

## The Locomotor Behavior of *Callicebus brunneus* and *Callicebus torquatus*

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### Key Words

*Callicebus* · Positional behavior · Habitat utilization · Platyrrhine

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### Abstract

This study presents data on the positional behavior of *Callicebus torquatus* and *Callicebus brunneus* collected from two different localities in Peru. *C. brunneus* primarily utilizes short-distance, bounding leaps, while *C. torquatus* relies predominantly on quadrupedal walking. Both species utilize small, horizontal and terminal branches more than any other substrate class. We relate the differences in locomotor behaviors between the two species to their utilization of different forest levels. *C. brunneus* tends to reside in the understory and brush layer forest levels. These more discontinuous strata necessitate higher frequencies of short-distance leaping. *C. torquatus* occupies the more continuous, interconnected canopy level, and much of its food is found in this level. Comparisons with other species show that *Callicebus* spp. locomote along smaller-sized, horizontal branches using quadrupedal progression and leaping.

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### Introduction

The genus *Callicebus* (titi monkey) is represented by numerous species of diurnal, monogamous, mostly frugivorous primates that range across central South America [Kinzey, 1981, 1997; Hershkovitz, 1990; van Roosmalen et al., 2002]. This genus has figured prominently in issues of platyrrhine evolution and ecology and is often viewed as analogous to a basal pitheciine or basal platyrrhine [Ford, 1986,

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1988; Kinzey, 1987; Kay, 1990; Ford and Davis, 1992; Rosenberger, 1992; von Dornum and Ruvolo, 1999]. By all accounts, this genus is characterized as ecologically and anatomically uniform [Ford, 1986; Robinson et al., 1987; Kinzey, 1987, 1992; Youlatos, 2004]. However, there are uneven amounts of ecological data collected on *Callicebus* spp. and the extent to which these species differ in morphology and behavior is not well understood [Kinzey 1997; van Roosmalen et al., 2002]. Some ecological and behavioral differences between species of titi monkey have been documented; for example, Kinzey and Gentry [1979; but see Defler, 1994] have suggested that in areas of sympatry, *C. brunneus* and *C. torquatus* occupy structurally and phenologically different habitat types and this has implications for differences in feeding ecology and positional behavior. More recent studies have also found that *Callicebus* species differ in their home range size, group size and feeding ecology [Muller, 1995, 1996; Price and Piedade, 2001; Bicca-Marques et al., 2002; Bossuyt, 2002]. These recent studies describe the influence of habitat use and ranging patterns on *Callicebus* social behavior, foraging strategies and demography. However, relationships between microhabitat, food distribution and specific positional behaviors remain only nascently understood for this genus [Kinzey, 1997].

In this paper, we document associations between the use of different forest levels, food distribution and positional behavior in two *Callicebus* spp. The motivation for this study is twofold: (1) to provide positional behavior data on two species for which little is known and (2) to examine the degree to which *Callicebus* can be characterized as an ecological generalist. Regarding the latter, many researchers suggest that *Callicebus* is minimally derived – both ecologically and anatomically – relative to other platyrrhines [Ford and Davis, 1992; Rosenberger, 1992; Youlatos, 2004]. For example, in a multivariate analysis of platyrrhine community ecology, Youlatos [2004, p. 190] suggests that *Callicebus* manifests ‘no particular adaptations to any specialized utilization of habitat, diet, or locomotion’. As positional behavior reflects anatomical and ecological adaptations pertaining to movement and feeding within a habitat, studies of positional behavior provide a window into the degree of ecological and behavioral specialization (or generalization) manifested by the species [Cant 1992]. Here, we present quantitative data on the positional behavior of *C. brunneus* and *C. torquatus*. Specifically, we examine the similarities and differences in locomotor behavior, substrate use and vertical location in foraging and travel contexts. We then compare our results to other studies of *Callicebus* positional behavior and habitat use.

