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ENTITLED The Positional Behavior of Cebus capucinus

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The Positional Behavior of *Cebus capucinus*

By

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I. Introduction

The history of every animal species is undeniably linked to its past and present environments. In order to investigate this linkage, it is necessary to study all aspects of a species: environment, behavior, and morphology. The study of the interactions between these aspects of an animal's ecology provides a basis on which to build evolutionary histories and relationships; an understanding of these relationships being the ultimate goal of primatology. The purpose of this paper is to examine in detail aspects of habitat utilization and positional behavior in a species of new world primate, *Cebus capucinus*.

The study of positional behavior provides insights into the evolution of primate locomotor systems. Because resources are found throughout the canopy on many different types of supports, differences in positional behavior and anatomy between species reflect the abilities of these species to exploit their respective habitats. A primate diet normally contains many different foods. The distribution of each resource in a habitat is restricted to a set of specific spatial conditions that include habitat zone, and the size, orientation, and flexibility of supports. Thus each resource in a habitat presents different problems of access to a primate.

The positional behavior of a primate is a compromise between its ability to exploit particular types of resources and its ability to exploit different types of supports in the habitat. Because the morphology of a species tends to constrain its positional behavior, the manner in which it exploits its environment is also constrained by morphology. For example, the Panamanian tamarin possesses claw-like nails and consequently is able to locomote on large vertical branches. Because they possess these specific morphological and behavioral characteristics, the tamarins are able to utilize exudates as an important food source (Garber, 1989). Other sympatric primates, such as *Cebus capucinus*, possess other morphological and behavioral qualities that enable them to use a different set of resources.

Functional associations between positional behavior and environment in living primates can often be applied to fossil primates. Fossil forms that resemble extant forms in morphology are likely to exhib

similar patterns of behavior. This method of comparison has provided insight into the ecology of many extinct primate groups such as *Simopithicus* (Day, 1979).

II. Ecology of *Cebus capucinus*

The white-faced capuchin is a well studied primate, and consequently much morphological and ecological data are available. *Cebus capucinus* is found throughout Central America south of Honduras, and has scattered populations in Northern Columbia and possibly Venezuela (Hernandez-Camacho, 1976; Oppenheimer, 1968). It inhabits virtually every type of forest in the neotropics, and wherever it is found it is fairly common. It is an adaptable, intelligent primate and is known to have a high degree of manual dexterity as well as possessing an insatiable curiosity (Oppenheimer, 1968; Hernandez-Camacho, 1976; Moynihan, 1976; Costello and Fragaszy, 1988).

This primate is generally classified as a medium-sized arboreal monkey, body size being between 2.5 and 4.0 kilograms. Sexual dimorphism is evident in *Cebus capucinus*, but not in the form of body size. Instead, there are differences in body shape between males and females: males have bigger shoulders than females, and the faces of males are said to be squarer than females. Also, the canines of males are bigger than those of females (Oppenheimer, 1968). Oppenheimer states that there is a difference in social maturation rates: females attain adulthood at four years, while males are not adults until eight years of age. *Cebus capucinus* is a long-lived species; individuals in captivity have lived longer than twenty-five years (Oppenheimer,1968).

Group size of *C. capucinus* averages between fifteen and twenty individuals. A dominant adult male in each group assumes reproductive and territory defense responsibilities (figure 1). Three trends appear evident in the group structure of this primate: the sex ratio is biased in favor of females, males between four and seven years of age spend a period of time in all male groups, and there are usually twice as many juveniles and infants as adults. Oppenheimer (1968) and Robinson (1987) believe that males between four and seven years of age are forced out of the group by the dominant male and form solitary bachelor bands.

Home range size is probably determined by insect foraging opportunities and averages around 0.9 square kilometers (Freese and Oppenheimer, 1981). Home ranges are defined by vocalizations, and although groups normally do not stray into other group territories, the adult males confront each other when two groups meet. It is also possible that territories are marked with urine (Oppenheimer, 1968). Robinson (1987) has pointed out that this social system is similar to that found in *Cercopithecus cephus* and *C. ascanius*, two species of old-world monkeys. He believes that *Cebus* and *Cercopithecus* converge on many aspects of ecology.

Cebus capucinus utilizes the entire vertical range of its habitat, from near the ground to the very top of trees. Although the pattern of activity varies greatly day to day, travel is the predominant activity. One or more rest periods of thirty to sixty minutes each are usually taken by the group every day. The activity budget of this primate is very much dependent on the food sources available; if resources are scattered and scarce, then almost all of the day is devoted to travel and feeding.

The diet of *C. capucinus* is omnivorous. The composition by weight of a typical daily diet is twenty percent animal prey, sixty-five percent fruit, and fifteen percent green plant material (Freese and Oppenheimer, 1981). *C. capucinus* does not appear to actively hunt or stalk its prey, but rather is an opportunistic forager, as most animals of small size are eaten.

Insect foraging is a time consuming activity and increases in frequency during the wet season. Insects from many families are eaten, but the most common prey is of the "hidden" type: ants, wasps, and beetle larvae (figure 2). The group normally forages for these prey in a spread out formation by opening dead leaves, inserting their hands into small openings, and breaking branches. They are often classified as "destructive foragers" (Terborgh, 1983).

Generalized Group Structure of *Cebus capucinus*

ages	females	males	total
8+ yrs.		2	2
4+ yrs.	3+		3+
2-4 yrs.	3	2	5
1-2 yrs.	1	1	2
0-1 yrs.	1	1	2
total	8	6	14+

figure 1
(Oppenheimer, 1968)

Diet of *Cebus capucinus*

plants commonly utilized by *C. capucinus* :

Sheelea zonensis
Ficus spp.
Cecropia spp.
Inga spp.
Olmedia aspera
Apeiba membranacea
Gustavia superba
Maripa panamensis
Faramen occedentalis

part of plant utilized:	# of species
New growth	6
Buds	3
Parts of flowers	6
Nectar	2
Receptacle	3
Aril or pulp	58
Seed	3

Insects commonly eaten from the following orders:

Orthoptera
Phasmatodea
Isoptera
Homoptera (nymphs)
Coleoptera (grubs and adults)
Lepidoptera (larvae and pupae)
Hymenoptera (adults, young and nest material)

figure 2 (Oppenheimer, 1968)

The diet of *C. capucinus* consists primarily of fruits. Over 72 species of plants are known to be utilized, but on the average about five to seven different species are eaten per day. *Cebus capucinus* are selective in their utilization of fruits; often they rely heavily on a tree species that occurs at a low density. Most of the plant material ingested consists of the pulp, aril, or other soft layer that surrounds the seed or pit of the fruit (Oppenheimer, 1968). Small berries, flowers, and new growth are also eaten. *Cebus* are very "sloppy" eaters; they eat just a tiny amount of pulp from a fruit and throw the rest away. This "wasted" fruit does not appear to be inspected before being rejected, rather it is just dropped (Oppenheimer, 1968; Freese and Oppenheimer, 1981). *Cebus capucinus* obtains its water from the food it eats and also from standing pools.

