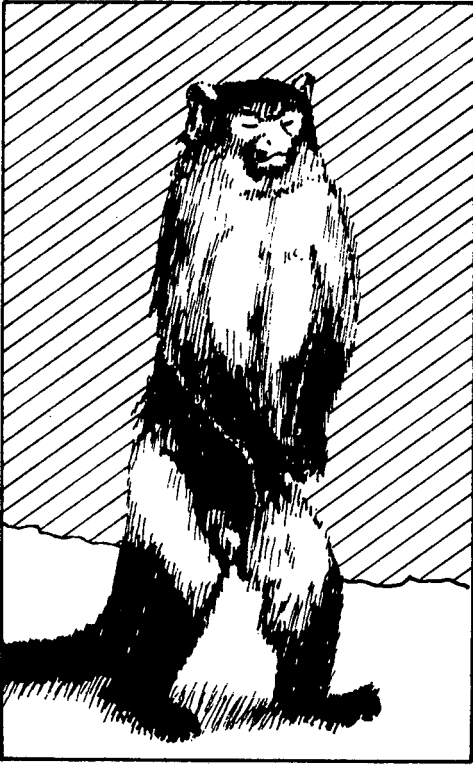


Fig. 4. Leg stand and Ears flick (*C.a. melanura*).

over another individual. "Activity" refers to any kind of body movement.

### 1.2. Relaxed postures

"Sit": head raised, hind legs retracted, hands on ground (fig. 3a). "Rest": sit with tail coiled between hind legs, when asleep forearms on ground and head falls forward (fig. 3b). "Sprawl": lie with legs relaxed.

### 1.3. Body postures

"Cringe": body withdrawn, arms extended, legs bent and spine curved (includes two patterns described by STEVENSON & POOLE (1976): cringe and withdrawal gesture). "Leg stand": bipedal position (fig. 4). "Flatten": head and trunk lower than hind



Fig. 5. A. Rump present (*C.a. melanura*); B. Tail coiled raised present (*C.a. argentata*); C. Tail raised present (*C.a. melanura*).

region, forearms on substrate, nearly always very near another marmoset and facing it. "Rump present": crouched posture, rear directed towards another animal or to a person, tail lowered (fig. 5a). "Tail raised present": display of genitals, tail extended or bent (fig. 5b). "Tail coiled raised present": display of genitals, tail coiled or completely coiled (fig. 5c). "Freeze": body flattened to substrate, legs bent and forearms on ground, immobile.

### 1.4. Face expressions and head movements

"Head cock stare": side to side movements,



Fig. 6. A. Tongue-in-out (*C.a. melanura*); B. Head cock stare (*C.a. melanura*). C. Slit stare (*C.a. melanura*).

fixed stare /+/. “Lipsmack”: mouth opens and closes rhythmically /+/. “Stare backwards”: head turned round, looking behind. “Tongue-in-out”: repetitive movement of the tongue in and out of the mouth /+/. it takes three forms: Slow (fig. 6a), Rapid with incomplete protrusion of the tongue and Very fast with complete protrusion. “Stare”: fixed gaze, eyes wide open (fig. 6b). “Slit stare”: fixed gaze, eyelids half closed /+/. (fig. 6c). “Open mouth”: mouth wide open but teeth not visible /+/. “Partial open mouth”: mouth slightly open, teeth not visible /+/. “Grin”: mouth open, teeth visible, lips not retracted. “Open grin”: mouth open, teeth visible, lips retracted. “Yawn”: open mouth, protrude tongue and close mouth /+/.

