

**Positional behavior of two sympatric guianan  
capuchin monkeys, the brown capuchin (*Cebus apella*)  
and the wedge-capped capuchin (*Cebus olivaceus*)**

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**Summary.** – Although brown (*Cebus apella*) and wedge-capped capuchins (*C. olivaceus*) are among the most widespread platyrrhines, quantitative data on their positional (locomotor and postural) behavior are limited. I collected and analyzed quantitative positional behavioral data for both species in French Guiana, where they are found micro-sympatrically. Both species used the middle and lower layers of the forest most often. In both species, quadrupedal walk/run ranked first in their locomotor behavior, while gap-crossing modes such as leaping and bridging were common during travel. During feeding, climbing/clambering increased while all other modes decreased. In *C. apella*, sitting was the predominant feeding posture, and was used most frequently on medium-sized substrates. *C. olivaceus* used an equal proportion of sit and stand, probably due to relatively more time spent in animal matter foraging.

**Résumé.** – Bien que les saïous (*Cebus apella* et *C. olivaceus*) soient parmi les platyrrhiniens les plus répandus, les données quantitatives sur leurs répertoires posturaux et locomoteurs sont bien limitées. Ces deux espèces sont sympatriques en Guyane française. Entre juillet et septembre 1993, j'ai collecté et analysé des données quantitatives sur leurs répertoires posturaux et locomoteurs. Les deux espèces utilisent très fréquemment les strates basses et intermédiaires de la forêt. Pendant le déplacement, les modes locomoteurs prépondérants sont la marche et la course quadrupèdes ainsi que les sauts et les « ponts » afin de franchir les discontinuités de la canopée. Durant l'alimentation, c'est le grimper en toutes directions qui domine. Chez *C. apella*, c'est la posture assise qui est la plus fréquente durant l'alimentation, utilisée surtout sur des supports moyens. Par contre, *C. olivaceus* utilise aussi fréquemment les postures assise et quadrupède, un fait probablement associé à ses habitudes d'un régime plus omnivore.

## INTRODUCTION

Capuchin monkeys, genus *Cebus*, are among the most widespread platyrrhines (Emmons and Feer 1990). More specifically, *C. apella* is the most widespread platyrrhine, found east of the Andes from Colombia and Venezuela south to Paraguay and northern Argentina (Emmons 1990). On the other hand, *C. olivaceus* has a more restricted geographic distribution, ranging from Venezuela east to the Guianas and northern Brazil (Emmons and Feer 1990). Both species are sympatric in French Guiana.

Several qualitative reports indicate that capuchins travel by walking quadrupedally and leaping, and feed mainly from a seated posture (Thorington 1967; Rose 1973; Izawa 1979; Freese and Oppenheimer 1981; Mittermeier and Roosmalen 1981; Terborgh 1983; Robinson 1986; Janson 1988; Janson and Boinski 1992). The first quantitative studies (Fleagle and Mittermeier 1980; Fontaine 1985) which analyzed the locomotor behavior of *C. apella* in Surinam, and *C. capucinus* in Barro Colorado Island (BCI) respectively, found *Cebus* to be primarily a quadrupedal monkey, with some leaping and to a lesser degree climbing in its repertoire. In stationary postural behavior, sitting and quadrupedal stand predominated. In contrast, Gebo's study (1992) of *C. capucinus* in Costa Rica revealed a lower proportion of quadrupedal walk and run, more climbing, and less leaping. Therefore, these studies all agree that *Cebus* locomotion is mainly characterized by quadrupedal walk, and to a lesser degree by leaping and climbing, and feeding postural behavior by sitting. However, differences in proportions of the different positional modes may reflect differences in methods of observation and data collection, definitions of modes, habitat structure (different sites or selective use within a site), or in the use of seasonal resources, as well as individual differences (see Dagosto 1995; Garber and Preutz 1995; Gebo and Chapman 1995).

In order to assess whether these differences are due to habitat structural differences or selective use (because seasonal differences can also be translated into structural differences; see Dagosto 1995), one has to study closely related species with extremely similar postcranial anatomies but different ecologies in the same habitat or the same species in different habitats (see Garber and Preutz 1995). Herein I analyze quantitative data on habitat utilization during locomotion, and feeding and foraging postures of the brown capuchin (*Cebus apella apella*), and the wedge-capped capuchin (*Cebus olivaceus*), which are found microsympatrically in the "Station des Nouragues" in French Guiana, where they are often seen to travel and forage together. Given that capuchin species show similar postcranial anatomies, similarities and differences in habitat use, and in locomotor and postural behavior likely reflect interspecific similarities and differences in patterns of microhabitat exploitation. The transitional, and early dry season chosen for the study is also important, as shortage of ripe fruit makes both species to shift to different alternatives (Terborgh 1983; Robinson 1986; Zhang 1995).

#### STUDY SITE AND ANIMALS

This study was conducted in the 'Station des Nouragues' (4°05'N, 52°40'W) in French Guiana, situated 100 km south of Cayenne, the French department's capital. This site is characterized by lowland wet high rain forest, with some patches of transitional, low, liana and pina palm forests (Zhang 1995). Annual rainfall varies from 3,000 to 3,250 mm and the mean annual temperature is 26.1 °C. The dominant plant families are the Ceasalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae. The study site is more extensively described in Juillot and Sabatier (1993) and Zhang (1995).