III. Study Area

In this paper I report on research I conducted on patterns of positional behavior and habitat utilization in *Cebus capucinus* on the Atlantic coast of Panama. The field site was located in Agua Clara Bay (9 N, 80 W). This bay is situated in the Gatun Lake area of the canal, and is five kilometers from the Smithsonian Tropical Research Institute at Barro Colorado Island (figure 3). The forest is a secondary, neotropical type that has a dry season extending from January through April. It is thought that much of the Agua Clara peninsula was a banana plantation about fifty years ago. Three other primates share this forest with *Cebus capucinus* : *Alouatta palliata, Aotus trivirgatus* and *Saguinus oedipus geoffroyi*. Humans do not inhabit this area.

IV. Methods

Data was recorded from 1-27-88 to 2-26-88 using the instantaneous time sampling technique as described by Altman (1974). A focal animal was chosen and individual activity records were recorded every two minutes. A total of 209 individual activity records were made in this manner. The following information was recorded: date, time,

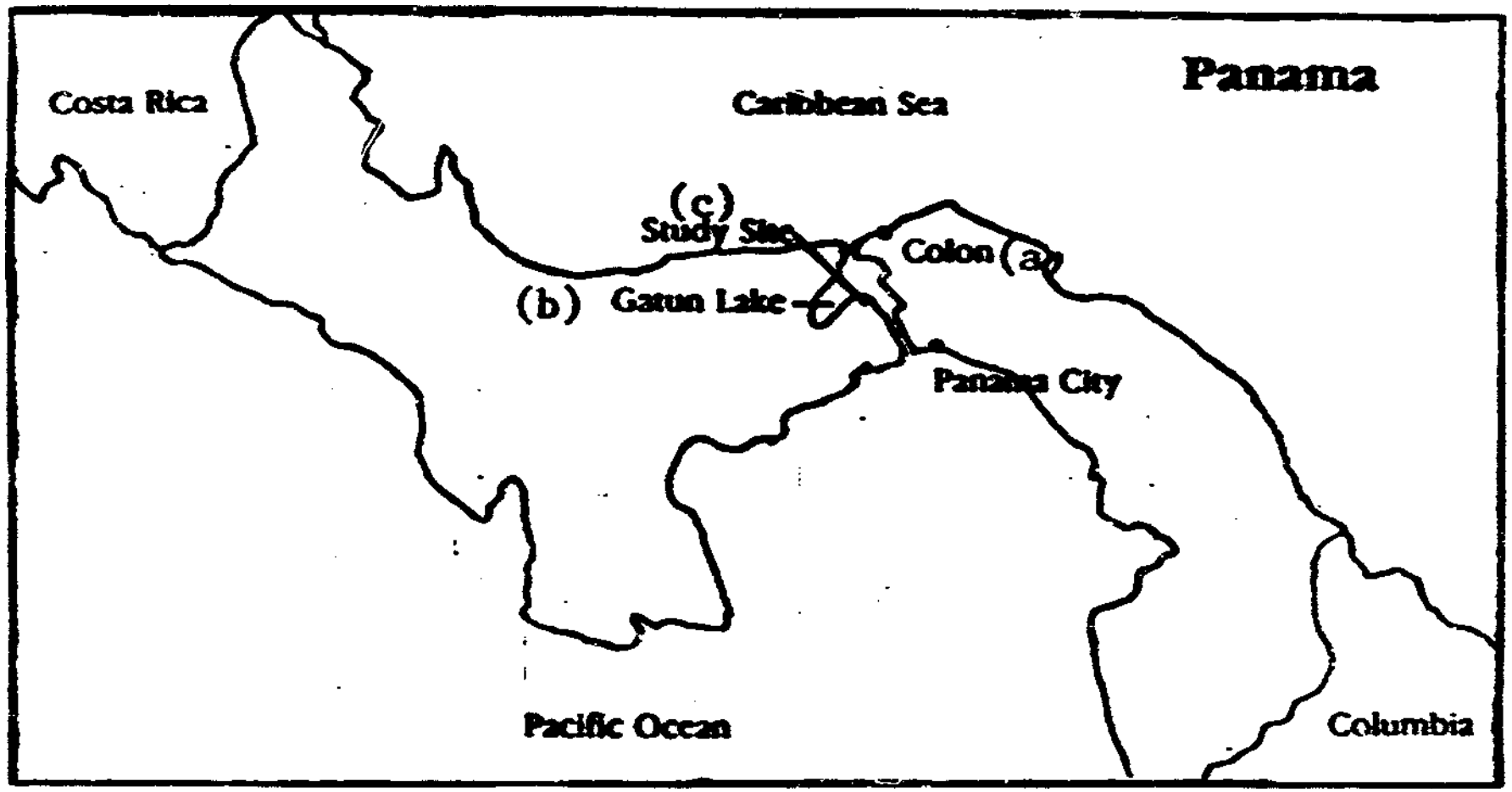


Figure 3 Panama and the location of the Study Site

location, size of the focal animal, posture or locomotion of the animal, and the nature of the support being utilized (circumference, orientation, flexibility, and height off the ground). Definitions for these terms are found in Appendix 1.

Data collected in the field were recorded directly on to a notebook. Later at night the data from each day were copied on to permanent data tables. When I returned home, the data from these tables were entered into a Macintosh computer and analyzed using the Double Helix II database package. Tables and charts of broad positional trends were then generated based on postures used in specific activities and the conditions under which these activities occurred. The tables and charts are presented showing percentages and sample sizes.

V. Results

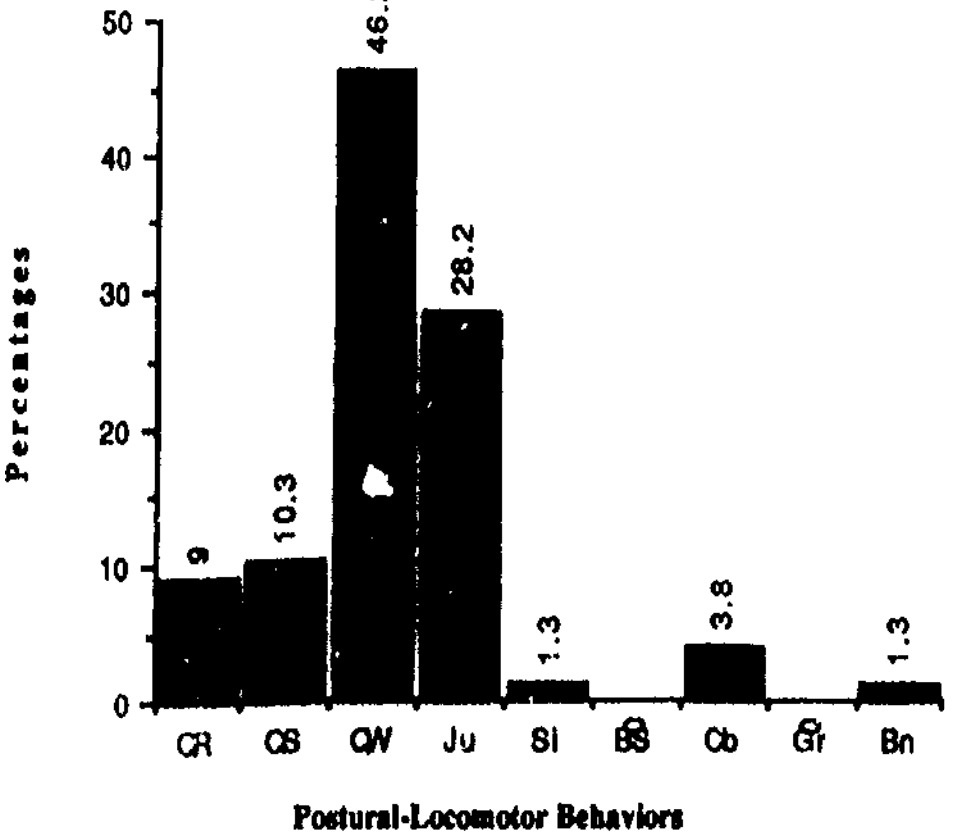
Cebus capucinus appears to be primarily a quadrupedal traveler. Sixty-five percent of travel time involves quadrupedal walking and running (figure 4), this method of travel occurring most often on horizontal and non-flexible branches (figure 5). Jumping accounts for almost thirty percent of travel time and is principally restricted to small, flexible branches that are either terminal or oblique in orientation (figure 6). Thus jumping and quadrupedalism occur on a different set of supports. When traveling quadrupedally or jumping, *C. capucinus* avoids both large branches and vertically oriented branches (figures 5 and 6). Overall, travel occurs most commonly on horizontal branches, with no preference observed between flexible and non-flexible branches.

