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TAIL-USE IN CAPUCHIN MONKEYS

Dionisios Youlatos

Introduction

Capuchin monkeys, *Cebus*, are among the most widespread of the platyrrhines (Emmons, 1990). The brown capuchin, *C. apella*, has the largest geographic range, found east of the Andes from Colombia and Venezuela, south to Paraguay and northern Argentina (Emmons 1990). The white-fronted capuchin, *C. albifrons*, occurs in the upper Amazon and central Colombia, the white-faced capuchin, *C. capucinus*, occurs in northern Colombia and Central America, and the weeper capuchin, *C. olivaceus* ranges from Venezuela east to the Guianas and the north-eastern Brazilian Amazon. *C. apella* and *C. olivaceus* are sympatric in French Guiana.

Capuchins, like the large-bodied atelines, have a prehensile tail. Anatomical studies have shown, however, some morphological differences between the tails of *Cebus* and the atelines, suggesting that this feature has evolved twice in platyrrhines, and also that they may use their tails in different ways (Ankel, 1972; Grand, 1977; German, 1982; Rosenberger, 1983; Lemelin, 1995). There has been only limited quantitative study in tail use in the prehensile-tailed

platyrrhines. Bergeson (1995), studying free-ranging howling, spider, and capuchin monkeys in Costa Rica, found that tail use was closely associated with feeding and foraging activities in all three species, but that capuchins used their tails less than their sympatric atelines. Freese and Oppenheimer (1981) and Janson and Boinski (1992) reported that capuchins also use their tails during climbing down and gap-crossing sequences in locomotion and that they may suspend themselves by their tails during feeding. It would appear, therefore, that the prehensile tail is an adaptation mainly associated with feeding/postural activities, and much less with locomotion.

Here I report on a study to determine the role and importance of the prehensile tail during locomotion and feeding and foraging postures in the brown capuchin, *Cebus apella*, and the wedge-capped capuchin, *C. olivaceus*.

Study site, subjects, and methods

This study was conducted at the 'Station des Nouragues' (4°05'N, 52°40'W) in French Guiana, 100 km south of Cayenne, the French department's capital. This site is characterized by lowland humid rain forest, with 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 study site is described in Zhang (1995).

Both *Cebus* species are found in the study area, with their home ranges widely overlapping (Zhang, pers. comm.). Data were collected between July and September 1993, during the transitional and early dry season (rainfall = 356 mm). Although previous studies have shown some differences in support and height use between age-sex classes (Robinson, 1986; Terborgh, 1983; Janson, 1988; Gebo, 1992), the sexes were not distinguished. Focal animal instantaneous sampling was carried out on adult individuals of both species (Altmann, 1974). Each focal animal was followed for 15 min. The session was discontinued if the focal animal was lost from view before the end of the 15 minutes.

Locomotor behavior was recorded at 20-second intervals determined by a beep from a stopwatch, and postural be-

havior was recorded by time bouts (Cant, 1987). A bout ended when one of the recorded variables changed. Total samples sizes for *C. apella* were: 1,218 intervals of locomotion during travel, 219 locomotion intervals during feeding, 174 intervals during foraging, 226 min feeding postural behavior, and 17 min foraging postural behavior. Those for *C. olivaceus* were: 412 intervals of locomotion during travel, 138 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 were considered significant.

The behavioral contexts recorded were *travel* (moving to and from sleeping trees, as well as between feeding trees), *feeding* (searching for, acquiring and processing plant foods within a single or adjacent feeding trees) and *foraging* (animal prey searching and processing). Locomotor modes recorded were: *Quadrupedal walk and run, bipedalism, pronograde clamber, climb up, climb down, bridging, air*. Postural modes recorded were: *sit, quadru/tripedal stand, bipedal stand, suspensory*. When the tail was not anchored, I recorded *tail free*. When the tail was anchored beneath the animal (or below the level of the midthoracic region in orthograde postures) I recorded *tail below center of gravity (CG)*. Lastly, when the tail was anchored above the level of the midthoracic region in orthograde postures) I recorded *tail above CG*.

