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The Howling Monkeys, Genus *Alouatta*

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I. DESCRIPTION OF THE SPECIES

The genus *Alouatta*, subfamily Alouattinae, includes six currently recognized species: *A. palliata, pigra, seniculus, belzebul, fusca* and *caraya* (see Hershkovitz, 1972) (Figs. 1-5), but several additional species may exist (see Mittermeier *et al.*, this volume). The howling monkeys are the second heaviest of the New World monkeys, trailing only *Brachyteles* in size (Zingeser, 1973), with adult males averaging 7 kg and adult females 6 kg. Napier and Napier (1967) describe the genus as follows:

"In all species, face is bare and deeply pigmented. Nostrils close together. Swelling beneath the chin, accommodating the specialized larynx, is outlined by a beard in the male; it is much more prominent in the male than in the female. The head is set low on the shoulders, giving a hunched appearance. The tail is very mobile; the distal quarter of the underside bears naked skin with papillary ridges. Arms and legs subequal. Big toe divergent and opposable. HAND: Digital formula: 3.4.2.5.1 or 3=4.2.5.1. Genitalia of both sexes are prominent. MAMMAE: 2 nipples situated near the axilla."

The two dominating external morphological features are the prehensile tail and the enlarged hyoid/larynx complex. Tail length is approximately that of head+body (Napier and Napier, 1967), and the naked portion is equipped with unusually extensive sensory innervation. The prehensile tail functions almost exclusively as a support device during locomotion and foraging. The Atelinae also possess this prehensile tail but are even more adept with it. The enlarged hyoid is a good example of a behavioral feature, the "howling" which characterizes the genus, generating a major morphological complex. It is probable that, once the elaboration of the hyoid/larynx complex had passed a certain point, the evolutionary possibilities for the taxon were sharply constrained.

Fig. 1 – *Alouatta seniculus* at HMG, Venezuela (photos by Andrew Young).

Fig. 2 – *Alouatta belzebul belzebul*. (photo by Russell A. Mittermeier).

Fig. 3 – *Alouatta fusca* (photo by Adelmar F. Coimbra-Filho).

All species show sexual dimorphism in weight. Thorington *et al.* (1979) estimate that adult female *caraya* weigh about 68% of adult males; likewise, adult female *seniculus* weigh about 69% of adult males. Adult female *palliata* are comparatively heavier, being 84% of adult male weight. Hyoids are larger in males than in females and their howling is softer (see Sekulic, 1983a). *A. caraya* and *A. fusca clamitans* are sexually dichromatic. Body size dimorphism and pelage color differences are discussed by Thorington *et al.* (1979, 1984).

Distribution

Alouatta is the most widely distributed genus of the New World monkeys, ranging from about 18°N in the Mexican State of Veracruz (Estrada and Coates-Estrada, 1984; Hall and Kelson, 1959, Map 167; Merriam, 1902) and 20°N in the Yucatan Peninsula (Smith, 1970) to about 27°S in the Argentinian State of Corrientes (Cabrera, 1939; Malinow, 1968) and perhaps to 28°S in the State of Rio Grande do Sul, Brazil (Cabrera, 1958). *Ateles* extends a little further north in Mexico, and *Aotus* and *Cebus* extend about as far south in Argentina, but these genera do not have the full extent of the latitudinal range of *Alouatta*. The howlers occupy forest regions throughout most of the area between its latitudinal limits, east of the Andes. In addition, they are found west of the Andes, as far south as the Tumbes Department in northern Peru (see Grimwood, 1965-1967, Appendix I). Hernandez-Camacho and Cooper (1976) report *seniculus* up to 3200 m in the central Andes of Colombia. *A. seniculus insulans* and *Cebus albifrons trinitatis* (Hill, 1960, 1962) are the only non-human primates to be found on Trinidad. We thus have the phenomenon of a large, lethargic, noisy primate, frequently hunted for food, which still maintains an enormous distribution in the Western Hemisphere. Elliot (1913) may describe the genus in derogatory terms ("slow... sullen... untamable... Their intelligence is of a

Fig. 4 – *Alouatta fusca* juvenile (photo by Russell A. Mittermeier).

Fig. 5 – *Alouatta caraya* female (photo by Adelmar F. Coimbra-Filho).

very low order, and altogether the animals of this genus are among the least attractive of the Primates."), but clearly *Alouatta* has been successful in an adaptive sense.

Alouatta palliata is the Central American howler, making a largely undetermined contact with *A. seniculus* along a line separating off western Colombia, Ecuador, and perhaps Peru, starting from the north in the Colombian state of Cordoba (Hernandez-Camacho and Cooper, 1976). An interesting, but still unresolved, taxonomic problem with behavioral implications, is Smith's (1970) proposal of the species distinctiveness of the taxon *pigra*, essentially of the Yucatan Peninsula and contiguous rainforest, from *palliata*. *Pigra* can supposedly be found sympatrically with *palliata mexicana*, and is clearly morphologically separated from it, and would be the type found at the important primate site of Tikal in lowland Guatemala. Horwich (1983b) presents behavioral and ontogenic data supporting Smith's (1970) suggestion. *A. seniculus* is the species with the widest distribution, being essentially that of northern South America including the Rio Orinoco basin, north of the Amazon River basin and south of the Amazon, west of the lower Rio Madeira. Heltne *et al.* (1975) place the boundaries between *caraya* and *seniculus* in Bolivia, and Crespo (1954) place those between *caraya* and *guariba (= fusca)* in the northeastern Argentinian territory of Missiones. *A. fusca* is the brown howler of the southeastern coastal region of Brazil; it is possibly divided into two subspecies, *fusca* (lacking sexual dimorphism) and *clamitans* (sexually dimorphic) (Kinzey, 1982), although further studies are needed (see Mittermeier *et al.*, 1982). *A. fusca* is suffering from habitat destruction within its range and populations are declining (Coimbra-Filho, 1972; Silva, 1981) and, if valid, the northern subspecies, *fusca*, is severely threatened with extinction (Mittermeier *et al.*, 1982). *A. belzebul* is the species south of the Amazon, east of the Rio Madeira. A subspecies of *belzebul*, *A. b. ululata*, is found on the northeastern coast below the mouth of the Amazon (Hill, 1962, Map I). In general, determination of boundaries between *belzebul*, *ululata*, *seniculus*, *caraya* and *fusca* require further studies. Particularly interesting behaviorally among these taxa may be *caraya* and the *clamitans* subspecies of *fusca* (Kinzey, 1982; pers. comm.), both of which are distinguished by color as well as size sexual dimorphism in adults.

II. PREVIOUS STUDIES

The number of studies which include significant information on howling monkey behavior must now be roughly similar to that for the African savanna baboons. It is impossible for us to comment on all these studies or to indicate the total number of ongoing projects, and we are painfully aware that we will undoubtedly omit or slight a number of important papers, for which we offer our apologies both to the authors and to our readers.

Captive Studies

The high frequency of mortality in captivity has produced the paradox that while *Alouatta* is the most frequently studied New World primate in the field, there have been very few observational studies on captive monkeys. Some information can be found almost incidentally, however, in reports and books written by zoo curators. We give below some of the most important colonies together with some indications of the chief significance of the reports from them.

(1) *Verlhiac Primate Center, France.* The colony of *seniculus* and *caraya* maintained at this center should eventually provide some of our most detailed information concerning maturation of both behavioral and physical features. The director, Scott Lindbergh (1976), has noted a tendency of same-sex animals to form cliques and fight against pariahs of the same sex; this kind of exclusionary behavior has also been noted from a number of other studies, such as at Gould's Monkey Jungle and the Riverbanks Zoo colonies. Lindbergh carried out a reintroduction program for captive bred *caraya* in the Brasília National Park (Lindbergh and Santini, 1984).[1]

(2) *Gould's Monkey Jungle, Miami, Florida, U.S.A.* Monkey Jungle includes an approximately 1.6 ha imitation of a South American rain forest based in a natural patch of subtropical Florida jungle, which has been supplemented by South American plants and an artificial sprinkling system (DuMond, 1967). A number of excellent primate studies have been based on some of the species bred there, which included (at the time of Fontaine and Hench, 1982) *Saimiri*, *Cacajao calvus*, two kinds of tamarins, and *Alouatta seniculus*. DuMond's (1967) report emphasizes the importance of the hostility of females in a group to females attempting to join that group and that adult females can adopt or facilitate the incorporation of juveniles into a group. In addition, he observed the immediate solicitation of the adult males by newly introduced adult females and the aggressive chasing of howler monkeys by two *Cacajao* monkeys.

(3) *Riverbanks Zoological Park, Columbia, South Carolina, U.S.A.* The very successful breeding colony of *A. caraya* at Riverbanks has produced useful data on the maintenance, maturation and behavior of this species (Shoemaker, 1978, 1979, 1982; Benton, 1976). Anne Gunter and Melvin Neville conducted three summers of studies on the allogrooming and proximity relations within social groups of these confined

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[1] Editors' note: this colony has now been disbanded.

caraya (Neville, 1979, unpubl. manuscript; Neville and Gunter, 1979), demonstrating patterns of affinities which determine the social structure of the group. Particularly important are the ties binding adult females together and the attraction of juvenile and adult females toward young infants. It is interesting to note that male-male hostility cropped up between two adults who had been together since at least juvenile age, and that there were several incidences of aggression toward pariah or just-introduced females; even the introduction of a female who had previously been in one group led to attacks upon her. Jones (1983a) has also studied dominance relations, grooming, copulation patterns and displays in these animals.

Naturalistic Studies

We indicate below some of the major studies, organized by study site and species, with a few abbreviations which will be used throughout the paper. Many more observations can be encountered in reports on sympatric species and even in the accounts of explorers.

(1) *Alouatta pigra*

The principal studies on *A. pigra* have been in the lowland rain forest site of Tikal, Peten Province, Guatemala. The area is protected because of important Mayan archaeological ruins. The park is a square of about 37,000 ha with a climax lowland seasonal dry tropical rain forest cover. Coelho *et al.* (1976a, 1976b, 1977) reported on an attempt to relate resource availability to energy budgets of the two sympatric primates, *Ateles geoffroyi* and the howler monkeys, and came to the controversial conclusion that food was in excess. Schlichte (1978) reported on the same population one year after Coelho *et al.* had studied them. Cant (1977) has contributed further data on the howlers while studying the spider monkeys. Inge Bolin has completed a study on *pigra* at Tikal and around Bermudian landing in Belize. She provides (1981, pers. comm.) importantly different data in that she saw a high percentage of monogamous social groups and unusually high frequencies of male parental care. Bolin points to the adaptability of the monkeys. The Belize site was very different from Tikal: gallery forests along the Belize river, isolated fig trees surrounded by grassland, and dry forest interrupted by plantations. Horwich (1983a) and Horwich and Gebhard (1983) report on short term studies of roaring rhythms and breeding behavior at Bolin's study site. Horwich (1983b) examined group sizes of *pigra*, and found them to be consistently smaller than those of *palliata*.

(2) *Alouatta palliata*

This is the most studied species, and the Smithsonian Research Station of Barro Colorado Island, former Panama Canal Zone, is the most important site. However, there are now numerous studies from other locations which are demonstrating interesting variability within the species. The following principal sites are given in approximate order north to south:

(a) *Los Tuxtlas. Veracruz. Mexico.* The Autonomous National University of Mexico maintains this 700 ha biological station in southeastern Veracruz, by the Gulf of Mexico. Estrada (1983) and Estrada and Coates-Estrada (1983) report on the site and the howlers found there. Los Tuxtlas is basically a tall evergreen forest in a hot humid climate, with mean annual rainfall of 4953 mm and a short, relatively dry period from March to May (Estrada, 1982). Estrada (1982) reports on group sizes, composition and densities of *palliata*. Long term studies of their feeding behavior, including comparisons with sympatric fruit bats, *Artibeus*, and other arboreal vertebrates, have been carried out since 1977 (Estrada *et al.*, 1977, 1984; Estrada and Trejo, 1978; Estrada, 1982, 1984; Estrada and Coates-Estrada, 1984a, 1985).

(b) *Finca La Pacifica (FLP), Guanacaste Province, Costa Rica.* This site, where studies were initiated by Kenneth Glander, has deciduous and riparian forests, falling into Holdridge's Lowland Tropical Dry Forest life zone. The ranch is 45 m above sea level. The average annual rainfall is approximately 1746 mm. The wet season is from April to October, with approximately 1691 mm of rainfall. Both forest types, covering about 4.4 km^2, are seasonal, with flowering and fruiting occuring mainly during the dry season (November to April). Glander worked on both sides of the Río Corobici, in a forest strip bounded by fields. The forests are lower (average tree height of 11 m in the riparian forest and eight meters in the upland forest) than those of Barro Colorado Island. *A. palliata* is the only monkey on the ranch, although *Ateles* also occurs in the region. The site is particularly valuable because the monkeys were captured and marked (see Scott *et al.*, 1976a). Glander also mapped all trees over four meters in height within the range of his main study group. Phenological studies and estimates of flower and fruit productivity were made on selected trees. Glander's (1975a, 1975b, 1977, 1978a, 1978b, 1979, 1981; Rockwood and Glander, 1979) speculations concerning the relationship between plant secondary compounds and the howler's folivorous diet produce a picture of sharply limited food supplies (see also Milton, 1980), very different from the conclusions of Coelho *et al.* (1976a, 1976b, 1977) at Tikal. The long term studies have also produced much-needed demographic data (Glander, 1980). Margaret Clarke (1981, 1982, 1983) conducted studies of social behavior and infant development. Her data correspond with those of Rudran (1979) and Crockett and Sekulic (1984) for *seniculus* in documenting infanticide and the migration of immatures. Both sexes may leave their natal groups as juveniles or subadults (15-40 months old). The females join a group as juveniles or subadults, whereas the males enter groups at about 40-60 months. Clarke also made observations on infant-nonmother interactions and the role of adult males. Clara Jones (1978, 1979, 1980a, 1982) reports on grooming patterns, and noted the importance of age and coalitions in dominance ranking. Her studies also included socioecological aspects of estrus, mating patterns, weaning and dispersal (1980b, 1985), and feeding behavior (1983b).

(c) *Santa Rosa National Park, Guanacaste Province, Costa Rica.* This is a tropical dry forest on the Pacific coast of northwestern Costa Rica. The park is 10.000 ha, with elevation ranging from sea level to over 350 m accompanied by considerable variation in terrain. Annual rainfall is 1750 mm, almost all occuring during the rainy season from June to November. The forest varies from five meters to 40 m in height and (roughly in correlation) from predominantly deciduous to evergreen. The primate species studied by Curtis Freese (1976) were *A. palliata*, *Ateles geoffroyi* and *Cebus capucinus;* the habitat variation in a protected park and the presence of three cebid species was the focus for Freese's analysis of habitat usage. The least abundant of the species was *Alouatta*, restricted to the evergreen forest.

(d) *Barro Colorado Island (BCI), Gatun Lake, Panama Canal, Panama.* This is the first and most important of the howler study sites. The island was formed in 1914 when Gatun Lake was filled after the damming of the Río Chagres during the construction of the Panama Canal. In 1923 the island was made a protected reservation of the Institute for Research in Tropical America, and in 1946 the island came under the administration of the Smithsonian Institution (Carpenter, 1965). Clarence Carpenter initiated work in December of 1931, and his original monograph (1934) remains the most important single report on *Alouatta* behavior: in a real sense, it was the "type" report for the description of not only the species but the genus. However, one of the most exciting aspects of the recent research is in pointing to the variability occurring within the genus.

The island's 1554 ha consists of a hilly terrain ranging from 26 m to 138 m above sea level. Carpenter (1934) describes the habitat as tropical rain forest with some trees over 38 m in height; about two-thirds of the island was primary rain forest at the time of his early study, with the secondary forest areas, remnants of agricultural activity prior to 1914, gradually converting to similar forest. The temperature range is about 19.4 to 37.8°C with humidity varying between 75% and 90%. The rainy season is from May to November. Other primate species which exist on the island include *Cebus capucinus, Aotus* sp. and *Saguinus geoffroyi. Ateles geoffroyi* disappeared from the island, but was reintroduced in 1959-1961.

As an indication of the productivity of this site, Table I reports published field studies resulting from BCI howler studies.

(e) *Hacienda Barqueta (HBC), Chiriqui Province, Panama.* The study site of John and Janice Baldwin was a 20 ha section of a 400 ha forest extending along the Pacific coast of southwestern Panama. The forest was at sea level, with the majority of trees 9-17 m tall with some emergents to 26 m. Their intensive study occurred during the dry season and involved *Alouatta palliata, Cebus capucinus,* and *Saimiri oerstedi* (Baldwin and Baldwin, 1972a, 1972b, 1973, 1974, 1976, 1978). The forest was destroyed a year after the study. Many of the interesting phenomena they observed, such as the extremely high howler density, are probably due to the crowding of the species within a diminishing forest; this naturally produced a situation of considerable interest in terms of stress on behavior patterns. It is a great pity that the reduced forest could not have been maintained in order to study equilibration processes.

(3) *Alouatta seniculus*

(a) *Bush Bush Island, Nariva Swamp, Trinidad.* Melvin Neville (1972a, 1972b, 1976a, 1976b) worked one summer in this forest which spreads out on and from an irregular, slightly-raised island with elevations under 4.5 m above the water level of the surrounding swamp. The heterogeneous forest is evergreen seasonal; temperatures are warm and humidity is high with an annual rainfall of about 2500 mm. *Cebus albifrons* is also present on Trinidad.

(b) *Hato Masaguaral (HMG), Guárico State, Venezuela.* This cattle ranch in the *llanos* area of Venezuela, north of the Orinoco, is essentially without terrain relief. There is strong seasonal variation in rainfall, temperature, and foliage; annual rainfall is very variable but averages 1600 mm (T. Blohm, pers. comm.). Two general areas are present: a riverine forest by the Río Guárico and Caracol stream with trees up to about 23 m (Oppenheimer and Oppenheimer, 1973) containing both *Alouatta* and *Cebus nigrivittatus,* and a more discontinuous forest with many thorny sections and residual fire effects in the working part of the ranch with only *Alouatta*. Neville (1972a, 1972b, 1976a, 1976b) reported on the basic behavior and demography resulting from census

TABLE I

Major published field studies on *Alouatta palliata* at Barro Colorado Island (BCI), Panama, arranged chronologically by date of field work and indicating the focus of the studies. [a]

Investigators	Field period	Purpose or focus	Chief reports
C. R. Carpenter	Dec 1931 – May 1932, scattered dates to Jan 1935	Basic behavior and ecology; censuses	Carpenter (1934/1964, 1953/1964, 1962/1964, 1965, 1974)
N. Collias & C. W. Southwick	Jan 1951 – Apr 1951	Census; behavior	Collias & Southwick (1952), Southwick (1955, 1962, 1969)
S. A. Altmann	Oct 1955 – Dec 1955	Social communication; ontogeny of behavior	Altmann (1959, 1966, 1968)
C. R. Carpenter *et al.*	Jun 1959 – Aug 1959	Census; movie: "Howler monkeys of Barro Colorado"	Carpenter (1960, 1962/1964, 1965); Southwick (1962)
I. S. Bernstein	Jan 1962 – Feb 1962	Behavior; activity frequencies	Bernstein (1964)
D. J. Chivers	Jun 1967 – Aug 1967	Howling behavior	Chivers (1969)
C. M. Hladik & A. Hladik	Nov 1966 – Jan 1968	Food sources of primates; primate effects on plants	Hladik (1972), Hladik & Hladik (1969), Hladik *et al.* (1971)
C. C. Smith	Sept 1967 – Jul 1968	Feeding and social structure	Smith (1977)
A. Richard	Jun 1968 – Aug 1968	Comparison of activity patterns of *Ateles* and *Alouatta*	Richard (1970)
R. A. Mittermeier	Sep 1970 – Dec 1970	Group activity and composition; census	Mittermeier (1973)
K. Milton *et al.*	Mar 1974 onwards, with scattered dates	Behavior; interaction of plants and monkeys; basal metabolism and physiology; census	Milton (1975, 1977, 1978, 1979, 1980, 1981, 1982), Nagy & Milton (1979a, 1979b), Milton *et al.* (1979, 1980)
R. W. Thorington, Jr., J. F. Eisenberg, J. W. Froehlich *et al.* [b]	Intermittently from 1964 onwards	Ecology and behavior; demographics (BCI fauna in general	Eisenberg & Thorington (1973), Scott *et al.* (1976a), Heltne *et al.* (1976), Otis *et al.* (1981), Froehlich *et al.* (1981), Froehlich & Thorington (1982a, 1982b).
F. C. Mendel	Jun 1974 – Sep 1974	Relation of locomotor anatomy to habitat	Mendel (1975, 1976)
O. P. Young	Jan 1974 – Jun 1974 Jan 1975 – Mar 1975	Behavioral observations	Young (1981a, 1981b, 1982a, 1982b)
M. Leighton & D. R. Leighton	Aug 1976 – Sep 1976	Feeding group sizes	Leighton & Leighton (1982)

(cont.)

Table I (Cont.)

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[a] Many other discussions on the island's howler population can be found in the writings of the various scientists who have worked on BCI, e. g., the general mammalian descriptions by Enders (1935), Chapman's incidental publications (1929a, 1929b, 1937, 1938), Oppenheimer's (1968) discussion of the relations between *Cebus capucinus* and *Alouatta*, and the comparative communication study by Moynihan (1967, see also 1976) based upon his many years as director and scientist on BCI.

[b] The variety and the promise of this work, which is not restricted to *Alouatta* nor to the primates, is immense. Space prohibits the listing of all the investigators of *Alouatta* behavior on BCI who have worked in connection with this program; at present, under the Smithsonian Environmental Sciences Program. A number of studies have compared BCI howlers with those of other localities in Panama or Costa Rica, e. g., Heltne *et al.* (1976) made comparisons with Fincas Taboga and La Pacifica in Guanacaste Province, Costa Rica; Milton & Mittermeier (1977) studied *Alouatta* and *Cebus capucinus* on Coiba Island, Panama; and Carpenter, in the 1930s, worked in both the Coto region of northwestern Panama and on Coiba Island.

work in 1969-1970 and 1972. The Smithsonian Institution in 1976 made HMG and Guatopo National Park the principal foci of their long-term study of the fauna and flora of northern Venezuela. An important part of this work was on the HMG red howler monkey. Mack (1979) obtained much-needed data on the ontogeny of infants. Rudran (1979) established that there was a high rate of immigration and emigration of juveniles and adult females as well as adult males into and from groups; observed infanticide by males taking over groups (which relates howlers to the pattern shown by many Old World monkeys), and confirmed the suspicions of Klein (1974) that this apparently pacific genus actually has much intermale physical aggression. Thorington, Rudran and Mack (1979) reported on the sexual dimorphism of *seniculus*, which begins earlier than *palliata* but then involves a curious imitation of the male genitalia by females. They also report on the capturing and marking success of the Smithsonian project on HMG. Studies of *A. seniculus* at HMG by Ranka Sekulic and Carolyn Crockett during the period 1979-1981 have provided insights regarding the function of roaring and its relation to group spacing and reproductive behavior (Sekulic, 1981, 1982a, 1982d, 1983a), feeding and ranging behavior (Sekulic, 1982b, 1982c), female behavior and emigration (Sekulic, 1982c, 1983b; Crockett, 1984), infanticide (Sekulic, 1982e; Crockett and Sekulic, 1984), gestation length and birth (Crockett and Sekulic, 1982; Sekulic, 1982a) and throat-rubbing behavior (Sekulic and Eisenberg, 1983).

The fauna on HMG represents a relict population in the sense that it and its habitat have been protected by the owner, Tomas Blohm. Private owners such as Mr. Blohm, Werner Hagnauer of FLP in Costa Rica, and Feliciano Abdalla in Brazil (see *A. fusca*) have performed a vital service in maintaining unofficial reserves and encouraging studies on their land.

(c) *Hato "El Frio", Apure State, Venezuela.* This ranch is located in the *llanos* south of the Río Apure, a tributary of the Orinoco. The forested areas are classified as semi-deciduous seasonal forests (Braza *et al.*, 1981). Francisco Braza and co-workers (Braza, 1978; Braza *et al.*, 1981, 1983) carried out studies of the reproduction, behavior and feeding habits of *seniculus* in a 30.000 ha area. Their behavior study provided the most complete ethogram yet made for this genus. Braza (1978) found seasonal variation in group size which he relates to a fluctuation in sexual attraction. Braza *et al.* (1983) analyzed their diet, in large part based on the contents of 61 digestive tracts and 380 feces samples.

(d) *La Macarena National Park, Meta Province, Colombia.* This 630,000 ha park ranges from the flood plains of the lowland to elevations over 2500 m (see Struhsaker, 1976). Lewis and Dorothy Klein worked in or near the flood plains in forests susceptible to occasional inundation. Their site was about 800 ha of continuous tropical rain forest on the northern bank of the Río Guayabero. The three dominant forest communities (of a total of eight) had tree elevations of 18 to 37 m with emergents to over 50 m. While the Kleins concentrated on *Ateles*, their careful work also provided data on behavior and habitat usage of *seniculus* (Klein and Klein, 1975, 1976). Thomas Struhsaker's (1974) census work in the park was near Cabana El Duda at the junction of the Duda and Guayabero rivers at an elevation of 400 m. Struhsaker (1974, 1976) reported that the Kleins' study site was no longer included within the park and was being destoyed by agricultural development, and that agricultural encroachment in general was a severe threat.

(e) *Río Peneya (of the Río Caquetá) and Río Putumayo, Colombia.* This is not a site but rather a general area. The Japanese Primate Centre sponsored some major investigations of primate densities and ecology in the Amazonian regions in Colombia (and into Brazil, including the Rio Negro). English language papers (Izawa, 1975, 1976; Tokuda, 1968) report very usefully on group size, composition, and ecology of *seniculus* as well as of other sympatric primates. Izawa felt that *seniculus* was mainly a one-male group species in his area.