Both *Cebus* species are found sympatrically in the study area, having the largest part of their home ranges overlapping (Zhang, pers. comm.). The data presented here were collected between July, 28 and September, 13, 1993, during the transitional and early dry season (rainfall = 356 mm). One troop of each species was followed. The troop of *C. apella* was the same one habituated and studied by Zhang (1995). In this

troop, at least five individuals were sampled (2 adult males and 3 adult females). The troop of *C. olivaceus* was not entirely habituated, and therefore the results presented here should be interpreted with caution. Both troops were ranging in the same area, and several times the two species traveled and foraged together. The mean body mass of *C. apella* adult males is 3.0 kg, vs 2.9 kg for *C. olivaceus* adult males, and 2.4 kg for adult females of both species (Ford and Davis 1992). No distinction between sex classes was made during sampling, although previous studies showed some differences in support and height use between age-sex classes (Robinson 1986; Terborgh 1983; Janson 1988; Gebo 1992).

## METHODS

I conducted focal animal instantaneous sampling on adult individuals of both species (Altmann 1974). Each focal animal was followed for 15 min, after which I shifted to the next available subject. If the focal subject was lost from view before the end of 15 minutes, I shifted to the next available subject.

Locomotor behavior was recorded at 20-sec intervals, adequate for recording the following variables: (a) behavioral context, (b) locomotor mode, (c) substrate characteristics (size, inclination and type), (d) tail use, and (e) forest layer.

Postural behavior was recorded by time bouts (Cant 1987). A bout ended when one of the recorded variables changed. The variables recorded were: (a) behavioral context, (b) postural mode, (c) substrate characteristics (size and inclination), (d) tail use, and (e) forest layer.

Total sample numbers for *C. apella* are: 1,218 intervals of locomotion during travel, 219 of locomotion during feeding, 174 of locomotion during foraging, 226 min feeding postural behavior, and 17 min foraging postural behavior; for *C. olivaceus*: 412 intervals of locomotion during travel, 138 of locomotion combining feeding and foraging, and 15 min of feeding/foraging postural behavior. G-tests were used for statistical comparison of frequencies and p values of 0.05 or less are considered significant.

The behavioral contexts recorded were TRAVEL (moving from and to sleeping trees as well as between feeding trees), FEEDING (searching for acquiring and processing plant food within a single or adjacent feeding trees) and FORAGING (animal food searching and processing).

Eight locomotor modes were recognized for both species:

(1) QUADRUPEDAL WALK/RUN: pronograde horizontal progression above and along single substrates using a diagonal sequence diagonal couplets gait (Fig. 1A; see also Hildebrand 1967). At higher speeds, capuchins trotted and galloped (see also Freese and Oppenheimer 1981; Gebo 1992). During walking, elbows and knees were only slightly abducted, the limbs moving mainly in parasagittal planes.

(2) BIPEDALISM: Progression above and along substrates involving only the two hindlimbs. The body was not kept completely orthograde but was always leaning forward. The hips were thus semi-extended, and the knees were abducted.

(3) PRONOGRAD CLAMBER: Horizontal displacement of the body on and across multiple, diversely oriented substrates (Fig. 1C). No particular gait was observed and limb movements were irregular. Arms and thighs were usually maintained abducted, and the joints were more extended than in walking.