Locomotor Behavior

Figure 1 shows the locomotor profiles of both species during travel, feeding, and foraging. In *C. apella*, quadrupedal walk/run was the principal locomotor mode used during travel (Fig. 1). The tail was rarely used (3.6% of the quadrupedal walk/run subsample [$n = 307$] in *C. apella*), and was kept in a curled-down position. Climbing/clambering (climb up, climb down, and pronograde clambering) was more important during feeding and foraging than during travel (travel vs feed: $G = 75.851$, $p < 0.001$, travel vs forage: $G = 61.577$, $p < 0.001$). The tail was used frequently in the climb down category (61.5% of the climb down subsample [$n = 65$] in *C. apella*). It anchored mainly above CG, supporting

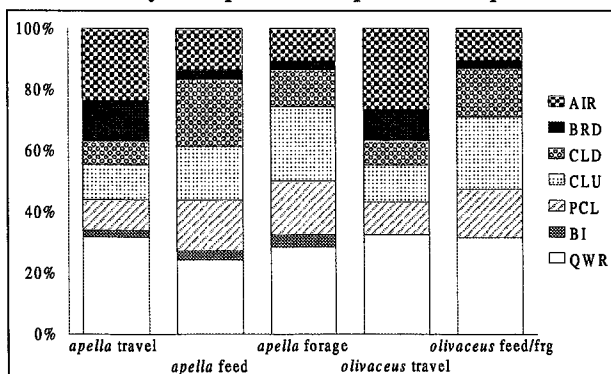


Figure 1. Percentages of locomotor modes of *C. apella* and *C. olivaceus* during travel, feeding and foraging. Sample sizes are: *apella* travel $n = 1218$, *apella* feed $n = 219$, *apella* forage $n = 174$, *olivaceus* travel $n = 412$, *olivaceus* feed/forage $n = 138$. QWR = quadrupedal walk and run, BI = bipedalism, PCL = pronograde clamber, CLU = climb up, CLD = climb down, BRD = bridging, AIR = leap, drop.

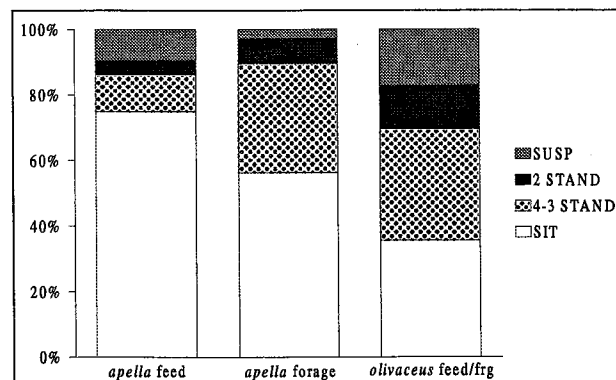


Figure 2. Percentages of postural modes of *C. apella* and *C. olivaceus* during feeding and foraging. Sample sizes are: *apella* feed $n = 226$ min, *apella* forage $n = 17$ min, *olivaceus* feed/forage $n = 15$ min. SIT = sit, 4-3 STAND = quadru/tripedal stand, 2 STAND = bipedal stand, SUSP = suspensory.

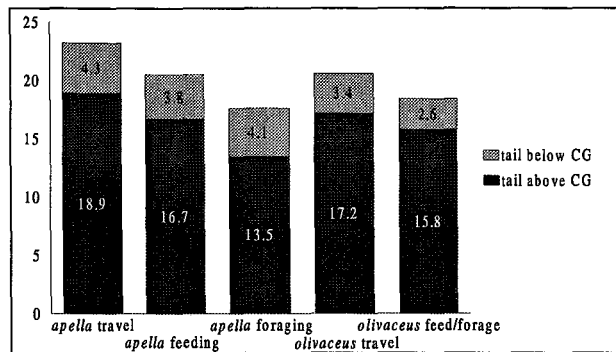


Figure 3. Use of the prehensile tail during locomotion. Labels on bars show percentages of use for each context (*apella* travel $n = 1218$, *apella* feeding $n = 219$, *apella* foraging $n = 174$, *olivaceus* travel $n = 412$, *olivaceus* feed/forage $n = 138$).

part of the body weight, controlling and braking the descent.

After leaping, bridging was the second most important gap crossing mode (Fig. 1). It was used extensively in travel, but its contribution decreased significantly in feeding and foraging (*apella*: travel vs feed $G = 23.72$, $p < 0.001$, *olivaceus*: travel vs feed/forage $G = 8.307$, $p < 0.05$). The tail was used very frequently during bridging (82.2% of the bridging subsample [$n = 129$] in *C. apella*; 87.8% of the bridging subsample [$n = 41$] in *C. olivaceus*) and was mostly anchored above CG, supporting the animal's weight. When employed, the tail was typically the last appendage to detach from the initial substrate giving the impression of controlling the passage and providing security.

No significant differences were detected in tail use during locomotion between the two species (travel *apella* vs *olivaceus*: $G = 1.439$, $p = 0.487$). The tail was anchored in less than 25% of the locomotor intervals in all contexts in both species (Fig. 3). In both species, the tail was anchored above CG in order to brake descents, control risky passages or in changes of direction. In *C. apella* there is a non significant tendency for the tail to be used less in feeding than in traveling (Fig. 3; travel vs feed: $G = 0.8$, $p = 0.067$; travel vs forage: $G = 2.941$, $p = 0.23$; feed vs forage: $G = 0.731$, $p = 0.694$).