#### 1.5. Ear positions and movements

“Ears flatten”: ears retracted towards the back of the head, immobile. “Ears flick”:

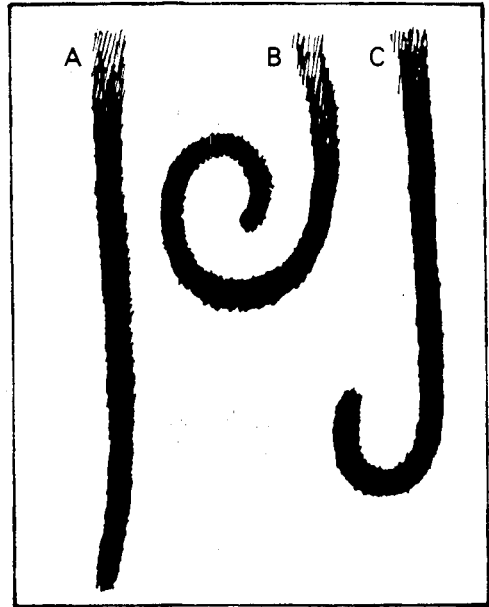


Fig. 7. A. Tail extended; B. Tail coiled; C. Tail tip coiled.

rapid movement of the ears back with return to normal position (fig. 4). “Ears forward”: anterior movements of the ears.

#### 1.6. Tail positions

“Tail extended”: relaxed tail in a straight or slightly bent position (fig. 7a). “Tail tip coiled”: terminal half of tail coiled (fig. 7c). “Tail coiled”: whole of tail coiled (fig. 7b).

#### 1.7. Interaction with objects

“Object bite and gnaw” /+/, “Object lick” /+/, and “Object muzzle rub” /+/: these terms are used in the normal colloquial sense.

#### 1.8. Patterns involving social contact

“Food steal”: take food from hand or mouth of other marmoset. “Lick”: lick an

area of body of a conspecific. "Nuzzle body": rub nose and sniff any region of the body of another marmoset (excluding ano-genital area). "Nuzzle genitals": rub nose and sniff other marmosets ano-genital areas. "Mount": hind legs on the ground, grip conspecific behind shoulders, ventre in contact with conspecific's back +/- . "Thrust": rhythmical pelvic movements, on a mounted position +/- . "Wrestle": grappling movements with hands and feet towards other marmosets +/- . "Extricate": wriggle or attempt to wriggle free when gripped by another marmoset +/- . "Pounce": jump on another animal +/- . "Hand": one hand touching another individual +/- . "Clap": bouth hands touch another individual +/- . "Cuff": hit the opponent lightly with fingers extended +/- . "Claw": more vigorous form of cuff, resulting in a scratch of the skin +/- . "Grip pelage": grab the hair of another marmoset with one or two hands +/- . "Bite": inhibited bite +/- . "Snap bite": sharp short bite +/- . "Uninhibited bite": bite resulting in injuries +/- .

### 1.9. Grooming

"Allogroom": part pelage of another marmoset, remove particles with mouth or hands +/- (fig. 8). "Autogroom": part own pelage, remove particles with mouth or hands +/- . "Scratch self": rhythmically scratch own body +/- .

### 1.10. Scent mark

"Anogenital scent mark": mark substrate by sit-rubbing anogenital region; may scent mark another marmoset (fig. 9). "Sternal scent mark" mark substrate by rubbing sternal region.

### 1.11. Patterns involving piloerection

"Arch Bristle Movement": walk with body arched, pelage fully erected +/- . "Arch



Fig. 8. Subadult Allogrooming adult (*C.a. melanura*).

"Bristle": body arched, stationary, pelage fully erected +/- . "Pilo body": pelage fully erected in all or most of the body. "Pilo crown": piloerection of hair on top of head, and slight piloerection of anterior part of the body. "Pilo base tail": progressive decreasing piloerection along the length of the tail towards its tip +/- (fig. 10c). "Pilo tail": full or semi-piloerection of the whole of the tail +/- (fig. 10a). "Pilo tip tail": full or semi-piloerection of the distal part of the tail +/- (fig. 10b). "Rampant": "Arch Bristle" position, with hands off the ground but not far from it.

## 2. Detailed description of specific situations

### 2.1. Amicable behaviour

Amicable behaviour includes any social activities that do not involve aggression, excluding sexual behaviour and play, such as grooming, greeting and resting in contact.