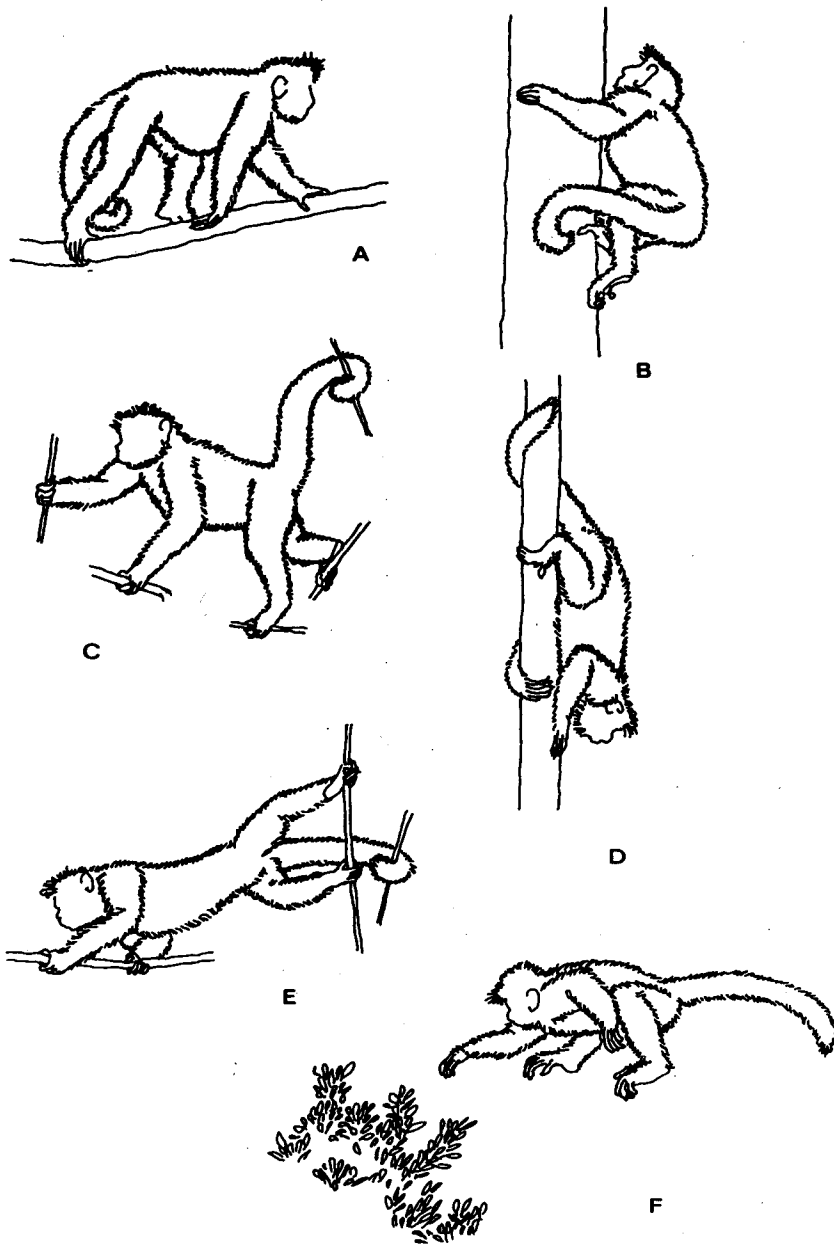


Fig. 1. — Locomotor patterns of the brown capuchin : (A) quadrupedal walk with diagonal gait, (B) climb up along a vertical trunk, (C) pronograde clamber across multiple twigs, (D) climb down along a vertical trunk, (E) bridging, (F) leaping.

(4) **CLIMB UP** : Continuous quadrupedal upward movement along a single vertical substrate (Fig. 1B), as well as upward body displacement across multiple substrates. Climbing up across multiple substrates was irregular and cautious with greater limb abduction and flexion. The arm was seldom raised above the shoulder joint.

(5) **CLIMB DOWN** : The same as climb up, but with downward body displacement on, along, and across substrates. Climbing down along single substrates included both head- (Fig. 1D) and tail-first movements, and was usually rapid. Climbing down across multiple substrates was cautious.

(6) **BRIDGING** : Active or passive deformation of the initial and terminal substrates of a gap so that the animal can cross it. There was never an airborne phase and progression was usually cautious. Limb maneuvers were similar to those observed during pronograde clambering and climbing down across substrates (Fig. 1E).

(7) **LEAPING** : Gap crossing mode always involving an airborne phase. The horizontal displacement is always longer than the vertical one. Limb thrust was produced by a rapid synchronous extension of the hip and knee joints. The forelimbs left the substrate first and were kept extended during the airborne phase (Fig. 1F). Landing was either by forelimbs first on rigid substrates, or by all four limbs on more flexible substrates.

(8) **DROPPING** : Gap crossing mode always involving an airborne phase. The body is mainly displaced vertically, although there may be some horizontal displacement. During the airborne phase all limbs were flexed and abducted, and landing was by all four limbs (and less frequently the tail).

Four postures were recorded in the field for both species :

(1) **SIT** : Sitting involved extreme flexion of all hindlimb joints (Fig. 2A) while the forelimbs collected and/or manipulated food items. On most occasions the ischium did not touch the substrate.

(2) **QUADRUPEDAL/TRIPEDAL STAND** : Capuchins supported themselves by either four or three limbs on a single or multiple substrates. Both fore- and hindlimbs were kept flexed at the elbow and knee joints, respectively (Fig. 2D).

(3) **BIPEDAL STAND** : Capuchins were supported by only the hindlimbs on a single or multiple substrates. Knees were always kept flexed, thighs were abducted, and feet grasped firmly the substrate (Fig. 2C). Bipedal stand, whether the body was kept orthograde or was leaning forward, was always tail-assisted.

(4) **SUSPENSORY** : Suspensory postures included hanging from the tail alone ; from the tail and two hindlimbs ; and from the tail, one forelimb, and the two hindlimbs. During suspensory postures the tail was always anchored above the center of gravity of the animal. No suspensory postures were observed that did not use the tail. During most of the suspensory postural behaviors, hindlimbs were flexed at the knee (Fig. 2B), thighs were usually abducted, and feet were inverted and plantar flexed. Forelimbs were usually protracted, but rarely above the elbow joint.

Substrates were classified in four size categories by estimated diameter : **SMALL** ( $\leq 2$  cm), **MEDIUM** ( $> 2$  cm,  $\leq 10$  cm), **LARGE** ( $> 10$  cm,  $\leq 20$  cm) and **VERY LARGE** ( $> 20$  cm).

Substrate inclinations were recorded relative to true horizontal : **HORIZONTAL** ( $0^\circ$ - $10^\circ$ ), **MODERATE** ( $10^\circ$ - $45^\circ$ ), **STEEP** ( $45^\circ$ - $80^\circ$ ), and **VERTICAL** ( $80^\circ$ - $90^\circ$ ). Substrate types were **TREE BRANCHES**, **LIANAS**, **VERTICAL TRUNKS** and **PALM FRONDS**.

The forest was vertically divided into 5 layers: GROUND/UNDERSTORY (0-15 m), LOWER LAYER (15-20 m), MIDDLE LAYER (20-25 m), HIGH LAYER (25-30 m) and EMERGENT (30 + m).