(f) *Finca Merenberg, Reserva La Plata, southwestern Colombia.* Gaulin (1977) and Gaulin and Gaulin (1982) carried out a 10-month study of *seniculus* in a cloud forest (2300 m elevation) at Finca Merenberg, 50 km west of La Plata in southwestern Colombia, on the eastern slope of the Central Cordillera of the Andes. Their study provides information on activity budgets, diet and ranging behavior.

(g) *El Tuparro National Park, eastern Colombia.* While studying *Cebus albifrons* and *C. apella* in forest patches and gallery forest in the llanos of this 548,000 ha National Park, Defler (1981) obtained data on densities and home range size of the sympatric populations of *seniculus.*

(4) *Alouatta caraya*

The first important study of this species resulted from the Oregon Regional Primate Research Center's expedition in 1964 to collect monkeys on the islands of Tragadero Sur, Tragadero Norte, and Isla Ulfeldt in the Río Paraná, northern Argentina (Malinow, 1968). Isla Ulfeldt, suggested as being typical, was surveyed over 413 ha. The island interiors were *pampa* or grassland; howlers ocurred in a narrow fringe of semi-evergreen, seasonal tropical rain forest. The dry season was September through February. The expedition was principally for the collection of material for atherosclerotic studies, but the data included many disease parameters, morphological and physiological characteristics and data on population structure and group size (Pope, 1966, 1968). The resident monkey populations were annihilated, which precludes building directly on the population data as such. However, the study of the dynamics of repopulation of the island could be very interesting, with the idea that the 1974 population was at equilibrium.

In 1983, Lindbergh and Santini (1984) carried out a study of the feeding and ranging behavior and the fate of two *A. caraya* groups, bred in the Verlhiac Primate Center (see Lindbergh, 1976) in France and introduced into the Brasília National Park, an area of *cerrado* forest *(cerradão)* and gallery forest in central Brazil.

The Argentinian Primate Center (CAPRIM) has been carrying out studies of *caraya* in gallery forest and forest patches in the Provinces of Formosa, Corrientes, Missiones and Chaco since, 1980. Colillas and Coppo (1978) report on preliminary studies regarding habitat preference, group sizes and breeding seasonality, and Thorington *et al.* (1984) on a census of a population of the Río Paraguay, near Puerto Bermejo.

(5) *Alouatta fusca*

The only published field studies of *A. fusca* are those of Chitolina and Sander (1981) in the Municipality of Sapiranga, near Porto Alegre in the state of Rio Grande do Sul, Brazil, with limited information on feeding behavior, Kuhlmann (1975) who analysed the contents of feces collected during 44 months in a secondary forest in the Parque Estadual das Fontes do Ipiranga in the municipality of São Paulo, Brazil (see also Carvalho, 1975), and Silva (1981), who carried out a survey of *fusca* in the Cantareira Reserve in the state of São Paulo. Silva presents information on the habitats they occupy, population characteristics, sleeping trees, feeding and the conservation status of the species.

Andrew Young (1983) carried out a two month study comparing the ecology, social organization and behavior of *fusca* with the sympatric muriqui, *Brachyteles arachnoides*, in the Caratinga Biological Station, of 880 ha, in the state of Minas Gerais, Brazil. The reserve is administered by the Brazilian Foundation for Nature Conservation (FBCN) and is one of the last remaining tracts of Atlantic coastal forest in Minas Gerais, in the privately owned Fazenda Montes Claros of Feliciano Miguel Abdalla. Further studies of *A. fusca* at Caratinga have been carried out by Sergio Mendes (1985) on the population size, behavior and ecology, and Daniel Louzada (in prep.) studied parasites, cytogenetics and morphometry in captured animals.

(6) *Alouatta belzebul*

The least studied of the *Alouatta* species, published information is limited to some data on habitat preference, population density and group sizes of the subspecies *nigerrima* in the Tapajós National Park of 1,200,000 ha in Brazilian Amazônia (Ayres and Milton, 1981; Branch, 1983). Cibele Bonvincino (in prep.) started a study of the feeding ecology of *belzebul* in a small patch of Atlantic forest in the state of Paraiba in northeast Brazil in 1983.

(7) General surveys and studies of primate communities

A number of studies have furnished data about the location, abundance, ecology and group composition of *Alouatta* species as part of general primate surveys. Notable are the surveys sponsored by the Pan American Health Organization which resulted in the following publications: Struhsaker (1974, 1976) on La Macarena; Struhsaker *et al.* (1974), Scott *et al.* (1976b) and Bernstein *et al.* (1976) in northern Colombia; Neville (1975), Neville *et al.* (1976), Freese (1975) and Freese *et al.* (1976, 1982) in Amazonian Peru; Muckenhirn *et al.* (1975) in Guyana; and Heltne *et al.* (1975) and Freese *et al.* (1982) in Bolivia.

In addition, Mittermeier (1977), Fleagle and Mittermeier (1980), and Mittermeier and van Roosmalen (1981, 1982) studied habitat utilization, diet, locomotion and postures, and the conservation of primates in Suriname. Izawa and co-workers surveyed primate populations in the Pando region of Bolivia, providing information on distributions and habitat preferences (Izawa and Bejarano, 1981; Izawa and Yoneda, 1981). Terborgh (1983) and colleagues are studying the ecology of sympatric primates in the Manu National Park, Peru. Since 1983, Rylands has been studying primate survival in forest fragments in central Amazonia in Brazil; part of the Minimum Critical Size of Ecosystems Project of the World Wildlife Fund and the Instituto Nacional de Pesquisas da Amazônia, Manaus (Rylands and Keuroghlian, in prep., Neves and Rylands, in prep.).

III. HABITAT

Alouatta is arboreal, using all forest levels, but most frequently the upper canopy and emergents. Mendel (1976) found *palliata* in the upper third of the canopy during 75% of his observations on BCI. Tokuda (1968), working on the Río Putumayo, Peru, reported that *seniculus* was found above 20 m. Freese (1977), working in Peru and Bolivia, reported that *Alouatta* inhabited the forest canopy, between 10 and 25+ m. He also found that *Ateles* occupied a similar niche and suggested that these two monkeys are separated by locomotor differences. *A. seniculus* uses mainly a slow quadrupedal progression, whereas *Ateles* uses mainly armswinging, brachiation and climbing (Fleagle and Mittermeier, 1980; see section on Locomotor and Postural Behavior). However, Mittermeier and van Roosmalen (1981), studying the synecology of eight Suriname primates, recorded *seniculus* in the middle and upper canopy and emergent layer in 81% of their 85 sightings. *Ateles* and *Chiropotes* were recorded more frequently in the upper canopy (55% and 52% of 27 and 142 sightings, respectively, compared to 28% for *seniculus*). *Cebus nigrivittatus* and *C. apella* were also frequently found in the middle canopy, but used the lower levels of the forest more than *seniculus*.

Fleagle and Mittermeier (1980) found that *seniculus* spent more than 50% of their travel time on arboreal supports larger than 10 cm, and about 50% of their feeding time on branches greater than 2 cm, but less than 10 cm.

Although primarily arboreal, howling monkeys can, and do, descend to the ground (Carpenter, 1934; Racenis, 1951; Izawa, 1975; Neville, 1972a; Silva, 1981; Sekulic, 1982b, 1982c), where they move with stealth, but can easily outrun a human (Glander, pers. obs.). In areas of discontinuous forest they move across large open spaces between trees (up to a kilometer or more in the sparsely forested Apure State, Venezuela; J. Ojasti, cited in Neville, 1972a). In Costa Rica, *palliata* routinely cross open areas between forests (Glander, pers. obs.). Howlers can also swim. Froehlich *et al.* (1981) reported marked animals moving from BCI to nearby Orchid Island; and captured Costa Rican howlers easily swam across 15 m of a moderately fast flowing river (Glander, pers. obs.).

Howlers are primarily folivorous, although they are not exclusively so, as are the Old World colobines. This relative lack of specialization may account for their widespread success. In addition to being widely distributed geographically, *Alouatta* occupy a wider variety of forest habitats than other New World monkeys. These range from sea level forests, to those at 3200 m altitude (Napier and Napier, 1967; Scott *et al.*, 1976b; Hernandez-Camacho and Cooper, 1976; Schlichte, 1978). Carpenter (1934) noted that howlers prefer primary forests but it is now clear that they are very adaptable and can ben found in such habitats as salt water mangrove swamps (*seniculus*, Scott *et al.*, 1976b; Mittermeier and van Roosmalen, 1981), deciduous forest (*palliata*, Jones, 1978), evergreen dryland forest (*palliata* on BCI, Carpenter, 1934, and others; *belzebul*, Ayres and Milton, 1981; *fusca*, Coimbra-Filho, 1972, Silva, 1981, Mendes, 1985; *seniculus*, Terborgh, 1983), montane forests at altitudes up to 2300 m above sea level (*seniculus*, Gaulin and Gaulin, 1982), gallery and riparian forest (*palliata* at FLP, Glander, 1975-1981; *caraya*, Lindbergh and Santini, 1984, Thorington *et al.*, 1984; *fusca*, A. Rylands, pers. obs.), seasonally inundated forests (*seniculus*, Mittermeier and van Roosmalen, 1982; *belzebul*, Ayres and Milton, 1981, Branch, 1983), forest patches in Amazonian savannas (*seniculus* and *belzebul*, A. Rylands, pers. obs.), dry deciduous thorn forest (*fusca*, A. Rylands, pers. obs.) and *llanos* habitats, comprised of a mosaic of short statured trees and grassland (*seniculus*, Neville, 1972a, Braza, 1978, and others).

In some areas *palliata* is restricted almost completely to mature evergreen forest (Freese, 1976), while in others the same species occupies deciduous and riparian forests (Glander, 1975a, 1978a, 1981; Jones, 1980b). Smith (1970) has proposed a possible ecological separation of *pigra* and adjacent *palliata*, *pigra* being more dependant on undisturbed forests (typical of its range) and *palliata* being more adaptable to secondary and even subxeric forests.

Mittermeier and van Roosmalen (1982) observed *seniculus* in 16 of the 18 forest types they identified for Suriname, and recorded it as common in high tropical rainforest, riverbank terra firme, marsh, and swamp forest. They also observed *seniculus* in low forest, savanna forest, liane forest and mangrove forest. Izawa and Bejarano (1981) observed *seniculus* in tall dryland forests with discontinuous and continuous canopies, as well as secondary forest of 10-20 m height, and recorded a preference for riverine forest in the Pando region of northwest Bolivia. *A. belzebul* is mainly Amazonian, allopatric to *seniculus* and occupies similar forest types.

A. caraya is typically found in gallery forest and tall forest patches throughout the central *cerrado* region of Brazil. Thorington *et al.* (1984) surveyed populations in gallery forests, with a canopy at 10-25 m, on the Río Paraguay in northern Argentina. *A. fusca* occurs in tall evergreen and semideciduous tropical forests of the Atlantic forest region and Rio Paraná basin in Brazil (Coimbra-Filho, 1972; Silva, 1981; Mittermeier *et al.*, 1982) but has also been found in dry deciduous thorn forest in the *caatinga* region of northeast Brazil (A. Rylands, pers. obs.).

Clearly the genus is very adaptable. They are often the only monkeys left in areas used by humans. *A. palliata* and *seniculus* appear to occupy a greater diversity of forest habitats, but they have also been the most intensively studied. It is reasonable to expect similar adaptability in other *Alouatta* species.

IV. DIET

Alouatta eat mature and young leaves, petioles, pulvini, buds, flowers, fruits, seeds, stems and twigs. Arthropods, especially, coleopterans are generally consumed inadvertently (Milton, 1980; Chitolina and Sander, 1981). The genus is characterized as folivorous, but this designation is based almost exclusively on the feeding behavior of *palliata* and fruit is known to comprise up to 95 percent of the diet of this species at certain times of the year (Altmann, 1959). Available data on *seniculus* (Klein and Klein, 1975; Gaulin and Gaulin, 1982; Braza *et al.*, 1983) indicate that they are also folivorous, but *pigra* (Coelho *et al.*, 1976a, 1976b, 1977; Schlichte, 1978) appears to be at least as frugivorous as *Ateles*. Categorization may be premature for *pigra* since it has not been observed year round. Relatively little is known about the diet of the other three *Alouatta* species, although it is evident that all regularly include mature leaves in their diet; a feature which separates them from all other New World monkeys.

Dietary characteristics of the studied species are indicated below in the order in which they were listed in the section on Naturalistic Studies. The length of each study and/or the number of observation hours are provided if available.

(1) *Alouatta pigra*

All of the dietary information for this species comes from Tikal. Coelho *et al.* (1976a, 1976b, 1977: three two-person teams accumulated 1,147 observation hours) reported that from June to August the diet of *pigra* is comprised of 86% *Brosimun alicastrum (ramón)* fruits and leaves, 7.9% *Achras zapota* fruits and leaves, and seven percent other. Schlichte (1978: four months and 907 five-minute observation units during one week), working in exactly the same place and presumably with the same population, found that from October to January the howlers ate food from only seven of the 36 most common tree species and spent 87.5% of their feeding time during a week ingesting *ramón* fruit, flowers, and leaves. The species and parts eaten are shown in Table II.

(2) *Alouatta palliata*

(a) *Los Tuxtlas, Mexico.*

Estrada (1984: 883 hours from September 1977 to August 1978) found that one group of *palliata*, observed during one year, fed from 120 trees of 27 species, although only eight species contributed 78% of the trees used and 89% of the total feeding time. The principal families involved were Moraceae and Lauraceae (Table III). Throughout the year, they spent an equal proportion of time consuming leaves and fruits, with young leaves and mature fruits contributing 39% and 41% of their feeding time, respectively. Young leaves were the principal dietary item during the second half of the wet season (September to February) and in the dry season (March to May), contributing up to 90% of the total feeding time. Mature leaves were eaten throughout the year, but contributed least to the diet during the first half of the wet season when ripe fruit was the main food type eaten. Young fruit contributed 8.5%, mature leaves 10% and flowers only 0.2% of the total feeding time. Estrada (1984) found that young leaves eaten by howlers are richer in protein content per dry weight, contain a higher proportion of digestible nutrients, more digestible energy and less fiber than mature leaves.

(b) *Finca La Pacifica, Costa Rica.*

Glander (1975a, 1978a, 1981: 2071 observation hours during June, 1972, to August, 1973) found that these howlers spent 19.4% of their feeding time eating mature leaves, 44.2% eating new leaves, 12.5% eating fruits, 18.2% eating flowers, and 5.7% eating petioles and pulvini (Table IV). Glander reported seasonal differences; mature leaf use was higher in the wet season and lower in the dry season. New leaves were used in an opposite fashion. Since new leaves were preferred, their availability directly affected feeding time on mature leaves. This was clearly reflected in the diet composition by month (Table IV). There was a significant negative correlation between mature and new leaves, between mature leaves and flowers, and between new leaves and fruits in the daily diet (Glander, 1981). In other words, the howlers ingested fewer mature leaves as more new leaves and flowers were eaten and new leaf use decreased as fruit use increased. Rainfall influenced the availability of fruits and flowers but not new leaves (Glander, 1981). Both flowers and fruits provided easily digestible carbohydrates, but neither were eaten all year since each was only seasonally available. The amount of time spent feeding on flowers and fruits increased or decreased as a function of their availability. Glander reported that the howlers obtained their food from 62 of the 96 tree species available. The distribution of feeding time by species is shown in Table V. All of the howlers' food for one 12-month period was obtained from 331 different trees, or 19.5% of all trees present in their 9.9 ha home range. In fact, 88 of the 331 food trees accounted for 79% of their total feeding time. Feeding time in a tree species was negatively correlated with tree abundance ($r_s = -0.287$, $n = 62$, $p \leqslant 0.05$); the more common a tree species was, the less it was used as a food source (Glander, 1981). Table VI contains the ten top food species and their relative densities. These ten food species accounted for 68% of the feeding time and only 11% of all tree species. Chemical analyses demonstrated that the leaves howlers ate contained significantly more water, total protein, more of all amino

TABLE II
Foods species of *Alouatta pigra*, Tikal, Guatemala

Species		Item	% time
Brosimum alicastrum	Moraceae	L, Fr, Bu	87.5
Ficus sp. A	Moraceae	L, Bu	3.0
Ficus sp. B	Moraceae	L, Fr	3.0
Bursera simeraba	Burseraceae	L	2.0
Aspidosperma megalocapon	Apocynaceae	L	1.0
Ximenia americana	Olacaceae	L	1.0
Achras zapota	Sapotaceae	Fr	0.3
Lianas		L, Fr	1.5
Others			0.7

Based on observation during one week by Schlichte (1978). L = leaves, Fr = fruit, Bu = buds.

TABLE III
Food species of *Alouatta palliata* at "Los Tuxtlas", Mexico

Species		Item	%
Ficus spp.	Moraceae	Yl, Ml, Fr	32.0
Nectandra ambigens	Lauraceae	Yl, Ml, Fr	22.6
Poulsenia armata	Moraceae	Yl, Ml, Fr	11.4
Brosimum alicastrum	Moraceae	Yl, Ml, Fr	7.4
Cecropia obtusifolia	Moraceae	Yl, Ml, Fr	6.1
Pterocarpus hayesii	Leguminosae	Yl	3.4
Cordia alliodora	Boraginaceae	Yl, Ml, Fr	3.2
Crateva tapia	Capparaceae	Yl, Ml	2.8
Pseudolmedia oxyphyllaria	Moraceae	Yl, Ml, Fr	1.5
Calatola laevigata	Icacinaceae	Ml	1.3
Sapium lateriflorum	Sapindaceae	Yl, Ml	1.0
Ulmus mexicana	Ulmaceae	Ml	0.9
Omphalea cardiophylla	Euphorbiaceae	Yl	0.9
Dialium guianense	Leguminosae	Fr	0.7
Ampelocera hottlei	Ulmaceae	Yl, Fr	0.7
Dipholis minutiflora	Sapotaceae	Fr	0.6
Robinsonella mirandae	Malvaceae	Yl	0.6
"Ola zapote"		Ml, Fr	0.5
Dussia mexicana	Leguminosae	Yl, Ml	0.5
Cassia doylei	Leguminosae	Yl	0.3
Coccoloba barbadensis	Polygonaceae	Yl, Ml	0.2
"Crespillo"		Yl	0.2
Cymbopetalum baillonii	Annonaceae	Ml	0.2
Tetrorchidium rotundotum	Euphorbiaceae	Ml	0.2
Spondias mombin	Anacardiaceae	Yl	0.1
Achras zapota	Sapotaceae	Fr	0.1
Zanthoxylum kellermanii	Rutaceae	Yl	0.1

Observations during 883 hours, one annual cycle from Estrada (1984). Ml = mature leaves, Yl = young leaves, Fr = fruit, % = percentage feeding time.

acids except isoleucine were more digestible, and contained significantly less fiber and ash than those leaves that they did not eat (Glander, 1981). In addition, there was seasonal and intraspecific variability in secondary compound content of the leaves. The howlers timed their food acquisition to coincide with those seasons when alkaloids were absent or only hydrolyzable tannins were present. Further, the leaves selected by the howlers of FLP contained significantly more methionine than those leaves not selected. Methionine may be a limiting amino acid for folivorous primates since it is found in very low amounts in most leaves.

(c) *Barro Colorado Island, Panama.*

Carpenter (1934: 7 months) listed 55 tree species that provided food for the howlers. Altmann (1959: 227 hours of observation during October 29 to December 1, 1955) reported that figs made up more than 50% of the daily diet. Hladik and Hladik (1969) found that the howler diet consisted of 40% foliage and 60% fruit, with figs being the primary fruit. Hladik *et al.* (1971) found that 80% of howler food came from 12 tree species with figs making up 50 percent of the diet. They calculated that the BCI howler diet consisted of 9.6% protids, 3.2% lipids, 21.7% reducing glucids, 13.6% cellulose, and 51.9% complimentary fractions.

Smith (1977: 407 hours of observation from February through July, 1968) reported that the dry season diet of BCI howlers had 46.1% fruits, 41.5% leaves, and 2.5% flowers. He indicated that the howlers concentrated their feeding on a few tree species and genera with a marked preference for *Platypodium elegans* leaves and fruits from *Ficus* spp. Based on assimilation experiments, Smith (1977) suggested that *P. elegans* leaves provide high amounts of nitrogen while the fig fruits provide easily used carbohydrates. He concluded that the howlers' daily food choice led to a balance

TABLE IV

Diet composition in percentages for Finca La Pacifica howling monkeys, *Alouatta palliata*

	%	Season Wet	Season Dry
Mature leaves	19.4	25.3	11.5
New leaves	44.2	31.2	56.5
Fruits	12.5	15.0	4.3
Flowers	18.2	21.0	18.0
Petioles & pulvinus	5.7	7.4	9.1

Tree Part	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec.
Mature Leaves	31.7	9.1	5.4	6.8	12.7	38.6	31.2	38.6	19.6	22.2	24.9	35.4
New Leaves	63.8	62.9	46.2	43.2	30.5	22.9	28.9	19.9	46.4	38.3	30.6	37.8
Fruits	1.0	4.6	3.0	16.8	13.6	17.4	22.5	40.2	27.9	6.8	11.6	5.4
Flowers	15.5	15.6	29.1	23.6	37.4	19.5	16.8	0	3.3	20.2	26.8	5.5
Petioles Pulvinus	6.1	7.9	16.1	9.5	5.8	1.4	0.6	1.3	2.8	12.6	6.5	15.7

After Glander, 1975a

TABLE V

Food species of Finca La Pacifica howling Monkeys, *Alouatta palliata*

Species	Feeding Time min	% of Total Feedtime	Nº Present	% of Total Present	Tree Parts Eaten [a]
Andira inermis	3118	12.15	28	1.65	Nl, Le, Pu
Pithecellobium saman	2577	10.04	11	.65	Le, Nl, Fl, Fr
Pithecellobium longifolium	2033	7.92	16	.94	Nl, Fl
Anacardium excelsum	1855	7.23	68	4.00	Pd, Pe, Fl, Nl, Le
Licania arborea	1812	7.06	29	1.71	Nl, Fl, Le
Manilkara zapota	1587	6.19	7	.41	Fl, Fr, Nl, Le
Astronium graveolens	1401	5.46	18	1.06	Le, Nl, Pe, Fr, Fl, Pu
Pterocarpus rohrii	1209	4.71	4	.24	Nl, Le
Muntingia calabura	967	3.77	9	.53	Fr, Le, Nl
Ficus glabrata	910	3.55	2	.12	Nl
Lonchocarpus nitidus	871	3.40	97	5.71	Fl, Nl
Spondias mombin	843	3.29	20	1.18	Fr, Pu, Le, Nl, Fl
Bursera simaruba	694	2.71	19	1.12	Le, Nl, Fl
Mastichodendron tempisque	523	2.04	6	.35	Fl, Nl, Le, Pe, Fr
Spondias nigrescens	428	1.67	10	.59	Pu, Nl, Pe, Fr, Fl, Le
Luehea candida	426	1.66	54	3.18	Fl, Nl
Schizolobium parahybum	360	1.40	6	.35	Fl, Fr, Pe, Nl
Gliricidia sepium	343	1.33	149	8.77	Le, Fl, Nl
Enterolobium cyclocarpum	341	1.33	13	.77	Le, Nl, Pu, Fl
Myrospermum frutescens	317	1.24	24	1.41	Le, Fl, Nl
Cecropia peltata	287	1.12	4	.24	Fr, Pe, Nl, Fl
Tabebuia ochracea	240	.94	32	1.88	Fl, Nl, Pe
Luehea speciosa	231	.90	2	.12	Fl, Nl, Le
Dalbergia retusa	221	.86	20	1.18	Fl, Nl
Albizzia adenocephala	173	.67	1	.06	Nl, Fl, Le
Eugenia salamensis	171	.67	75	4.41	Fr, Le
Inga vera var. *spuria*	168	.65	5	.29	Nl, Fl, Le
Hymenaea courbaril	159	.62	64	3.77	Nl, Fl, Le
Cordia dentata	153	.60	197	11.60	Fr
Trichilia cuneata	124	.48	3	.18	Le, Nl
Tabebuia rosea	120	.47	34	2.00	Nl, Fr, Fl, Le, Pe
Lonchocarpus hondurensis	118	.46	2	.12	Fl, Nl
Spondias purpurea	112	.44	31	1.82	Le, Nl, Fr
Lysiloma seemannii	104	.41	24	1.41	Nl, Fl, Le
Zanthoxylum procerum	94	.37	4	.24	Le, Nl
Coccoloba caracasana	92	.36	9	.53	Fr, Nl
Byrsonima crassifolia	73	.32	2	.12	Fr
Trichilia sp.	69	.27	12	.71	Le, Fl, Nl, Pe
Sweetia panamensis	33	.13	5	.29	Nl, Le
Ficus ovalis	28	.11	1	.06	Nl
Lonchocarpus costaricensis	26	.10	7	.41	Fl
Chlorophora tinctoria	24	.10	7	.41	Fl, Le
Cordia alliadora	23	.09	42	2.47	Le
Cordia panamensis	19	.07	6	.35	Fl, Le, Pe
Sterculia apetala	18	.07	4	.24	Le, Nl, Pe
Calycophyllum candidissimum	18	.07	17	1.00	Le
Guazuma ulmifolia	17	.07	201	11.83	Le, Nl
Cochlospermum vitifolium	16	.06	30	1.77	Fl, Pe
Sloanea terniflora	14	.05	16	.94	Le, Pe, Nl

(cont.)

Table V (Cont.)

Species	Feeding Time min	% of Total Feedtime	Nº Present	% of Total Present	Tree Parts Eaten [a]
Bombacopsis quinata	13	.05	4	.24	Le
Cedrela mexicana	13	.05	8	.47	Fl
Bourreria quirosii	11	.04	2	.12	Nl
Ceiba pentandra	9	.04	6	.35	Nl
Guettarda macrosperma	9	.04	2	.12	Le
Carica papaya	7	.03	1	.06	Le
Chomelia spinosa	6	.02	5	.29	Le
Thouinidium decandrum	5	.02	26	1.53	Le
Cordia collococca	3	.01	23	1.35	Nl
Diospyros nicaraguensis	3	.01	2	.12	Le
Simarouba glauca	2	.01	6	.35	Nl, Fr
Casearia arborea	1	.01	7	.41	Nl
Genipa caruto	1	.01	5	.29	Le

[a] The tree parts are arranged in their order of importance in the diet. Le = mature leaves; Nl = new leaves; Fr = fruit; Fl = flowers; Pe = petiole; Pd = pedicel; Pu = pulvinus. After Glander, 1981.