Marmosets usually rest in contact in the "Rest" and "Sit" positions. Resting periods





vidual will "Roll", "Stalk" and "Slide" while staring and uttering soft calls to a conspecific and occasionally show Rapid "Tongue-in-out" and "Lipsmack". This behaviour may elicit play response from the addressee. Play invitation may also consist of approaching another marmoset and grabbing its tail or show the "Clap" behaviour, which very often elicits "Cuff" from the addressee.

#### 2.4. Solitary play

Solitary play usually results as a consequence of unsuccessful bouts of Play invitation. The main differences with Play invitation are the absence of staring and approaching another member of the group and the addition of the "Ears flick" pattern.

#### 2.5. Intragroup aggression

Intragroup aggression is very rare amongst Silvery marmosets. Only two encounters ending in fights were observed during the course of the study. Two other instances of intragroup aggression were observed, one was after a fight, the other involved the animals being separated since the aggressor had previously been involved in very severe fights.

The two encounters which resulted in fights were observed for approximately one hour previous to the fight, and all patterns involved noted.

One of them was between an adult female (Mandy) and an adult male (Sidney) of *C.a. melanura*, in which the animals had been paired for several months. Mandy chastised Sidney for approximately one hour. She repeatedly walked towards Sidney while showing "Stare", Very rapid "Tongue-in-out", various degrees of "Pilo-tail", "Ears forward" and occasional "Object muzzle rub" of a branch; Sidney showed "Flee", "Pilo body", "Cringe" and "Ears flatten" and uttered loud calls while showing "Grin" or

"Open grin". On several occasions the animals were very near each other and cuffed or grabbed each others pelage. This encounter ended up in a fight in which the patterns "Claw", "Uninhibited bite", "Grip the pelage", "Extricate", "Wrestle" and "Pounce" were displayed by both marmosets. As a result of this fight both animals had injuries, but only Sidney's were severe.

The other encounter ending in a fight was between two females and one male of *C.a. argentata*. An adult male (Stan) was introduced to an adult breeding female (Maria) and to her subadult daughter (Shura) two weeks after the breeding male of the group died. Shura chastised Stan for nearly an hour, while Maria showed no more than slight aggression, but when the fight commenced between Shura and Stan, Maria joined in. Shura chased and walked towards Stan while uttering faint hoarse calls with "Pilo body", "Pilo tail", Very fast "Tongue-in-out", "Stare" and occasionally showed "Tail raised present" while Stan displayed "Flee", "Pilo tail", "Cringe", "Partial open mouth" while uttering hoarse and loud calls. On several occasions Shura cuffed him and grabbed his pelage. Both females showed simultaneous "Arch bristle movement" with "Tail tip coiled". The patterns associated with the fight were the same ones as described for *C.a. melanura*. All animals received mild injuries.

In all intragroup aggressive encounters the animal being chastised spent most of the time in the lower part of the cage except when it showed "Flee" when it ran all over the cage.

#### 2.6. Display and alarm

This section includes any aggressive or defensive reaction provoked by stimuli outside the group, thus including as well any displays directed towards humans.

When there is a sudden alarm in the room, the group may show simultaneous "Flee" with "Pilo body" and "Pilo tail"

Table 3. Contexts in which behaviour patterns occur. *C.a. argentata*: O (common),/(rare); *C.a. melanura*: X (common),/(rare).