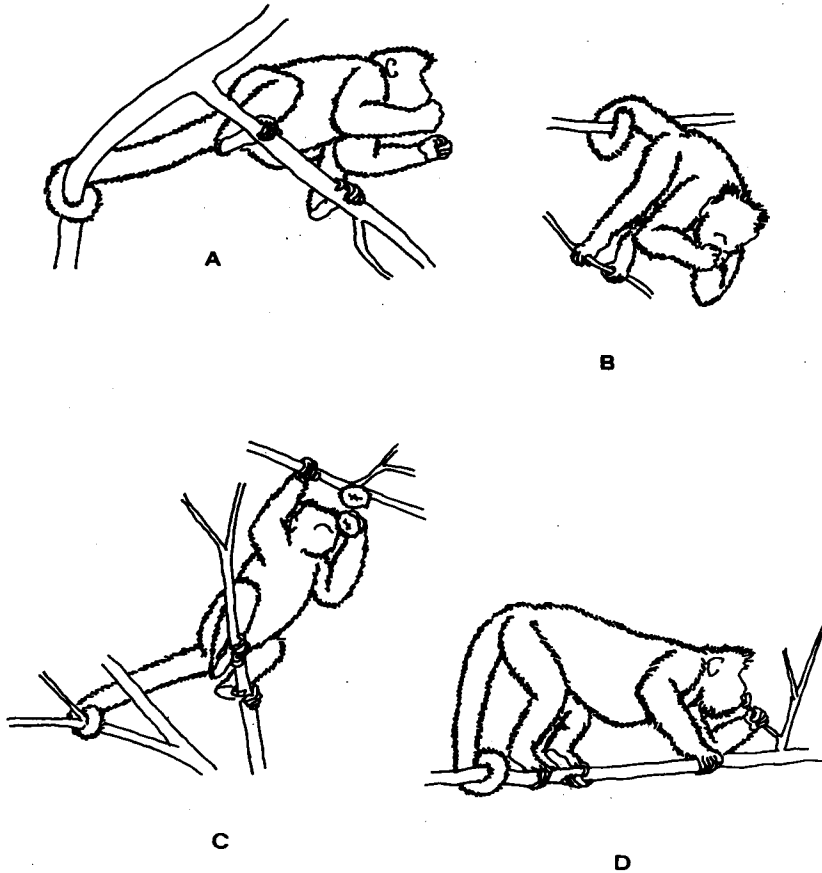


Fig. 2. — Feeding and foraging postures of the brown capuchin: (A) sit with tail anchored below CG, (B) tail-2hindlimb hang, (C) forelimb-assisted bipedal stand with tail anchored below CG, (D) tripod stand with tail anchored below CG.

## RESULTS

### *Habitat Use*

*C. apella* and *C. olivaceus* showed no significant difference in the use of forest layers during travelling ( $G = 1.875$ ,  $p = 0.599$ ). Both species used mostly the middle and high layers of the forest (Fig. 3). During travelling, lianas were not used frequently (Fig. 4). In *C. apella*, liana use was significantly less in feeding than travel (0.8%  $n = 219$ ;  $G = 38.16$ ,  $p < 0.001$ ). Palm fronds were relatively used when travelling, but

were used extensively in feeding and foraging locomotion in both species (17.4 % in *C. apella*, 8.0 % in *C. olivaceus*).

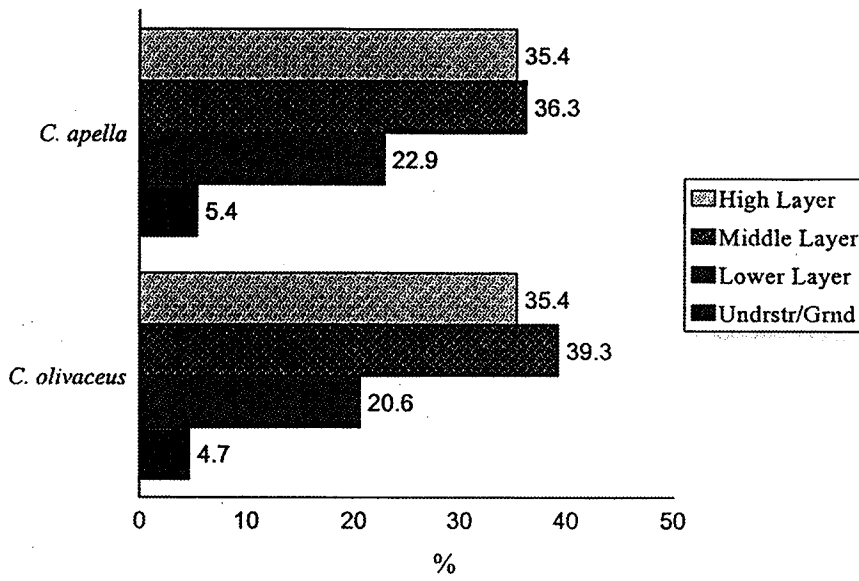


Fig. 3. – Forest vertical layer use during travel. Labels on the right side of the bars show percentages of use for each species (*C. apella* n = 1218, *C. olivaceus* n = 412).