TABLE VI

Top ten food species with their relative densities for *Alouatta palliata* at Finca La Pacifica

Species	% Feeding Time	% Relative Density
Andira inermis	12.15	1.65
Pithecellobium saman	10.04	0.65
Pithecellobium longifolium	7.92	0.94
Anacardium excelsum	7.23	4.00
Licania arborea	7.06	1.71
Manilkara achras	6.19	0.41
Astronium graveolens	5.46	1.06
Pterocarpus hayseii	4.71	0.24
Muntingia calabura	3.77	0.53
Ficus glabrata	3.55	0.12
Totals	68.08	11.31

After Glander, 1981.

TABLE VII

Diet composition in percentages for Barro Colorado Island howling monkeys, *Alouatta palliata*

Tree part	Year	Season	
		Wet	Dry
Leaves [1]	48.2	48.8	35.2
Fruits	42.1	46.1	46.9
Flowers	9.6	4.9	17.9

	Jan	Feb	Mar	Apr	Jul	Aug	Sep	Oct	Nov
Leaves [1]	76.4	36.0	26.9	12.4	37.2	53.9	62.3	50.5	36.2
Fruits	15.2	51.3	62.4	47.0	61.0	41.6	37.0	49.7	55.1
Flowers	8.4	12.1	10.6	40.0	2.0	4.7	0	0	8.3

[1] Maturity not given. After Milton, 1977.

between foods which are rich in protein and those rich in digestible carbohydrates, and that the seasonal changes in the percentage of feeding time on various tree parts paralleled changes in availability of those types of food.

Milton (1977, 1978, 1980: 1020 hours of observation during July-November, 1974, February-April, 1975, and mid-December 1975 – mid-January 1976) found that howlers spent 48.2% of their overall feeding time eating leaves (no maturity given), 42.1% eating fruits, and 9.6% eating flowers (Table VII). She found seasonal differences; more leaves and fewer flowers were eaten during the wet season than the dry season. Fruit use was consistent for both seasons. Milton notes that young leaves were preferred to mature leaves and that the howlers ate more leaves when less fruit was available; also observed for *palliata* at Los Tuxtlas (see above). Both fruit and flower use were correlated with their respective availability and affected leaf consumption as shown by the monthly diet composition (Table VII). Milton found a negative correlation between eating flowers and eating fruit and suggested that flowers substituted for fruit in the diet. Milton's two study groups ate from a total of 109 tree species (Table VIII) of the estimated 135 species present during the study and ate seven to eight different tree species every day, but a few food species were used rather heavily. The top ten food species accounted for 63% of the total feeding time but only 11% of all trees present (Table IX). Milton (1979, 1980) reported that the foods the howlers preferred were generally of high nutritional quality (high protein: fiber ratio) and down-played the role of plant-produced secondary compounds in determining leaf choice. Nagy and Milton (1979a) conclude that the diet diversity results at least in part from the necessity for balance, particularly in terms of certain minerals such as copper, sodium and phosphorus.

The most comprehensive data on the diet of howlers comes from these studies of Glander and Milton on *palliata* at different sites. A comparison of diet composition (Tables IV and VII) demonstrates some similarities (flower use during the dry season was similar at both sites) but many more differences exist between the FLP and BCI *palliata* populations. The major difference is the amount of fruit in the BCI diet. A comparison of Tables V and VIII indicates very little overlap in food species between FLP and BCI. The abundance of *Ficus* on BCI and its absence at FLP is the most striking difference. Even though there is no overlap in the top ten food species from each site (Tables VI and IX) the totals are very similar, indicating that both populations of *palliata* are obtaining a majority of their food from relatively rare tree species in their home ranges.

Milton and co-workers (Milton, 1978, 1979, 1981; Nagy and Milton, 1979a, 1979b; Milton *et al.*, 1979, 1980) have carried out a series of studies on the digestive processes, metabolism, dietary quality, nutrient assimilation and water balance in *A. palliata*, examining particularly the physiological and behavioral adaptations for their, at times, largely folivorous diet. *Alouatta* have long colons and a slow passage rate of food through the gut to permit sufficient fermentation by cellulolytic microorganisms (Milton *et al.*, 1980; Milton, 1980). Fermentation end products are believed to be important sources of energy during times when fruit availability is low (Milton *et al.*, 1980). Milton *et al.* (1979) report that the standard metabolism of *Alouatta* is similar to other mammals of the same body mass and Milton (1979, 1980) argues that adaptations

TABLE VIII
Food species of two groups of Barro Colorado Island howlers, *Alouatta palliata*, **(Old Forest group and Lutz Ravine group).**

Species	Percent of Feeding Time	Percent of Trees in Sample	Tree Parts Eaten
	Old Forest		
Ficus yoponensis	15.32	.39	L, F
Brosimum alicastrum	11.25	.59	L, F
Poulsenia armata	6.04	3.13	L
Ficus insipida	5.91	.78	L, F
Inga fagifolia	5.18	.40	L
Platypodium elegans	4.20	1.37	L, Fl
Cecropia insignis	3.44	.98	L, F, Fl, P
Hyeronima laxiflora	3.23	.98	L, F, Fl
Pseudobombax septenatum	2.21	1.17	Fl
Ficus costaricana	1.99	.20	F
Quararibea asterolepis	1.86	5.28	L, F
Anacardium excelsum	1.79	.39	L, F, P
Tabernaemontana arborea	1.64	.39	L
Trichilia cipo	1.50	6.65	L, F
Eugenia cerstedeana	1.46	.78	L, F
Ceiba pentandra	1.40	.59	L
Arrabidaea patellifera	1.24	v	L
Bignoniaceae sp.	1.13	v	L
Clusia odorata	1.23	v	L, Fl
Chrysophyllum panamense	.96	.39	F
Dipteryx panamensis	.91	.98	F
Ormosia coccinea	78	1.57	L
Topobaea praecox	.68	v	L, Fl
Abuta racemosa	.67	v	L
Maripa panamensis	.64	v	L, Fl
Acacia glomerosa	.64	v	L
Cordia alliodora	.55	1.96	L
Ficus obtusifolia	.55	0	L
Tetragastris panamensis	.50	1.76	L, F
Calophyllum longifolium	.50	0	F
Protium panamense	.48	.78	L
Hiraea sp.	.45	v	Fl
Paragonia pyramidata	.42	v	L
Arrabidaea candicans	.38	v	L
Inga goldmanii	.37	.98	L
Ficus trigonata	.35	v	L, F
Mascagnia hippocrateoides	.34	v	Fl
Ficus hartwegii	.32	v	L, F
Souroubea sympetala	.32	v	L
Drypetes standleyi	.31	0	L, F
Ficus paraensis	.31	v	L, F
Ficus citrifolia	.28	0	L, F
Triplaris americana	.27	.39	L
Paullinia sp.	.27	0	L
Tabebuia guayacan	.27	.59	Fl
Martinella obovata	.27	v	L

(cont.)

Table VIII (Cont.)

Species	Percent of Feeding Time	Percent of Trees in Sample	Tree Parts Eaten
	Old Forest		
Entada gigas	.25	v	L
Ormosia sp.	.25	0	L
Guatteria dumetorum	.25	2.15	Fl
Tachigalia versicolor	.25	.39	L
Prioria copaifera	.24	1.17	L, F
Ficus tonduzii	.20	.20	L, F
Machaerium arboreum	.19	v	Fl
Cordia sp.	.18	0	L
Desmopsis panamensis	.15	0	L
Serjania sp.	.15	v	L
Luehea seemannii	.15	1.17	L
Inga sp.	.15	0	L
Philodendron radiatum	.13	v	P
Mangifera indica	.13	0	F
Socratea durissima	.11	0	F
Pterocarpus rohrii	.10	0	L, F
Machaerium purpurascens	.10	v	L
Licania platypus	.09	0	L
Eugenia nesiotica	.08	.20	L
Celtis shippii	.08	.20	L
Alseis blackiana	.06	5.09	L
Beilsehmiedia pendula	.03	1.37	F
Omphalea diandra	.03	v	L
Tynnanthus croatianus	.03	v	L
Virola surinamensis	.03	2.74	L
Unomopsis pittieri	.03	0	L
Hybanthus prunifolius	.03	0	L
	Lutz Ravine		
Ficus yoponensis	25.95	2.15	L, F
Ficus insipida	22.88	1.16	L, F
Platypodium elegans	6.94	1.98	L, Fl
Spondias radlkoferi	4.96	1.65	L, F
Lacmellea panamensis	3.16	.17	F
Pterocarpus rohrii	2.48	2.97	L, F, Fl
Inga fagifolia	2.04	.17	L
Maquira costaricana	1.59	1.16	L, F
Brosimum alicastrum	1.48	0	L, F
Poulsenia armata	1.48	2.15	L
Ficus trigonata	1.41	0	L, F
Anacardium excelsum	1.17	3.80	L, F
Luehea seemannii	1.10	4.62	L
Inga sapindoides	1.07	0	L
Cecropia insignis	1.17	.17	L, F, Fl, P
Inga sp.	.93	.10	L, Fl
Hyeronima laxiflora	.90	4.62	Fl
Inga goldmanii	.89	.17	L
Inga punctata	.87	0	L
Zanthoxylum panamense	.82	.83	L, Fl
Ceiba pentandra	.81	.17	L
Eugenia coloradensis	.74	0	L, F

(cont.)

Table VIII (Cont.)

Lutz Ravine			
Species	Percent of Feeding Time	Percent of Trees in Sample	Tree Parts Eaten
Protium panamense	.77	.99	L
Machaerium purpurascens	.71	v	L
Dioclea reflexa	.70	v	Fl
Socratea durissima	.49	0	F
Entada gigas	.44	v	L
Hasseltia floribunda	.43	.83	F, Fl
Trophis racemosa	.43	1.98	L, F, Fl
Gnetum leyboldii	.36	v	Fl
Cordia alliodora	.36	.66	L
Ficus tonduzii	.32	.17	L, F
Tetragastris panamensis	.28	0	L, F
Prioria copiafera	.29	0	L, F
Quassia amara	.24	0	L
Machaerium pachyphyllum	.22	v	L, Fl
Arrabidaea patellifera	.22	v	L
Bignoniaceae sp.	.19	v	L, Fl
Cavanillesia platanifolia	.19	.17	L
Pseudobombax septenatum	.19	0	Fl
Virola sebifera	.18	2.81	L
Tabebuia guayacan	.17	0	Fl
Miconia argentea	.16	0	F
Maripa panamensis	.13	v	L
Ormosia coccinea	.12	0	L
Tetacera sp.	.12	v	L
Terminalia amazonica	.12	.83	L
Inga sp.	.11	0	L
Philodendron radiantum	.11	v	P
Alseis blackiana	.10	7.26	L
Hippocratea volubilis	.09	v	L
Doliocarpus olivaceus	.09	v	F
Calophyllum longifolium	.09	.17	F
Aspidosperma megalocarpon	.07	0	L
Apeiba membranacea	.06	.99	L
Martinella obovata	.05	v	L
Guatteria dumetorum	.04	0	Fl
Phrygenocydia corymbosa	.04	v	L
Petrea volubilis	.04	v	L
Clusia odorata	.04	v	L
Bombacopsis sessilis	.03	.83	L
Tabernaemontana arborea	.03	0	L
Macfadyena unquis-cati	.02	v	Fl
Dipteryx panamensis	.02	.17	L, F
Gustavia superba	.02	3.30	L
Triplaris americana	.02	.50	L
Connarus panamensis	.02	0	L
Protium tenuifolium	.02	.99	L
Unonopsis pittieri	.02	.17	L
Ficus bullenei	.02	0	L
Virola surinamensis	.02	3.36	L, Fl
Piper arboreum	.02	0	L
Doliocarpus major	.02	v	F

L = leaf; F = fruit, Fl = flower; P = petiole; v = vine, liana, epiphyte. After Milton, 1980.

TABLE IX

Top ten food species, with their relative density, for *Alouatta palliata* at Barro Colorado Island

Species	% Feeding Time	% Relative Density
Ficus yoponensis	20.95	1.34
Ficus insipida	14.89	0.98
Brosimum bernadette	6.08	0.27
Platypodium elegans	5.65	1.70
Inga fagifolia	3.86	0.27
Poulsenia armata	3.63	2.60
Spondias mombin	2.63	0.98
Cecropia eximia	2.24	0.54
Hieronyma laciflora	1.99	2.95
Lacmellea panamensis	1.67	0.09
Totals	63.59	11.72

After Milton, 1980

to leaf-eating in this genus are mainly behavioral (see also Braza *et al.*, 1983, below). These behavioral adaptations include a selective diet, preferably a mixture of fruit and immature leaves, using a wide range of species which are not necessarily the most common ones in the group's home range (Glander, 1981, and see below) and ranging and activity patterns which optimize their use of these resources.

(3) *A. seniculus*

(a) *Hato Masaguaral, Venezuela.*

The key resources for a group of 9-10 *seniculus* at HMG were strangler figs, *Ficus* spp., a palm, *Copernicia tectorum* (an important host for the figs), and *Albizia cf. caribea*, which occurred at very high densities; 18 *Ficus*/ha, 189 *Copernicia*/ha and 12 *Albizia*/ha (Sekulic, 1982a). Taking into account range overlap, Sekulic estimated that the group had exclusive use of approximately 25 *Albizia*, 153 adult palms, and 44 fig trees, including 23 medium to large figs. This high density of food resources is believed to explain the very small home ranges used by the howling monkeys in this site (see below).

(b) *Hato "El Frío", Venezuela.*

Braza *et al.* (1983: Braza's field study covered May 1975–June 1976, but the bulk of this report deals with the contents of 63 stomachs and 57 intestines) reported on a number of interesting features. Males were significantly larger (5.6 kg vs 4.0 kg) but their stomach contents were only insignificantly heavier. Leaves and fruits were most emphasized in the diet: they appear in three quarters of the stomachs, over half of the intestines, and almost all of the feces collected. The howlers discriminate a lot regarding fruit species available throughout the year, choosing only some of them at a given time. Legume pods and young leaves in general were probably very important sources of protein, fleshy fruits of carbohydrates, and palm fruits of lipids. Females appeared to be more selective than males with respect to taking in legume pods, flowers, woody stalks, grasses, and bark. They note that howlers appeared to be only slightly specialized for leaves because their stomachs and caeca are only slightly longer than those of other Cebidae, but that the digestive surface is sufficiently increased that Hladik (1967) classifies them as folivorous. 'Therefore, relative digestive surface together with long intestinal microvellosities... could compensate for the shortness of

TABLE X

Food species of *Alouatta seniculus* at Finca Merenberg, Colombia

Species		Item
Brunellia comocladifolia	Brunelliaceae	Yl, Fl
Eupatorium sp.	Compositae	Ml, Yl
Sapium cuatrecasasii	Euphorbiaceae	Yl
Quercus humboldtii	Fagaceae	Ml, Yl, In
Nectandra sp.	Lauraceae	Yl
Souroubea sp.	Marcgraviaceae	Fr
Guarea sp.	Meliaceae	Yl
Morus sp.	Moraceae	Ml, Yl, Fr, In
Cecropia tessmannii (?)	Moraceae	Fr
Cecropia sp.	Moraceae	Ml, Yl, Fr, Pe
Ficus cundinamarcensis	Moraceae	Ml, Yl, Fr
Ficus insipida	Moraceae	Yl, Fr, UFr
Ficus garcia-barrigae	Moraceae	Yl
Ficus caucana	Moraceae	Yl
Ficus gigantosyce	Moraceae	Yl
Ficus dendrocyda	Moraceae	Fr
Ficus boyacensis	Moraceae	Fr
Ficus sp. A	Moraceae	Yl, UFr
Ficus sp. B	Moraceae	Yl
Ficus sp. C	Moraceae	Yl, Fr
Prunus integrifolia (?)	Rosaceae	Fr
Solanum sp.	Solanaceae	Ml
Calatola sp.	Sic.	Yl
Billia colombiana	Hippocastanaceae	Yl
Psammisia falcata	Ericaceae	Yl, Fr
Ladernbergia macrocarpa	Rubiaceae	Ml, Fl

Observations during 340 hours over 10 months (Gaulin and Gaulin, 1982). Ml = mature leaves, Yl = Young leaves, Fr = fruit, UFr = unripe fruit, In = inflorescence, Fl = flower, Pe = petiole.

the intestine. The problem is partly solved if... howlers prefer young leaves over mature ones, since the former's low fibrous content do not make necessary complicated digestive specializations.' As noted already, young leaves do seem to be greatly preferred.

(c) *La Macarena, Colombia.*

Klein and Klein (1975: 70 hours of observation during October 1967-November 1968) reported that a major part of the *seniculus* diet consisted of mature and young leaves and mature and young fruits, with figs being the primary fruit.

(d) *Río Peneya, Colombia.*

Izawa (1975) reports on clay-eating by *seniculus* at clay-licks ("salado-sites") and also observed them eating *Pourouma* fruits.

(e) *Finca Merenberg, Colombia.*

Gaulin and Gaulin (1982 and Gaulin, 1977: 340 hours of focal observation during 10 months) reported that *seniculus* spent an average of 12.7% of their 12-hour activity period in feeding. They estimated that 7.5% of the total feeding time was spent eating mature leaves, 44.5% new leaves, 42.3% fruit, 5.4% flowers and 0.1% petioles. The main species used were *Ficus, Cecropia, Morus* and *Quercus*. Table X lists the species and items eaten, which include 12 species of ripe fruits, two of unripe fruits (possibly seed predation), nine species of mature and 24 of young leaves, floral material of four species and one species for leaf petioles. Although more time was spent eating leaves (53% of feeding time) than fruits (42%), Gaulin and Gaulin (1982) estimated that leaves contributed only 25% of the total dry matter ingested, and that fruits contributed more than 70%.

(4) *A. caraya*

The only information available on the feeding behavior of *caraya* comes from studies by Lindbergh and Santini (1984) of one of two captive bred groups introduced into a gallery forest in the Brasília National Park. During four months following release, the group used 11 of the 17 tree species existing in the forest (Table XI). They were observed eating old and new leaves, leaf buds, flowers and fruits.

(5) *A. fusca*

The brown howler has been observed feeding on old and young leaves, leaf buds, fruits, flowers (including pollen and nectar), vine stems and twigs. Young (1983: 100 contact hours from June to August, 1983) compared the feeding behavior of *fusca* with that of the sympatric *Brachyteles*. *A. fusca* spent more time feeding on leaves and leaf buds (88% compared to 66%) but less time feeding on fruit (5% compared to 26% of the feeding time). Young concludes that, at least during the dry season, the most important food item for both *fusca* and *Brachyteles* was mature leaves but, whereas fruits took second place for *Brachyteles*, young leaves were the second most eaten category for *Alouatta*. Of interest is that *fusca* were not observed eating the fruits consumed by *Brachyteles*. Fig trees were not fruiting during Young's study, but he indicates that they are an important food source at other times of the year. The diurnal patterns of feeding show morning and afternoon peaks of leaf-eating, with fruit-eating being more frequent as midday. The same pattern was observed by Chitolina and Sander (1981: 32 observation days during nine months). Species and food items recorded by Chitolina and Sander are shown in Table XII. Kuhlmann (1975) lists 76 plant species identified in fecal samples of *A. fusca*, obtained over a period of 44 months in a 327 ha secondary forest patch in the municipality of São Paulo (Table XII).

TABLE XI

Food species of *Alouatta caraya*, Brasília National Park, Brazil

Species		Item
Tapirira guianensis	Anacardiaceae	Ml, Yl, Bu
Protium sp. 1	Burseraceae	Ml, Yl, Bu
Protium sp. 2	Burseraceae	Yl, Bu
Richeria obovata	Euphorbiaceae	Ml, Yl, Bu
Callophyllum brasiliensis	Guttiferae	Yl, St
Salacia crassifolia	Hippocrataceae	Yl
Cecropia sp.	Moraceae	Ml, Yl, Fl
Pseudolmedia laevigata	Moraceae	?
Mauritia flexuosa	Palmae	Ml, Fr
Euplassa inaequalis	Proteaceae	Yl, Bu
Ferdinandusa speciosa	Rubiaceae	Ml, Yl, Bu, Fr, Fl
Styrax camporum	Styracaceae	Ml, Yl

Observations of a captive group released in the Brasflia National Park, over four months (Lindbergh and Santini, 1984). Ml = mature leaves, Yl = young leaves, Bu = buds, Fr = fruits, Fl = flowers, St = stem.

Mendes (1985: 493 hours during 11 months) compared the diet of *fusca* during the wet and dry seasons. In the dry season, 77% of feeding time was devoted to leaves, 11% leaf buds, 9% flowers and only 2% fruits. This confirms Young's (1983) finding of the infrequency of fruit-eating at this time. During the wet season, fruit eating,

TABLE XII

Food species of *Alouatta fusca* at Sapiranga, Rio Grande do Sul, (Chitolina and Sander, 1981) and the Parque Estadual das Fontes do Ipiranga, São Paulo (Carvalho, 1975; Kuhlmann, 1975) in Brazil.

Species		Item
Sapiranga, Rio Grande do Sul [1]		
Unidentified	Compositae	L
Ajonea saligma	Lauraceae	Fr
Unidentified	Lauraceae	L
Arabidea sp.	Bignoniaceae	Fr, L
Inga marginata	Leguminosae	L, Se
Piptadenia rigida	Leguminosae	Fr
Cecropia adenopus	Moraceae	Fr
Ficus anthelmintica	Moraceae	L, Yl, Fr
Ficus sp.	Moraceae	L, Fr
Aracastrum romanzoffianum	Palmae	Fr
Eugenia pungens	Myrtaceae	Fr
Unidentified	Solanaceae	L
Celtis talla	Ulmaceae	L, Fr
Parque Estadual das Fontes do Ipiranga, São Paulo [2]		
Abbevillea sp.		Fr
Alibertia myricifolia	Rubiaceae	?
Allophyllus edulis	Sapindaceae	Fr
Aniba sp.	Lauraceae	Fr
Buchenavia sp.	Combretaceae	Fr
Byrsonima ligustrifolia	Malphigiaceae	Fr
Calyptranthes sp.	Myrtaceae	Fr
Casearia parvifolia	Flacourtiaceae	Fr
Crecopia aff. *leucocoma*	Moraceae	Inf
Chrysophyllum cuspidatum	Sapotaceae	Fr
Cissus paullinifolia	Vitaceae	Fr
Campomanesia chrysophylla	Myrtaceae	Fr
Campomanesia guaviroba	Myrtaceae	?
Capsicodendron dinizii	Canellaceae	?
Celtis aff. *ferruginea*	Ulmaceae	?
Cissampelos sp.	Menispermaceae	?
Cissus erosa	Vitaceae	?
Coccoloba crescentiaefolia	Polygonaceae	Fr
Coccoloba scandens	Polygonaceae	Fr
Cordia aff. *sellowiana*	Boraginaceae	Fr
Coussarea contracta	Rubiaceae	Fr
Cryptocarya moschata	Lauraceae	Fr
Diclidanthera elliptica	Polygalaceae	Fr
Didymopanax angustissimum	Aracaceae	Fr
Didymopanax calvum	Aracaceae	Fr
Duguetia lanceolata	Annonaceae	?
Eugenia sp.	Myrtaceae	Fr
Ficus luschnathiana	Moraceae	?
Ficus sp.	Moraceae	Inf
Guatteria parvifolia	Annonaceae	Fr
Guettarda viburnoides	Rubiaceae	Fr
Heisteria silviani	Olacaceae	?
Ilex amara	Aquifoliaceae	Fr
Inga sellowiana	Leguminosae	Fr
Lauraceae spp.		Fr
Maytenus alaternoides	Celastraceae	Fr
Maytenus sp.	Celastraceae	?
Mendoncia coccinea	Mendonciaceae	?
Mendoncia velloziana	Mendonciaceae	Fr
Miconia cabucu	Melastomataceae	Fr
Miconia candolleana	Melastomataceae	?
Miconia cubatensis	Melastomataceae	Fr
Miconia eichlerii	Melastomataceae	?
Miconia sp.	Melastomataceae	?
Mouriri chamissona	Melastomataceae	?
Myrcia aff. *rostrata*	Myrtaceae	Fr
Myrciaria jaboticaba	Myrtaceae	Fr
Myrtus psedicaryophyllus	Myrtaceae	Fr
Ocotea sp.	Lauraceae	?
Odontocarya sp.	Menispermaceae	Fr
Ouratea sp.	Ochnaceae	Fr
Paivae langsdorffi	Myrtaceae	?
Prunus sphaerocarpa	Rosaceae	Fr
Piptocarpha macropoda	Compositae	L
Psidium (cattleyanum)	Myrtaceae	Fr
Psychotria hancorniifolia	Rubiaceae	Fr
Psychotria saturella	Rubiaceae	Fr
Posoqueria acutifolia	Rubiaceae	Fr
Rapanea ferruginea	Myrsinaceae	Fr
Rapanea umbellata	Myrsinaceae	Fr
Reedia gardneriana	Guttiferae	Fr
Rollinia sericea	Annonaceae	Fr
Rollinia sylvatica	Annonaceae	Fr
Salacia sylvestris	Hippocrataceae	Fr
Salacia sp.	Hippocrataceae	?
Solanum bullatum	Solanaceae	?
Solanum excelsum	Solanaceae	?
Solanum inaequale	Solanaceae	Fr
Solanum paniculatum	Solanaceae	Fr
Solanum rufescens	Solanaceae	Fr
Symplocos nitidiflora	Symplocaceae	Fr
Tapirira guianensis	Anacardiaceae	Fr
Tapirira marchandii	Anacardiaceae	Fr
Tibouchina sp.	Melastomataceae	Fr
Torrubia olfersiana	Nyctaginaceae	Fr
Vernonia diffusa	Compositae	L

L = leaves, Yl = young leaves, Fr = fruits, Se = seeds.