## Methods

Positional data for *C. brunneus* were collected by P.C.W. at Manu National Park, Peru. Following Fleagle [1976], a locomotor bout sampling method was used, and 749 positional bouts were collected. Details of *C. brunneus* habitat structure are primarily drawn from Wright [1985 and unpublished data] and Terborgh [1983]. Positional behavior data for *C. torquatus* were collected by S.P.E. at Estacion Biologica *Callicebus* (EBC), northeastern Peru. Using an instantaneous time sampling technique [Altmann, 1974], a total of 7,997 individual samples were collected on *C. torquatus*. Details of habitat structure for *C. torquatus* are taken from Easley [1982] and Kinzey [1977]. Both data sets covered full ‘*Callicebus*’ days. For ease of comparison, only frequencies of behaviors are presented and likelihood-based G tests are used to determine statistical significance (with significance set at  $p < 0.05$ ). The G test is similar to the Pearson  $\chi^2$  test. However, the G test compares the observed values with expected values generated from a multi-

**Table 1.** Ethogram and definition of forest variables used in this study

|   |   |
|---|---|
| <i>Locomotor and postural behaviors</i>                   |   |
| Quadrupedal walk  | progression along a substrate in which all four limbs follow a regular pattern of movement  |
| Quadrupedal run   | rapid progression along a substrate   |
| Climb   | movement up or down steeply angled substrates   |
| Leaping   | movement between substrates that involves an in-air phase where the hindlimbs provide the propulsive force  |
| Sitting   | a stationary position where the animal rests on its hindlimbs in a pronograde or semi-pronograde posture  |
| Vertical cling  | a stationary position where the animal rests on a vertical support; forelimbs are in tension and hindlimbs are flexed   |
| (Other postural behaviors include standing and sprawling) |   |
| <i>Context of behavior</i>                                |   |
| Foraging/feeding  | movement associated with feeding activities and/or searching for food   |
| Travel  | movement within and between crowns of trees where no feeding and foraging is observed   |
| Rest  | periods of idleness or a stationary posture where the animal is not observed eating or moving   |
| <i>Substrate size</i>                                     |   |
| Terminal branches   | a small collective mass of distal branches that supports an animal where no single branch bears the majority of weight of the animal; branches are usually less than 0.5 cm in diameter |
| Small support   | a substrate greater than 0.5 cm and less than or equal to 4 cm in diameter  |
| Medium support  | a substrate greater than 4 cm and less than or equal to 25 cm in diameter   |
| Large support   | a substrate greater than 25 cm in diameter  |
| <i>Substrate orientation</i>                              |   |
| Horizontal substrate                                      | a substrate between 0 and 15° from the horizontal   |
| Oblique substrate   | a substrate between 16 and 74° from the horizontal  |
| Vertical substrate  | a substrate between 75 and 90° from the horizontal  |
| <i>Vertical location</i>                                  |   |
| Ground layer  | the forest floor  |
| Brush layer   | the forest stratum consisting of mostly small shrubs and tall plants  |
| Understory  | the forest stratum consisting of discontinuous substrates and/or vertical trunks with few branches spreading out laterally  |
| Canopy  | the forest stratum in which the majority of the tree branches spread out laterally above the forest floor, often connecting with branches from other trees                              |
| Emergent crown  | the forest stratum where the topmost portions of the trees emerge from the horizon created by the canopy  |

nomial probability distribution. The test statistic is a ratio of the probabilities of the observed versus expected frequencies and is a  $\chi^2$  distributed random variable. The G test is particularly suited to observational studies since it imposes the fewest a priori assumptions about row and column totals (these totals are used to calculate expected values); in essence, the G test treats the row and column totals as population parameters, not fixed values [Gotelli and Ellison, 2004].