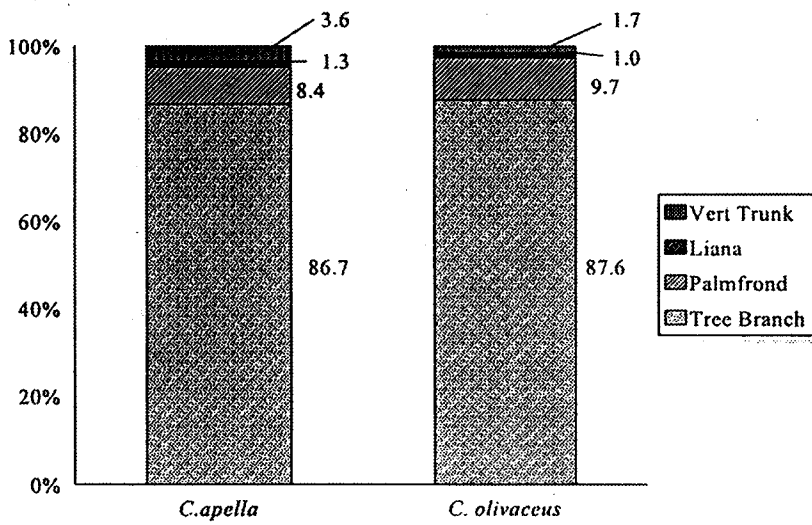


Fig. 4. – Substrate types used during travelling locomotion. Labels on bars show percentages of use for each species (*C. apella* n = 1218, *C. olivaceus* n = 412).

*Locomotor Behavior*

Table 1 shows the locomotor modes used by both species in travelling, feeding and foraging. In *C. apella*, quadrupedal walk/run was the principal locomotor mode used during travel, but its frequency decreased significantly in feeding locomotion ( $G = 5.198$ ,  $p < 0.05$ ). In both species, quadrupedal walk/run in travel mainly occurred on medium-sized substrates [68.1% of the subsample ( $n = 307$ ) in *C. apella*, and 67.1% of the subsample ( $n = 134$ ) in *C. olivaceus*].

In *C. apella*, climbing/clambering (climb up, climb down, and pronograde clambering) was more important during feeding and foraging than during travel (travel vs feed:  $G = 5.851$ ,  $p < 0.001$ , travel vs forage:  $G = 61.577$ ,  $p < 0.001$ ). In *C. apella*, climbing/clambering was more frequently used on small substrates than quadrupedal walk/run ( $G = 199.9$ ,  $p < 0.001$ ).

Leaping was the main gap crossing mode for both species. It was very frequent during travel, but its percentage decreased significantly during feeding and foraging (Table 1; *C. apella*: travel vs feed  $G = 9.351$ ,  $p < 0.05$ , *C. olivaceus*: travel vs feed/forage  $G = 13.29$ ,  $p < 0.001$ ).

Both species covered horizontal distances as long as 5 m in a single leap, but the majority of leaps were between 1 and 3 m (Table 2). In travel, no significant difference

TABLE 1. – Locomotor modes used during travel, feeding and foraging (entries of columns are percentages for each context).

	<i>C. apella</i>			<i>C. olivaceus</i>	
	Travel (%) <i>n</i> =1218	Feeding (%) <i>n</i> =219	Foraging (%) <i>n</i> =174	Travel (%) <i>n</i> =412	Feed/Forage (%) <i>n</i> =138
Quadrupedal Walk/Run	31.8	24.2	28.4	32.5	31.6
Bipedalism	2.1	3.0	4.1	0.0	0.0
Pronograde Clamber	10.1	16.7	17.6	10.7	15.8
Climb up	11.4	17.4	24.3	12.1	23.7
Climb down	7.7	22.0	12.2	8.0	15.8
Bridging	13.3	3.1	2.7	10.0	2.6
Leaping	19.7	11.3	9.6	23.8	10.5
Dropping	3.9	2.3	1.1	2.9	0.0

TABLE 2. – Distribution of leaping horizontal distances during locomotion in different behavioral contexts. Entries of columns are percentages for each context (total number of leaps in each context are shown in brackets).

	<i>C. apella</i>			<i>C. olivaceus</i>	
	Travel (%) ( <i>n</i> =188)	Feeding (%) ( <i>n</i> =15)	Foraging (%) ( <i>n</i> =7)	Travel (%) ( <i>n</i> =98)	Feed/Forage (%) ( <i>n</i> =4)
0-1 m	5.3	46.7	57.1	8.2	0.0
1-2 m	28.2	33.3	42.9	35.7	50.0
2-3 m	32.4	13.3	0.0	30.6	50.0
3-4 m	22.3	0.7	0.0	19.4	0.0
4+ m	11.8	0.0	0.0	6.1	0.0



was found between leaping behavior in the two species ( $G = 4.507$ ,  $p = 0.342$ ). In *C. apella*, leaping distances covered during travel were significantly longer than those in feeding ( $G = 22.68$ ,  $p < 0.001$ ).

Bridging was the second most important gap crossing mode (Table 1). It was used extensively in travel, but its proportion decreased significantly in feeding and foraging (*C. apella*: travel vs feed  $G = 23.72$ ,  $p < 0.001$ , *C. olivaceus*: travel vs feed/forage  $G = 8.307$ ,  $p < 0.05$ ). The tail was used very frequently, and was typically the last appendage to detach from the initial substrate giving the impression of controlling the passage, providing security.

Small substrates were frequently used in all contexts by both species (Fig. 5). Table 3 shows slightly but significantly greater use of medium-sized substrates during feeding than in travelling in both species (*C. apella* travel vs feed:  $G = 8.359$ ,  $p < 0.05$ ; *C. olivaceus* travel vs feed:  $G = 13.28$ ,  $p < 0.05$ ). In *C. apella*, gap crossing occurred mainly between small substrates [92.2 % of the bridging subsample ( $n = 129$ ), 78.2 % of the leaping subsample ( $n = 188$ ) and 86.8 % of the dropping subsample ( $n = 38$ )]. On the other hand, quadrupedal and bipedal walk/run occurred more frequently on medium-sized substrates (67.6 % of the quadrupedal/bipedal subsample,  $n = 327$ ). These differences in substrate use between quadrupedal and bipedal walk/run and gap crossing modes (leaping, bridging, and dropping) were significant ( $G = 26.28$ ,  $p < 0.001$ ).