[1] Observations during 32 days over nine months by Chitolina and Sander (1981).

[2] From fecal samples collected during 44 months (Kuhlmann, 1975; Carvalho, 1975).

increased to nearly 29% of feeding time at the expense of leaves (66%), flowers (5%) and leaf buds (0.7%). Mendes found that they eat more mature than young leaves in the dry season but the reverse was true in the wet season.

Water

Carpenter (1934) was the first of many to suggest that howling monkeys obtained their necessary water either from their food or by licking rain from leaves or themselves. Several investigators (Carpenter, 1934; Racenis, 1951; Izawa, 1975) reported that howlers came to the ground near water but were not observed to drink. However, there are now documented cases of howlers drinking, not from terrestrial sources but from arboreal reservoirs. Glander, (1975b, 1978b) observed *palliata* drinking from arboreal cisterns during the wet season in Costa Rica. Glander (1978b) suggested that drinking or the lack was linked to the kinds of foods available rather than to water availability. When succulent new leaves comprised a large part of the diet, supplemental water was not required but when new leaf ingestion was low drinking was necessary to supply additional water. Coelho *et al.* (1977) reported that *pigra* drank from water cisterns in trees as well as pools of water collected on the tops of pyramids. *A. seniculus* has been observed to drink from bromeliads (Gaulin, 1977) as well as arboreal reservoirs (Rylands, pers. obs.).

V. POPULATION DYNAMICS

Group Size and Composition

Studies of the relative proportions of the age/sex categories and the total numbers in average groups have long been a basic part of the description of a species, and indeed a tremendous amount of information is implied by these simple numbers. There are two questions of general interest, however: (1) Do the averages of the various numbers stemming from the groups studied tend toward some abstract, yet useful, species-specific characterization? Carpenter in his various papers follows this approach with his "central grouping tendencies" (= "apoblastosis" of Eisenberg *et al.*, 1972). This would mean that other features of the behavior and ecology of the species result in a set of forces which produces groups tending toward a particular size and composition. A principal task of initial field studies would then be to establish these group composition norms in a sense similar to the taxonomist describing the proportion of vertebral bones to be classified as cervical, thoracic, or lumbar. At a much later stage one would hope to be able to connect the rest of the behavior and ecology to the group composition, and to that end the study of *interspecies* variation may be of most interest. (2) As an alternative, do apparently species-characteristic compositions result from our limited number of samples of the species, and as we expand our data base will we be able to study the effect of environment on behavior by studying the variation in group compositions within the species? The level of primary interest may then be *intraspecies* variation. We will follow the first approach in which one hopes to be able to describe, through the group composition, a set of species-specific characteristics, but we will also indicate studies in which important and consistent intraspecies variation seems to be appearing.

TABLE XIII

A comparison of the age categories for *Alouatta palliata* immatures used by Carpenter in his early work (1934/1964, Table 2) and more recently (1965, Table 8-2). [a]

Class	Est. size (gm)	Color	Relation to mother	Play	Est. age 1934	Est. age 1965
Infant-1	600	Grayish-brown	Carried ventrally.	+	Under 1 mo	Birth to 5-6 mo
Infant-2	900	Brownish-black	Carried dorsally, still close association.	+ +	About 6 mo	5-6 to 10-12 mo
Infant-3	1500	Black	Occasionally travels alone during group movement. [b]	+ + +	About 12 mo	10-12 to 18-20 mo
Juvenile-1	2500	Black	Weaning period: relatively independent of mother, but occasionally assisted by her over crossings; group play.	+ + + +	About 18 mo	20 to 30 mo
Juvenile-2	4000	Black with reddish mantle	Usually with other young; occasionally with mother and younger siblings.	+ +	About 25 mo	30 to 40 mo
Juvenile-3	6000	Black with distinctly red mantle	Entirely independent: dominates play groups; some avoidance of males.	+	About 36 mo	40 to 50 mo

[a] "Est." = estimated. The comments are often paraphrases of Carpenter's descriptions. Baldwin & Baldwin (1973) present a similar comparison of Carpenter's terminologies. See text here for Glander's (1980) very different age intervals.

[b] Description from the 1965 table. Carpenter (1934) included occasionally being assisted or carried over critical crossings and the appearance of the lower incisors at 11 months.

It is first necessary, however, to consider the problems caused by the use of different aging criteria by the various authors. Lack of a discrete birth season, which would identify age-sets of immatures, and the scarcity of howlers in captivity are to blame for our dilemma.

Carpenter (1934) did such an excellent job of specifying his criteria for age categories of *palliata* that most other workers on that species have followed him. However, his estimated ages appear to be guesses which he changed in his 1965 paper (Table XIII). Froehlich *et al.* (1981) made a detailed study of tooth wear patterns of *palliata* on BCI and, through longitudinal observations of known individuals, produced a method for aging both immature and mature animals. They used Carpenter's (1934) age categories (Table XIII) which they calibrated in years. By regressing body weight against the age estimates, they also obtained maturation curves for both sexes. Glander's (1980) longitudinal studies on the same species in Costa Rica have led to a very different set of age estimates: Infant-1, zero to two days; Infant-2, two to 21 days; Infant-3, 21 to 90 days; Juvenile-1, three to six months; Juvenile-2, six to 30 months; subadult female and subadult male, 30 to 48 months. The juvenile stage has adult pelage; in males the scrotum remains black and the testes have not yet descended. On average, subadult females bear their first infant at about 43 months of age. Secondary sexual characteristics appear during this stage for both sexes. Adulthood for females is judged to occur with full size, while for males the scrotum is in its last stages of whitening and the other secondary sexual characteristics become fully developed. We have not attempted to revise population statistics based upon Carpenter's age criteria. If by "infant" one refers to a young monkey under one year of age (which would have the advantage of using a designation roughly comparable to other monkeys), then some of Glander's juveniles would become infants.

Neville (1972a, 1976) used criteria involving the shape of the female genitalia, the head and throat of the males, and size in classification of ages of *seniculus*. The ages are again estimates based upon piecing together longitudinal observations on different individuals, but they indicate an infant stage from zero to 10-12 months, juveniles up to *ca.* 2.5 years, subadult females probably until *ca.* 3.5 years and subadult males very provisionally until 4.5 years. These age categories correspond better with the early Carpenter estimates (1934). Rudran (1979) classified immatures 10 months or less as infants and females then up to three years and males up to 3½ or four years as juveniles. Thorington (1979) and Braza (1978) consider the anatomical changes by presumed age and sex classes for *seniculus*.

Age estimates can also be given for *caraya* on the basis of the large collection of specimens from the Oregon Regional Primate Research Center's expedition to Argentina plus observations over at least two years on two young males maintained at the center. On the basis of the estimates of Malinow *et al.* (1968), the males were about three months old at time of capture. Their weight gain was as follows: from an assumed birth weight of *ca.* 250 gm to *ca.* 1.7 kg at six months, 3.0 kg at one year, 3.7-4.3 kg at 1.5 yr., 4.5 kg at two yr., and to *ca.* 4.8 kg at 2.3 yr. Permanent lower dentition appeared as follows: M1 at about seven mo, I1 at *ca.* nine mo, M2 at *ca.* 11 mo, I1 at *ca.* 12 mo, C, P1 and P2 at *ca.* 18 mo, and P3 and M3 at about 19 mo. Stahl *et al.* (1968) noted that sexual maturation in both sexes occurred at a body weight of about 4.0 kg. If these weights are equivalent to weights of similar-aged *palliata*, and if the Oregon group's estimates for the age at capture is correct, then, as suggested by Glander's (1980) work, even Carpenter's (1934) age estimates are inflated.

Froehlich *et al.* (1981), however, argue that the aging technique (dental strontium-90 content) used by Malinow *et al.* (1968) and Pope (1968) is inaccurate (see also Rosenthal, 1968). Pope's dental wear data are similar to those of Froehlich *et al.* for *palliata* but according to them the correlates between Pope's relative adult ages and absolute ages estimated by strontium-90 content are very low. The developmental data presented by Stahl *et al.* (1968) are, for these reasons, biased by overestimating the young ages (Froehlich *et al.*, 1981). Thorington *et al.* (1984) conclude that if the rate of tooth wear is similar for Pope's (1968) *caraya*, *palliata* on BCI (Froehlich *et al.*, 1981) and in their population of *caraya* on the Río Paraguay, then all three populations have similar age profiles.

The problems of the use of different criteria by different workers, even with respect to the same species, and the difficulty of making estimates while observing free-ranging monkeys should be kept in mind when making comparisons of age-category proportions among the various studies. See also Smith (1977) for comments on the resulting problems.

As noted earlier, *A. palliata* has been studied so much more than the other species that it is often used as a kind of *type* species to indicate the major aspects of behavior in the genus. The extensive studies and repeated censuses on BCI have provided an image of the howling monkey as living in groups averaging three to four adult males, seven to 10 adult females, and roughly the same number of immatures, with an average group size of 15 to 19 (Carpenter, 1934; Milton, 1975, 1977, 1982; see Table XIV). Milton (1982) found no statistical difference in her group size and composition estimates from those of Carpenter in 1932 and 1935 (Carpenter, 1959). The most extreme BCI census figure is that of Collias and Southwick (1952) in 1951 with severely reduced group sizes. They suggested that the census was recording the effects of a yellow fever epidemic (to which howlers are extremely susceptible). Indeed, the high mortality rates of *Alouatta*, *Aotus*, and *Saguinus* from jungle yellow fever have been used as a way of detecting the beginning of epidemics in Panama which could endanger humans (Galindo and Srihongse, 1967). Recently, Rudran (1979), on the basis of his observations of infant-killing in *A. seniculus*, suggested that infanticide may have significantly contributed to the 1951 population crash, though it is not clear why it should have been so severe at that particular time. The 1967 censuses of Chivers (1969) and Smith (1977) are also relatively low. Froehlich *et al.* (1981) suggest that there are variations in juvenile mortality dependant on extreme oscillations in environmental conditions. The population age profile they provide for the BCI howling monkeys in 1976 shows a lack of seven year old animals. Extremely heavy rains in the early dry season affected pollination adversely, leading to a failure in the fruit crop in 1970 (Foster, 1982) and they suggest that this caused a high mortality of one year old juveniles which had inadequate toxin tolerance to cope with a nearly total leaf diet. Froehlich *et al.* suggest that an absence of 15-16 year old males in the 1976 profile might be the result of a similar early dry season phenomenon in 1963, when they would have been 2-3 years old. Milton (1982) also emphasizes food availability as the important limiting factor to population growth and that group size and composition and the distribution of groups on the island reflect adapatation to the distribution and quality of their foods.

TABLE XIV

Group composition averages from published studies with large data bases. [a]

Site Author (date publ.), date of study	Number groups	Group composition AdM	AdF	Juv.	Inf.	Group size Mean + s.e.	Nº 1M groups	Soc. sex ratio	Repro. rate	Largest group
				Alouatta palliata						
Barro Colorado Island, Panama										
Carpenter (1934/1964), 1932 [b]	23	2.7	7.4	4.0	3.1	17.3 ± 1.5	4	0.34	0.42	35
Carpenter (1934/1964), 1933 [b]	28	2.9	6.9	4.2	3.4	17.5 ± 1.3	3	0.43	0.51	29
Carpenter (1934/1964), 1935 [b]	15	3.3	7.0	5.4	2.5	18.2 ± 1.8	2	0.47	0.36	34
Collias & Southwick (1952), 1951	29	1.2	4.7	1.1	1.2	8.2 ± 0.6	23	0.27	0.27	17
Carpenter (1962/1964), 1959 [b]	44	3.3	9.1	3.1	3.0	18.5 ± 1.4	6	0.36	0.34	45
Chivers (1969), 1967	12	3.3	6.0	2.9	2.5	14.7 ± 0.7	0	0.56	0.42	18
Smith (1977), 1967	25	2.9	7.0	1.8	2.1	13.8 ± 1.2	3	0.42	0.30	31
Mittermeier (1973), 1970	6	3.2	5.8	4.3	2.8	16.2 ± 1.7	0	0.54	0.49	23
Milton (1975), 1974	6	3.8	7.7	6.7		18.2 ± 1.1	–	0.49	–	–
Hacienda Barqueta, Chiriquí Province, Panama										
Baldwin & Baldwin (1973), 1970-71 [c]	8	3.9	8.0	3.8	3.3	18.9 ± 2.4	0	0.49	0.41	28
Santa Rosa National Park, Guanacaste Province, Costa Rica										
Freese (1976), 1971-72	9	1.4	3.2	1.8	0.8	7.2 ± 2.6	5	0.45	0.24	24
Finca La Taboga, Guanacaste Province, Costa Rica										
Heltne *et al.* (1976 1966-71 (nine censuses)	11.3	2.4	5.5	2.4	1.2	11.5 ± 2.1	–	0.44	0.21	39
Finca La Pacífica, Guanacaste Province, Costa Rica										
Heltne *et al.* (1976) 1967-70 (three censuses)	5	2.3	5.5	2.3	1.5	11.7 ± 1.7	–	0.42	0.28	27
Los Tuxtlas, Veracruz, Mexico										
Estrada (1982)	17	3.0	4.1	0.8	1.2	9.12 ± 2.9	1	0.73	0.29	16

(Cont.)

TABLE XIV (Cont.)

Site Author (date publ.), date of study	Number groups	Group composition AdM	AdF	Juv.	Inf.	Group size Mean + s.e.	Nº 1M groups	Soc. sex ratio	Repro. rate	Largest group
				Alouatta pigra						
Bermuda landing, Belize										
Bolin(1981)	13	1.1	1.1	1.3	0.7	4.2 ± 1.5	12	0.93	0.6	7
Horwich & Gebhard (1983)	9	1.6	2.1	2.0	0.4	6.8 ± 1.8	4	0.79	0.21	10
				Alouatta caraya						
Tragadero Sur Island, Paraná River, Argentina										
Pope (1968), 1964 [d]	17	3.2	2.8	1.6	0.4	7.9 ± 0.8	3	1.13	0.13	14
Chaco Region, Paraguay (or Brazil?)										
Krieg (1928) [e]	9	2.1	2.8	0.2	0.8	5.9 ± 0.8	3	0.76	0.28	10
Rio Paraguay, Puerto Bermejo, Argentina										
Thorington *et al.* (1984) [j]	11	1.9	3.7	2.3	0.9	7.6 ± 3.3	5	0.52	0.24	14
				Alouatta seniculus						
Northern Colombia (census survey)										
Struhsaker *et al.* (1974), 1974 [f]	20	3.5	2.9	1.7	1.1	9.5 ± 1.1	2	1.21	0.36	26
Hato Masaguaral, Guárico State, Venezuela [g]										
Neville (1972a), western 1969-70	26	2.5	2.8	1.8	1.4	8.5 ± 0.3	3.5	0.87	0.51	14
Neville (1972a), eastern 1969-70	5	2.8	3.4	1.4	2.0	9.6 ± 1.8	1	0.82	0.59	14
Neville (1976), western 1972	19	2.3	2.8	2.2	1.4	8.6 ± 0.6	6	0.82	0.49	15
Rudran (1979), 1976-78	28	1.7	2.5	3.3	0.7	8.9 ± 2.5	7.5	0.68	0.28	14
Hato del Frio, Apure State, Venezuela										
Braza (1978), 1975-76 (La Carmena) [h]	5	1.8	3.0	1.4	1.4	7.6 ± 1.1	2	0.60	0.47	11
Braza (1978, 1981), 1975-76 (general) [h]	141	1.6	2.6	1.0	1.1	6.3 ± 2.1	–	0.64	0.44	13
El Tuparro, Colombia										
Defler (1981)	10	1.9	2.4	1.1	1.1	6.5 ± 2.1	3	0.79	0.46	9

(Cont.)

TABLE XIV (Cont.)

Site Author (date publ.), date of study	Number groups	Group composition AdM	AdF	Juv.	Inf.	Group size Mean + s.e.	Nº 1M groups	Soc. sex ratio	Repro. rate	Largest group
				Alouatta fusca						
Cantareira Reserve, São Paulo, Brazil Silva (1981)	25	1.8	2.4	1.2	0.4	5.8 ± 2.5	9	0.55	0.16	11
Caratinga Ecological Reserve, Minas Gerais, Brazil Mendes (1985)[j]	19	1.2	2.3	2.1	0.9	6.8 ± 2.0	16	0.50	0.41	10

[a] Groupings of only one or two monkeys are not included. AdM = adult males, AdF = adult females, Juv = juveniles, Inf = infants. Nº 1M groups = number of groups with only one adult male. Soc. sex ratio = socionomic sex ratio = AdM/AdF. Repro. rate = reproduction rate = Inf/AdF.

[b] Carpenter's "mothers" and "females" (1934/1964, Table 1) are summed into AdF, and his three subdivisions each of infants and juveniles are lumped into "Inf" and "Juv" respectively.

[c] Three of the groups occasionally travelled peacefully together for aggregations of up to 65 monkeys; the other groups showed normal intergroup hostility (Baldwin & Baldwin, 1972b).

[d] The entire population of the island was collected except for some females with infants spared by the hunters. Solitary males were added to the composition of the nearest group: this artificially increases the socionomic sex ratio. Pope's pregnant and non-pregnant females were lumped (17 of the 58 females were pregnant).

[e] Males undergoing color change have been added into the adult male category. Krieg's "not grown males" have been classified as juveniles. Four of 25 females were pregnant.

[f] The only survey included in this table because of the necessary inaccuracies of survey counts. Even this survey noted possible duplicate and incomplete counts. The group mean count includes an average of 0.26 unsexed adults. "Subadult males" are lumped here with juveniles because of their definition of subadult males as males smaller than adult males with undescended testes: *seniculus* differs from *palliata* in having early testes descent (Thorington *et al.*, 1979).

[g] "Western" refers to areas west of the main highway dividing the ranch, "eastern" to the riverine forest area east of the highway. Most or all of Rudran's census appears to be in the western forests. Rudran's total includes 0.6 subadults per group and is from the terminal counts on groups. Neville's counts group subadults with adults and are averages (when available) of initial and terminal counts. The number of one-male groups for both Neville's and Rudran's censuses are given as averages of initial and terminal counts and for groups in which one adult and no subadult males appear; if groups qualify for this category which have one adult male and any number of subadult males then the numbers are 14 (Neville 1972a, western), 1 (Neville 1972a, eastern), 10 (Neville 1976, western), 12.5 (Rudran 1979). See text for discussion of age-group problems.

[h] "La Carmena" is the forest area intensively studied; "general" refers to encounters with social groups of more than two monkeys throughout the ranch and hence would reflect many replicate counts.

[j] Subadults included as juveniles.

Another *palliata* population with small groups occurs on Coiba Island off the Pacific coast of Panama. Milton and Mittermeier (1977) counted an average of six in four groups (plus a solitary male and a heterosexual pair), two of those groups having only one adult male and two, three adult males. No juveniles and only three infants were seen, which suggests that either the counts were incomplete or that the animals were under severe pressure of some sort. Froehlich *et al.* (1981, 1982b) compare the BCI *palliata* population with that of the small Orchid Island, nearby and to the north. They found that 50% of the Orchid Island population was over 13 years old in 1976 and that infant survival and juvenile recruitment had been extremely low during the previous decade. They suggest that the population is severely food-limited.

Freese's (1976) data from Santa Rosa National Park also indicated small groups (Table XIV), though five of the counts may be incomplete; also, he noted that the habitat seemed inferior for *Alouatta* because of the restricted evergreen forest. Similarly, Heltne *et al.* (1976), doing repeated censuses at two Costa Rican sites in Guanacaste Province, found small groups on the average (though the largest groups compared with those of BCI) and felt that the situation was "a picture of a distressed and declining population." Yellow fever was ruled out as a cause of (presumed) population decline. At Taboga, where the data most clearly indicated such a decline, howlers were seen fighting and injured, and forest cutting was continuing.

Cohen (1969) has attempted a mathematical analysis of Carpenter's proposition about central tendencies in *palliata* group composition and size. Cohen's BIDE model is based upon assumptions of independence among individuals within a group. Birth, death, and emigration rates are considered strictly proportional to the size of the group (or of the age/sex category, if this is being examined), and the probability of an extra-group animal joining a group is considered independent of the group's size. This leads to the prediction of a Poisson distribution of frequencies, which corresponds fairly well with the actual distributions. Donald Sade has reasonably objected to the constancy-of-immigration assumption of the BIDE model, and Cohen (1972) has suggested an adjustment. Such model-building involves a spiral of proposing evermore complicated (and biologically realistic) models and testing these with evermore massive amounts of data. As Cohen puts it, "A field worker who invites home a realistic model has opened the door to a creature with an enormous appetite for data. Yet if quantitative studies of the genetic structure of primate populations are to have a firm foundation in population dynamics, there is no other choice.".

It remains possible that the intraspecies variation away from the "norm" of BCI, which is being discovered in *palliata*, is a result of environmental stresses and is, in a sense, evidence of strikingly unfavorable conditions rather than simply representing a series of variations in response to varieties of normal howler habitat.

If *A. pigra* is indeed a separate species from *A. palliata*, or if *pigra* represents a subspecies of *palliata* with significantly different behavior as well as morphology, then Bolin's (1981) and Horwich's (1983a, 1983b, Horwich and Gebhard, 1983) studies of *pigra* at Tikal in Guatemala and around the Bermuda Landing in Belize are of major importance in demonstrating a taxonomic behavioral difference. Bolin (1981, pers. comm.) found that all of the three groups she worked with at Tikal and 11 of the 13 she studied in Belize had a monogamous structure of one adult male with one adult female plus offspring. Thirteen groups at the Bermuda landing averaged 4.4 animals with a 1:1 sex ratio. Horwich (1983b) later observed nine groups averaging 6.22

individuals at the Bermuda Landing and Coelho *et al.* (1976b) observed four groups averaging 6.25 individuals per group at Tikal (Table XIV). Even if the data turn out to not have taxonomic relevance, they are still very exciting in presenting a problem concerning the factors producing this unexpected group structure. One possibility, of course, is that this is the end result of population stress in very marginal habitat (where the stress and marginality may stem from human activities). As noted earlier, Bolin (1981) saw unusual degrees of paternal behavior, which one would predict in a naturally monogamous species or which would indicate an unsuspected degree of behavioral plasticity if the monogamous structure is a result of recent stresses.

A comparison of *A. palliata* to *A. caraya, A seniculus* and *A. fusca* (Table XIV) shows that the latter three species are more similar to each other than to *palliata*. The limited information for *belzebul* indicate that group sizes are also smaller than those of *palliata* (2-8 individuals per group; Branch, 1983). Ayres and Milton (1981) suggest that groups are typically one-male. The socionomic sex ratio tends to be low in *palliata* and roughly one in *caraya* and *seniculus*, while the group sizes of *palliata* on BCI (most years) and even at the overcrowded HBC site of Baldwin and Baldwin (1973) are about double those reported for *caraya, seniculus* and *fusca*. Even in the Collias and Southwick (1952) census of BCI and at those other *palliata* sites where the groups are roughly the size of typical *caraya* and *seniculus* groups, the socionomic sex ratio remains typically *palliata*. Scattered reports from the literature giving the counts of one or a few *seniculus* groups tend to correspond also to the larger *seniculus* samples.

Particularly extensive discussions of the implications of the age-sex compositions reported in various studies can be found in Carpenter (1934, 1953), Collias and Southwick (1952), Chivers (1969), Heltne *et al.* (1976), Neville (1976), Thorington *et al.* (1979, 1984), Rudran (1979), Otis *et al.* (1981) and Froehlich *et al.* (1981).

Population Density

Population density figures can be used for various purposes. They can testify as to the appropriateness of a particular habitat for the species studied, they can (through the estimation of "carrying capacity") on occasion predict maximal steady-state populations of that species, they can indicate through their variation in time the alteration of conditions in an area, and they can be used (if sufficiently accurate) to predict total species populations in a larger area (e. g., census work through transects). There are a number of problems with the accuracy or meaning of population density figures. If they are derived from a rapid survey, they will be dependent upon the chance of spotting the monkeys and the representativeness of the portion of the habitat surveyed. If they are derived from one particular habitat, their extension to another is problematical; this problem is increased when one considers that habitat alteration effects by humans can be as subtle as variation in hunting pressure. Calculation of population density figures also depends upon whether portions of the area have been excluded as being unrepresentative of the general habitat or area that is being analysed. Thus Rudran (1979) obtained two different population density estimates for the HMG *seniculus* by excluding different portions of the area on various environmental grounds: these two estimates differed considerably (118 and 150 howlers/km^2). The HMG estimates also demonstrate the usefulness of population density figures in tracking changes in populations. Neville (1972a) obtained a figure of 87/km^2 for his 1969-1970 work using a calculation methodology comparable to that which produced Rudran's 118, and Neville's (1976) 1972 census indicated that overall population growth was occurring. Rudran felt that his figures demonstrated a continuation of the trend and attributed much of the population expansion to protection of the flora and fauna by the ranch owner.

As is to be expected, the BCI figures present the clearest demonstration of population variation over time. Carpenter's 1932 and 1933 (Carpenter, 1934) surveys indicated an increase from 26 to 31 *palliata*/sq.km, the Collias and Southwick (1952) 1951 study, presumably just after a yellow fever epidemic, recorded a reduction to 15/sq.km, and subsequent surveys have shown some oscillation around slightly higher figures. In particular, Chivers (1969), from intensively worked areas on the island, estimated a population density range of from 60 to 82 per km^2. He also predicted a maximal carrying capacity for the island of 249/sq.km, or 3860 monkeys in all. Smith (1977) calculated that the increase between 1951 and 1959 was 241% and between 1959 and 1967 about 37% or approximately 4% a year; a slowing which indicates that the howling monkey population was near saturation in 1967. Froehlich *et al.* (1981), however question this on the basis of the age profile and conclude that at least part of the BCI population was still growing at an annual rate of 1.5%. Milton (1982) analyzed demographic data for BCI from censusing during three years (1977-1980). She concluded that there had been no population growth during the previous six years and that, as predicted by Smith (1977), the island was saturated with howler monkeys. Milton discounts the yellow fever argument for the population decline and argues that food availability (particularly severe periodic shortages, see Foster, 1982 and section on Group Size and Composition) sets the limit to population size. She ruled out immigration and emigration, and concluded that mortality, resulting from food scarcity and parasitism particularly affecting juveniles (see Froehlich *et al.*, 1981), is the key factor involved.