To ensure that our results for the two species were comparable we undertook the following steps. The data collected by P.C.W. were recorded onto audiotape in a narrative and highly descriptive fashion under the rubric of locomotor bout sampling [Fleagle, 1976]. Because locomotor bout sampling defines a bout as a change in positional behavior, the descriptive sentence ‘[the adult male quadrupedally walks 3 feet down a small, 2.5 cm, horizontal support], [sits for 1 min], [then leaps 2 feet, to a small 2.5 cm, oblique branch], [then sits...’ can be broken down into 4 bouts (denoted by brackets). These bouts were tallied and entered into a spreadsheet and statistically compared with the point-sample bouts collected by S.P.E. In order to make our postural results comparable between the two species, we broke up long bouts of sitting in *C. brunneus* into 5-min intervals [Doran, 1992]. We did this because under locomotor bout sampling, a single 20-min episode of sitting would constitute 1 bout, whereas under point sampling this same behavior could be broken down into numerous bouts of sitting depending on the sample interval. A study by Doran [1992] compared instantaneous time sampling versus locomotor bout sampling and found that few differences emerge between the two methods when locomotor bouts are weighted by distance. In addition, a similar study by Wright [1996] indicates that these two sampling methods yield similar results when collected on arboreal, small-bodied New World primates. Following the findings of Wright [1996], we did not need to weight quadrupedalism bouts by distance because both species tended to travel short distances before changing their positional behavior. Given that the data for *C. brunneus* were collected in a descriptive and narrative fashion we were able to define positional behaviors and substrate categories for *C. brunneus* that were directly comparable to the behaviors and substrate categories defined for *C. torquatus* by S.P.E. Regarding substrate categories, for example, S.P.E. defined substrate diameter as ‘small’ when the substrate was between 0.5 and 4 cm. To match this definition, we pooled all substrate diameters between 0.5 and 4 cm (as described in the audiotapes) into the category ‘small’. Table 1 presents definitions of the variables used in this study. Throughout this study, we follow the taxonomic revisions of van Roosmalen et al. [2002].

## Results

Frequencies of positional behaviors, support use and vertical ranging patterns are presented in tables 2–4. We summarize the major findings in this section. Locomotor behaviors differed significantly between *C. brunneus* and *C. torquatus* ( $G = 21.6$ ,  $d.f. = 3$ ,  $p < 0.01$ ). As evidenced in table 2, *C. brunneus* relies primarily on leaping and quadrupedal walking (38.3 and 32.5%, respectively) whereas *C. torquatus* uses quadrupedal walking for the majority of sample points (62.4%). Frequencies of postural behaviors during foraging are not significantly different ( $G = 4.5$ ,  $d.f. = 2$ ,  $p = 0.10$ ), although frequencies during resting are significantly different ( $G = 14.0$ ,  $d.f. = 2$ ,  $p < 0.01$ ). Both species utilize sitting as the most frequent postural mode during resting and foraging (>70% for both species). However, *C. brunneus* also exhibits vertical clinging during foraging (11.1%) while *C. torquatus* engages in a variety of ‘other’ postures during resting (24.7%); these latter postures mostly include sprawling [Easley, 1982].

Substrate use is given in table 3. During both foraging and travel, *C. brunneus* relies primarily upon small and medium-sized branches. Small branches are used in 63.1% while foraging and in 50.0% while traveling, and medium branches are used in 21.2% while foraging and in 38.8% while traveling. *C. torquatus* most often utilizes terminal branches during foraging (36.0%) and during travel (43.2%). Frequencies of branch size utilization are significantly different between the species both during foraging ( $G = 60.5$ ,  $d.f. = 3$ ,  $p < 0.01$ ) and travel ( $G = 71.0$ ,  $d.f. = 3$ ,  $p < 0.01$ ). Both species utilize horizontal supports most frequently across all contexts (>50.0%).