Feeding is done primarily while adopting a sitting or grasping posture (figure 10). In this position part of the animal's body weight rests on its body as opposed to on its arms or legs. Feeding almost always occurs on small, flexible branches that are non-vertical in orientation. As shown in figure twelve, foraging is both a locomotor and a postural activity. Forty percent of foraging involves quadrupedal activities, and thirty-five percent is associated with climbing or grasping among small branches. As in feeding, *C. capucinus* forages almost exclusively on small, flexible, non-vertical branches. Thus, feeding and foraging appear to

occur on similar types of supports, although feeding is accomplished using a less diverse set of postures. Feeding and foraging occur at about the same height in the canopy. This level is higher than the height at which traveling and resting occur (figure 11). *Cebus capucinus* normally utilizes n(a-flexible, non-vertical medium or small supports while resting.

Some general trends are indicated in this analysis. *Cebus capucinus* is best described as an arboreal quadruped. Jumping occurs principally on small, flexible supports, and vertical and large supports are avoided in all activities. This is not surprising as small to moderate sized primates utilize this type of support much more easily than the large-bodied *Cebus* (Fleagle and Mittermeier, 1980). Because *C. capucinus* is an opportunistic forager, it is advantageous for the monkeys to travel and forage on an otherwise wide variety of support types to maximize the likelihood of finding insect prey. This, in fact, is what I observed.

Posture/Locomotion While Traveling



n=78

figure 4

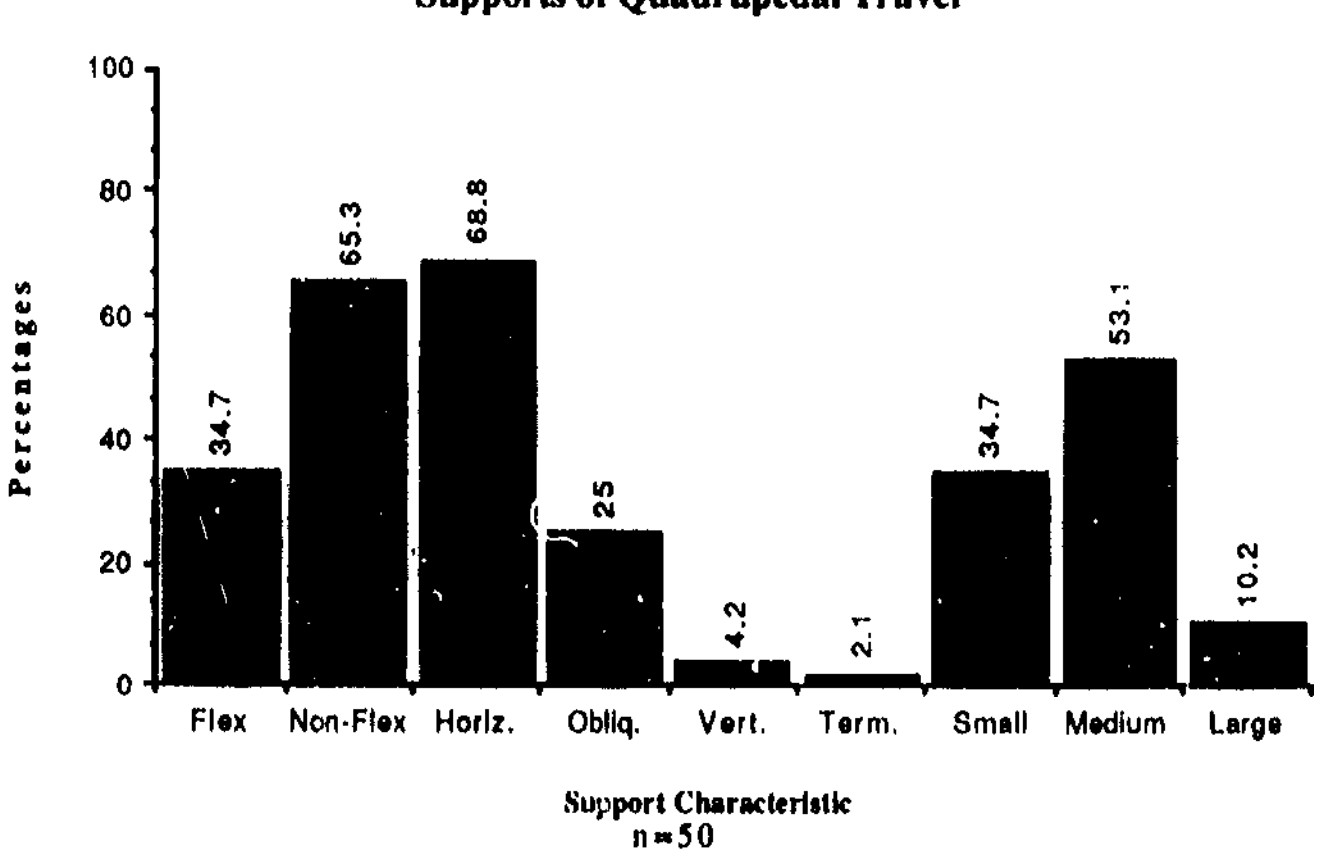
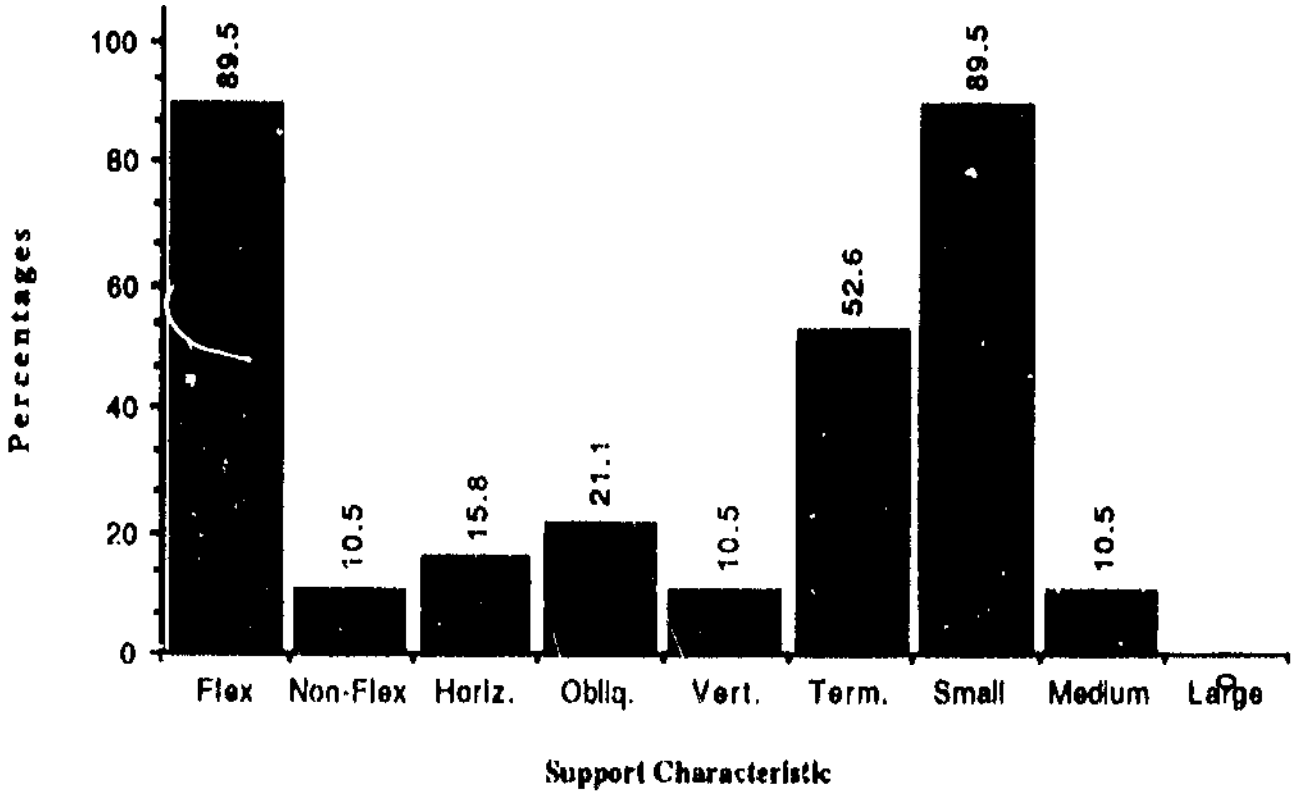