Eisenberg and Thorington (1973) demonstrated the relative importance of *Alouatta* and of the primates in the mammalian fauna of BCI. The edentates, particularly the sloths (arboreal folivores), make up over 52% of the non-chiropteran biomass. The Dasyproctidae (Rodentia: *Agouti paca* and *Dasyprocta punctata*) are the most important family with 8.5%, and the Cebidae are the third most important group with 6.8% for *Alouatta* and 0.8% for *Cebus capucinus*. This they compare with biomasses calculable from data resulting from the "Operation Gwamba" salvage conducted by the International Society for the Protection of Animals during the flooding of lowland behind the Afobaka Dam on the Upper Suriname River (Walsh and Gannon, 1967). Deer and tapirs were much more important than other mammals in Suriname (in biomass), but the sloths still contributed over 22% of the non-chiropteran biomass and *Alouatta seniculus* 5.7%. On BCI the arboreal browsers (the sloths *Bradypus tridactylus* and *Choloepus didactylus* plus *Alouatta*) therefore contributed about 60% of the nonchiropteran biomass, about twice that of the Suriname site; but at both sites the biomass invested in arboreal browsers is impressive. Eisenberg *et al.* (1979) compared BCI estimates (somewhat revised by subsequent work) to those made by various means in Guatopo National Park in the northern coast ranges of Venezuela and at HMG. At these sites the arboreal folivore component of the fauna was greatly reduced compared to BCI, which the authors attributed to the extensive secondary forest component of the Venezuelan areas. General biomass estimates ("crude", with no areas excluded from the computation) were 176.3 and 86.0 kg/sq.km for *A. seniculus* at HMG west and east of the main highway bisecting the ranch and 68.8 kg/sq.km at Guatopo.

Many of the other published long-term studies or surveys on *Alouatta* contain implied or actual population density estimates. Of these perhaps the most striking is that coming from the Baldwins' (1972b) study at HBC, where the *palliata* density estimate was 1050/sq.km. This exceedingly high figure is undoubtedly due to compression of the population by the progressive deforestation (which continued until the forest was destroyed). Some low density figures are indications of marginality of the habitat for howlers. Freese (1976) estimated 0.7-1.0 *palliata*/sq.km at Parque Nacional Santa Rosa in Costa Rica and emphasized the higher population levels of *Cebus* and *Ateles*, suggesting that the relative lack of mature rain forest was to blame. A special problem is presented by the lowland rain forest of Tikal in Guatemala: Coelho *et al.* (1974) estimated only five "*palliata*" (= *pigra*)/sq.km with *Ateles* density nine times as high. They felt that the howler population was greatly below the carrying capacity of the forest. Cant (pers. comm.) and Bolin (1981), who conducted longer studies at the site, confirm the relatively low number of howlers.

Day Range

This variable also relates to foraging needs. Mason (1968) defines *path length* as the total distance travelled, regardless of direction, and *travel distance* as the straight-line distance separating the remotest points on a day's trajectory. The data on path lengths are limited for *Alouatta*, partly because of the extended observation time necessary each day. The best published data are again from BCI. Bernstein (1964) reported a dry season average exceeding 200 m/day with some days over 1000 m, while Carpenter (1934) reported day ranges varying from 46 to 830 m with an average of *ca.* 180 m for his group 1 (the Laboratory Group) during the dry season. Altmann (1959) indicated an average of 109 m/day at the end of the rainy season, while Chivers gave an average of 284.4 m/day on a total of 56 group-days of three groups. Richard (1970) reported day ranges at the beginning of the rainy season varying from less than 23 m to 320 m and contrasted these with *Ateles* day ranges varying from less than 320 m to 2700 m. Finally, Milton (1980) estimated a mean travel rate of 360 m per hour and a mean distance of 443 m per day. Minimum distance was 104 m and maximum 792 m. They have a pattern of regular daily travel, not usually remaining in one place for several days and then travelling a large distance (say 1000 m or more) to a new section of their home range as was suggested by Carpenter (1934), Richard (1970) and Schlichte (1978). The Baldwins (1973) at HBC recorded ranging varying from 30 to 400 m/day (average 272) for their eight groups.

Neville (1972) estimated a day range of 580 m for *A. seniculus* in Trinidad. Sekulic (1982a) provides day range estimates for four groups of *A. seniculus* at HMG. The median was between 340 m and 445 m, with a minimum day range of 20 m and a maximum of 840 m. Gaulin and Gaulin (1982) emphasize the importance of including vertical as well as horizontal ranges when discussing field energy budgets. They estimated a typical day range of 706 m and vertical movements of 382 m per day. This larger day range is associated with the larger home ranges of *A. seniculus* in extensive and continuous forest compared to the small forest patches at HMG (see section on home range).

Young (1983) provides an estimate of 225 m as a typical day range for *A. fusca* at Caratinga. Mendes (1985) indicated slightly longer day ranges for groups of the same population; between 197 m and 540 m. No published data are available for *A. caraya* and *A. belzebul*.

Activity Patterns

For *palliata*, the best published analyses and descriptions appear in Carpenter (1934), Chivers (1969), Richard (1970), Mendel (1976), and Smith (1977), all with reference to BCI. Richard directly compared *Ateles geoffroyi* with the howlers: the spider monkeys were engaged in movement and social interaction much more than the howlers, spent much less time resting, and spent almost equal time in feeding. The pattern of foraging was different, with *Ateles* spending brief periods in any food tree, whereas *Alouatta* delays for long periods in suitable trees. Chivers (1969) recorded weather-related variations during the day and during the change from the dry season into the wet. The daily patterns were clearest in June, the driest and sunniest month: a very distinct feeding bout during the first few hours after dawn and another, less distinct, in late afternoon. Resting peaked at midday. In rainier July and August, the frequencies tended to smooth out, with feeding perhaps showing three peaks: shortly after dawn, late morning, and late afternoon. Activity was depressed during rainfall and also during periods of intense sun. From the reduced morning travel, Chivers suggested that the groups are moving out from habitual sleeping sites, returning to them nightly, and he also noted that there may be some ability to anticipate weather changes. These aspects, with perhaps the exception of Chivers' idea of habitual night positions, correspond with the general impression with respect to other *Alouatta* species or locations. All observers agree that what howlers do best is rest. Smith's (1977) statistics, for example, show adults resting at least 74% of the daytime, searching for and consuming food 15 to 22%, and engaging in social activities only 4%. Smith hypothesizes that low intragroup activity, as well as howling, serve to reduce intergroup activity which allows blood to be primarily directed to the digestive system rather than the voluntary musculature, and hence is a part of the howler folivore-frugivore adaptive specialization in relatively indigestible foods (see also Milton *et al.*, 1980; Milton, 1981).

Braza *et al.* (1981) contributed an extensive analysis of *seniculus* activities in the principal group in Hato del Frio. Their analysis is extracted from eight complete daylight periods in the rainy season and eight in the dry season, with observations taken from concealment to avoid disturbing the monkeys. The rainy season and dry season statistics showed that the howlers spent 18 and 15% of their time, respectively, in locomotion, 20 and 24% in feeding, 38 and 43% in sleeping, and 24 and 18% in other activities and resting. These statistics agree with the *palliata* data. The general schedule of the *seniculus* activities involved the most intense howling bouts after awakening until nine a.m. and again between four p.m. and 6:30 p.m., lasting until night fall. The most intense foraging is soon after awakening, during which time movement in the general area of the sleeping tree may occur. However, a nap will often follow, and later around midday there will be two naps (rainy season) or one (dry season). Activities may occur at any time throughout the day, however.

Sekulic (1982a) observed a seasonal change in the diurnal distribution of roaring bouts of *A. seniculus* at HMG. Although roaring is most frequent in the early morning in both seasons, the dry season was characterized by a higher frequency of early morning bouts and a reduced frequency around midday. Roaring bouts were more evenly distributed throughout the day in the wet season. Chivers (*palliata;* 1969) and Horwich and Gebhard (*pigra;* 1983) found similar seasonal patterns. Sekulic (1982a) suggests that this is, at least in part, related to climate. The cooler wet season imposes fewer restraints on the howler's activity but temperatures above 30°C and/or increased insolation around midday reduce their activity, when they seek shade. The phase of the moon influences the time of onset of the dawn chorus; it started as early as 169 minutes before dawn at full moon, less than a full moon was correlated with a later start, and no full moon generally resulted in the howlers starting their dawn chorus about 50 minutes before sunrise. Regarding other activities, Sekulic noted that the howlers spent progressively more time feeding and less time resting during a typical day in the wet season, whereas there were early morning and late afternoon feeding peaks in the dry season. The groups tended to arrive at their sleeping tree later in the day and remain active for longer in the dry season.

Sleeping Sites

No special work has been done on sleeping sites. The monkeys appear to use the horizontal branches of medium to large-sized trees, often ones in which they have been foraging. They sleep singly or in small groupings, with occasional shifts of location during the night being reported from the few overnight observations which lacked, however, special equipment for night viewing (Neville, 1972b). Neville (1972a) suggested that attacks by small predators on sleeping adult and subadult *seniculus* males, who often were separated from the other huddles in the group's sleeping tree, might account for scars, torn ears, and missing fingers seen on these monkeys. However, recent data, to be discussed in the section on "Intragroup Social Behavior", strongly indicate that intermale aggression caused the damage.

Silva (1981) recorded that members of *A. fusca* groups usually split into small parties of two or three when taking up their sleeping sites. They sit in a hunched position, huddled together, with their prehensile tails curled around the branch. The subgroups may use the same or different trees. Silva (1981) noted that howlers of his study area most frequently used the tops of *Araucaria angustifolia* pines and that this may result from the fact that, at a distance, the brown clusters of dead leaves and branches hide the monkeys.

Home Range

Table XV leaves the impression that home range data are only broadly comparable. This is to be expected, as habitat quality, population density, and group sizes will vary. Short studies should tend to underestimate group ranges: this is clearly proven by Chivers (1969), who showed the ranges drifting somewhat with each month, though there was little overlap in a given month. This led to the exclusively-used portion of his Group AA's range exceeding 90% each month but totalling only 37.5% over three months. Smith (1977), working at approximately the same time as Chivers, found no exclusive range. Collias in 1951 also recorded over 90% exclusively-used range for the BCI Laboratory Clan group during 30 days of following (Southwick, 1962). In Mittermeier's (1973) study, the percentage of range exclusively used by a group varied from 100% to 83% among six groups during a six-week period. Altmann (1959), with the Laboratory Group, had found only 71%. As shown by Chivers, longer-term data demonstrate less exclusive ranges.

The Baldwins' (1972b) study at HBC also produced extensive overlap, as three of seven groups had no exclusive range, and of the rest the greatest percentage of exclusive range was about 35%. Further study would probably have reduced known exclusive ranges. Their data fit the picture of the monkeys being compressed into ever-smaller forest by the ongoing habitat destruction.

Considerable variation in range size was shown by the groups at the beginning of the BCI studies when the population pressure was low, and this tendency was shown again by Clan 2 during the 1951 low population study. On the basis of the comparison with other studies, one wonders whether the estimation of the range used by the group studied by Hladik and Hladik (1969) was off by a factor of two: they report the area as approximate, and their indicated population density falls into the range of the studies by Mittermeier (1973) and Chivers (1969). The HBC (Baldwin and Baldwin, 1972b) and HMG (Neville, 1972a) studies, both based on seven groups instead of one, show a reduction of range per monkey, with population densities higher than those of BCI.

The most detailed study of ranging at BCI was carried out by Milton (1980). Two groups had home ranges ("supplying areas") of 39.23 and 43.73 ha. These could be traversed in a little more than an average day's travel (about 1.5 hours). Use of the ranges was related directly to the distribution of preferred food sources, particularly *Ficus*. From one to four different groups used various parts of the study groups' ranges, and for one of them a second group overlapped by 100%. When fruit supply was low, Milton noted more intergroup competition for food sources but no increase in territorial behavior, that is the patrol and defense of an exclusive area.

Howler monkeys are often pictured as classically territorial animals, with groups defending a relatively strictly delimited area, mainly by howling. However, the current view is that they are not so much territorial but, rather, antagonistic towards conspecifics not of their own group; that "they defend the place where they are" (Carpenter, 1965; Milton, 1980). Scent-marking may be involved in this defense. Howlers rub their throats and various other parts of the body on branches. Milton (1975) reported urine washing by *palliata*, which was performed more by adults than immatures and particularly often by adult males during social stress. Throat-rubbing is performed in both inter-and intragroup hostile interactions (Sekulic, 1982d; Sekulic and Eisenberg, 1983). Sekulic and Eisenberg (1983) found that both males and females rubbed equally on the approach of males but females rubbed more than males on the approach of females. Urination and scent marking are discussed in the section on "Expression and Communication". Feces could also be involved. Braza *et al.* (1981) indicate that the accumulation of excrement may be important in denoting sleeping sites.

Most observers have noted the preponderance of roaring (=howling) around dawn or during the hour after sunrise (Carpenter, 1934; Chivers, 1969; Baldwin and

TABLE XV

Some home ranges in relation to group size and overall population density

Study and group	Home range (ha)	Group size	Range/ group size	Pop. density (monkeys/ha)
Alouatta palliata (Barro Colorado Island, Panama)				
Carpenter (1934/1964) [a]				
Group I (Laboratory Clan)	76.0	30	2.5	0.31
Group 2	44.6			0.31
Collias & Southwick (1952) [a]				
Clan 1 (Laboratory Clan)	16.2	17	0.95	0.15
Clan 2	12.3	6	2.1	0.15
Altmann (1959), Laboratory Group [a]	15.1	14	1.08	–
Bernstein (1964) [a]				
Laboratory Group (Laboratory Clan)	17.5	17	1.03	–
SW Group	19.5	16	1.22	–
Chivers (1969) [a]				
AA (Laboratory Clan, monthly average)	7.9	12	0.66	0.60-0.82
AA (total range over three months)	11.6	12	0.97	0.60-0.82
Hladik & Hladik (1969)	25.0	13	1.92	*ca.* 06
Mittermeier (1973), over six weeks				
Group 1	7.3	14	0.52	0.52-0.66
Group 2	7.5	23	0.33	0.52-0.66
Alouatta palliata (Hacienda Barqueta, Panama)				
Baldwin & Baldwin (1972b), aver, seven groups	4.9	20.6	0.24	10.5
Alouatta palliata (Finca La Pacifica, Costa Rica)				
Glander (1974)	9.9	13	0.76	1.31
Alouatta palliata (Los Tuxtlas, Mexico)				
Estrada (1982, 1984), over 16 months				
Group S	60.0	14	4.29	0.23
Alouatta seniculus (Bush Bush Forest, Trinidad)				
Neville (1972a), WHT group	6.6	7.5	0.88	1.14
Alouatta seniculus (Hato Masaguaral, Venezuela)				
Neville (1972a), aver. seven groups	3.2	7.9	0.40	0.6-1.1
Sekulic (1982a)				
Group 71	5.1	9	0.56	1.77
Group 72	7.4	13	0.57	1.76
Group 73	3.9	9	0.43	2.31
Group 74	5.8	11	0.53	1.90
Alouatta seniculus (El Tuparro, Colombia)				
Defler (1981), aver. 10 groups	23.75	6.8	3.49	0.27
Alouatta seniculus (Finca Merenberg, Colombia)				
Gaulin and Gaulin (1982)				
Group 1	22.0	8.5	2.58	0.38
Alouatta fusca (Caratinga Biological Station)				
Mendes (1985), aver. 19 groups	5.8	6.8	0.85	1.17

(Cont.)

Table XV (Cont.)

[a] Calculations from Neville (1972a, Table 8).

Baldwin, 1976; Sekulic, 1982b, 1982d; Horwich and Gebhard, 1983), although Mendes (1985) and Young (1983) record a peak in howling by *fusca* groups in the late afternoon, between 1600 and 1800. Chivers (1969) concluded that howling was important in maintaining a distance between the groups and influenced the daily ranging patterns of each. Neville (1976b) and Mendes (1985) noted that the howling or proximity of another group or solitary individual increased the probability of howling. Close groups may even approach each other (Neville, 1976b; Chivers, 1969). Horwich and Gebhard (1983) found indications of territorial defense in *pigra*. For one of their groups, 91% of the calling bouts were within 100 m of the range border (see also Mendes, 1985). In three incidents, an invading group was chased across the border.

Sekulic (1982a) found no relationship between the position of the group in the home range and the onset of the dawn chorus in four *seniculus* groups at HMG. The frequency of intergroup encounters (defined as vocal response to a group within 100 m) was similar between the dry and rainy seasons, although the howlers called more during encounters in the former. Sekulic suggests that this may be partly due to defense of more restricted food supplies. Sekulic (1982d) concludes that, although the dawn chorusing may serve as a positional cue for groups using overlapping home ranges, the principal function is not in territorial defense but as a means of female defense; assessing opponents, while avoiding chasing and fighting. This is discussed further in the section on howling behavior.

Howling was also a typical reaction at densely-populated Barqueta when two groups came within 50 m of each other. In agreement with Sekulic (1982d), the Baldwins (1974) feel that the appearance of howling in some fear situations indicates that rather than a territorial marking, such intergroup roaring "is to be related to fear, retreat and avoidance responses." Howling can regularly occur between mutually-visible groups at zoos, where one might have expected habituation to take place given the impossibility of avoidance and the regularity of visual contact.

The nature of intergroup relations will be returned to in the sections on "Relationships among Adult Animals and Peripheralization of Group Members".

Relations with Other Animals

(1) *Other monkeys*

Howlers have generally been observed to be neutral in their relations with other monkeys. When interactions occur, they are usually initiated by other species. Kidnappings of howler infants by *Ateles* females have been noted by a number of observers on BCI: these appear to result in the death of the infant through lack of nourishment after it has been carried by one or more of the females for a few days (Richard, 1970; Eisenberg and Kuehn, 1966). Klein (1974) in Colombia saw three approaches of *Ateles* monkeys towards *Alouatta seniculus* females with infants. The mothers shielded the infants or withdrew with them. DuMond (1967) described howler deaths resulting from chases by uakari monkeys in a mixed-species compound at Monkey Jungle in Florida. Young (1983) and Mendes (1985) observed *Brachyteles* displacing *A. fusca* groups from their feeding trees but interactions with *Cebus apella* were generally characterized by little reaction from either species (Mendes, 1985).

(2) *Predators*

Healthy adult howlers in trees are probably only threatened by the Felidae, large Mustelidae (e. g., possibly *Eira barbara*) and snakes among the nonhuman predators. Young howlers, however, could potentially by carried off by large birds. This presumably explains the alarm behavior that Carpenter (1934) noted in an interaction with a flock of black vultures *(Cathartes urubu)*, though he also reported indifference during proximity to Gresibreck's hawk *(Leucopternis ghiesbreghti costaricensis)*, guans *(Penelope cristata cristata)* and toucans *(Rhamphastos swainsonii)*. Some South American birds are potent predators of small monkeys. Fowler and Cope (1964) found that *Cebus* monkeys were the most common prey at two different nests of the harpy eagle *(Harpia harpyja)* in Guyana. Rettig (1978) also found that *Cebus*, along with the two-toed sloth, *Choleopus*, were the most frequent prey of *Harpia* in Guyana, according to remains at a nest during 328 days. They found evidence of just one howler, *A. seniculus*, taken during this time.

Interactions with other mammals are also rare. Carpenter (1934) saw an attack by an ocelot *(Felis pardalis*, semi-arboreal), which was driven off by the adult males, who rushed toward the wounded juvenile "roaring as I have rarely heard howlers roar." Rohl (1959, Fig. 41) reproduces an illustration from Brehm's *Tierleben* which shows a jaguar *(Panthera onca)* in a tree facing a band of excited *Alouatta*. Howlers do not like to be on the ground but will descend if necessary (e. g., on occasion for water or for movement from one tree group to another: Rudran, 1979; Neville, 1972a; Braza, 1978). On the ground, however, they are subject to predation by terrestrial animals, and, particularly in the vicinity of human establishments, dogs probably kill some howlers.

(3) *Humans*

Carpenter (1934) described various reactions of *palliata* to human observers; ignoring an accustomed, neutral observer; an initial burst of vocalizations followed by usual activities when contact with man is frequent and non-harmful; continued aggressive vocalizations when contact is infrequent; and a quick and silent disappearance when the animals have been hunted. The major vocalizations would seem to be (using Altmann's 1959 terminology) C and D barks with A and B roars and wails indicating greater excitement; these correspond roughly with Carpenter's types 9 and 1 (1934: Table 4)." (Neville, 1976b)

In addition, many observers have reported that excited howlers break off and drop branches, urinate, and defecate. Neville (1976b) found that branch-breaking behavior was variable among locations, groups, and individuals for *seniculus*. Defecation and urination as defense also appear variable. Neville postulated that the tendency of the monkeys to approach the observer under some conditions, together with the natural reaction of elimination under stress, has led to the appearance of fecal or mictural attack, and indeed the success of the behaviors has probably led to selection for conditional approach. Branch-breaking was often done by distant monkeys, but again the success of the reaction when the monkey was overhead has probably reinforced approach tendencies. It would be interesting to know to what extent there is a genetic backing for the howlers' defensive behavior.

Howlers were not hunted for food on BCI nor on some of the protected ranches. However, howlers are sometimes shot for sport, scientific purposes, or, in many parts of the tropical Americas, are intensively hunted for food. Mittermeier (1977) found that *A. seniculus* is the most frequently shot of the Suriname monkeys, and Soini (1982) reported that the distribution of *seniculus* in Amazonian Peru is patchy because of extensive overhunting. The PanAmerican Health Organization Census of Peruvian primates estimated (Castro *et al.*, 1975-6; Neville, 1974) that a minimum of 167 howlers were sold for food in the markets of Iquitos alone over a period of approximately six months in 1973. In the remainder of the protein-starved Peruvian Amazon, howlers were still more important as food, and it can be assumed that this is true throughout much of tropical lowland South and Central America. Some howler behaviors, such as the group-spacing vocalizations, barking at observers, and approaching to urinate, defecate, or drop a branch over an enemy, are counter-productive when the enemy has a gun.

VI. INTRAGROUP SOCIAL BEHAVIOR

Birth and Development of the Young Animal

We refer the reader to the criteria used in establishing age-stages which were given earlier (in the section on "Group Size and Composition" and in Table XIII). An overall picture of the alteration in behavior which accompanies physical maturation can be obtained by fitting together descriptions of various aspects of the process which appear in a number of papers; unfortunately, the papers treat one or the other of the three most-studied species, but it is reasonable to assume that behavioral ontogeny follows a fairly similar course in all three. The following developmental descriptions are largely taken from Carpenter's (1934) monograph and Altmann's (1959) observations on a young mantled infant during the (estimated) age period of seven through 34 days, Neville's (1972b) and Mack's (1979) papers on HMG *seniculus*, and Neville's (1979) studies of the *caraya* groups at Riverbanks Zoo. Mack's study, which focused on eleven infants between the ages of one to nine months during five months, can be specially emphasized for its quantitative data. In addition, Baldwin and Baldwin (1978) present much developmental material for HBC *palliata* in their discussion of phases of exploration and play: this will be considered in both this and the following subsections. After the preliminary treatment of maturational changes, we will consider the relation between adults and immatures.

We are not familiar with any detailed published observations of the actual birth, though Carpenter (1934) describes the mothers handling and licking presumably just-born infants, who actively climb up their ventrums. Glander (1980) has seen still-wet newborn. Glander also reports that females loose aggressiveness and drop in dominance during the week prior to parturition, and that new mothers (except for the primiparous) continue to avoid confrontations after the birth. Newborns are relatively immobile; their tails, which later play such an important role in locomotion and suspension, tend to dangle in nonfunctional corkscrews. At first, the infant's tail is so short that when it is carried well forward on its mother's ventrum, it could not be employed in any case in the classic wrap-around-the-base of its mother's tail which it uses later. The tail tip begins to be appropriately used at about one and one-half to two months of age. The classic dorsal riding position involves the infant mounted on the lumbo-dorsal section of its mother's back with its tail wrapped around her tail root. Altmann saw it as early as the 14th day and Carpenter between the third and fourth week, while Neville saw it at ten weeks and Mack notes a general change-over from ventral to dorsal after two months in red howlers. Occasional ventral carries during the fourth month have been noted by both Mack in red howlers and Neville in black. Altmann's mantled infant could hang by its tail by its 31st day.

Altmann's mantled infant left its mother at 15 days of age, while Neville saw a red howler infant leave its mother at less than seven weeks and two of the Riverbanks zoo black howlers moved independently on their 56th and 66th days respectively. Thereafter, the infant's independence and its degree of interaction with other monkeys increases rapidly, though Mack notes that during the first four months the infant is rarely more than two meters from its mother. However, an infant may leave its mother much earlier than this because it has either accidentally crawled onto an adjacent monkey or because it has been "kidnapped" or borrowed from its mother. This latter phenomenon results from the great interest which especially adult and juvenile females express in young infants (see below).

Mack comments that "the frequency and duration of nursing did not decline through the ninth month..., even though an infant begins eating solid foods as early as the second month...". Judging from the breasts of their mothers, Neville felt that red howler infants could still be nursing at ten months, and Mack felt that juveniles up to 18 months would regularly nurse for long periods when resting next to their mothers. It is very possible, of course, that the latter nursing provided only "comfort". Carpenter (1934) estimated that weaning "occurs when the juvenile is between a year and a half and two years old".