**Table 2.** Frequencies (%) of positional behaviors for *C. brunneus* and *C. torquatus*

|                                    |      |                |       |       |
|------------------------------------|------|----------------|-------|-------|
| Locomotor behaviors (all contexts) | Walk | Run            | Leap  | Climb |
| <i>C. brunneus</i>                 | 32.5 | 16.8           | 38.3  | 12.4  |
| <i>C. torquatus</i>                | 62.4 | 4.5            | 23.9  | 9.2   |
| Postural behaviors (foraging)      | Sit  | Vertical cling | Other |       |
| <i>C. brunneus</i>                 | 88.1 | 11.1           | 0.8   |       |
| <i>C. torquatus</i>                | 88.8 | 3.6            | 7.6   |       |
| Postural behaviors (resting)       |      |                |       |       |
| <i>C. brunneus</i>                 | 90.9 | 2.5            | 6.6   |       |
| <i>C. torquatus</i>                | 71.4 | 3.9            | 24.7  |       |

**Table 3.** Frequencies (%) of substrate use for *C. brunneus* and *C. torquatus*

|                               |            |         |          |          |
|-------------------------------|------------|---------|----------|----------|
| Substrate diameter (foraging) | Large      | Medium  | Small    | Terminal |
| <i>C. brunneus</i>            | 0.0        | 21.2    | 63.1     | 15.7     |
| <i>C. torquatus</i>           | 14.4       | 32.9    | 16.7     | 36.0     |
| Substrate diameter (travel)   |            |         |          |          |
| <i>C. brunneus</i>            | 0.0        | 38.8    | 50.0     | 11.2     |
| <i>C. torquatus</i>           | 8.9        | 41.7    | 6.2      | 43.2     |
| Substrate angle (foraging)    | Horizontal | Oblique | Vertical |          |
| <i>C. brunneus</i>            | 49.7       | 28.6    | 21.7     |          |
| <i>C. torquatus</i>           | 67.2       | 24.0    | 8.8      |          |
| Substrate angle (travel)      |            |         |          |          |
| <i>C. brunneus</i>            | 51.8       | 32.7    | 15.5     |          |
| <i>C. torquatus</i>           | 52.5       | 28.0    | 19.5     |          |

**Table 4.** Frequencies (%) of vertical location for *C. brunneus* and *C. torquatus*

| Vertical location   | Ground | Brush layer | Understory | Canopy | Emergent |
|---------------------|--------|-------------|------------|--------|----------|
| Foraging            |        |             |            |        |          |
| <i>C. brunneus</i>  | 0.0    | 20.2        | 77.9       | 1.9    | 0.0      |
| <i>C. torquatus</i> | 0.1    | 2.0         | 21.5       | 68.0   | 8.4      |
| Travel              |        |             |            |        |          |
| <i>C. brunneus</i>  | 0.0    | 17.8        | 67.5       | 14.7   | 0.0      |
| <i>C. torquatus</i> | 0.2    | 1.0         | 18.2       | 76.5   | 4.1      |
| Resting             |        |             |            |        |          |
| <i>C. brunneus</i>  | 0.0    | 33.3        | 58.7       | 8.0    | 0.0      |
| <i>C. torquatus</i> | 0.0    | 2.0         | 37.7       | 54.9   | 5.4      |

Oblique supports are the next most frequently traversed substrate in all contexts. While foraging, *C. brunneus* uses a greater percentage of vertical substrates than *C. torquatus* (21.7 vs. 8.8%). Frequencies of branch angle between the two species differed significantly during foraging ( $G = 9.1$ , d.f. = 2,  $p = 0.01$ ), but not during travel ( $G = 0.7$ , d.f. = 2,  $p = 0.69$ ).

Vertical ranging patterns are given in table 4. Overall, *C. brunneus* tends to stay more in lower forest levels than *C. torquatus*. Across all contexts, *C. brunneus* principally uses the understory (77.9% while foraging, 67.5% while traveling and 58.7% during resting) and brush layer (20.2% while foraging, 17.8% while traveling and 33.3% while resting). *C. torquatus* primarily occupies the canopy level (68.0% while foraging, 76.5% while traveling and 54.9% while resting) and understory (21.5% while foraging, 18.2% while traveling and 37.7% while resting). Vertical ranging patterns are significantly different between the two species during foraging ( $G = 147.4$ , d.f. = 3,  $p < 0.01$ ), travel ( $G = 99.8$ , d.f. = 3,  $p < 0.01$ ) and resting ( $G = 83.1$ , d.f. = 3,  $p < 0.01$ ).