figure 5



n=22

figure 6

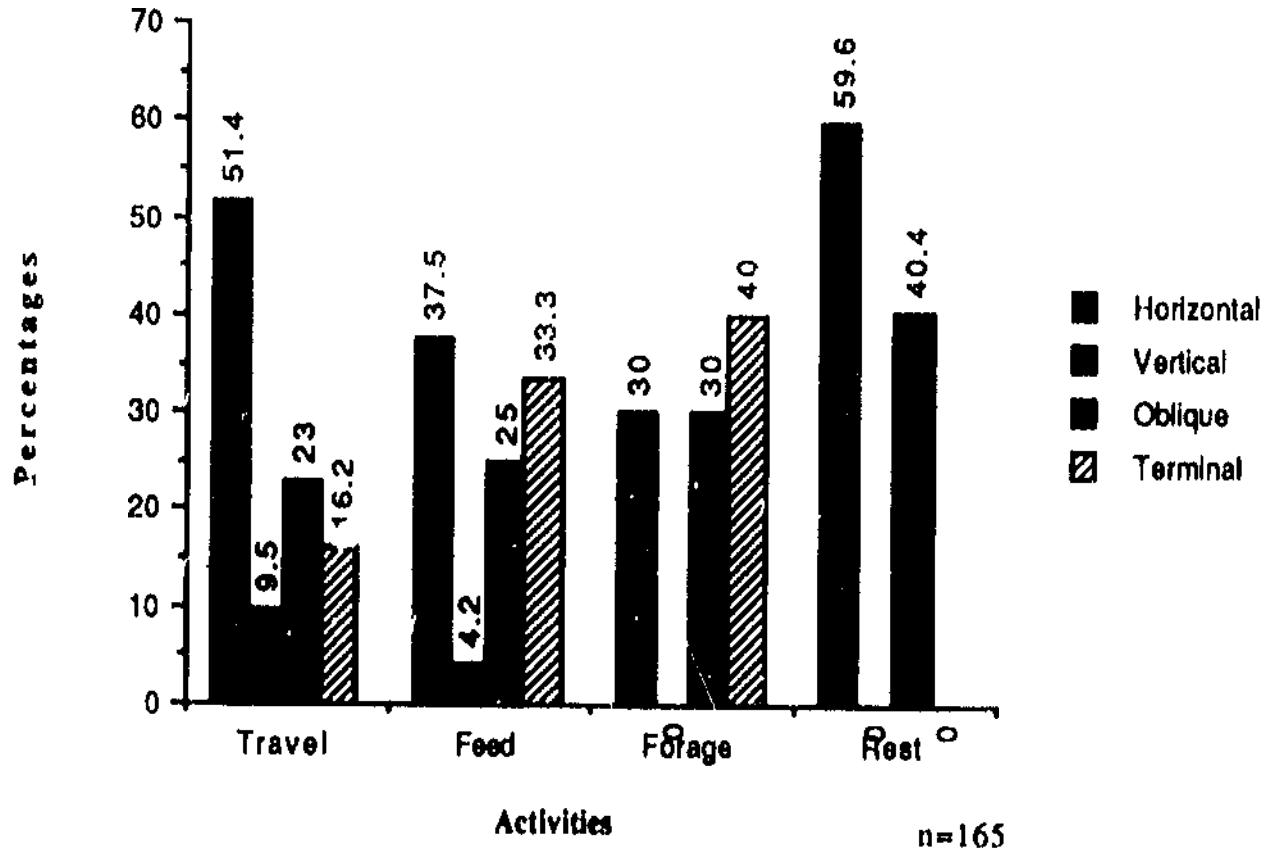


figure 7

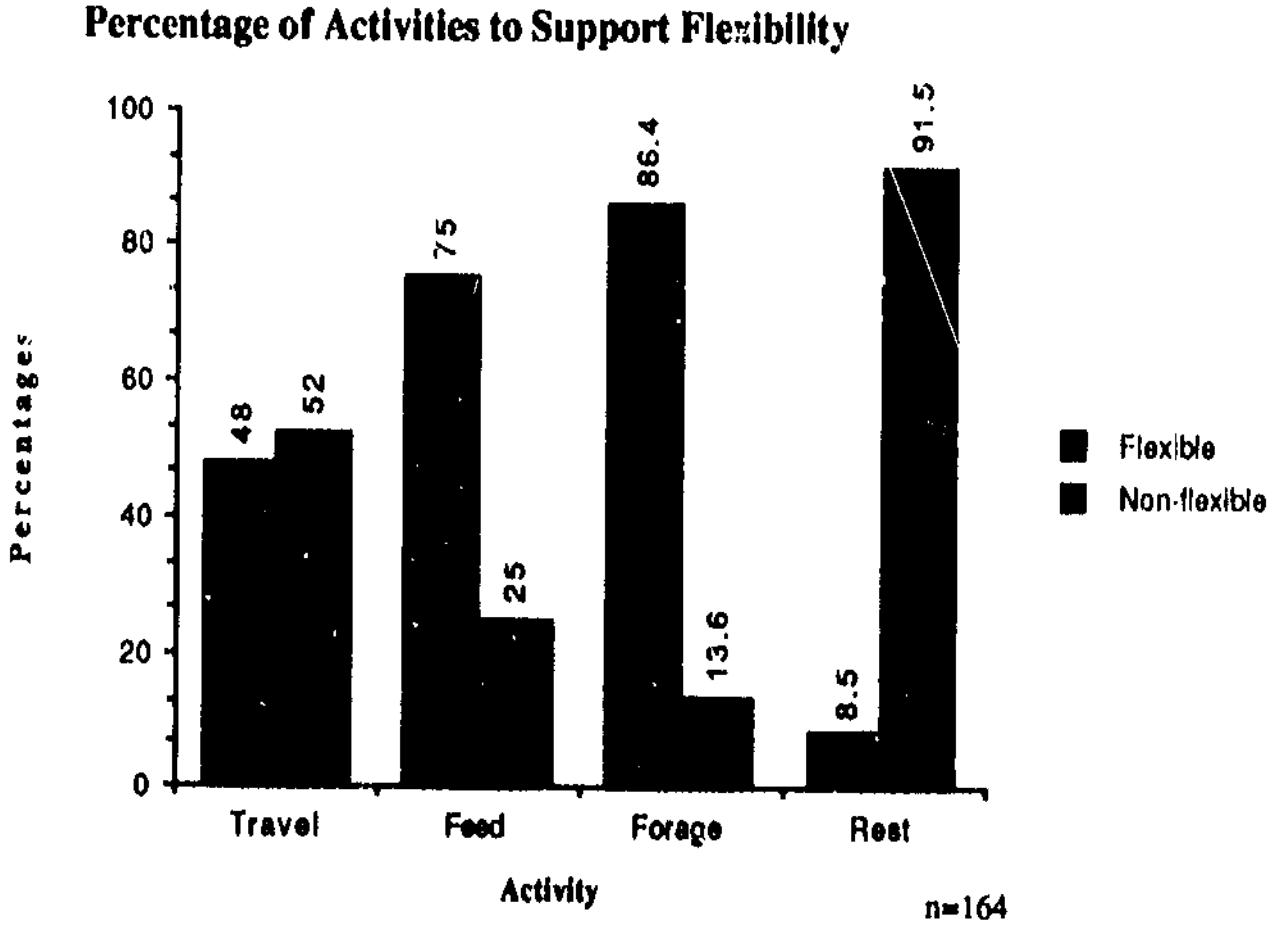


figure 8

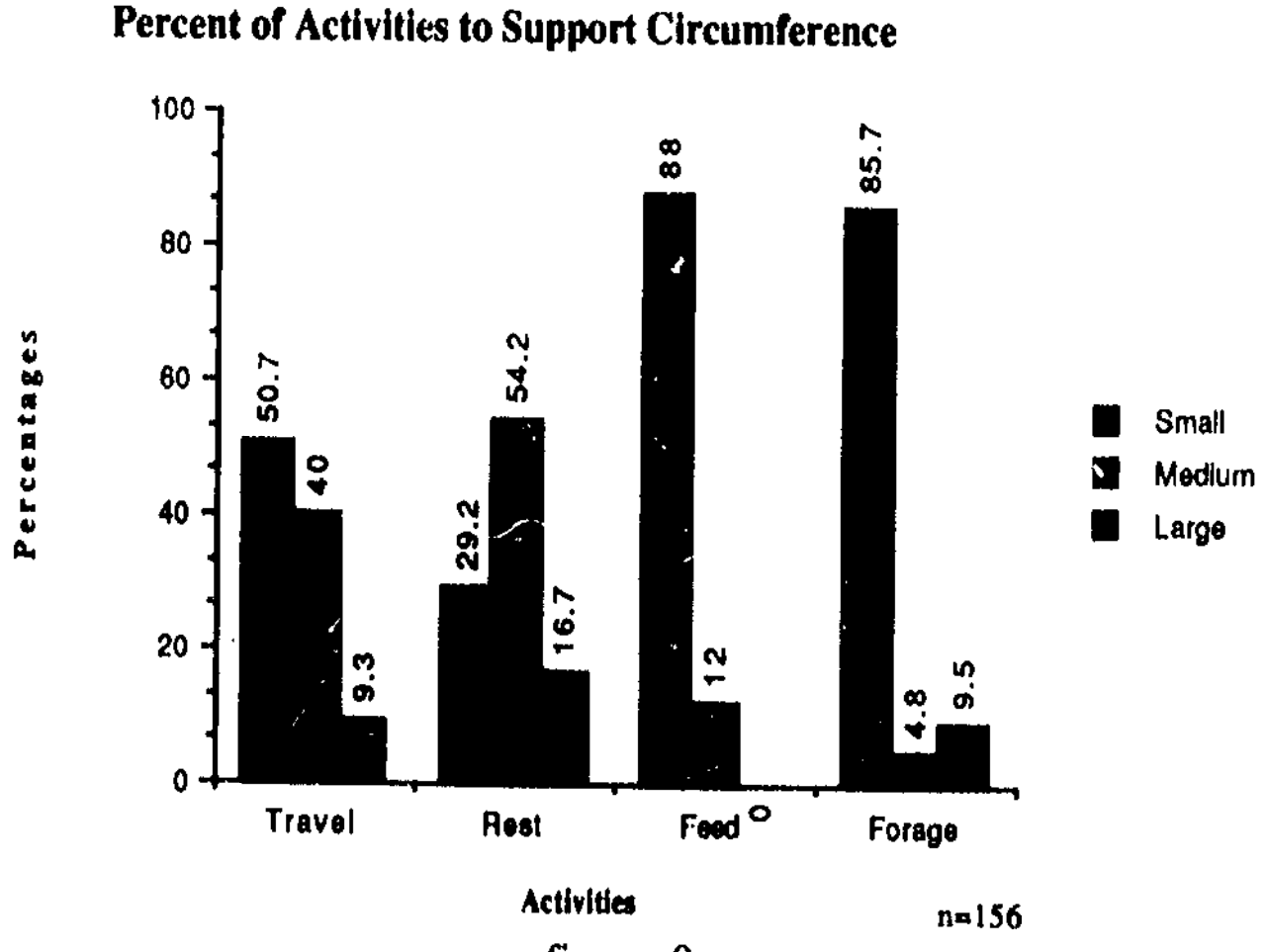


figure 9

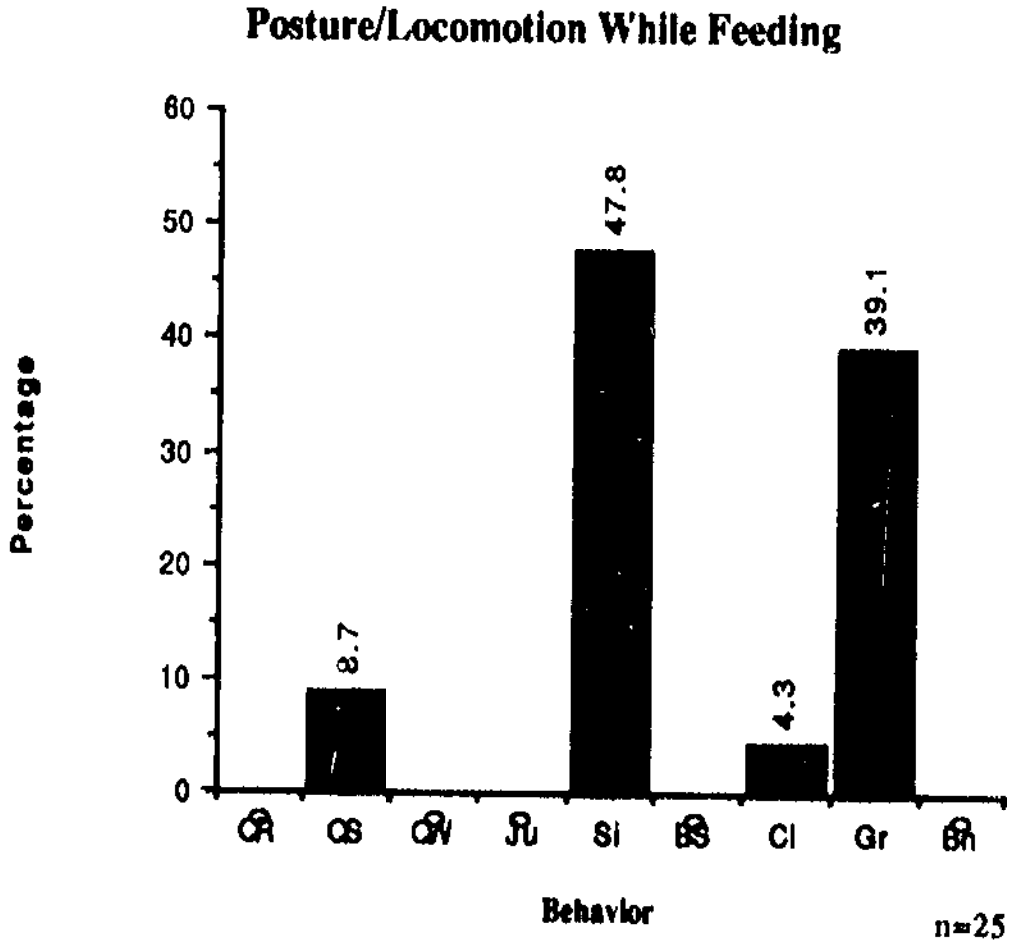


figure 10

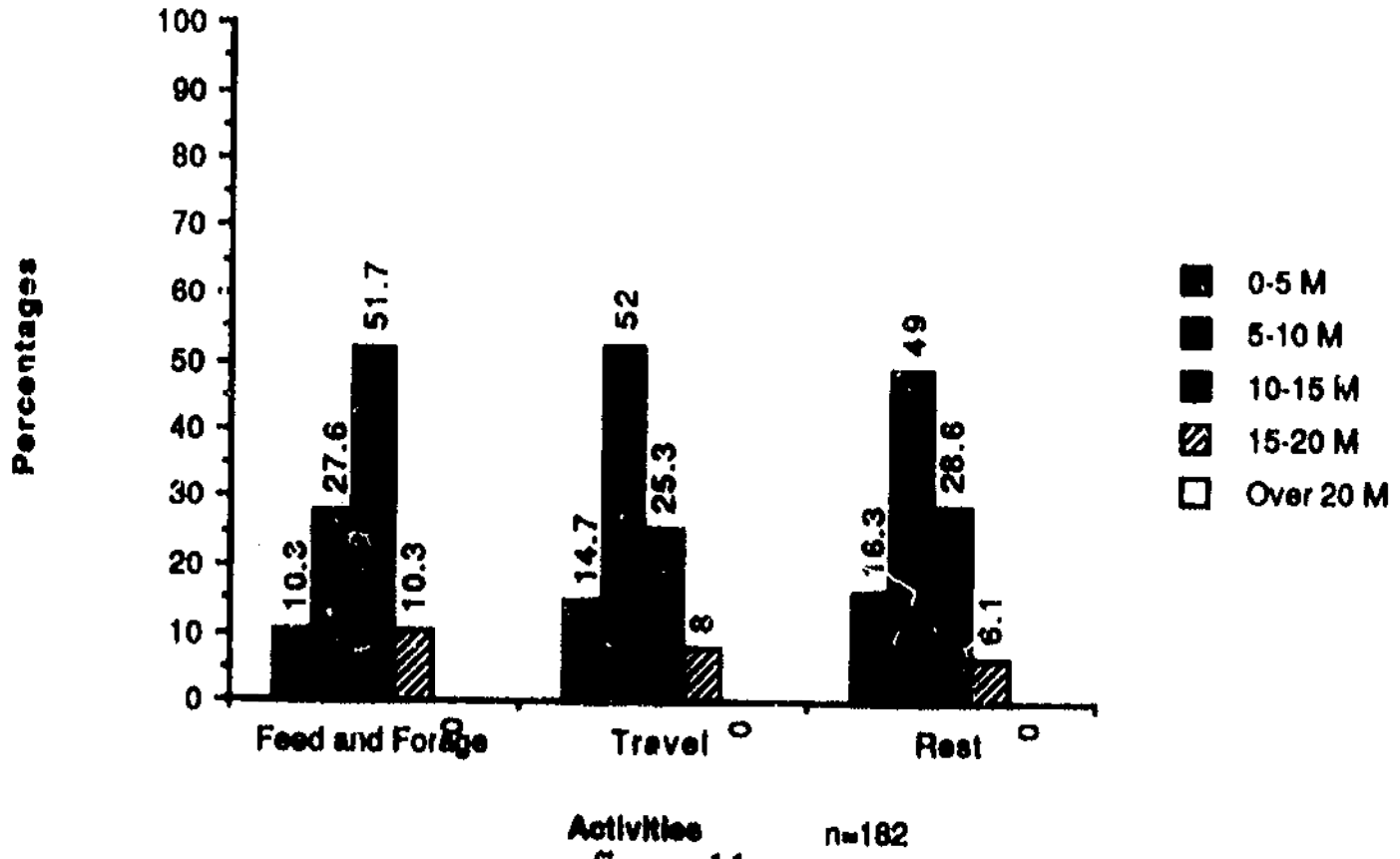


figure 11

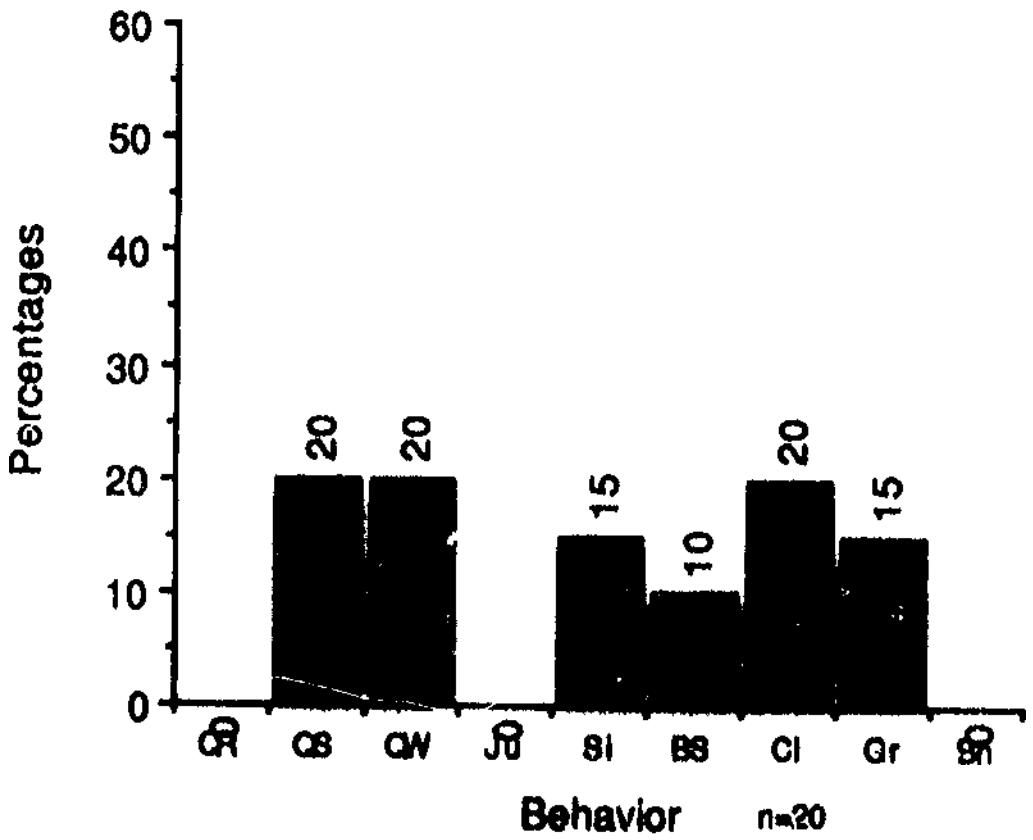


figure 12

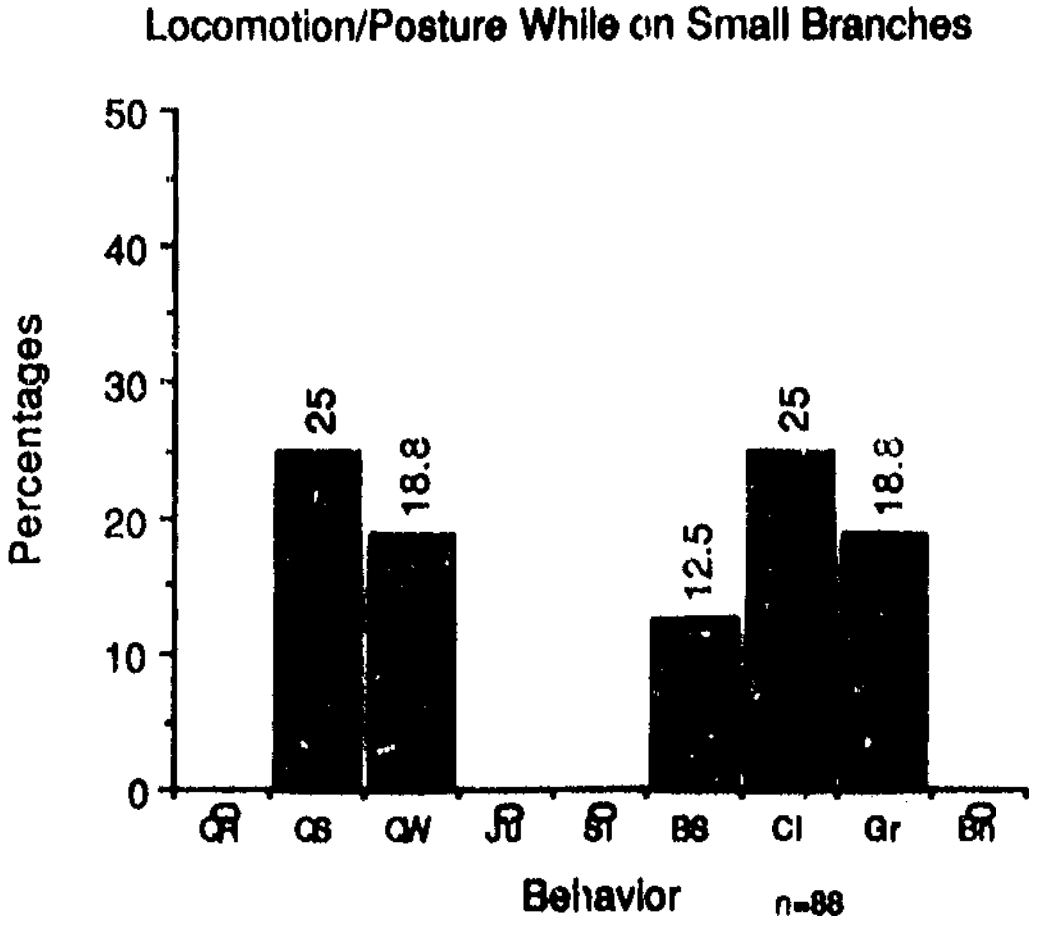


figure 13

These data have some limitations that need to be addressed. The relatively low number of individual activity records severely limits the depth of productive data analysis. It would be of little value to calculate trends in a situation that was