Both male and female black howlers pass through a color change from the juvenile lemon-yellow phase which leaves the males coal-black and the females a dark yellow. Shoemaker's (1978) data indicate that for both sexes the color change begins at about two and one-half years of age and is completed approximately six months later. Males are larger than females of the same age throughout this time; during the darkening they pass through a female-colored phase. Neville (unpubl. manuscript) saw sexual activity, including copulation and tongue-flicking, in a pre-color-change, two-year old male, and Shoemaker (1978) indicates that it probably occurred for another male at about the same age. Shoemaker (1979) presents data suggesting that a *caraya* female became pregnant at about two years of age and delivered a live infant approximately six months later; certainly Neville (1979) saw copulation by at least 31 ½ months for a female. These early ages for the commencement of sexual activity suggest that monkeys that function socially as juveniles in the wild may have the potential for reproduction much prior to the time that they physically appear fully adult. *A. palliata* also give birth as subadult females, that is, before 48 months of age (Glander, 1980).

We now consider specifically the relationship between adults and immatures, taking as topics (1) the infant to the mother, (2) the infant to other females, (3) the infant to the adult male, and (4) the juveniles and subadults to adults.

(1) Howler infants appear to receive rather passive mothering, with the mother showing few positive reactions, including little grooming, but rather being accomodative and tolerant (Carpenter, 1934; Altmann, 1959; Neville, 1972b). Baldwin and Baldwin (1973), in the most detailed analysis of the development of the relationship between mothers and infants, came to a similar conclusion, but did manage to demonstrate the subtleties of a relationship which is actually more extensive than others had indicated. Even with infant-1s, however, they report that most of the mother-infant interaction was due to the infant's initiative or was in response to an independent behavior of the mother, even to the infant securing itself for transport. They report that the infant-2 may travel independently of the mother during slow group progressions, but usually remained within two meters of her. The mother would often wait for her infant to mount for a transfer over a gap. "Squeak" vocalizations were sometimes made as the infant approached the mother to ride, and this vocalization was also used by infants seeking contact with a "base-of-explorations" adult female (one not its mother). Others have also commented on this vocalization by an infant on approaching its mother (Neville, 1972b; Lundy, 1954). Carpenter (1934) reported seeing a female give a terminal twig with buds to a small infant-2 associated with her after the female had eaten some of the buds. No one else has reported one howler feeding another except through lactation, and, indeed, reports of such feedings are very rare among monkeys in general.

Infant-3s spent four to eight hours per day off the mother, and usually travelled separately but within 10 m of her. The Baldwins note that a "caw call" as well as the "squeak" was used by the infant-3s during separation from their mothers in difficult locomotor situations. The Baldwins also document responses by the mother to the infant's approach: "The mother's gesture was to reach out her arm closest to the infant, gently put it over the infant's back and pull the infant toward her lap with the loose, relaxed arm". "Eh" vocalizations were used by approaching infants or infants waiting for maternal response. Response to an endangered infant, however, was very variable. One fallen infant not even not retrieved: the mother moved to rejoin her group after only a two-minute wait for the silent infant to reappear after it had failed to complete a difficult jump (the silence of the infant may have been an important factor in this desertion). The Baldwins commented that falls were more infrequent at HBC than on BCI, and that this, and the low level of adult response to the falls, might be due to the lower and more densely foliated forests of Barqueta. Females involved in exciting activities, e.g., consort relations with males or vocal confrontations with another group, tended to ignore their infant-3s.

(2) Other females are often interested in infants, especially young infants. Carpenter (1934) observed that females and unsexed juveniles would surround a

mother with a newborn infant and attempt to touch it: the mother, in the two cases observed, attempted to thwart these contacts. Altmann (1959) also noted this interest in the young infant he was following. During the estimated age period of seven to fourteen days, other adult females with their associated infants would approach the new infant, whose mother quickly carried it away. During the period of 21 to 27 days, however, the infant was interacting more directly with the other group members. Altmann describes as typical an instance when the infant climbed onto the back of an adult female, who, with her associated juvenile-2, had approached the infant and her sleeping mother. The other female, carrying the infant and with her juvenile, moved three meters away, and for 20 minutes the infant clambered over and around the two. The mother finally came up to the grouping, and, when the infant had crawled onto her shoulders, returned to her position.

The Baldwins described little interest in infant-1s other than the approach by an adult female to gaze at the infant. They noted three occasions when the crawling infant was carried up to one meter away by another female, but the infant in each case "scampered back to its mother when the adult female stopped". Adult females twice carried an infant-2 other than their own, the infant returning to its mother when the female had stopped. They saw the occasional use by an infant-2 of an adult female other than the mother as a "base of operations", to be returned to or touched periodically or even clung to for up to 30 seconds during periods of exploration or play. The females were tolerant but unresponsive to such contacts. The one infant-3 the Baldwins observed generally avoided adult females other than its mother, except during play bouts.

Neville (1972b) could emphasize the interest in *seniculus* infants more than the Baldwins did in their HBC *palliata:*

> "Adult, subadult, and juvenile females often, but not always, showed interest in the recent infant of another adult female through overt approaches, attempts to touch, and attempts to induce transfer, and infants as old as 10 weeks were still interesting to other females. Transfer would occur when a young infant crawled off its mother onto the fur of an adjacent howler. There was no indication that the change-over was intentional on the part of the infant; but the other howler would sometimes withdraw with the infant attached, as if to prevent its moving back onto its mother. Mothers usually tolerated transfer. A transfer was recorded for an infant less than 11 days old, and on one occasion a mother tolerated transfer onto another adult female for at least 24 min. The mother then reclaimed her infant two min. after it had retransferred onto a female juvenile. One juvenile female demonstrated responsibility to the extent of restraining an infant in its attempt to crawl off down a branch".

The strength of this interest was also demonstrated by a female who, despite being a recent mother, was still interested in the older infant of another female. In contrast to Neville's findings, Sekulic (1983b) reports that females with infants spent less time near new mothers than did immature females and adult females without infants. Sekulic suggests a subtle relationship between male infanticide and the pattern of association between recent mothers and adult females. The latter may be avoiding neonates during times when there is conflict between adult males for dominance because the association with the neonate, which is susceptible to infanticide, may increase the chances that her own neonate will also be killed. Sekulic notes that intragroup male conflict may last six months or longer (Crockett and Sekulic, 1984; Sekulic, 1982c) before the winning male kills the previous male's infants.

Neville (1979) noticed a kidnapping in the captive *caraya* howlers of Riverbanks Zoo as early as the sixth day of an infant's life: an adult female pulled the infant off the the mother when she was suspended by all four limbs and her tail from the roof grating. Interest in young infants was not totally restricted to females in that group, however; the juvenile brother of this infant kidnapped it a few days later. Recovery in both cases involved the mother pursuing while the kidnapper evaded, although the mother appeared to have her attention fixed on the infant rather than on the carrier, and no overt hostility occurred.

In general, the birth of an infant can have profound repercussions on the patterns of relationships within a group as the adult and juvenile females divert much of their attention to the new monkey and, probably as a stratagem to gain access to the infant, to its mother.

(3) Adult males are generally tolerant of or indifferent to infants. Adult male *palliata* have been observed "bridging" gaps for infants (Collias and Southwick, 1952) and Carpenter (1934) describes them as responding to the distress cries of a fallen infant-2 and a fallen infant-3 by approaching and howling. This could facilitate the approach and rescue of an infant by the mother in dangerous situations, although Carpenter did see situations in which the rescue was not completed. On one occasion a male rescued the infant-3 of a female with whom he had been consorting. Carpenter had shot the female and the infant had fallen with it to within eight meters of the ground. The infant was carried off on the male's back and was seen over the next few days in close proximity to, or nestling against, the male who seemed to adjust his pace to the infant's needs. Chapman (1929) recounts an incident in which an adult male and an adult female remained near a fallen infant for six hours, accompanied by another monkey for three of them. There were also vigorous vocalizations from the group. The adult female (presumably the mother) did not go to the ground, but was probably inhibited by Chapman's presence. The infant finally died and proved to be in poor physical condition, including a heavy botfly larva infection.

Glander (1974) reported cases of adult and immature male *palliata* carrying infants, but male *seniculus* spend little time with infants and have never been seen to initiate affiliative interactions with them (Mack, 1979; Sekulic, 1983b). Infant care and protective behaviors by adult *pigra* males were studied by Bolin (1981). She found that 7.4% of the total time an infant spends interacting in a social manner was with adult males. The interactions were divided into clinging (the least frequent (8.5%) and of the shortest duration (5%)), affiliative (51% frequency and 72% duration) and play, usually initiated by the infant (41% frequency and 23% duration). Males were generally merely tolerant although sometimes they moved away and at others playfully pulled at the infant. Vigorous play between adult males and infants was never observed. Interactions between males and infants increased as the infant grew older (Infant-1 to Infant-3 of Carpenter, 1965). Although similar data are not available, Bolin concludes that, despite considerable variability between groups, adult male-infant interactions are more frequent than in other *Alouatta* species, and relates this to their monogamous social system. Similarly, the difference between the patterns observed in *seniculus* and *palliata* may also result from their social systems; age-graded in *seniculus* and multi-male in *palliata*. Infanticide by adult males is discussed after the section on "Relationships among Adult Animals".

(4) There is little published information dealing specifically with relations of adults with juveniles and subadults. Perhaps the most important finding is that in both *palliata* (in the wild) and *caraya* (in captivity) females initiate competition for rank while still in the subadult stage (Jones, 1978, 1980, 1983a).

The *caraya* male's retention of a juvenile pelage, which is similar to that of the juvenile female, and then passing through a color phase like that of the adult female, may function to alleviate problems which might derive from the group's adult male or males (see also Shoemaker, pers. comm. in Jones 1983a). In *seniculus,* juvenile and subadult males may be evicted from the group by the adult males (Rudran, pers. comm. to Jones, 1983a). Rudran (1979) suggested that the mimicry of male genitalia by female *seniculus* (which is only partial, as the two sexes in *seniculus* can be relatively easily distinguished at an early age) is related to the mobility of young females between groups. He feels that the mimicry, together with the similarity in body size between the sexes (at what might be termed the subadult and young adult ages) and the apparent increase in body size through female's pilorecting, can function as medium to long range visual signals, causing extragroup males to reduce contact with such females; inducing group males to approach them, investigate them, and hence discover in a favorable setting that they are female. This may also give a group added protection by giving the appearance that extra males are present.

Juveniles remain associated with their mothers spatially and are in contact at night (presumed on the basis of night huddles which include adult females and juveniles). There is also considerable social play during the juvenile period, as will be discussed in the section on "Play". Female juveniles have been noted as being very interested in infants, whereas male juveniles show little or no interest (Glander, 1974; Sekulic, 1983b). Male juveniles on the other hand sometimes remain close to the adult males during intergroup howling.

Carpenter (1934) noted that partial weaning occurs prior to the birth of a sibling, and that mothers could behave rather "viciously" toward a youngster attempting to suckle. Examples include cuffing of a juvenile-2 and a juvenile-1 and display of teeth by the presumed mother.

Bernstein (1964) saw a male which "was almost always closely associated with a small juvenile. This male frequently rested with the juvenile in the ventral position that infants use in travel, but never travelled more than a metre or so carrying the juvenile".

Other rare interactions include play and aggression. Both Carpenter (1934) and Neville (1972b) saw rare instances of play between adult or subadult males and immatures in free ranging howlers. Carpenter saw snapping and growling between an adult male and a juvenile-1 in 1932 and noted that aggression was also seen between a male and a juvenile in 1959 (Carpenter, 1965).

A behavior of exceptional interest is that of "bridging" in which an adult of either sex forms a link between two branches over which an immature can then cross. Carpenter (1934) provides the classical description of this behavior, which is evidently usually performed by a mother for her infant or juvenile; the behavior is also depicted in his film (1960). Chapman (1937) and Bernstein (1964) also reported on bridging. Southwick saw a male howler form a bridge for an infant (Collias and Southwick, 1952). Neville (1972b) did not report bridging for *seniculus,* although DuMond (1967) saw it in a captive *seniculus* female for an adopted infant. Young (1983) describes bridging in *A. fusca.*

Bridging behavior has also been reported for *Ateles* (see Bernstein, 1964; Eisenberg and Kuehn, 1966; Mittermeier, 1978), *Lagothrix* (Kavanagh and Dresdale, 1975) and *Brachyteles* (Young, 1983), although the form is very variable.

Play

Descriptions of play appear in many of the studies, such as Carpenter (1934) and Altmann (1959) on BCI *palliata,* Glander (1975a) on HLP *palliata,* Baldwin and Baldwin (1978) on HBC *palliata,* and Neville (1972b) on *seniculus* in Trinidad and Venezuela. Of these, the most extensive report comes from the Baldwins, who describe patterns for Carpenter's three infant age stages (Table XIII), two juvenile age-stages, and adults. Unfortunately, immature *palliata* cannot be readily sexed by field observers, so that potential sexual differences in patterns are missing. The Baldwins' descriptions can be summarized as follows:

Infant-1: passively clings to the mother while she is active, but nurses, rests, or explores while she is inactive. Coordination is poor, especially off the mother. On occasion they explore for up to 60 seconds off the mother. Exploration was principally locomotor rather than object-manipulation, though very brief social play and mouthing or manipulation of vegetation occurred.

Infant-2: much more active and coordinated, but still clumsy. Most of its time off its mother was spent in nonsocial exploration. Early infant-2s could hang by their tails for up to three minutes and wandered up to 10 m away from the mother. Older infant-2s spent up to 40 minutes at a time away from their mothers. Their social contact with each other occasionally involved clumsy wrestling but more often resembled exploratory manipulation.

Infant-3: spent much more time in independent locomotion, and often made group moves independently. They actively wrestled or pawed at each other during social play; frequently while one or both hung from their tails. Play could occur with older animals, except for adult males. Early juveniles were the most playful of the age categories. Play bouts of wrestling could last 15 minutes in an "on-off" fashion (social play alternating with asocial activities). Chasing play appeared in infant-3s and continued in juveniles.

The Baldwins explained the decline in play with juvenile-3s as being a result of the increasing need to spend the time foraging. Carpenter (1934) had an alternative explanation: as play patterns become rougher, play became less rewarding and was "extinguished". The Baldwins themselves explained the frequency of play between peers, as opposed to infrequency between nonpeers, as resulting from the mutually reinforcing nature of peer play: "Because similar age gives two players similar strength, skills and interaction styles, age-mates can generate mutually reinforcing play with minimal interference costs". They noted that "effortful behavior is a negative reinforcer" and hence explained the decline in such play in late juvenile and adult monkeys and the increase in wrestling while dangling by the tail.

They noted no play with adult males, but rather the appearance of an adult male would terminate play behavior of the immatures. Neville (1979) observed play between immatures and the adult male of a *caraya* group at Riverbanks Zoo. With young immatures, the play patterns were initiated by the immature and the male was a passive recipient of pokes and pulls. With older juveniles, especially male juveniles, the male was a pursuer in chases that often came close to being actual agonistic behavior. At such times the monkeys were very excited and tense. Other observations of aggressive "play" involving adult males were noted earlier in this subsection.

The Baldwins draw attention to a further interesting feature: the variability in play pattern frequencies among groups at Barqueta and among the various *palliata* sites. Thus Carpenter observed a type of follow the leader play not seen at Barqueta, and Glander similarly observed a pattern of playing that consisted of running down from the top of a tree to the bottom and then running back up to the top for another cycle.

Relationships among Adult Animals

Howling monkeys appear strikingly docile in their intragroup behavior, especially to anyone who has observed macaques or baboons. The Kleins (Klein, 1974) saw "only three clear-cut cases of intragroup agonistic interactions" during 70 hours of observation on *seniculus*. Neville (1972b) recorded only 41 occurrences of agonistic behavior (disregarding the sex of the participants) during 603 hours of observation at HMG. These included harrassment of mating monkeys, appropriation of food or a food site, screeches in an unseen group, mothers forcing infants to dismount, and other behaviors (excluding play contexts and mothers giving mock-bites at females interested in their infants). Jones (1980a) suggests that "a limiting supply of palatable leaves may create intense intraspecific competition for group membership", leading to a hierarchical organization of males and females, and that "the energetic constraints imposed by a folivorous diet appear to restrict the expression of aggression to 'ritualized' forms" (see also Jones, 1983a).

Adult females. Carpenter's original monograph (1934) stressed the close association and peaceful interrelations of the adult females in a *palliata* group. This tendency to be in proximity was seen when feeding, resting, sleeping and during group progression. He hypothesized that the females were not specifically cooperating with each other, but that the similarity of their reactions, their physical proximity, and mutual facilitation could lead to a common response to stimuli. This same trend is noticeable in *seniculus* in the field and *caraya* in captivity, though it is possible that if group sizes of these latter two species were as large as those of the BCI *palliata* new effects might be seen.

In *palliata*, *seniculus* and *caraya* groups, females form a hierarchy in which rank correlates negatively with age: a rare type of social system for primates (Jones, 1978, 1981, 1983a; Rudran, pers. comm. to Jones, 1983a; Crockett, 1984). All adult females are subordinate to adult males. The maintenance of this hierarchy is evidently achieved through subtle behaviors and rarely through overt agression. Carpenter (1934) did not report any incidents, while Collias and Southwick (1952) observed a number of aggressive interactions, including one which involved bared teeth by both females, lunges, and "rather metallic cackling sounds". However, both Glander (1975a) and Jones (1978) reported that aggression was common among *palliata* at FLP and that adult males broke up dominance fights among the females. Neville (1972b) observed some minor instances, including displacement, grimacing with bared teeth, a "squeaky door screech" vocalization (possibly homologous to the "metallic cackling" of Collias and Southwick), and male interference in a female fight. During 1500 hours of direct observation of *seniculus* groups at HMG, Crockett (1984) saw only one fight between

females that involved physical injury. However, of 74 adult females at least 29 had scars or injuries. Thirteen of these females obtained their wounds during the study, four were believed to have resulted from fights between females and in only two cases was there no evident link with female-female conflict. Crockett (1984) suggests that injuries to females may result from male infanticide attempts, both when young and when defending their infants. Hostile behavior by females toward nongroup females is described in the section on "Peripheralization of Group Members".

Young (1981a) reports on an incident of copulation interrupting between two female *palliata* at BCI, and indicates that it is a form of dominance assertion. Jones (1978, 1981, 1983a) and Glander (1980) provide information which links, in a complicated sense, female dominance status to reproductive success. Both observed that female dominance was inversely related to age, although Glander found that "no infants of 3 to 4 year old primiparous, alpha females survived. Since primiparous females gave birth to their first infants about the same time they were obtaining the alpha position, the death of their infants may be linked to their behavior while achieving this position". Glander found that females below the alpha position, but above the lowest dominance positions, had the highest reproductive success. Crockett (1984) argues that female emigration is caused by reproductive competition resulting from ecological constraints on group size.

Adult and, more frequently, immature female howling monkeys show considerable interest in mothers with newborn infants (Glander, 1974; Sekulic, 1983b). In *palliata*, females without infants often follow mothers and attempt to "take" the infant by "presenting their necks" (Glander, 1974). Responses of the mothers vary from none to turning away and females observed carrying other's infants were referred to by Glander as "baby-sitters". Although Sekulic (1983b) observed that *seniculus* mothers did not show interest in the infants of others, Glander (1974) reported that female *palliata* may carry infants in addition to their own.

Adult males. Carpenter (1934) emphasized the peaceful and cooperative relations among group males, noting that he had not seen them "compete for sexually receptive females, for food, or for positions". This view of howlers as markedly pacific became "conventional knowledge" and influenced Neville (1972a) to interpret major scars, torn ears and missing fingers, apparent in about one-eighth of his subadult and adult *seniculus* males, as due to predator attacks rather than intermale hostility. Klein (1974), however, pointed out that howlers possess less obtrusive behaviors which may well have agonistic relations and which should be examined. He also drew attention to the low rate of behavioral interactions which reduces the significance of the low agonistic rate.

Male *palliata* form dominance hierarchies in which age and rank are negatively correlated (Jones, 1978, 1980). Adult *seniculus* males, however, form hierarchies dependent on body size and, therefore, probably positively correlated with age (Rudran, pers. comm. to Jones, 1983a), and Jones (1983a) believes that the same is true for *caraya*. Jones (1978, 1980, 1982, 1983a) emphasizes the importance of subtle behaviors, such as supplantations (frequently involving lunges), interindividual distance, grooming, ritualized displays and vocalizations, as opposed to overtly aggressive behavior, in the establishment and maintenance of dominance hierarchies in howler societies. Glander (1975a) could measure dominance in terms of access to food, sleeping places, and (between two adults of his group) estrus females, and found that adult males were dominant over other age/sex categories. Clarke (1983) and Jones (1985) report that dominant male *palliata* usually maintain priority of access to estrus females. During Clarke's study, consorting and copulating during a female's peak estrus was restricted to one male in 42 of 49 female estrus cycles. The exceptions occurred when two females were in estrus at the same time (the dominant male concentrated his attentions on the dominant of the two) (3 cases) and when a low ranking male consorted outside the group (6 cases). In captive *caraya*, Jones (1983a) found that the alpha male showed the lowest copulatory rate in the group, but importantly was solely responsible for the few copulations during the females peak estrus. Peripheral or subordinate males, therefore, do infrequently manage to copulate. Apart from rank, female choice and copulation interruptions were mainly responsible for this pattern.

Jones (1982) examined the relations between three adult males in a *palliata* group in Costa Rica. She had found that the relative status among males is reflected by the distances they maintain and in the rates of vocalizations between them (Jones, 1978). When she removed the third ranking in a three-male group during five days, the interindividual distance between the first- and second-ranked males decreased and the vocalization rates between them increased. On returning the third-ranked male to the group, these parameters resumed their original levels. During the absence of the third-ranked male, the second-ranked was able to achieve closer proximity to the females and was evidently attempting to displace the dominant male. Jones documents that the second-ranked male was eventually expelled from the group when a fourth male entered the group and formed a coalition with the first-ranked male. She concludes that male coalitions may be important in the regulation of male-male competition (see also Lindbergh, 1976).

Sekulic (1982d) studied the function of howling bouts between groups and between groups and solitary males (see below), and also described intragroup aggressive interactions between adult male *seniculus*. These involved piloerection, throat rubbing (see Sekulic and Eisenberg, 1983) and growling at each other from a distance (more than 5 m). She suggests that the growling may function to allow competing animals to assess each other.

Rudran (1979) has been the most decisive to date in emphasizing the presence of physical aggression and damage among adult males, especially during male group takeovers. He found the dead body of a dominant male who had been chasing two others and who was replaced in group leadership by one of them immediately afterward. He saw other males with wounds that could be related to dominance struggles and who later disappeared and concluded that intermale aggression, along with infanticide and senility, is one of the most frequent causes of death. Glander (1975a) also witnessed a fight between two males: the younger, who had been subordinate, beat the older in a 90-second fight in which the older acquired head wounds. The older male became peripheral, and the younger then copulated with all the females he could. From then on the younger male also interfered in dominance fights among females, a role reminiscent of the behavior of cercopithecoid alpha males.

Infanticide

Collias observed a male outdistance a mother approaching her infant female which was giving distress calls, bite the infant's tail in half, and throw it to the ground 15 m below (Collias and Southwick, 1952). Clarke (1983) also documented infant-killing in *palliata* in Costa Rica and the same phenomenon has been observed for *seniculus* at HMG (Rudran, 1979; Sekulic, 1981; Crockett and Sekulic, 1984). Occurrences of infanticide by adult males are associated with male takeovers, in a situation strikingly similar to that reported for langurs (Hrdy, 1977; Rudran, 1979). The males involved may be resident or extragroup. Rudran (1979) observed one case of infanticide by an invading adult male, found two infant bodies in which teeth marks clearly implicated male guilt, and reported a fourth infant disappearing after a male takeover in his group. This is believed to be a male reproductive strategy to decrease the interbirth interval of the group's females. In *seniculus* at HMG, group tenure by adult males is estimated at 5.1 to 6.7 years (Crockett and Sekulic, 1984) indicating the importance of shortening the interbirth interval for male reproductive success. Clarke (1983) reports that, depending on the age of the infant, the interbirth interval of *palliata* could be shortened to as little as seven months when the average interval (infant surviving) is 22.5 months (Glander, 1980). Similarly, Crockett and Sekulic (1984) observed that females could return to a receptive condition only one or two weeks after losing infants, although they never concieved in this first cycle, only in the second; 35-84 days after the infant's death. They suggest that this may be a female strategy; biding time to assess the permanence of the male's occupation, or, by quickly returning to estrus, she may be precipitating the resolution of, as yet undecided, male-male conflict. The mean interbirth interval (death of infant to birth of sibling) recorded by Crockett and Sekulic (1984) was 10.5 months compared to 16.6 months when the infant survived. Only infants killed when younger than 9 months resulted in a shortening of the interbirth interval and they found that most were killed when four months old or less.

Clarke (1983) found that while infants of high ranking females disappeared following a male takeover, infants of lower ranking females remained unharmed. She suggests that this might be a function of the association between the immigrant male and the lower ranking females, suggesting that the new male discriminates infants which may be his own. Crockett and Sekulic (1984) record, however, that in a few cases the new adult male probably also killed his own infants.

Infanticide is evidently a significant cause of mortality within these howler populations. Recording nine male takeovers, Crockett and Sekulic found that 15 of the 20 infants less than nine months old in the groups at the time were killed. Rudran (1979) felt that "infanticide, intermale aggression and also probably senility appeared to be the most frequent causes of mortality" in the *seniculus* at HMG. He extrapolated to a model in which primate population size fluctuated with declines caused by increasing infanticide by males and increases occurring when declines had produced a lower adult-to-immature ratio with a resultant decrease in infanticide. This model is proposed as general. He, thus, suggests that it explains the decline in populations which Collias and Southwick (1952) documented in their BCI census. However, despite the high infant mortality recorded by Clarke (1983), she concludes that infant killing does not occur more frequently at high densities and believes that it is a regular phenomenon best understood in terms of a male's simply maximizing his reproductive success.