## Discussion

### *C. brunneus* Locomotor Behavior

The vertical distribution of food and forest microhabitat influences the type of locomotor behaviors exhibited by *C. brunneus*, although other factors such as interspecific competition may also be important. *C. brunneus* tends to feed on leaves in the dry season (the season when these locomotor data were collected), particularly genera such as *Miconia*, *Acalypha* and some bamboo species. Sixty-four percent of all feeding minutes during the dry season include episodes of leaf eating and many of the leaf sources are found on vines, lianas or small-crowned trees of less than 10 m in diameter [Wright, 1985]. These trees are characterized by, ‘...slender, unbranched trunks with a narrow topknot of foliage...[and]...few opportunities to spread out laterally below’ [Terborgh, 1983, p. 79]. Moreover, many of these food sources are located in successional and edge habitats which are characterized by tangled and dense vegetation with a high density of vines [Terborgh, 1983; Wright, 1985].

Ninety-eight percent of all foraging activities take place in the subcanopy levels (table 4). These areas are structurally complex and there are few options for uninterrupted, horizontal travel, given the high density of lianas, vines and small-crowned trees. In these habitats, *C. brunneus* primarily uses short-distance leaping. Seventy-five percent of all leaping behaviors in *C. brunneus* were short-distance, bounding leaps of less than 2 body lengths [Lawler, 1999]. This type of leaping behavior often occurs between small horizontal and oblique substrates that are of varying heights relative to the take-off substrate. When leaping was not utilized, *C. brunneus* relied on quadrupedal travel and other positional behaviors. Bouts of locomotion in these areas are of short distance (3 body lengths or less) and occur mostly on small horizontal and terminal branches. Quadrupedal progression in the subcanopy levels is almost always used in conjunction with leaping behavior. From the perspective of *C. brunneus* – a small-bodied quadruped – the irregular substrate horizon in this type of habitat would also require those behaviors that impose nonuniform limb movements. Janson [cited in Kinzey, 1981, p. 245; see also Wright, 1985] describes the *C. brunneus* habitat as ‘broken up’ and such habitat discontinuity tends to be associ-

ated with locomotor behaviors that require relatively more leaping or asymmetrical gaits [Fleagle and Mittermeier, 1980; Fleagle et al., 1981]. These include trunk-to-trunk leaping, climbing and upward hoisting; collectively, these behaviors make up 21.5% of the locomotor behaviors of *C. brunneus* apart from bounding leaps [Lawler, 1999]. Other researchers have also noted the use of dense undergrowth by *C. brunneus* [Mason, 1966; Hernandez-Camacho and Cooper, 1976; Moynihan, 1976; Kinzey, 1981; Crandlemire-Sacco, 1988; Emmons, 1997]. When feeding in these habitats, *C. brunneus* relies on sitting, although vertical clinging is also utilized (11.1% of all foraging postures).

The use of lower forest levels by *C. brunneus* may also be linked to interspecific feeding competition. Group size in *C. brunneus* is about 3–4 individuals [Wright 1985]. The small group size and diurnal foraging pattern – when compared to other primates at Manu – impacts how *C. brunneus* uses the forest [Wright, 1989]. This, in turn, can influence positional behavior by forcing *C. brunneus* to lower forest levels. *C. brunneus* is excluded from large-crowned, upper-level, feeding trees by other primates in the Manu community [Terborgh, 1983; Wright, 1985, 1986, 1989]. Many of the larger-bodied frugivores such as *Cebus albifrons*, *Ateles paniscus* and especially *Cebus apella* and *Saimiri* will chase *C. brunneus* from these food sources [Wright, 1985]. In July and August – when these data were collected – *C. brunneus* was chased out of fruiting trees at least once a day during observation periods [Wright, 1985, fig. 19]. The small-bodied *Saimiri* does not suffer the same fate by virtue of its large group size. Because *C. brunneus* is excluded from these large fruit trees it tends to use smaller, lower-level, food sources. As Wright states, ‘...during the day *Callicebus* are chased from the big trees by many groups of each of the species of large monkey... Denied access to the figs and nectar resources, the dusky titi monkeys resort to leaf eating’ [Wright, 1989, p. 642]. These items are found in lower forest levels and necessitate short-distance leaps and quadrupedalism to access them.