Postural Behavior

Figure 2 shows the percentages of postural behaviors for both species during feeding and foraging. The species differed in the use of modes during feeding postural behavior (Fig. 2; *apella* vs *olivaceus* feeding postures: $G = 10.80$, $p < 0.05$). Sitting was the dominant feeding posture in both species (Fig. 2). the tail was very frequently used during sitting (*apella* 64.5%, and mostly below CG). On the other hand, percentages of tail-anchoring below and above CG in quadru/tripedal postures were more similar (*apella* above CG 28.5%, below CG 37.4%).

Suspensory postures were quite infrequent in *C. apella*, while they represented a considerable proportion in *olivaceus* (Fig. 2; but this could be an artifact due to the small sample size for *olivaceus*). In both species, the most frequent suspensory posture was tail-2hindlimbs hang,

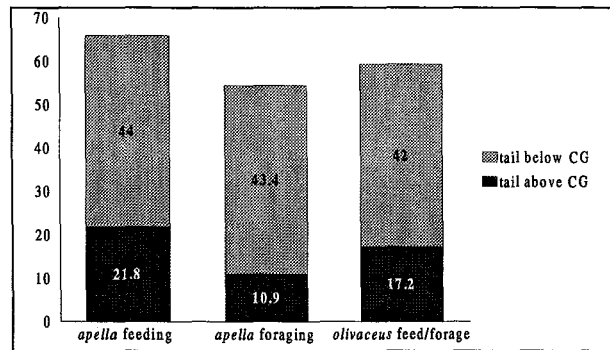


Figure 4. Use of the prehensile tail during feeding and foraging postural behavior. Labels on bars show percentages of use for each context (*apella* feeding $n = 226$ min, *apella* foraging $n = 17$ min, *olivaceus* feed/forage $n = 15$ min).

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. The tail was always used in suspensory postures.

The prehensile tail was frequently used in feeding postural behavior (*apella* feed 65.8%, *apella* forage 54.3%, *olivaceus* feed/forage 59.2%), mainly anchoring below CG (Fig. 4). No significant difference was found in tail use during feeding postural behavior between the two species ($G = 0.685$, $p = 0.71$).

Discussion

Bergeson's (1995) results from free-ranging sympatric howling, spider, and capuchin monkeys in Costa Rica, showed that capuchins used their tail much less (36.3%) than howlers and spiders (58.3% and 71.3%, respectively). Youlatos (1994) reported similar results for sympatric howling and spider monkeys in French Guiana, with spider monkeys using their tail in 62% of the locomotor sample, and howling monkeys only 25%. These results are more or less similar to Bergeson's, showing that there is a tendency for decreasing tail use from spiders to howlers and capuchins.

During locomotion, the tail was used very frequently in irregular modes (for example, climbing down, bridging) occurring on, below, and across slender substrates. In such modes, the tail was anchored mostly above CG suggesting that it supported a significant part of the body weight. Both bridging and climbing down require caution in the choice of different, diversely oriented substrates, and, as the principal body displacement is obliquely or vertically downward, both forelimbs and hind limbs are frequently loaded under tension. The tail grasp brakes the movement, secures body displacement, and offers an additional limb in weight distribution above slender substrates. Grand (1984) qualitatively underlined the importance of such functions for the prehensile tail, and Youlatos (1993) showed the importance of tail use in bridging behavior in red howlers. These findings would appear to agree with previous qualitative observations and expectations for prehensile tail use (Rosenberger, 1983; Grand, 1977). *Cebus* may use its prehensile tail in a rather conservative way, and only in critical

situations within the canopy. Anchoring of the tail above CG during locomotion suggests that the tail must be loaded under tensile and torsional forces. The frequent action of such forces is partly responsible for anatomical features indicating prehensility in *Cebus* tails.

The tail was used very frequently in feeding postures, more often than in locomotion. This suggests a close association between feeding postures and tail use as argued by Thorington (1967) and Rose (1974), and shown quantitatively by Bergeson (1995). In *C. apella*, sitting was the most frequently used feeding posture, as it is among platyrrhines and catarrhines (Rose, 1974; 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 fruit and nuts (Izawa and Mizuno, 1977), breaking open branches, and unfurling leaves. Manipulation and processing of hard-shelled fruit is time consuming, which may also justify the exceptionally long sitting bouts of capuchins.

In general, suspensory postures help arboreal primates to expand their feeding and foraging activities within the terminal twigs (Grand, 1972; Janson and Boinski, 1992). In both capuchins, the tail was always used during suspensory postures. However, since tail-only postures are rare and very brief, the tail may help distribute the weight in 3 or 4 limbs in tail-assisted suspensory postures, thus stressing the other limbs less.