Patterns	Amicable behaviour	Sexual behaviour	Social play	Solitary play	Intargroup aggression	Display and alarm	Mild aggression	Scent mark	Other or non-specific
Walk		OX			OX			OX	OX
Run					OX				
Flee					OX	OX			
Climb									OX
Jump			OX	OX					
Bouncing gait			OX	O					
Stalk			OX	OX					
Slide			OX	OX					
Roll			OX	OX					
Side to side						OX			
Hop over						O /			
Sit	OX								OX
Rest	OX								OX
Sprawl	OX								OX
Cringe					OX				
Leg stand						X			
Flatten		OX	O						
Rump present						) X			
Tail raised present						OX			
Tail coiled present						O			
Freeze						OX			
Head cock stare									OX
Lipsmack	O	OX	O /						
Stare backwards		OX							
Tongue-in-out	OX	O	/						OX
Slow									
Rapid	/	OX	) /	) /		O			
Very fast		O			OX	O /			
Stare	) /	OX			O /	X			
Slit stare		OX				) X			
Open mouth		/	OX	O					
Partial open mouth		O	O	O	O	OX			
Grin					OX				
Open grin					OX				
Yawn	OX								OX
Ears flatten					OX	O /			
Ears flick				OX	/	OX			
Ears forward					X				

Table 3. (Continuation).

	Amicable behaviour	Sexual behaviour	Social play	Solitary play	Intergroup aggression	Display and alarm	Mild aggression	Scent mark	Other or non-specific
Tail extended	O X	O X	O X	O X	O X	O X			O X
Tail tip coiled		O X	)		O				
Tail coiled		O X							
Object bite and gnaw								O X	O X
Object lick									) /
Object muzzle rub	O X				X				O X
Food steal									O X
Lick	) X								
Nuzzle body	O X	O X				O			
Nuzzle genitals	O X	O X							
Mount		O X	)						
Thrust		O X	)						
Wrestle			O X		O X				
Extricate			O X		O X				
Pounce			O X		O X				
Hand	O X		O X						
Clap	O X	O X	O X						
Cuff					O X		O X		
Claw					O X				
Crip pelage			O X		O X		O X		
Bite			O X						
Snap bite							O X		
Uninhibited bite					O X				
Allogroom	O X	/							
Autogroom	O X								
Self scratch									O X
Anogenital scent mark						O X			
Sternal scent mark						O X			
Arch bristle movement					O	O X			
Arch bristle						O /			
Pilo body					O X				
Pilo crown					X	O X			
Pilo base tail					O X				
Pilo tail			O		O X	O X			
Pilo tip tail				O X	O X				
Rampant						O /			

while uttering the sharp loud calls; this only lasts for a few seconds and then the animals "Freeze" with "Ears flatten" and "Partial open mouth". Gradually the marmosets start moving again, very slowly at first until they resume their normal activities.

Aggressive displays towards other marmosets or humans are usually performed simultaneously by other members of the group, excluding the infants. It is usually based on "Arch bristle movement" combined with other patterns.

Both subspecies combine and/or alternate "Arch Bristle", "Ears flick", "Pilo tail", "Pilo base tail", "Pilo body", "Pilo crown", "Tail coiled", "Tail tip coiled". "Tail raised present" and "Rump present" with "Arch bristle movement" display.

*C.a. argentata* alone shows "Tail coiled raised present". During and after "Arch bristle movement" the marmosets may approach each other and then "Hop over" or "Nuzzle". "Rump present" occurs very rarely and "Arch bristle" very often.

*C.a. melanura* marmosets show different patterns during their displays. They alternate between "Arch bristle movement" and "Leg stand". They commonly alternate "Rump present" with "Arch bristle movement". "Leg stand" and "Rump present" are shown combined with "Tail coiled", "Slit stare", "Ears flick" or very rarely "Ears flatten". Unlike *C.a. argentata* "Leg stand" or "Rump present" are never combined with any type of "Tongue-in-out".

### 2.7. Encounters involving mild aggression

Mild aggression is used to stop a conspecific from "Allogrooming", "Food stealing" or take infants away.

The behaviour patterns observed in mild aggression are "Cuff", "Snap bite", "Grip the pelage" and hoarse calls.

These encounters are regarded as mild aggression because "Grin" and "Open grin" were not associated with them.