#### *C. torquatus* Locomotor Behavior

At EBC, *C. torquatus* procures the majority of its food in the canopy and generally uses quadrupedal locomotion to reach these items. In particular, 74.6% of all fruit consumed by *C. torquatus* is obtained in the canopy and more than 50% of leaves and insects are also obtained in this level [Easley, 1982]. Similarly, 77% of its movement (i.e. travel) was in the canopy. As table 4 shows, *C. torquatus* tends to occupy these strata because of the vertical distribution of food items it exploits. Both movement to a food patch and feeding take place primarily within the canopy.

Its reliance on quadrupedal travel is broadly consistent with its occupation of the canopy level. The *C. torquatus* study group often resides in high/dry ‘varillal’ forest that is characterized by large-crowned trees with a continuous canopy and very few epiphytes and lianas [Kinzey, 1977; Easley, 1982]. Kinzey’s study – also at EBC – showed that *C. torquatus* locomotion in the ‘varillal’ forests is predominated by horizontal and terminal branch use and that these areas contain important feeding trees. In the present study, *C. torquatus* uses horizontal branches at a frequency of 67.2% and terminal branches at a frequency of 36.0% when foraging. On both substrate types, movement is achieved through quadrupedal progression [Easley, 1982]. In the canopy, there is a predominance of terminal branches that tend to connect rain forest trees above the forest floor. Animals inhabiting the canopy take advantage of these interdigitated branches and move in a somewhat continuous fash-

ion along this level with relatively less leaping than may be required of other forest levels [Napier, 1962, 1966; Kinzey, 1977; Fleagle and Mittermeier, 1980; Terborgh, 1992; Cannon and Leighton, 1994; Emmons, 1996]. This is not to say, of course, that there are no gaps within the canopy; gaps do occur and they often require leaping to cross [Cannon and Leighton, 1994]. Nevertheless, in a continuous canopy, one would expect relatively less leaping and climbing from a small-bodied primate such as *Callicebus*, as there are relatively fewer gaps to leap across and fewer steep vertical disjunctions which require climbing to ascend or descend [Fleagle and Mittermeier, 1980; Fleagle et al., 1981].

The locomotor profile of *C. torquatus* also indicates that this animal engages in leaping at a frequency of 23.9% (table 2). Leaping in the canopy consists of quadrupedal jumping (>3 body lengths), while leaping in the understory consists mostly of leaping between vertical substrates [Easley, 1982]. Much of the quadrupedal jumping behavior relates to the exploitation of the palm nuts, *Jessenia polycarpa*. This tree species is characterized by a large, smooth trunk with no midtrunk branches and leaf stems that emanate directly from the top portion of the trunk. The large fructescence of the tree forms a horizontal platform. This species is found in areas with a discontinuous canopy, and *C. torquatus* was never observed climbing up these palm trees [Easley, 1982]. To reach this tree, *C. torquatus* leaps from neighboring trees in the discontinuous canopy making a long, quadrupedal jump from a stationary position. Once there, the animal spends time feeding and moving about on the horizontal fructescence. Thus, a major portion of the leaping behavior in *C. torquatus* is accounted for by its manner of reaching this food resource. Easley [1982] found that this resource accounted for 13.7% of all feeding samples and comprised 22.7% of all fruit consumed by *C. torquatus*. Insect feeding also accounted for a portion of the leaping behavior in *C. torquatus*, especially in the understory [Easley, 1982]. The understory was the second most used forest level during foraging and travel, and movement in this area included both quadrupedal travel and vertical leaping.