In both species, the tail was used to stabilize the animals in either above-branch, or suspensory feeding postures, but not as a supportive fifth limb as in atelines. During locomotion, capuchins seem to use their tails rather conservatively in risky crossings and downward movements, braking, and securing the movement of the body.

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Dionisios Youlatos, Muséum National d'Histoire Naturelle, Laboratoire d'Anatomie Comparée, 55 rue Buffon, 75005 Paris, France. *Address for correspondence*: 35, Agathoupoleos Street, 11252 Athens, Greece.

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AGGRESSION AND DOMINANCE REVERSAL IN A CAPTIVE ALL-MALE GROUP OF *CEBUS APPELLA*

Antonio Christian de A. Moura

Capuchin monkeys, *Cebus*, live in multimale-multifemale societies, with a dominant male and a dominant female (Fedigan, 1993; Izawa, 1980; Janson, 1984; Perry, 1996). Hierarchies are based mainly on age, size and sex, and older and larger individuals usually have higher rank (Freese and Oppenheimer, 1981). In the brown capuchin monkey, *C. apella*, the dominance order among males is directly related to age (Izawa, 1980, 1990). Aggressive interactions within the group are rather infrequent (Izar and Sato, 1997; Izawa, 1980), and dominance reversal events are rare (Robinson and Janson, 1987). However, Santini (1984), studying a captive *C. apella* group that had been split into three sub-groups, observed aggression among males when the group was re-united. After reunion the males skirmished among themselves in order to attain the alpha position. Byrne et al. (1996) reported on a dominance reversal and aggression among males in a captive *C. apella* group, but the reasons for the initial fight between the higher-ranking males were unknown. Izawa (1990) related two cases of dominance reversal in a wild group of *C. apella*. In one case a younger animal was supplanted by an older animal that had entered the group and in the other, reversal occurred between animals of the same age, but one was larger than the other. Moreover, neither of the dominance reversals involved the alpha male. In this note I relate a case of aggression and dominance reversal in a captive all-male group of *C. apella* apparently due to the increase in size of a juvenile.

The group was composed of three unrelated males: Chico, more than 20 years old, the dominant male; Tadeu, more

than eight years old; and Paulinho about five years old, a juvenile-subadult. They were maintained at the Laboratório Tropical de Primatologia (LTP) at the Federal University of Paraíba, in a large wire mesh enclosure (3.8 m x 4.2 m x 2.6 m), containing natural branches and platforms. They received three meals a day. The enclosure was subject to normal environmental and climatic conditions, since the LTP is located in a 5 ha remnant of coastal Atlantic forest. The animals had lived together, for at least two years.

The dominance order in the group was related to age, and the relationships between the group members was generally peaceful. In spite of this, Tadeu occasionally bullied Paulinho, mounting him, and sometimes barring his access to food. On 27 October 1996, there was a fight involving Paulinho, Tadeu and Chico. Paulinho and Chico attacked Tadeu, whose face was injured as a result. It was not possible to determine who started the fight nor who was more aggressive. However, most of Chico's attacks against Tadeu were prevented by the keepers using a hose to direct water at him, and likewise to stop Paulinho's attack. Due to the injuries suffered, Tadeu was isolated for medical treatment. About one week later he returned to the group. After that, on several occasions Tadeu avoided Paulinho, he became frightened of him, and usually screamed when Paulinho approached him. Tadeu, as such, became subordinate to Paulinho. Interestingly, after this event, when a person approached the cage only Chico and Paulinho would go to the netting to "greet" them.

On one occasion, the keepers observed Paulinho blocking Chico's access to food. On 19 May 1997, Paulinho attacked the dominant Chico. The fight was serious, and Chico was wounded on the right hand and suffered a perforation on the right leg and some injuries on the face. Externally Paulinho showed no sign of injury. Following this event Paulinho was isolated and transferred to another facility.

In the two events reported here the severity of aggression was unusual. The *C. apella* males typically use aggressive vocalizations and facial intimidation in agonistic interactions, physical injury is rather infrequent (Santini, 1984). Izawa (1980, p.453), for example, never found any injuries in the animals he studied in wild (but see Byrne et al., 1996).

Although the reasons for the aggression and dominance reversal reported here are unknown, I believe that it was favored by Paulinho increasing his body size. The captive conditions may also have contributed, but hormonal changes due to puberty (increasing testosterone levels) may have been responsible for Paulinho's aggressiveness, and his increase in body size could have made him more self-confident. However, his aggressiveness may be explained merely by a more aggressive personality.

Interesting was the active participation of the alpha male during the first aggressive outbreak. Janson (1984) observed a dominant male intervening to support juveniles, although an older unrelated juvenile was never defended by the alpha male. A primate male's rank may change many times