Both species made extensive use of oblique (moderate and steep) substrates during travel (69.9 % for *C. olivaceus* and 65.9 % for *C. apella*). The differences between the two species in substrate inclination use during travel were not significant ( $G = 2.306$ ,  $p = 0.316$ ).

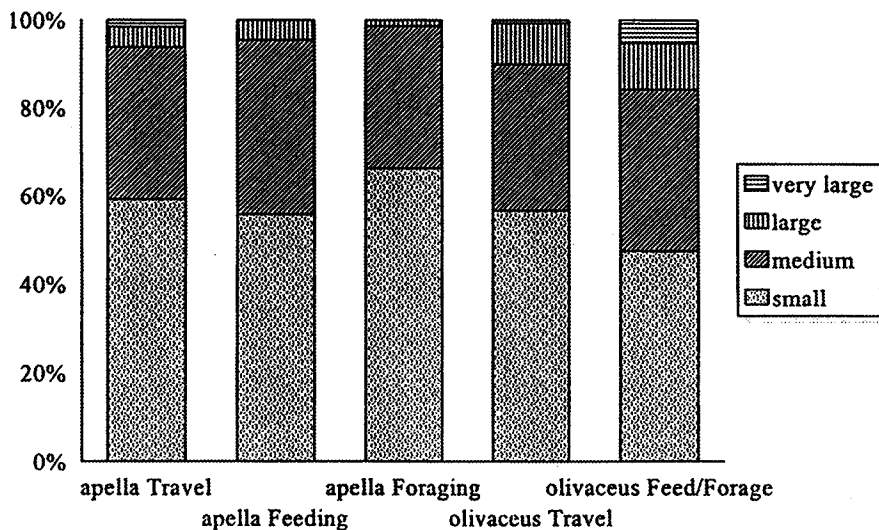


Fig. 5. – Size of substrates used during locomotion (*C. apella* travel  $n = 1218$ , *C. apella* feeding  $n = 219$ , *C. apella* foraging  $n = 174$ , *C. olivaceus* travel  $n = 412$ , *C. olivaceus* feed/forage  $n = 138$ ).

TABLE 3. – Size of substrates used during locomotion (entries of columns are percentages for each context).

	<i>C. apella</i>			<i>C. olivaceus</i>	
	Travel (%) n=1218	Feeding (%) n=219	Foraging (%) n=174	Travel (%) n=412	Feed/Forage (%) n=138
Small	59.2	55.7	66.2	56.6	47.4
Medium	34.6	39.7	32.4	33.3	36.8
Large	4.6	4.6	1.4	9.4	10.5
Very Large	1.6	0.0	0.0	0.7	5.3

### Postural Behavior

The species differed in the use of modes during feeding postural behavior (*C. apella* vs *C. olivaceus* feeding postures:  $G = 10.80$ ,  $p < 0.05$ ). Sitting was the most frequent feeding posture in *C. apella*. It occurred mainly on medium-sized substrates (Fig. 6) and lasted a mean of 98 sec per bout ( $n = 61$  sitting bouts). In both species, sitting was used not only for acquisition of food items but also for manipulation and processing of hard-shelled and large-sized fruit. In *C. olivaceus*, sitting and quadrupedal stand were almost equally used (Table 4). Quadru-/tripedal stand was an important foraging posture in both *C. apella*, and *C. olivaceus* (Table 4). In *C. apella*, quadrupedal stand occurred significantly more frequently on small substrates than sitting ( $G = 10.55$ ,  $p = 0.001$ ).

Bipedal stand represented a appreciable proportion of *C. olivaceus*' postural behavior [(Table 4) although this could be due to the small sample ( $n = 15$  min)], while it

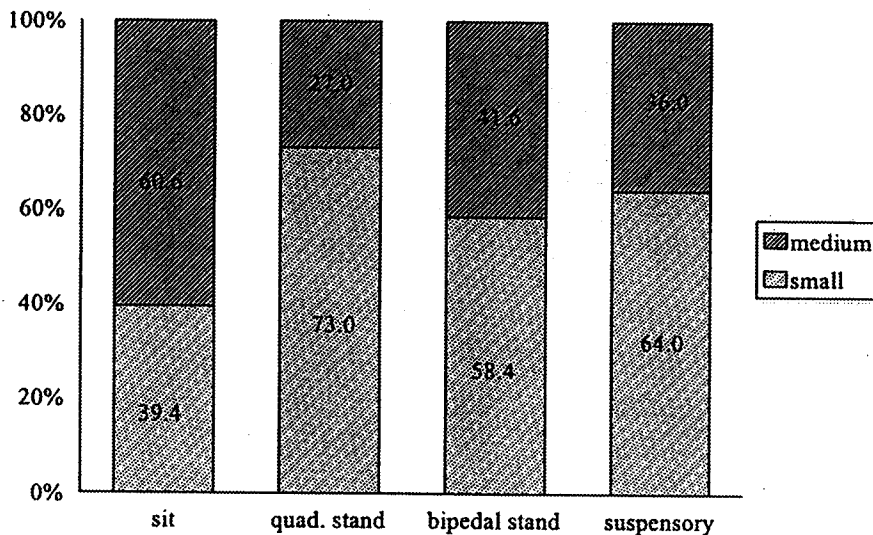


Fig. 6. – Size of substrates used in feeding postures in *C. apella*. Labels on bars show percentages for each posture (sit  $n = 169$  min, quadrupedal stand  $n = 26$  min, bipedal stand  $n = 10$  min, suspensory  $n = 21$  min).