#### *Comparative Evidence and Conclusions*

Numerous researchers have suggested that *Callicebus* species are generalized arboreal quadrupeds [Ashton and Oxnard, 1964; Stern, 1971; Ciochon and Corrucini, 1975; Moynihan, 1976; Kinzey, 1977; Ford and Davis, 1992]. The results presented in this study broadly concur with this description. Both *Callicebus* spp. rely on quadrupedal locomotion to move within their habitat. Walking and running make up 50% or more of each species' locomotor behavior. However, both species also leap a fair amount, accounting for almost 25% of their total locomotor repertoire. *C. brunneus* uses short-distance leaps associated with its occupation of brushy, broken up habitats whereas *C. torquatus* uses longer leaps, particularly associated with its exploitation of palm nuts. Both species rely on small and medium horizontal branches during foraging and travel. Patterns of food distribution influence the locomotor behaviors of these two species. Foraging for leaves in the dense underbrush accounts for the combination of short-distance leaping and quadrupedal walking observed in *C. brunneus*. For *C. torquatus*, most of its food is found in the canopy level and it uses quadrupedal walking and running in combination with longer quadrupedal jumps to obtain these items. Comparisons with other field studies are congruent with our findings. Table 5 gives comparative information on positional behaviors and associated variables from other investigations of *Callicebus*. Although

**Table 5.** Comparisons of positional behaviors and associated variables among *Callicebus* spp.

| 1st and 2nd most frequently used | <i>C. torquatus</i> <sup>1</sup> | <i>C. torquatus</i> <sup>1</sup> | <i>C. brunneus</i> <sup>1</sup> | <i>C. brunneus</i> <sup>2</sup> | <i>C. cupreus</i> <sup>3</sup> |
|----------------------------------|----------------------------------|----------------------------------|---------------------------------|---------------------------------|--------------------------------|
| Locomotor behaviors              | QW and LP                        | QW and LP                        | LP and QW                       | QW and ?                        | QW and LP                      |
| Substrate diameters              | TM and ?                         | TM and MD                        | SM and MD                       | SM and TM                       | SM and TM                      |
| Substrate angles                 | HO and ?                         | HO and OB                        | HO and OB                       | HO and OB                       | HO and OB                      |
| Vertical locations               | CY and BL                        | CY and US                        | US and BL                       | MS and US                       | US and CY                      |
| References                       | Kinzey [1977, 1981]              | this study and Easley [1982]     | this study                      | Crandlemire-Sacco [1988]        | Youlatos [1999]                |

QW = Quadrupedal walk; LP = leaping; MD = medium; SM = small; TM = terminal; HO = horizontal; OB = oblique; CY = canopy; MS = midstory; US = understory; BL = brush layer.

<sup>1</sup> Refers to travel context only.

<sup>2</sup> Refers to foraging context.

<sup>3</sup> Refers to all contexts.

this table does not include data on the eastern ranging *C. personatus*, it does include data from species distributed along the western side of the Amazonian rain forest. Due to differences in data collection and presentation, we only present rank order information on the two most frequently used locomotor behaviors, substrate types and forest levels used by each *Callicebus* sp. We also note that the data presented for *C. torquatus* in this study and the data obtained by Kinzey [1977] were collected at the same location.