only observed five times. Also, the monkeys were not habituated to my presence; they would often run away when they saw me. Because of this, any activity budget calculated from these data would probably not be representative of what normally happens under natural conditions. For example, an activity budget calculated from these data would probably show an inflated percentage of travel bouts. To avoid these problems, in my analysis I focused on broad trends in the postural-locomotor budget within specific activities.

VI. The *Cebus* Foraging Method

A study conducted by Fleagle and Mittermeier (1981) on *Cebus apella* and *Saimiri sciureus* provides data that are comparable to the data I collected while observing *Cebus capucinus*.

Travel:

Cebus capucinus	*Cebus apella* *
n=78	n=363
65% Quadrupedal	85% Quadrupedal
28% Leaping	10% Leaping
4% Climbing	5% Climbing

Feed and Forage:

Cebus capucinus	*Cebus apella* *
n=45	n=438
67% Quadrupedal	85% Quadrupedal
0% Leaping	4% Leaping
33% Climbing	11% Climbing

(* Fleagle and Mittermeier, 1981)

A comparison of data collected on both species reveals a common reliance upon quadrupedal locomotion both in travel and foraging. This reliance represents an adaptive pattern that is found in all four species of the genus *Cebus* (Moynihan, 1976; Fleagle and Mittermeier, 1980). Quadrupedal locomotion is an important element of the distinctive foraging method used by *Cebus spp.*

While traveling, *Cebus spp.* spend a great deal of time inspecting and manipulating their surroundings. They unroll leaves, break branches, inspect knotholes, and look under bark (Defler, 1979; Terborgh, 1983; Oppenheimer, 1968; Fleagle and Mittermeier, 1981). This should not be dismissed as an insignificant manifestation of their "curious nature". This habit represents an adaptive foraging pattern that enables *Cebus* to obtain sufficient animal prey to supplement the frugivorous component of their diet.