Table 4. Differences in the occurrences of behaviour patterns associated with aggressive display between *C.a. argentata* and *C.a. melanura*. C: commonly observed; R: rarely observed; N: never observed.

	<i>C.a.a.</i>	<i>C.a.m.</i>
Rump present	R	R
Ears flatten	C	R
Very fast Tongue-in-out	C	R
Hop over	C	C
Slit stare	R	N
Tail coiled raised present	C	N
Rapid Tongue-in-out	C	N
Nuzzle	C	N
Leg stand	N	C

### 2.8. Scent mark

Both subspecies show "Anogenital scent mark" and "Sternal scent mark", usually preceded by bouts of "Object bit and gnaw" branches. "Anogenital scent mark" is sometimes associated with aggressive displays and may be performed simultaneously with other group members.

"Sternal scent mark" was seen much less often than "Anogenital scent mark" and most of the times associated with patterns related to social behaviour such as "Nuzzle genitals", Rapid "Tongue-in-out" and "Nuzzle".

On a few occasions both *C.a. argentata* and *C.a. melanura* were seen to "Anogenital scent mark" other group members.

### 3. Differences between *C.a. argentata* and *C.a. melanura*

Table 3 shows in what context the behaviour patterns previously described in this paper are used. It also shows whether these behaviours have frequently or rarely been recorded in both subspecies. Quantitative data on these differences are given by OMEDES (in prep.).

Most behaviour patterns have been observed in both subspecies. *C.a. argentata* alone shows "Tail coiled raised present".

Table 5. Differences in the combination of patterns during aggressive displays between *C.a. argentata* and *C.a. melanura*. C: commonly observed; R: rarely recorded; N: never recorded.

		Rapid Tongue-in-out	Very fast Tongue-in-out	Slit stare	Ears flatten
Arch bristle	<i>C.a.a.</i>	C	C	R	C
	<i>C.a.m.</i>	N	N	C	R
Rump present	<i>C.a.a.</i>	C	C	R	C
	<i>C.a.m.</i>	N	N	C	R
Leg stand	<i>C.a.a.</i>	—	—	—	—
	<i>C.a.m.</i>	N	N	C	R

“Ears forward” and “Leg stand” have only been recorded for *C.a. melanura*.

During sexual behaviour several differences were noted: *C.a. argentata* shows “Stare” before and during copulation much more often. The combination of “Nuzzle genitals” and close following showed by males was very frequent in *C.a. argentata* and extremely rare in *C.a. melanura*. Periods of sexual activity were much longer in *C.a. argentata* and in general more pre-copulatory patterns were shown per mating.

Table 3 shows that during intragroup aggression neither “Ears forward” and “Object muzzle” were shown in *C.a. argentata* nor “Tail raised present”, “Partial open mouth”, “Arch bristle movement” and “Tail tip coiled” in *C.a. melanura*. It also shows several differences in which patterns were shown by the aggressive or the submissive animal. The fact that only two fights occurred during the study enables any generalization to be made.

Aggressive display is the context in which the qualitative differences of use of behaviour patterns between both subspecies becomes more obvious. Table 4 shows which patterns were commonly, rarely or never used during displays towards humans or other marmosets. Some face expressions and ear movements were combined with the three stationary body postures that were seen in aggressive displays (see table 5). *C.a. melanura* never shows “Tail coiled raised present”, Rapid “Tongue-in-out” or “Nuzzle”

and rarely “Ears flatten”, Very fast “Tongue-in-out”, and “Hop over”. *C.a. argentata* never shows “Leg stand” and very rarely “Slit stare”.

## DISCUSSION

The Behavioural repertoire of Silvery marmosets was found to be very complex and it was observed that the meaning of a display which is used in more than one context varies depending on the situation in which it was used.

Most of the behaviour patterns were present in both subspecies and in general similar to the ones described for *Callithrix j. jacchus* by STEVENSON & POOLE (1976).