The general picture emerging from table 5 is that *Callicebus* spp. employ quadrupedal walking and leaping on smaller-sized horizontal or oblique supports in the canopy or subcanopy forest levels. These species do not systematically make use of the large vertical supports or utilize the ground or emergent forest levels. *Callicebus* spp. appear to prefer smaller-sized horizontal substrates, and this makes sense given their reliance on quadrupedalism. All studies report that *Callicebus* has a generalized diet consisting of fruits, insects and leaves. Crandlemire-Sacco [1988] found that *C. brunneus* uses quadrupedalism almost exclusively when navigating through very dense brush. At other sites, *Callicebus* sp. engages in a combination of quadrupedal walking in conjunction with leaping to move within their habitat. Leaping behaviors varied between sites. In the present study, and that of Youlatos [1999], *Callicebus* sp. engaged in a fair amount of trunk-to-trunk leaping. Vertical leaping was reported as ‘infrequent’ in Kinzey’s study [1977] and was not observed at all in the study by Crandlemire-Sacco [1988]. Vertical leaping is used by *C. brunneus* and *C. torquatus* at Manu and EBC as a means to move around in the understory or brush layer of the forest, usually during foraging. The habitat structure at Yasuni may also necessitate vertical leaping as it consists of an open canopy with many lianas [Youlatos, 1999]. *C. torquatus*, as reported in this study and that of Kinzey, ranges in higher forest levels than *C. brunneus* or *C. cupreus*. Both Crandlemire-Sacco [1988] and Youlatos [1999] found that their study species primarily uses noncanopy levels. This is similar to our findings for *C. brunneus* at Manu.

Although there seems to be a fair amount of consistency in locomotor behavior among these *Callicebus* spp., it is difficult to determine the extent to which these factors are entrained to similarities in anatomy, habitat or both. Our data and those of Crandlemire-Sacco [1988] show similar positional profiles for *C. brunneus* at two different study sites. This lends support to the idea that two populations of the same species in different localities will retain a consistent locomotor pattern due to shared anatomical constraints [Garber and Pruetz, 1995]. However, qualitative descriptions of these two sites suggest that the forests may be similar. Both contain an abundance of lianas, scrub-like brush and small-crowned trees (see above) [Crandlemire-Sacco, 1988]. In the absence of more controlled, systematic studies on habitat structure, it is not possible to sift out the anatomical and ecological components that impinge on locomotor behavior in these two populations of *C. brunneus*.

On the whole, the comparative data lend credence to the idea that the genus *Callicebus* is characterized by ecological generalism [Kinzey, 1987; Ford and Davis, 1992; Youlatos, 2004]. Collectively, *Callicebus* spp. fall on the primitive end of the platyrrhine morphocline in terms of dental and postcranial adaptations [Ford, 1986; Kinzey, 1992] and – relative to other platyrrhines – they do not show major ecological specializations pertaining to diet, habitat preference, substrate choice or forest type [Ford and Davis, 1992; Kinzey, 1992; Rosenberger, 1992; Youlatos, 2004]. As Youlatos notes [2004, p. 190]: ‘*Callicebus* exhibits variable rates of frugivory, insectivory, and folivory while moving by quadrupedal walk and leaping in all forest layers and types.’ Basic predictions from optimal foraging models suggest that niche breadth should increase with decreasing resource availability [Emlen, 1966, 1968]. In all parts of South America, *Callicebus* is sympatric with primate species that tend to be larger-bodied and/or reside in large social groups [Kinzey, 1997] and many sympatric species have been observed displacing *Callicebus* spp. from feeding sites [Wright, 1989; Kinzey, 1992]. This extrinsic factor, coupled with a plesiomorphic postcranium [Ford, 1988] and body size that falls near the switchpoint of ‘Kay’s threshold’ [Fleagle, 1999], could account for the seeming ecological generalization observed in *Callicebus* [Kinzey, 1981]. Thus, while individual *Callicebus* spp. will sometimes focus on particular food sources (e.g. *Jessenia polycarpa* in *C. torquatus*) or habitats (e.g. broken-up, brushy habitats in *C. brunneus*), the overall niche of *Callicebus* does not harbor any fundamentally unique features witnessed in other platyrrhines [Ford and Davis, 1992; Rosenberger, 1992; Youlatos, 2004]. As always, more empirical data are needed to determine the number and type of variables that define niche space in *Callicebus* and other platyrrhines. In addition, theoretical models that generate null expectations about what a niche should look like in the absence of competition would also be illuminating [Gotelli and Graves, 1996].

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