Although cebus monkeys are quite omnivorous, they feed almost exclusively on cryptic, stationary prey such as Hymenoptera, snails, or grubs (Terborgh, 1983; Oppenheimer, 1968; Robinson, 1987; Defler, 1979). This tendency is probably not the result of preference, but of opportunity. Terborgh has noticed that *Cebus* does not routinely capture large prey, but when it does it devours it eagerly. He believes that *Cebus* is simply unable to catch larger, mobile prey. Cebus monkeys do not actively hunt or stalk their prey. John Terborgh (1983) compares the opportunistic searching of *Cebus apella* with the active stalking of *Saguinus spp*. He found that the tamarin typically foraged in leaves for non-hidden prey such as Orthoptera and Lepidoptera, while *Cebus apella* spent more time on branches searching for cryptic prey:

	Cebus apella n=5408			*Saguinus imperator* n=682		
	trees, vines	palms	other	trees, vines	palms	other
Leaves	28	17	1.5	86	1.4	0.4
Branches	29	16	5	8	0.2	1.0
Knotholes	2	0.2	0.1	0.6	0.0	0.2

(Numbers reflect percent of time)

Terborgh observed that although the tamarins spent less time foraging than *Cebus apella*, their overall yield was much higher. In addition, Robinson (1987) found that although *Cebus* spends sixty to seventy percent of its time foraging for insects, animal material makes up only twenty percent of the items ingested in its diet. Because of this low success rate, cebus monkeys forage for most of the day (Terborgh,1983). The difference in insect capture success rates reflects the different forage techniques of *Cebus* and *Saguinus*. *Cebus* forage rapidly over the environment and will look anywhere for food (Terborgh, 1983; Oppenheimer, 1968). They need to, as they are among the largest of arboreal insectivorous primates and require relatively large amounts of protein in their diet (Richard, 1985). The omnivory of *Cebus* allows them

to be non-selective in forage sites as they are not especially selective in what food they will eat.

Saguinus, on the other hand, is much smaller than *Cebus* and is able to exploit exudates as a food source as well as insects and fruit (Garber, 1980). They do not need to spend as much time foraging for insects as *Cebus* because their protein requirements are not as great. They can afford to be selective in their forage sites, and take enough time to stalk or hunt their prey. Thus, whereas *Cebus* forage rapidly and are not selective in their foraging sites, *Saguinus* forage more slowly and selectively. Consequently, *Saguinus* has a greater success rate at insect capture.

Several aspects of *Cebus capucinus* ecology combine to constrain its insect diet to hidden prey and keep its forage success rate at low levels. Cebus monkeys usually travel in large, noisy groups of ten or more individuals. These groups, although very active and mobile, remain fairly cohesive through frequent vocalizations. Active, non-cryptic insects are likely to detect the cebus monkeys and avoid them long before the monkeys have a chance to catch them. Some cryptic prey can also detect the *Cebus* group, but their escape strategy relies not on outdistancing predators but rather on avoiding detection. Thus cryptic prey often remain stationary and vunerable to the Cebus monkey forage method of search and inspection. Because of its low success rate, this forage method requires a highly omnivorous diet. The monkeys will eat whatever they can catch.

Due to their particular manner of insect foraging, it is often difficult to distinguish foraging from traveling. A case can be made for the inappropriateness of such a distinction in the first place. Travel is not an end in itself but rather a means to many ends. In the case of *Cebus capucinus*, foraging is similar to traveling because these animals are always on the lookout for forage sites. Thus, travel in *Cebus capucinus* is constrained by their forage method. For cebus monkeys to be able to search while traveling, locomotion must be primarily quadrupedal and devoted mainly to small to medium branches. Approximately 65% of travel was quadrupedal and 88% of this quadrupedal travel was done on small or medium supports (figures 4 and 5).

Not surprisingly, *Cebus capucinus* is morphologically well suited to

this foraging method. They have greater manual dexterity than most new world primates, and possess a semiprehensile tail (Moynihan, 1976). Manual inspection of the habitat is an important component of the foraging method of *Cebus capucinus*, and the high degree of manual dexterity allows easier and more efficient manipulation of the environment (Costello and Fragaszy, 1988). Also, good manual dexterity probably helps *Cebus capucinus* locomote on small branches. As shown in figure 13, sixty-nine percent of locomotion on small branches is done either quadrupedally or by climbing. Both of these methods require complex movements of the hands. The semiprehensile tail is often used for anchoring or balancing on a branch. This frees the hands of the monkey for more efficient manual inspection of its surroundings.

VII. Conclusions

Cebus capucinus, like all cebus monkeys, is highly quadrupedal and avoids vertical and large supports. Jumping is done almost exclusively on small, flexible branches but is not the dominant form of locomotion for this primate. The highly quadrupedal nature of travel is due to the fact that *Cebus capucinus* forages while traveling, and opportunistically and destructively searches for insect prey. This method provides the most opportunities for invertebrate foraging. The diet of *Cebus capucinus* is very omnivorous, although insect capture is restricted to cryptic, stationary prey. This restriction is probably not one of choice, but results instead from a limited ability to capture mobile prey.

Appendix 1

Definitions

Activities:

Travel - Locomotor behavior whose sole purpose is spatial displacement.

Feed - A food item has been selected and manipulated. Normally a postural behavior.

Forage - Actively searching or collecting food items. Much slower and more deliberate than travel; Postural or locomotor behavior.

Rest - Stationary and very little movement for extended periods of time. Postural behavior.

Groom - Extended tactile contact in a social setting. Postural.

Locomotor or Postural Behaviors:

Bound - Front feet operate as one unit; all feet may be in air at given moment.

Quadrupedal Stand - No directional movement; weight borne by all feet.

Quadrupedal Walk - At least one front foot and one back foot on ground at any given time.

Quadrupedal Run - Same as QW except much faster.

Jump - The act of moving from one support to another when supports are not touching. Animal is briefly in midair.

Sit - The weight of the animal is resting on its body, not its appendages.

Climb - The act of travelling while weight is supported by many branches. Usually associated with terminal branches.

Grasp - Like climbing only no directional movement.

Bipedal Stand - Weight borne on two back feet.

Support Characteristics:

Small - The animal can completely close its fist around the perimeter of the support.

Medium - The animal cannot close its fist around the support, but can encircle its arms around it.

Large - The animal cannot encircle its arms around the perimeter of the support.

Horizontal - The support is at a 0 to 15 degree deviation from precise horizontal.

Oblique - 15 to 75 degrees from precise horizontal.

Vertical - 0 to 15 degrees from precise vertical.

Terminal - The support is found among a large number of small branches of various orientations. One branch does not bear entire weight of animal.

Flexible - The support bends under the weight of the animal.

Non flexible - The support does not bend under the weight of the animal.

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