The variety of facial expressions and head movements was limited to movements and positions of ears, mouth, tongue and eyelids. REDICAN (1975) reviews facial expressions in non-human primates and it can be seen that Old World monkeys display a much greater variety of face expressions and it is probably due to the fact that marmosets lack of facial musculature to perform the same movements (HILL, 1957; VAN HOOFF, 1962). MOYNIHAN (1967) suggests that patterns involving piloerection used by marmosets are substitutes for the facial expressions in Old World monkeys. “Yawn” did not seem to have a communicative function.

Facial expressions were displayed in most

situations and played an important part in visual communication particularly in aggressive and sexual interactions. VAN HOOFF (1962) defines two categories in which face expressions can be placed: attack, aggressive threat, scared and crouch face and grin, lipsmack and teeth chatter face. TINBERGEN (1959) suggests the possibility that grinning and the associated laughter of man proves to be a ritualized threat movement. "Ears flatten" which was seen as a sign of fear in Silvery marmosets was described by ANDREW (1963a) in Lemuridea and Lorisidea as a sign of threat against equals and superiors.

Lipsmacking behaviour was solely associated with the sexual context. In Cercopithecids this movement is exactly as those of sucking or eating soft food (ANDREW, 1963b).

Facial expressions seemed to be very important during sexual behaviour and were shown continuously through courtship and copulation, the "Stare backwards" of the female facilitated the interchange of visual communication during mating.

The "Frown" pattern which is used in apes and man as a threat (ANDREW, 1963b) as well as in most species of Callithricids was not seen in this species of marmoset.

Tongue movements constitute a very important part of Silvery marmoset visual communication and the different speeds at which the tongue is protruded determines the context of this pattern: groom and feeding if it is Slow, sexual and play (only for *C.a. argentata*) Rapid, and aggressive when Very fast. CARPENTER (1940) suggests that tongue protrusion given by *Hylobates lar* with a grin in friendly greeting derives from grooming movements.

Playful behaviour had many behaviour patterns in common with aggressive encounters and fights and some with social behaviour, mainly sexual activities. CHALMERS (1978) defines "play markers" which are patterns that only happened in play, other patterns are regarded as playful depending on the context in which they

are used and are called "context-dependant" play components. Solitary play and play invitation shared many behaviour patterns but only during the latter "Stare" and "Clap" were present.

Friendly and greeting activities were mainly represented by contacts with hand and muzzle but lacked the Body rub pattern described by STEVENSON & POOLE (1976) for the common marmoset.

Behaviour patterns in which faeces, urine, glandular secretion and saliva are deposited occur in many Prosimians and South American Primates. *Callithrix argentata* mark mainly with glandular scent and occasionally with urine.

Scent marking was only performed using the anogenital and sternal glands although PERKINS (1969) describes in *C.a. argentata* the presence of a large apocrine gland with hair follicles in the suprapubic skin. Scent marking behaviour, mainly "Anogenital scent mark", was usually associated with gnawing of wood which agrees with what was observed in the wild (STEVENSON & RYLANDS, in press) for *Callithrix j. jacchus*.

In general "Anogenital scent mark" was more related to aggression in contrast to "Sternal scent mark" which was associated with sexual behaviour. In the Common marmoset scent mark is temporally associated with piloerection behaviour (SUTCLIFFE & POOLE, 1978). These authors also report that as in *C.a. argentata* sternal marking occurs infrequently but, in common marmosets is associated with "Anogenital scent mark". EPPLE (1970b) suggests that scent marking in marmosets plays a role in sexual communication and perhaps territorial behaviour and has an important function in the demonstration of social dominance of *Callithrix j. jacchus*.

Silvery marmosets show, under normal conditions, considerable sociable and friendly behaviour and agonistic encounters between members of a family group are rarely observed, although occasionally mild aggression is displayed.