Howling Behavior

Carpenter (1934), commenting on the coordinated roaring of the howler group, noted that "as a rule, every male of the clan participates simultaneously in the roars. In some situations, each of the males of the group appears to be equally and simultaneously stimulated". Both males and females roar (Sekulic, 1983a; Mendes, 1985). The male howling (here used interchangeably with roaring, although Chivers (1969) suggests a difference) probably corresponds to Altmann Type A1 and A2 vocalizations, while those of the female are probably homologous with Altmann Type B (Altmann, 1966, 1968). The most common time of occurrence is around dawn, but howling can often be heard at other times during the day and even at night (see section on "Activity Patterns").

Sekulic (1982b, 1982c, 1982d, 1983a) carried out a detailed study of the roaring behavior of *seniculus* at HMG. As noted by Neville (1976b), howling is usually initiated by the dominant male when observing the approach of another group or solitary males. The group move close together, and two males (those which rest together) call side by side while others roar from a distance (more than five meters). Females usually join in the roaring shortly after. During close encounters between groups, males may head throw, and throat-rubbing is also shown at this time (Sekulic and Eisenberg, 1983). Aggressive encounters between males of the same group may also involve roaring. Sekulic (1982d) also observed that howling may occur when subadult males return to the group after several hours or days of absence. Sekulic (1982d) concludes that howling is used to assess opponents in male competition for females. She found that males in groups with few males roared more than did males in groups with several other resident males. This, she believes, is because the main threat in the former comes from the outside of the group, hence the greater neccessity for assessment, whereas in the latter it is from the subordinate resident males.

The female calls are softer than those of adult males and in *palliata* they are higher pitched (Baldwin and Baldwin, 1976; Sekulic, 1983a). Sekulic (1982b, 1983a) observed that roaring by troop females was directed at solitary females (both sexes disperse) and indicates that the function is probably similar to that for male roaring. Roaring between group females may also occur as a means of preventing access to the dominant male, and simultaneous roaring with males Sekulic indicates is important in strengthening the pair bond. She found that females roared with males with whom they had recently mated and with the father of their infant, even though he may not be the dominant male. Sekulic (1983a) also observed that females roared at, and elicited roaring by, extragroup males, possibly as a strategy of assessment by the female of the staying power of the dominant male; important when considering the possibility of infanticide as a result of a male takeover (see above). One would predict that female roaring in this context would be most frequent between estrus periods.

Various stimuli other than extra-group howlers, potential predators, or human observers seem to be capable of eliciting roaring. Carpenter (1934) notes wind, rain, or aeroplanes as stimuli. Lundy (1954) added a shot as a stimulus to howling on the basis of his experiences in Panama. Bernstein (1964) described the howler roaring response to rain or aircraft as "invariable", and noted a frequent response of Altmann's "oodle type E" to wind gusts. Baldwin and Baldwin (1974) reported howling as stimulated by loud noises of low frequency, specifically loud aeroplanes, rain, wind, thunder, and the vocalizations of other animals (see also Sekulic, 1982d). Neville did not note a response to aircraft at either of his major *seniculus* sites. Advancing rain fronts at Bush Bush Forest in Trinidad could be followed by the howls, but rain only reduced general activity at HMG. Poley (1972) makes an intriguing contribution to the answer of why these phenomena might produce howling: an adult male *caraya* at Duisburg Zoo could not be stimulated into howling through tape recording playbacks of the vocalization (also tried with negative results by Neville at HMG), but he would consistently react to the play of a stream of water onto the wooden seat of a chair. The frequency of howler roaring and of the drumming of the water seemed to be the same.

Group Progression

Carpenter (1934) described the selection of the day's route as involving individual exploration by the group's males followed by cooperation when one of the males signalled his satisfaction through deep clucking vocalizations (Carpenter Type 2 or Altmann Type H vocalizations). The males had a strong tendency to be found in the lead or last positions, but there was no evidence that any particular male was more likely to be in either. There was a tendency for females with infants to be in the last positions. The clucking of the males and their starting or stopping was influential on the others. Collias and Southwick (1952) saw more influence by the adult females, which they correlated with the smaller socionomic sex ratio at the time of their census, though the males were still leading progressions more frequently than their numbers in the overall population would have predicted if the lead position occurred only by chance. Females carrying infants were more wary, which accounted for the unusual frequency of this category of either leading or lagging. Collias and Southwick also commented on male clucks as attracting group attention and noted the existence of female clucks. Females also emitted clucks at dusk when the "Laboratory Clan" was spread out, and this might have had a contact function. Collias and Southwick provided clear evidence that the single adult male of the group could not always have controlled the progressions. Bernstein (1964) also observed that low vocalizations were common during progressions, and additionally recorded the occurrence of Altmann'a "incipient roar Type A2" (Altmann, 1959) during travel. Milton (1975) presented evidence of a scent trail produced by urine-marking by a moving group.

Both Bernstein (1964) and Altmann (1959) noted the breaking off of small objects such as epiphytes and small branches by the adult males in relation to the line of march, and Altmann commented that the howlers' most common routes were free of epiphytes. An alternative interpretation to marking of the route might be "branching" defense (detachment and dropping of twigs, etc.) caused by the stress of movement near the observer.

Neville's (1972b) limited data on *seniculus* progressions suggested that the last monkey tended to be an adult male. Though juveniles were probably more active within any tree, they usually travelled close to their mothers, and when they did not, they sometimes had to return to the group after having outdistanced it. In sharp distinction to the BCI reports, Neville (1976b) did not hear vocalizations associated with group progressions.

Grooming

Grooming has been traditionally deemphasized by most commentators on howler behavior. Carpenter (1953) termed it rare and did not even mention it in his monograph (1934) or summary chapter (1965). Bernstein (1964) saw allogrooming on five brief occasions during 221 hours of direct observation of the BCI *palliata*. Richard (1970) was able to say that these "howlers never allogroom". Jones (1979) saw 23 bouts of allogrooming during 516 hours of observation of *palliata* at FLP. However, Neville (1972b) recorded five allogrooming bouts for *seniculus* at the Bush Bush forest, Trinidad, and 216 bouts at HMG during 51.5 and 603 hours respectively, providing evidence that there is a major difference between these species with respect to this behavior.

A. caraya appears to be more similar to *seniculus* than to *palliata* with respect to allogrooming rates, as it is with group size and composition. Thorington *et al.* (1984) noted that grooming is a common behavior in *caraya* in the wild. In captivity, Neville and Gunter (1979; Neville, unpubl. manuscript) recorded 163 bouts during 40 hours of observation of a captive group of seven *caraya* at the Riverbanks Zoo, a rate of 4.75/hr. Jones (1983a) recorded 245 bouts of grooming in 40 hours of observation of a captive group of five, a rate of 6.35/hr. This is quite a bit more than the HMG rate Neville (1972b) obtained of 0.36/hr with an average group size of 8.5, but they are greatly in excess of even Jones' (1979) rate of 0.3/hr in her more active *palliata* group. Mendes (1985) observed grooming to be a common behavior in *fusca*. *A. pigra*, like *palliata*, rarely groom, although males may infrequently groom infants (Bolin, 1981).

A. palliata and *pigra* very rarely groom, therefore, whereas it is a common behavior in *caraya*, *seniculus* and *fusca* (no information is available for *belzebul*). Why this difference is difficult to say. BCI howlers have heavy botfly infestations (Carpenter, 1934/1964; Milton, 1982), while this is not true of the HMG *seniculus*, although the reverse is true with respect to lice (Thorington *et al.*, 1979). Smith (1977) notes that he never saw allogrooming among wild *palliata* on BCI but that it took up 20% of the "maintenance activity" (elimination, grooming, and resting) time during some hours among young captive individuals (nine to 18 months old). Hence the caged state of the Riverbanks *caraya* may be an important factor influencing the grooming frequency. Smith (1977) also drew attention to the possible link between the lack of ticks on the BCI *palliata*, resulting from their almost total lack of ground activity, and the absence of allogrooming. Both *seniculus* at HMG and *caraya* go to the ground on occasion in their native habitats. This could relate to the early stages of the evolution of the behavior, when perhaps the bodily function aspect of allogrooming was more important than that of social communication. The usefulness of allogrooming with respect to control of ectoparasites remains to be established, however, and the differences between allogrooming rates in the different species requires further study. Jones (1983a) emphasizes more the social aspect of allogrooming and suggests that ecological constraints are involved (minimization of time devoted to activities unlikely to promote reproductive success). She proposes that the lack of grooming in *palliata* is linked with a more restrictive diet and also with their multimale group structure, as opposed to harem or age-graded in *caraya* and *seniculus*.

Neville and Gunter (1979; Neville, unpubl. manuscript) used the relative frequency of allogrooming dyads to indicate social bonding within the *caraya* groups, and Neville (1972b) also estimated the relative frequency of grooming amongst various age/sex combinations in *seniculus*. In the latter, results indicated that the most frequent interaction was subadult females grooming adult females. Following, in order, came adult female grooming adult males, subadult females/adult males, adult females/juvenile females, juvenile females/adult females, subadult and juvenile females/adult males, and finally a number of rare combinations. This ordering was corrected for the bias of different numbers of age-sex categories in the groups. Notable is the fact that males are generally the groomees and females the groomers both in adults and juveniles, whereas juvenile males are little involved in grooming interactions. The direction of grooming reversed with age in the females; adult females groomed juvenile females 1.6 times (in duration) more than vice-versa, but subadult females groomed adult females 3.2 times more than vice-versa. For *caraya*, Neville (unpubl. manuscript), considering both allogrooming dyads and dyad proximities, concluded that the most striking patterns include grooming by mothers of their immatures, the general interest of juvenile through adult females in young infants (which extends to grooming of the mothers by adult females and inducement of grooming from the mother by the other females, probably usually in order to "gain proximity to the infant"), and a relative affinity as shown in both proximity and allogrooming, among adult females. Additionally, the adult male was attracted to the adult females and was groomed by them. During a consortship, the male's relationship with the estrus female was strengthened, and he groomed her more. At this time, the mother's interactions with her immatures decreased and the male's interactions with individuals other than the consort also fell off sharply.

In a detailed study of the social context of grooming in captive *caraya*, also at Riverbanks Zoo, Jones (1983a) concluded that, within the hierarchies of each sex, the subordinates groom the dominants, and observed a close link between sex and status in the grooming patterns. In *palliata*, although a rare behavior, dominants usually groom subordinates (Jones, 1979). Mendes (1985) found that all six members of his *fusca* group participated in grooming, although, following the pattern in *seniculus*, and in the *caraya* studied by Jones (1983a), females were the most frequent groomers, but he was not able to draw any conclusions regarding dominance relations and grooming dyads.

Solicitation to groom is not observed in *palliata*, but in *caraya* the solicitor lies on his back in front of the potential groomer or, more rarely, adopts a rear-present posture (Jones, 1979, 1983a). Grooming solicitation in *seniculus* involves the groomee merely positioning himself in front of the potential groomer (Neville, 1972b).

Peripheralization of Group Members

In this section, we discuss the problem of group membership, transfers between groups, and the existence of non-group howlers. Transfers occur in two different ways: (1) splitting or amalgamation of groups, and (2) individuals leaving their group, becoming temporarily solitary, and then joining another group.

Males and, less frequently, females disperse, including juveniles and, more frequently, subadults and adults (Rudran, 1979; Jones, 1980; Sekulic, 1982c, 1982d;

Crockett, 1984; Crockett and Sekulic, 1984). Emigrant male *seniculus* are generally older than female emigrants (Crockett, 1984). Group transfer patterns are sometimes complex, with males, for example, invading and leaving groups successively (see Rudran, 1979; Mendes, 1985). The process can be prolonged (Rudran, 1979; Sekulic, 1982c), although Crockett (1984) found that, whereas males tended to come and go from a group for several months prior to emigration, females tended to leave abruptly.

It seems unlikely that strange groups would ever coalesce. However, temporary, peaceful amalgamations have been reported by Coelho *et al.* (1976b) for up to four small *pigra* groups at Tikal; by Baldwin and Baldwin (1972b) for three groups of *palliata* at HBC; and by Crockett (pers. comm.) for *seniculus* at HMG. Bolin (1981) suggests that unusually large groups of *pigra* may have resulted from mergers. Possibly in each case the groups represent a recently-split ancestral group. The early stages of group fission may have been seen in a few cases. Carpenter (1934) suggested hat very large groups may split "because of the impossibility of the proper oordination of all animals in a single body" and because of the increase of adult males in large groups, the "potential independent leaders of a new group". Carpenter also suspected that a strongly coalesced subgrouping including an adult male may gradually split off from a group. He further proposed that some group monkeys may leave to become associated with a "complemental male", his term for a male who is moving in proximity to the group but who has not yet been accepted into it. Collias and Southwick (1952) observed two males in Clan 26 who howled at dawn on several days in trees so widely separated that they at first suspected that the males belonged to different groups, but who came together peaceably. They also suggested that Carpenter's Clan 1 might have fragmented into the groups which they found using Clan 1's old home range: given the conservative behavior of howlers with respect to their ranges, this seems quite possible.

Chivers (1969) had felt that his group YY was unstable because of its excessive howling, tendency to travel in two subgroups, and the presence of five adult males in a group totalling 18 monkeys. Mittermeier (1973) found that the same group (his group 6) still tended to travel in separate subgroups but fed peaceably together in the laboratory clearing, and he suggested that the loss of the adult males between 1967 and 1970 might account for the two subgroups still remaining associated. He also noted two subgroups, sometimes separated by as much as 200 m, for Group 2 (five adult males in a group of 23 monkeys). Neville noted an apparently unstable group of 16 monkeys, large for *seniculus*, in eastern HMG.

Regarding dispersal of individuals, the actual number of solitary monkeys is difficult to estimate because of problems of observability and identification. Carpenter (1934) saw five "complemental male" *palliata* in 1932 and six in 1933; he never observed females and young separated from their groups. Carpenter provided a description of the slow incorporation of a solitary ("complementary") male into one group over three months; the male was wounded during the process. Collias and Southwick (1952) saw two solitaries, one a young male which might have been loosely associated with the "Laboratory Clan", and the other a juvenile of estimated age three years, whose condition was indicated by their comment that "no other individual so heavily infested with botflies was seen". The Baldwins (1972b) saw six solitary howlers at HBC, four of which were juveniles. Mendes (1985) describes a temporary invasion by a solitary adult male (Alien) in his *fusca* study group.

Neville (1972a) saw a number of solitaries and isolated pairs of *seniculus*, including adult females and adult female-with-immature combinations as well as isolated males or subgroups of males. Neville (1976b) hypothesized that one reason for these pairs or solitaries was the apparent lack of an appropriate vocalization: a group could easily leave behind a dozing member; and he noted apparent searching behavior by some solitaries. Rudran (1979), however, has produced data which suggest that solitaries and small combinations may be a common feature in *seniculus*. These fragments were unstable, however, not lasting more than a few months at best. All extra-group adult females were nulliparous and some might not have been sexually mature. All triplets contained at least an adult male and an adult or subadult female. Pairs came in various combinations, but subadult male pairs were most common. Quartets seemed to have unusual stability. He also noted the immigration of 13 males, including one juvenile, and two females "nearing sexual maturity". Some of the male incursions were in connection with group invasions. He calculates a male incursion every 43.7 group-months into a bisexual group. Eight emigrations included two adult males, four subadult males, a juvenile male, and a subadult female. Not surprisingly, Rudran emphasizes the social mobility between groups which howlers have, and in particular "in *A. seniculus*, where females are nearly half as mobile as males, it is interesting that the female external genitalia closely resemble those of males". The model in which he proposes a connection between genital mimicry and social mobility has been mentioned earlier.

What are the reasons for howlers leaving their groups? Rudran (1979), Jones (1980) and Crockett (1984) emphasize intense intrasexual competition for group membership resulting from limits on group size. An unstable group promotes dispersal. One of the two adult males had to be removed from a *caraya* group at Riverbanks Zoo in which all the male and female adults had grown to maturity together (Shoemaker, pers. comm.). The remaining adult male's play with a maturing juvenile male bordered on aggression. Attacks by females (including a pre-color change, but sexually active, female of 31 months) on females either being reincorporated into their group after a long absence or relatively recently associated with the attacking female, were observed by Neville at Riverbanks (unpubl. data). One of the clearest illustrations of such aggressive dynamics is provided by DuMond's (1967) report on the introduction of two adult males, two adult females and a juvenile male to a grouping of two *seniculus* at Florida's Monkey Jungle. The two original females immediately solicited to the adult males (one pair copulated within ten minutes) and chased off the new females, who subsequently died (cause unknown). One female adopted the young male, including carrying it, responding to its calls, and letting him use her body as a bridge. Later, with only one adult female left alive, 14 more howlers were introduced; the original female was "responsible for the adjustment of the four that survived, and for the rejection that led to the death of the remaining 10". This indicates that group membership is not easily won and that the peripheralization process is probably quite violent, as emphasized by Rudran (1979).

For males, and probably females, group transfer is evidently a reproductive strategy. Crockett (1984) argues that inbreeding is not the reason for female dispersal because females leave groups in which the breeding male is not the father, and natal females are sometimes recruited into groups where the male is probably the father. Most important are the conditions for successful breeding which a female finds within a group. This depends on a complex of factors which include the female's age, reproductive status (whether she has already bred and with whom, implying that the structure and stability of the male hierarchy is involved), as well as the relationship between her and the other group females and their relationships with the group males. When conditions are lacking, the female's option is to disperse, even though this incurs costs in terms of increased mortality and lost breeding time, which may be considerable taking into account that entry to another group may be a lengthy process (Crockett, 1984). Sekulic (1982c) made a detailed study of a solitary female attempting, unsuccessfully, to enter a group with two resident females over 11 months. Interactions with the group were characterized by aggression and howling from the resident females and disinterest by the males. This disinterest is explained by Sekulic as resulting from the possibility of stress-induced ovulatory failure by the female, the low probability of successful breeding while not a group member, and also the possibility that the time spent with the solitary female would increase the chances of a male take-over of the two resident females. The emigration of adult males as a result of a male take-over involves costs both in terms of lost reproductive potential and also the possibility of the killing of his infants by the new male or males (see section on "Infanticide").

Both Sekulic (1982c) and Crockett (1984) emphasize that females are responsible for female emigration and males for male emigration. The implication is that limiting food supplies restrict the possibilities for breeding within each group (female competition) whereas males compete directly for access to peak estrus females. Coalitions may be involved (at least among males) in this competition, which takes the form of a hierarchical ranking within the sexes (see section on "Relationships among Adult Animals"). Rudran (1979) also recorded cases where males dispersed and invaded another group together.

VII. REPRODUCTIVE BEHAVIOR

Seasonality

There is no strong evidence for a mating season or birth season, although this does not rule out the possibility of seasonality at some times in parts of the genus' range. Birth peaks do occur, however. Carpenter (1934) had the impression that births were more frequent at BCI in late December and January, as opposed to April or May. Milton (1982) found no evidence for a discrete birth season, although in some years births were more clustered than others and generally fewer infants were born in the late rainy season. Milton points out that the pattern of infant births in any one year reflected the pattern of infant mortality in the previous year.

Glander (1980) reported that births at FLP were scattered during some years and clumped in others. Jones (1980b) recorded a birth peak at FLP at the time of a peak in food availability in the middle dry season. Neville (1972a) also reported more HMG *seniculus* births in the dry season months (December to May) than in the wet season, though the skewing was far short of statistical significance. Braza (1978), working with *seniculus* at Hato "El Frío" in Venezuela, found reproduction throughout the year but with a peak in the second half of the dry season (January-February), with an immediate increase in male sexual activity, reaching a peak in June and July. For *caraya* in northern Argentina, the observations of Colillas and Coppo (1978) and Thorington *et al.* (1984) conflict. Whereas Colillas and Coppo, who observed *caraya* over a wide area, report that births are more frequent at the end of the dry season (January-April), Thorington *et al.*, studying *caraya* at one locality, Puerto Bermejo, report a birth peak in the middle of the dry season in July. The evidence suggests therefore a tendency for birth peaks, which, following the arguments of Jones (1980b), are probably dependent on the variable patterns of food availability during the year.

Gestation

Glander (1980) estimated the average gestation length in *palliata* by counting from the birth backward to the last maximal ("double-plus") swelling of the sexual skin of the mothers. The average was 186 days (range 180 to 194 days, n = 4). Crockett and Sekulic (1982) recorded the duration of 13 pregnancies in wild *seniculus* at HMG, six of which they believe to have been sufficiently accurate to indicate a gestation length of 184-194 days with an approximate mean of 191 days. As they point out, this is within the range of that for *palliata*, but because they were unable to pinpoint the date of conception during several estrus days, any slight but significant difference was obscured.

A female *caraya* gave birth to a male infant in the Lincoln Park Zoo, 233 days after her last contact with a male in the Riverbanks Zoo. However, it lived for only four days, weighed approximately 239 gm at birth, and was believed to have been overdue (M. Warneke, pers. comm.).

Glander (1980) estimated an interbirth interval of 22.5 months for *palliata* at FLP. His oldest female was estimated to be 16 years old, and even the older females continued to produce infants every two years. At BCI, the interbirth interval is perhaps rather shorter. Milton (1982) estimated an average of 17 months, using data from three females during four years. *A. seniculus* females may give birth soon after weaning their previous infants, when aged nine months (Mack. 1979). Finally, Shoemaker (1982) catalogued 23 captive *caraya* births, which provided an average interval of 11 months (range 7-16, n = 16 intervals). The interbirth interval recorded by Crockett and Sekulic for HMG *seniculus* was 16.6 months. This may be shortened, however, to 10.5 months if the infant dies within the first four months of life (see section on "Infanticide").

Estrus

Estrus is usually inferred from the increase in sexual behavior and soliciting of the female. Glander (1980), however, observed sexual skin swelling in female *palliata*, involving increasing tumescence of the vulva and perianal regions, color change from white to ligth pink, and exposure of the labia minor at peak swelling correlated with sexual activity. Copulations were only observed during maximal swelling, and no skin changes occurred during pregnancy. Jones (1985), following Glander's (1980) observations, distinguished three graded stages of tumescence and detumescence: (1) minimal tumescence when the vulva is swollen but not pinkish, (2) moderate tumescence when the vulva is pinkish and swollen but not "ruddy", and when no vaginal fluid is evident, and (3) maximal tumescence ("peak estrus") when the vulva is swollen and "ruddy" and exudes a viscous vaginal fluid, and the urine has a pungent odor.

Crockett and Sekulic (1982) report that the genitalia of female *seniculus*, however, did not appear to show reliable changes in shape or coloration correlated with estrus behavior, although they sometimes observed a slight swelling of the labia and erection of the clitoris. Also, confusing the issue, the females showed considerable variation in the size, shape and coloration of their genitalia.

In *palliata*, adult females copulate during a two to four day portion of their cycles, which average 16.3 days (range 11-24, n = 23; Glander, 1980). Jones (1985) estimated average cycle lengths of 15.5 ± 4.9 days (n = 25 cycles) for one *palliata* group and 16.1 ± 4.3 days (n = 12) for a second group at FLP. In the first group, peak estrus lasted an average of 1.3 days, and in the second 2.25 days. The two groups were in different habitats (riparian forest and deciduous forest, respectively) and that in the more seasonal deciduous forest showed greater estrus synchrony among its females (Jones, 1980b, 1985). Two estrus periods observed by Crockett and Sekulic *(seniculus)* lasted two and a half and three days, and estrus cycles showed a median of 17 days (n=5; Crockett and Sekulic, 1982; Sekulic, 1982c). Horwich (1983a) recorded an instance of a female *pigra* in peak estrus for six days. Colillas and Coppo (1978), using vaginal cytology as an indicator, estimated an estrus cycle of 20 days for *caraya*.

Mating Patterns

During peak estrus, the dominant male shows interest in the female (consorting) and prevents other males from copulating. The males routinely check the urine of the female by sniffing urinated spots, and Glander (1980) and Jones (1985) could distinguish receptive from non-receptive females by the pungent odor of the former. Males also "sampled urine directly by placing their noses and mouths into the urine flow and then raised their head with lips slightly parted, a behavior resembling *flehmen* in ungulates and cats..." (Glander, 1980). Horwich (1983a) reports urine sniffing in male *pigra* similar to that observed for *palliata*. He also saw the male giving a chewing response following sniffing but never the lip-curl or grimacing. Crockett and Sekulic (1982) observed that *seniculus* males routinely muzzled and licked the genitalia of females during inferred estrus. On occasion, males would also do this at other times but females usually responded with a wide grimace and a "cackle" vocalization (Neville's (1972b) "squeaky-door screech") and moved away. Mendes (1985) observed an adult male *fusca* licking and smelling the female's genitalia prior to copulation.

Sexual solicitation involves a ritualized tongue flicking or "lingual display"; rapid tongue movements in an out and up and down, first described for *palliata* by Carpenter (1934). This behavior is also shown by *caraya* (Neville, unpubl. data; Jones, 1983a), *seniculus* (although lacking the rhythmicity characteristic of *palliata;* Neville, 1972b, and sometimes given as an aggressive signal; Rudran, pers. comm. to Jones, 1983a), *pigra* (Horwich, 1983a), and *fusca* (Mendes, 1985) and in all may be quickly followed by copulation. Tongue-flicking by *caraya* is particularly distinctive because the adult's tongues are pink on the upper surface with borders and underside black.