TABLE 4. - Postural modes used during feeding and foraging (entries of columns are percentages for each behavioral context).

	<i>C. apella</i>		<i>C. olivaceus</i>
	Feeding (%) (n=226 min)	Foraging (%) (n=17 min)	Feed/Forage (%) (n=15 min)
Sit	74.9	56.3	35.6
Quadru/Tripedal Stand	11.3	33.2	34.0
Bipedal Stand	4.3	7.7	13.2
Suspensory	9.5	2.8	17.2

was rare in *C. apella*. In the latter, small and medium-sized substrates were more or less used equally during bipedal stand (Fig. 6).

In both species, the most frequent suspensory posture was tail-2hindlimbs hang, while tail-only hang or tail-2hindlimbs-forelimb hang were used very rarely. Suspensory postures were adopted not only for food acquisition but also for processing of mostly soft-tissue food items. In *C. apella*, suspensory postures occurred more than sitting on small substrates ( $G = 3.869, p < 0.05$ ), and lasted a mean of 42 sec per bout ( $n = 21$  suspensory bouts).

Feeding and foraging postures occurred slightly more on medium than small substrates in *C. apella*, and more on small ones in *C. olivaceus* but the differences were not significant (Fig. 7; *C. apella* feed vs *C. olivaceus* feed/forage:  $G = 7.218, p = 0.166$ ). In *C. apella*, medium-sized substrate use increased in foraging, but not significantly (Fig. 7; feed vs forage:  $G = 0.163, p = 0.686$ ).

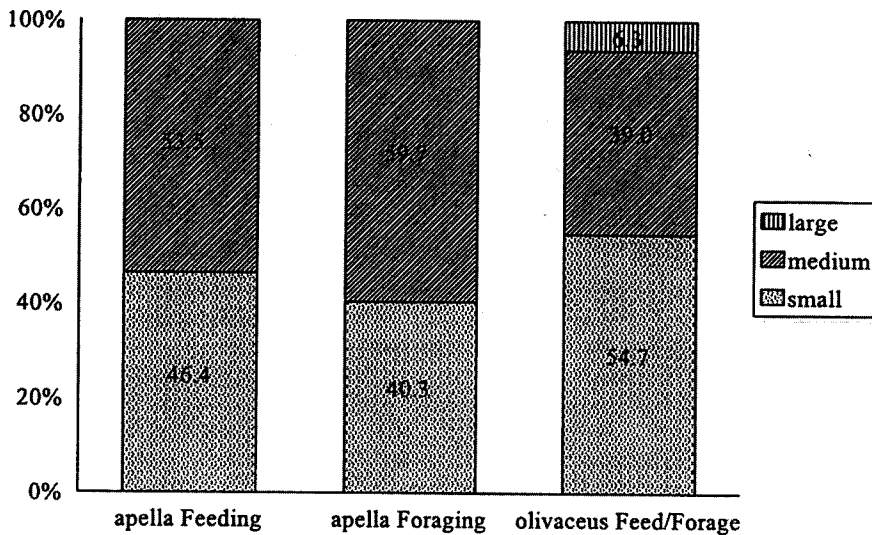


Fig. 7. - Size of substrates used during feeding and foraging postural behavior. Labels on bars show percentages of use for each context (*C. apella* feeding  $n = 226$  min, *C. apella* foraging  $n = 17$  min, *C. olivaceus* feed/forage  $n = 15$  min).

## DISCUSSION

*Habitat Use in C. apella and C. olivaceus*

*C. apella* and *C. olivaceus* showed no significant differences in the use of the forest layers and their activities were confined largely to the middle and lower forest layers. The substrate surfaces in these layers are slightly discontinuous (Oldeman 1974). Thus, a relatively high proportion of gap-crossing modes such as leaping and bridging was used by both species during travel. Lianas, which usually interconnect separate tree crowns, also provided important travel substrates for capuchins (see also Grand 1984).

During feeding locomotion, *C. apella* used palm fronds relatively frequently. This species relies heavily upon palm nuts during periods when fruit abundance decreases (Izawa 1979; Terborgh 1983; Janson and Boiski 1992; Zhang 1995). In the transitional period, when sampling occurred, *C. apella* fed very frequently on nuts from several palm species. In contrast, *C. olivaceus*, a ripe fruit specialist, which still depends on ripe fruits and invertebrates during periods of fruit scarcity (Robinson 1986), showed, as expected, less frequent use of palm fronds.

Both species showed significant differences in locomotion between travel and feeding and foraging. These differences are due to the decrease in the use of quadrupedal walk/run and leaping, bridging, and dropping, and the increase of climbing and clambering while feeding/foraging. The same pattern has been observed in other New and Old World monkeys (Fleagle and Mittermeier 1980; Gebo and Chapman 1995b). During feeding and foraging, as capuchins usually move within a single tree, gaps to cross are shorter in size and fewer in number, and therefore can be dealt with by other modes such as walking or clambering. Furthermore, in feeding and foraging, capuchins used mainly the peripheries of tree crowns, where small and flexible substrates are abundant. To move within the same crown, in between feeding and foraging sites, the animals are compelled to clamber and to climb up or down on slender substrates.