When a strange marmoset is introduced in the group it is chased by the family members and the behaviour patterns involving piloerection and facial expressions are the ones mainly used. The behaviours shown by the strange animal and by the members of the group are clearly different with the exception of those of piloerection and tail coiling. Piloerection of the whole or of areas of the body show a graded intensity. In addition to piloerection the tail also shows degrees of coiling. It seems that the combination of both represent the various levels of arousal of the animal and hence the presence of them in both the marmoset attacking and the one being attacked. It is reasonable to assume that some patterns are clearly associated with the concept of dominance or aggression ("Stare", "Very fast Tongue-in-out" and "Ears forward" plus the addition of "Tail raised" for *C.a. argentata*), others with submission or defense ("Cringe", "Open grin", "Flee", "Ears flatten" and "Grin"). "Ears flatten" and "Grin" have been described as aggressive patterns by EPPLE (1967, 1968, 1975) for the common marmoset.

The fact that the patterns shown during aggression towards strangers (i.e. marmosets from other groups or humans) and the ones displayed during intragroup mild aggression are different suggest that inter and intragroup aggression are different.

Display behaviours are of very varied nature and involve many behaviour patterns that appeared alternated and/or combined. "Arch bristle movement" represents the maximum expression of group display and it is usually performed by all members of the family towards a stimulus outside the group. EPPLE (1967) describes "Arch bristle" and "Arch bristle movement" in *C.a. argentata* as a defensive threat. It is interesting that "Arch bristle movement" was not observed by RYLANDS (1981) in the closely related species *Callithrix humeralifer intermedius*.

Most behaviour patterns described in this study were present in both subspecies of Silver marmosets with the exception of "Tail

coiled raised present" which was only used by *C.a. argentata* and "Ears forward" and "Leg stand" that was only recorded in *C.a. melanura*. The main differences between both subspecies are not in which patterns are used but in which context they are used, at what frequencies are performed and in the way they are associated with each other.

More of those differences were found related to aggression and display than any other context. The different markings in the pelage of both subspecies seems to be important (OMEDES, 1979) since *C.a. melanura* while displaying "Leg Stand" and "Rump present" shows the light patches in its thighs. *C.a. argentata* which lacks the contrasting patches of colour on the pelage of the trunk and limbs but has got a much darker tail than the rest of the body which could account for the fact that this subspecies uses "Tail coiled raised present" instead of the other two patterns. "Rump present" in *C.a. melanura* and "Tail raised present" in *C.a. argentata* appear to be equivalent. "Tail present" in *C.a. melanura* and "Tail coiled raised" present in *C.a. argentata* also seem to have corresponding meanings, the last two representing a much stronger response to the stimulus.

*Callithrix humeralifer intermedius* has a similar thigh stripe to *C.a. melanura* but is not seen to "Rump present" and only occasionally "Tail present" (RYLANDS 1981). COATES and POOLE (in press) report that some behaviour patterns emphasize the bright colours of the pelage of *Saguinus labiatus labiatus*, and that instead of "Arch bristle movement" they show "Leg stand" while piloerect the anterior part of the body which enhances the contrast between the black neck and the orange venter.

Genital displays represent aggressive behaviour in marmosets (EPPLE, 1967, 1968, 1975).

GOULD (1980) gives the two criteria that have to be satisfied to subdivide a species into subspecies:

1/A subspecies must be recognizable by features of its morphology, physiology or

behaviour, that is, it must be "taxonomically (and by inference, genetically) different from other subspecies; and 2/A subspecies must occupy a subdivision of the total geographic range of the species.

Although most behaviour patterns and calls were recorded for both *C.a. argentata* and *C.a. melanura* many differences exist between the two subspecies in the frequencies of behaviours and calls and in the context in which they are used. Both subspecies are morphologically different and from what is so far known about their distribution their geographic ranges do not overlap.

It is thus reasonable to postulate that *C.a. argentata* and *C.a. melanura* are two subspecies of the *Callithrix argentata* species, since to describe subspecies consists in separating a spectrum of variation into discrete packages with distinct geographic borders and recognizable traits.

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