Leaping in both species represented the most important gap crossing locomotor mode. The leaping distances varied between 1 and 3 meters, matching those reported by Fontaine (1985). This similarity in leaping distances most likely indicates a similarity in habitat constraints.

*Comparison of C. apella and C. olivaceus*

The behavioral data on both species presented here were collected during the same period of the year. Both species were ranging at largely overlapping areas, were often travelling and foraging together, and used the same horizontal and vertical space. Therefore, any difference in positional behavior may be due to variations in either anatomical design, individual behavior or microhabitat use. An assessment on individual variation, as provided by others (Dagosto 1995) is beyond the scope of this study.

No significant difference was found in travel, feeding and foraging locomotion between the two species. Both used quadrupedal walk and run extensively during travel. Climbing/clambering also represented an important proportion of travelling, but especially of feeding and foraging locomotion. For both species the main modes for crossing gaps were leaping and bridging. Both species used mostly small and oblique substrates during locomotion in all contexts. Thus it appears that both species use similar if not the same paths while travelling between feeding sites, implying a choice

of route at least compelled in part by similar postcranial anatomies and habitat structure.

In contrast, there were clear species differences in feeding postural behavior. Sitting was predominant in *C. apella*, while *C. olivaceus* showed high proportions of quadrupedal and bipedal stand. Previous studies have shown that *C. olivaceus* depends more on invertebrates than *C. apella* and spends more time searching for this food source especially in periods of fruit shortage (Robinson 1986; Janson 1990). This activity may explain the relatively shorter bouts and the frequent use of quadrupedal and bipedal postures in *C. olivaceus*, both behavioral features associated with foraging for animal prey. Since both species were sampled during the transitional period when fruit becomes increasingly scarce (Zhang 1995), these differences reflect differences in feeding techniques and, most likely, microhabitat use. Such subtle differences may not have been detectable in a period of fruit abundance.

#### *Comparison of C. apella with previous studies*

In Surinam, Fleagle and Mittermeier (1980) found that *C. apella* was primarily a quadrupedal monkey (84 % of bouts) with only a small proportion devoted to climbing (grouping, according to the authors, vertical climbing, bridging, and clambering). Leaping was also noted to be far less frequent than in the present study. Given that French Guianan and Surinamese forests are more or less floristically and structurally similar, these differences may reflect differences in sampling methods (instantaneous vs bout). Capuchins tend to use long quadrupedal walking bouts while clambering bouts are usually fairly short, and such a difference could bias for walking bouts. However, these differences may also be due to seasonal, microhabitat and individual behavioral variation, as some recent studies have pointed out (Dagosto 1995; Gebo and Chapman 1995a). Fontaine's study (1985) on *C. capucinus* showed results similar to Fleagle and Mittermeier's study: quadrupedal walk and run predominated, while leaping ranked second (12.11 %), and vertical climbing third (7.87 %). Bridging was rare (1.48 %). These differences, especially those between leaping and bridging, suggest differences in habitat structure between the French Guianan and Panamanian forests, the latter probably being more uniform in presenting fewer and smaller gaps. Gebo (1992), in a deciduous forest in Costa Rica, showed that white-fronted capuchins mostly walked and ran quadrupedally (54 %). He also found a very low percentage of bridging (3 %). Percentages of climbing (including my categories of climb up, climb down and pronograde clambering) and leaping, however, are not very different from my results. Therefore compiling previous data with the ones presented in this study, all capuchin species studied seem to be primarily above branch quadrupedal walkers with substantial proportions of time devoted to both climbing/clambering and leaping.

In *C. apella*, sitting was the most frequently used feeding posture, as in most platyrrhines and catarrhines (Rose 1974; Mendel 1976; Mittermeier 1978; Fontaine 1985; Cant 1986, 1988; Gebo 1992). By sitting, an animal enlarges its contact surface with the substrate and simultaneously lowers its center of gravity (Grand 1977). Anchoring the tail below the center of gravity lowers further the position of the center of gravity. The animal's equilibrium is thereby enhanced by counteracting the destabilizing torques resulting from sitting on narrow substrates (Rose 1974). This biomechanical stability allows capuchins to both acquire and manipulate food items, as in cracking open hard-shelled fruits and nuts (Izawa 1979). Manipulation and processing of such fruits is time consuming, a fact that may justify the exceptionally long sitting bouts of capuchins.

## CONCLUSIONS

The two sympatric Guianan capuchins, *C. apella* and *C. olivaceus*, showed no significant differences in habitat use. Both species used extensively the middle and lower forest layers, and used lianas moderately. Only during feeding did *C. apella* use a little higher proportion of palm fronds than *C. olivaceus*.

During travelling locomotion, both species used quadrupedal walk/run primarily, and climbing/clambering and leaping with relatively high frequencies. The absence of significant differences in locomotion in all behavioral contexts shows that both species used the same pathways compelled by their similar anatomies and habitat structure.

During feeding and foraging postures, *C. apella* sat more frequently than *C. olivaceus*. The large proportion of sitting in *C. apella* is probably due to the exploitation of hard-shelled nuts requiring special manipulation. In contrast, the equal proportion of sitting and quadrupedal stand in *C. olivaceus* may be due to its more extensive foraging behavior.

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