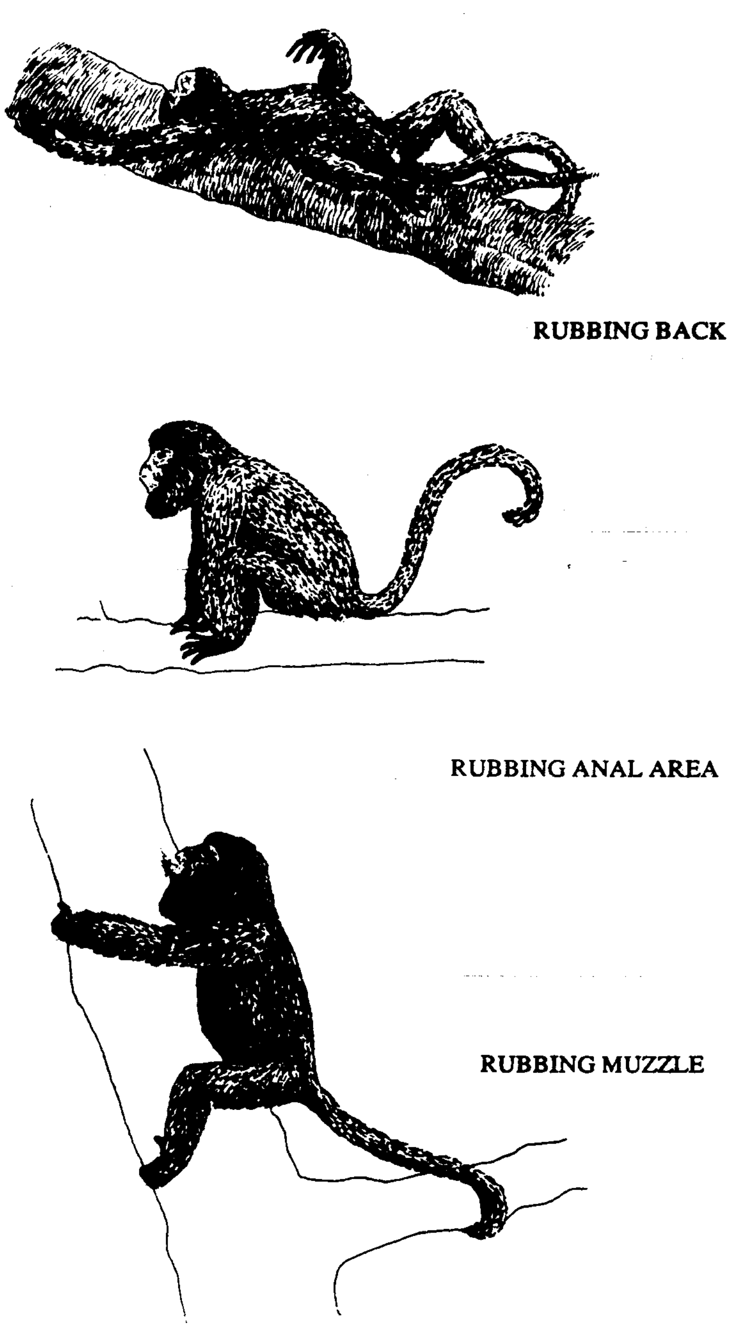


Fig. 6 – Behaviors of *Alouatta*. See text and Table XVI.

Carpenter (1934) and Jones (1985) also describe a rear-present posture (submissive) by either sex as part of sexual soliciting. In *caraya*, Jones (1983a) describes "vulval, scrotal and clitoral displays" but indicates that only the "vulval display" has a sexual context, the other two being observed in agonistic situations. Females may also solicit by licking the male's face, hands or genitalia and males may smell the female's genitalia, urine or vaginal fluids, but Carpenter (1934) never observed manual exploration. Sniffing and licking of genitalia does not always occur in a sexual context. Glander (1980) reports this behavior as part of a stereotyped "greeting ceremony" between females, especially during reproductive cycling. Small amounts of urine are deposited and they may also sniff each others axillary regions. Horwich (1983a) reports a similar ceremony in *pigra*.

As stated, copulations may quickly follow a lingual display. Carpenter (1934) observed 29 copulations. The basic stance has two versions, both with the male's tail attached to his support but differing in whether the male has his feet on the branches or on either side of the female's hips. The hands in at least one case were on the female's shoulders, as shown also for *pigra* by Horwich (1983a). Horwich (1983a) illustrated three copulation postures. Mendes (1985) described *fusca* copulating with both male and female remaining with their hands and feet on a horizontal branch. Neville (unpubl. data) recorded that *caraya* may give very low "growl-screeches" during thrusting series but he was unable to determine the vocalizer. Braza (1978) describes two copulations in *seniculus*. In one the male inspected the fur of a female lying by him, smelled her inferior flank, she rose and he mounted her. After some small thrusts, they separated, sat back to back, and then went to sleep next to each other. The duration was approximately two minutes. The second copulation also ended in the pair sleeping together.

Fig. 7 – Behaviors of *Alouatta*. See text and Table XVI.

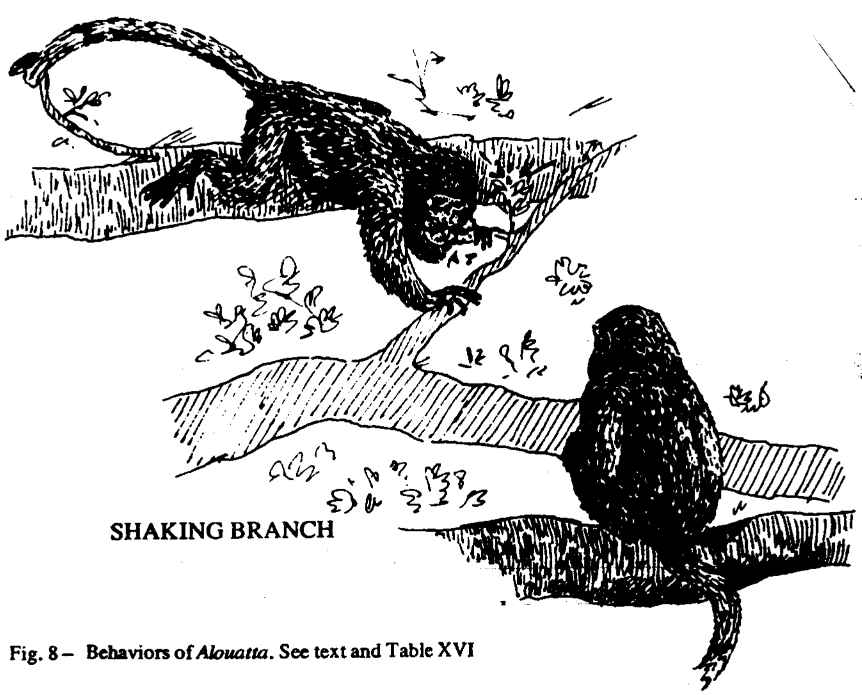


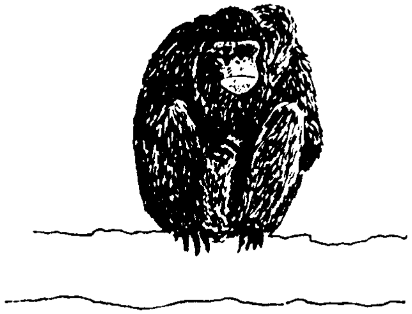
Fig. 8 – Behaviors of *Alouatta*. See text and Table XVI

Jones (1985) determined the occurrence, or otherwise, of ejaculation by the presence or absence of an ejaculatory pause prior to ending intromission. Copulations may occur in series, with intervals between successive copulations of between 17 and 45 minutes (Carpenter, 1934). The average duration recorded by Carpenter was 32 seconds and the number of thrusts varied from eight to 24 per copulation (average 16.9). Young (1981a) recorded BCI *palliata* copulating, with preliminaries involving tongue-flicking and rear-presenting. One copulation lasted 30 seconds with only four thrusts but was then interrupted by an adult female of the group. Copulation interruptions and harrassment (also observed for *seniculus* by Neville, 1972b) may be a form of dominance assertion among females (see section on "Relationships among Adult Animals").

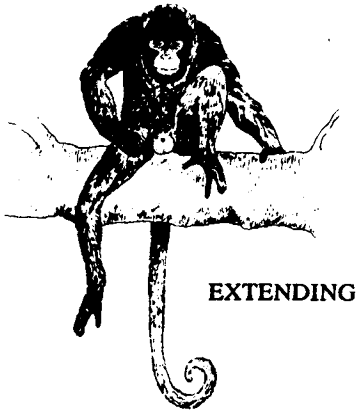
VIII. EXPRESSION AND COMMUNICATION

There have been more studies of howlers in their natural environment than of any other New World species. However, the literature contains information on expression and communication principally in two species: *palliata* and *seniculus*. In Table XVI we present an ethogram based mainly on these two species. While we hope that the table will be of use to other observers of howling monkeys, we are aware that, in summarizing the available information, some details of the descriptions of the patterns and of the social context, which may be of importance, may have been omitted.

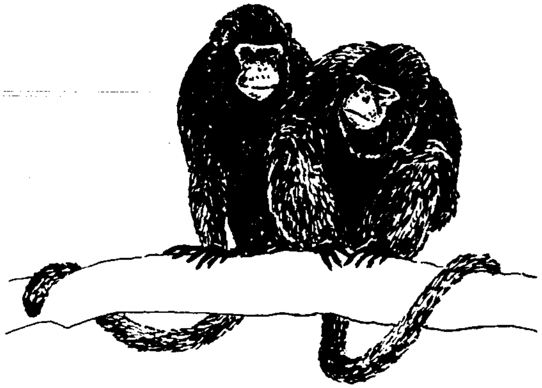
As mentioned earlier, captive studies have lagged far behind those in the wild because of the difficulties, until recent years, of their maintenance in captive



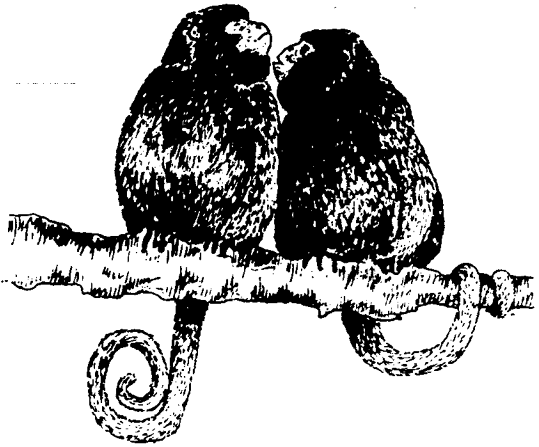
CROUCHING



EXTENDING LEG

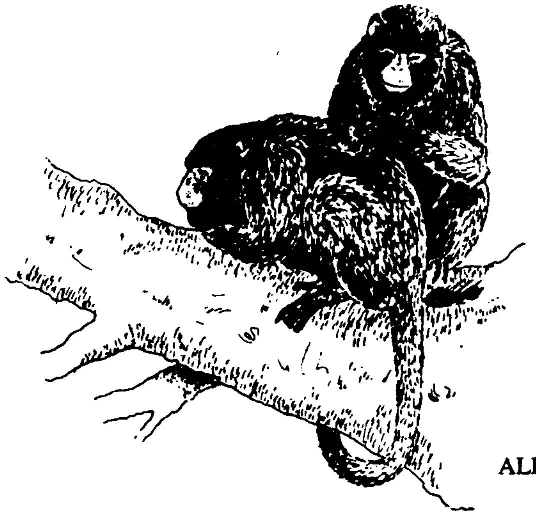


PUSHING AWAY



MOUTH TO MOUTH

Fig. 9 – Behaviors of *Alouatta*. See text and Table XVI.

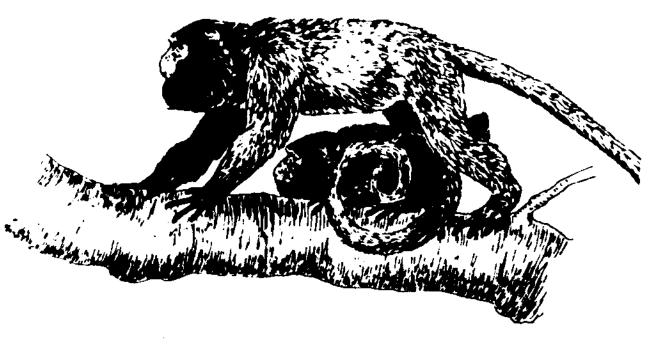


ALLOGROOMING

COPULATION

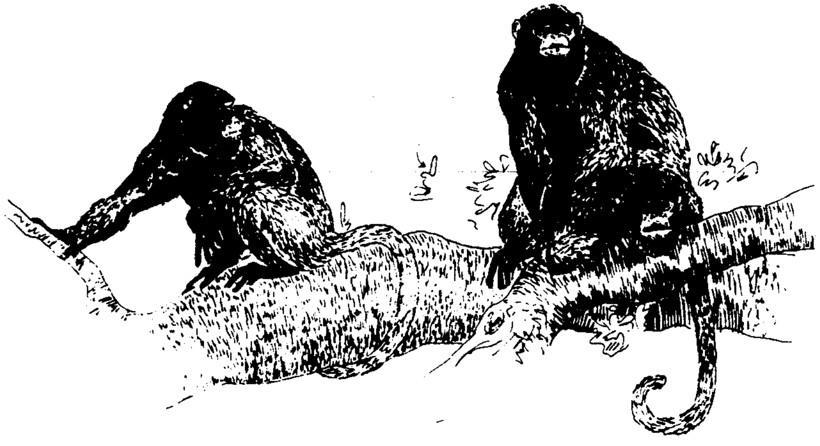
Fig. 10 – Behaviors of *Alouatta*. See text and Table XVI.

conditions. Detailed studies, rather than anecdotes, of specific behaviors and displays and their social contexts are, therefore, rather few. The more sophisticated long term studies in the wild have provided the most information (for example, Carpenter's and Glander's studies of *palliata*). Sekulic and Crockett's research on roaring, female and male dispersal and infanticide in *seniculus*, and Jones' (1980a, 1980b, 1982, 1985) studies of reproductive strategies in *palliata*, to name only some. The more classical ethological captive studies are limited to those for *caraya* at Riverbanks Zoo by Neville (1979) and Jones (1983a). Jones analyzed the frequencies, rates and escalation probabilities of 16 behaviours in a group of five *caraya*; including supplanting, grooming, play, huddling, fighting, and copulation. Supplanting by means of vocal signals clearly followed the dominance hierarchy amongst the males. Visual and tactile



WALKING OVER

APPROACHING AND STOOPING

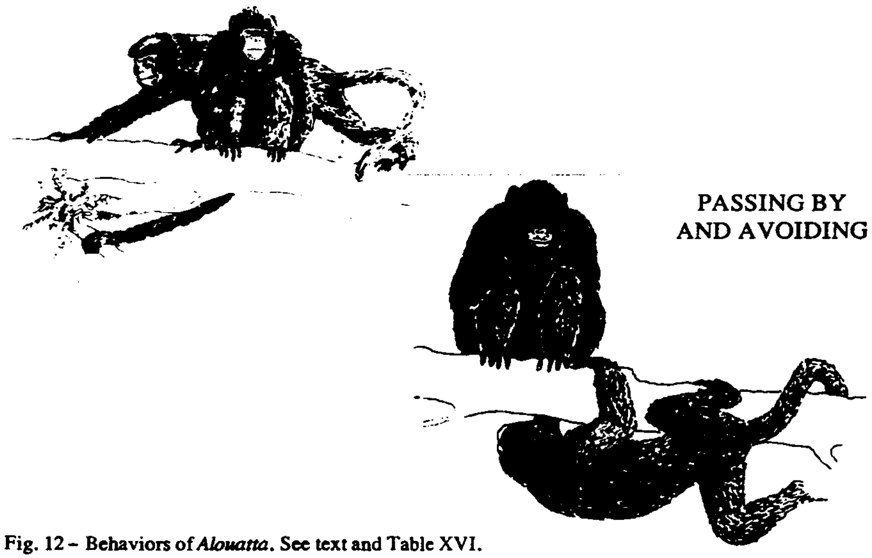


RESTRAINING

Fig. 11 – Behaviors of *Alouatta*. See text and Table XVI.

behaviors used for supplanting by subordinates attempting hierarchical reversals were ritualized, which Jones argues results from the fact that ritualized displays minimize the chances of a fight. She identified four ritualized displays: the lingual gesture and clitoral, vulval and scrotal displays. The first is sexual, although in *seniculus* it may also be aggressive (see section on "Mating Patterns"), and Jones concludes that it functions to communicate receptivity, solicit copulation or as a component of courtship. The other three occur in agonistic situations. The clitoral display is rarely shown by subordinates as an appeasement gesture to dominants. The vulval display is similarly given in tense social situations and serves to inhibit overt aggression. The scrotal display is the male equivalent, given by males to males. The scrotal display was never observed to lead to a fight. Jones indicates that these behaviors are rare because tense situations are generally avoided. Studies of this type are lacking for other species, but would provide some fascinating insights to the variability in the social behavior of this genus and its relation to the extraordinarily wide range of habitats that howlers occupy.

When Table XVI is considered as a whole, attention is directed to the sexual dimorphism in body size and the general aspects which bear some relation to their behavior. Thus, we see that male protectors respond to external alarms and coordinate the movements of the group, but very rarely participate in the daily social interactions of the females, juveniles, and infants of their own group. Howler group life is generally remarkably placid, and Milton (1978, 1979, 1980) and Jones (1980a, 1983a, 1985) suggest that the nature of the diet has selected for relatively low rates of energy expenditure. They spend a high proportion of the day resting (digesting and conserving energy), and Moynihan (1976) indicates that the lack of variety of facial expressions, ritualized displays and tactile signals (at least in *palliata*) results from the cohesiveness of the group in their idleness and, for this reason, group members are able to monitor subtle unritualized visual signals and intention movements which are frequent.



PASSING BY
AND AVOIDING

Fig. 12 – Behaviors of *Alouatta*. See text and Table XVI.

However, as Kudran (1979), among others, has emphasized, behind this placidity is a struggle for dominance among both males and females which can be violently expressed in vicious fights, group expulsion and infanticide. The picture, threfore, is of a deceptively calm daily life with a considerable degree of aggressive restraint and energy conservation, but with strong underlying competition. We can expect, therefore subtle but important communication systems, with non-damaging behaviors such as grooming, play and supplanting being significant and frequent and ritualized displays being used less often in more tense social situations (Jones, 1983a). The social environment of howlers is highly dynamic, as has been well illustrated through the studies at HMG and, with more detailed studies, it might be found that their communication systems are sufficiently complex to retract their categorization by Moynihan (1976) as stupid. Certainly, taking into account the elements of the ethogram we can conclude that the howlers have reached a level of specialization or ritualization (for example, "extended leg", ritualized genital displays, "walking over", "restraining" and "rubbing back") which is similar to other cebids. As indicated above, the challenge for the future will be studies of species differences; for example, the context and form of the lingual display evidently differs between the species; the lack of allogrooming in *palliata;* the effects of differences in group size and structure; and the evidently monogamous social groups of *pigra* indicating a very different behavioral repertoire, if only in terms of rates and frequencies, from *palliata*.

Regarding vocalizations, Carpenter (1934), Altmann (1958) and Baldwin and Baldwin (1976) provide classifications of *palliata* calls. We have chosen to eliminate from Table XVI some vocalizations mentioned in the literature (roar terminus, variations of incipient roar, incipient roar accompaniment and variations of whisper, grunt and hiccup) either because they are included in previously mentioned categories or because the information was insufficient. We also draw the reader's attention to the fact that tapes giving illustrations of the categories of *palliata* vocalizations have been made by Altmann (1966; see also 1959 for an initial discussion and 1968 for a systematic comparison to Carpenter's scheme) and also Baldwin and Baldwin (1976) placed tapes on file with the Laboratory of Ornithology, Cornell University. Thorington *et al.* (1984) provide a comparison of the grunts, barks and long calls of *caraya, seniculus* and *palliata* based on the recordings by J. Eisenberg, analysed by R. Sekulic. They found that the calls of *caraya* are more similar to those of *seniculus* than of *palliata*, and that male *palliata* long calls were higher pitched and showed more frequency modulation.

Keleman and Sade (1960) and Schön (1971 and earlier publications) describe the anatomical adaptations for howling in *seniculus* and *palliata* and Chivers (1969: *palliata)* and Horwich and Gebhardt (1983: *pigra)* discuss the contexts and possible function. Although the sounds related to the behaviors have always been of interest, howler accoustic communication is still poorly understood. A great advance was made by Sekulic (1982a, 1982d), who studied the contexts and function of howling of *seniculus* at HMG. She demonstrated that although the dawn chorus may be important for groups to localize each other, howling functions as a ritualized aggression in the male's defense of his group's females. Females may roar in more subtle contexts such as inciting male competition, but also do so in aggressive display to other females (Sekulic, 1982c, 1983a). Roaring is discussed in more detail in the sections on Howling Behavior, Activity Patterns and Home Range. Undoubtedly, most of howler vocalizations are fundamentally related to individual recognition, the use of space and in agonistic situations. In defense against danger, howlers are able to communicate different intensities of alarm using different sounds. We believe that howler vocalizations are organized in one or more gradients, and that different messages are delivered during the modulation of the call along the gradient.

Rubbing various parts of the body on branches and conspecifics, and smelling and licking urine and genitalia are probably all important in olfactory communication, as well as being unmistakable visual and tactile (when on conspecifics) displays. Authors have described chin rubbing, throat rubbing, chest rubbing, back rubbing and anogenital rubbing (Collias and Southwick, 1952; Altmann, 1959; Neville, 1972b; Braza, 1978; Young, 1982a; Sekulic and Eisenberg, 1983) and also urine washing of the hands, feet, tail and throat (Kirchshofer, 1963; Milton, 1975).

Altmann (1959) described anogenital rubbing by *palliata* females. "This was done by keeping the front legs in a standing position, bending the hind legs, and moving the rump back and forth in the sagittal plane". Altmann felt that this might have been a form of masturbation also seen in males: "the monkey scratched at the genital region for several seconds to a minute, whereupon about two fluid ounces of watery fluid, presumably urine, was emitted..." Collias and Southwick (1952) observed anogenital rubbing by a female and the sole adult male in the Laboratory Clan at BCI showing scrotal pulsations, scrotal rubbing and genital region scratching with a similar emission of fluid. An estrus female was present in the group at the time. Throat, neck and chest rubbing were observed for an adult male in a sexual context (following copulation) by Young (1982a). Neville (1972b) observed anogenital rubbing in *seniculus* and also face, back and chin rubbing. Back rubbing was particularly frequent after or during rains. Other monkeys were not observed to investigate the sites. Neville (1972b) recorded chin and neck rubbing in possibly sexual contexts in the Trinidad *seniculus*, possibly as a result of excitement because of the proximity of an estrus female. Of 30 instances of muzzle and chin rubbing observed by Braza (1978), 15 were by adult males, 11 adult females, three a young female and one by a young male. The throats of both male and female *seniculus* have skin glands (Epple and Lorenz, 1967) and so this form of rubbing probably involves olfactory communication. Back rubbing may well be purely scratching, although Kirchshofer (1963) recorded a juvenile male rubbing its back on a urinated portion of a branch. Throat rubbing by *seniculus* is described by Sekulic and Eisenberg (1983). It was found to be associated with a hostile reaction to conspecifics (particularly adult females in aggression to other females) and was usually accompanied by howling and/or piloerection.

Urine washing is described in detail by Milton (1975). She saw 26 incidents by adult males, 22 by adult females, and eight by immatures, during 270 hours of observations of six *palliata* groups. Twenty of these urine washes were observed immediately prior to group travel.

In summary, the various rubbing activities, carried out predominantly by adults, are undoubtedly important in olfactory communication; frequently involving the distribution of urine and also, in the case of throat rubbing, scent glands. The motivations for these behaviors are evidently multiple and probably include aggression, dominance assertion and sexual relations. More detailed explanations of scent-marking and the use of urine in olfactory communication will depend not only on experimental manipulation of captive groups but also further studies in the wild.

TABLE XVI
Behavior patterns of howler monkeys 1

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
VISUAL PATTERNS			
Pivoting *A. seniculus*	d – Supported on four legs swings towards receiver, often repeated. f – Rare.	s – During play in juveniles and when conspecifics near by or touch performer, in adults. p – All.	m – Aggressive or playful. f – Mild threat or play releasing. r – Aggression when agonistic play when play releasing.
Rapid approach *A. seniculus* *A. caraya* *A. fusca*	d – Walking quickly at increasing speed toward receiver, sometimes involving lunging. f – Very common.	s – When conspecific near by, mainly when feeding. p – Adults of both sexes.	m – Aggressive. f – Threat. r – Moving away.
Chasing (Fig. 7) *A. seniculus* *A. palliata* *A. caraya* *A. fusca*	d – Rapid chase in erratic trajectory (short duration). f – Rare.	s – Conspecifics near by. p – Adults of both sexes.	m – Aggressive. f – Threat. r – Moving away or fight.
Play chasing *A. seniculus* *A. palliata* *A. caraya*	d – Rapid chase in erratic trajectory, of long duration and not moving far away. f – Rare.	s – Members of group resting or feeding together. p – Juveniles.	m – Playful. f – Play functions. r – Group juveniles start. playing.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Walking over (Fig. 11) *A. seniculus* *A. caraya*	d – Peformer walks over receiver, with feet on substrate and no body contact. f – Rare.	s – When receiver in walking trajectory of performer. p – Mainly oldest male of group and sometimes female carrying infant.	m – Self assertion f – Dominance. r – Crouching.
Staring *A. seniculus* *A. pigra* *A. fusca*	d – Self explanatory. f – Common.	s – Proximity and when receiver approaches performer. Pre-copulatory associated with lingual display. p – Adults of both sexes.	m – Aggressive or sexual. f – Mild threat or soliciting. r – Receiver immobilizes, moves away, threatens or attacks. Copulation.
Baring teeth *A. seniculus* *A. palliata* *A. caraya*	d – While raising chin mouth-corners are retracted backwards and lips slightly opened. f – Rare.	s – When performer threatened or disturbed. Also when juveniles attempting sucking are rebuffed by mother. Also in play. p – Most frequently adult females and juveniles of both sexes.	m – Frustated. f – Threat. r – Receiver threatens, moves away, or no response.
Shaking branch (Fig. 8) *A. seniculus* *A. palliata* *A. pigra*	d – Moving erratically, grasping branches and shaking them. Also sometimes biting branches with lateral nodding head movements. f – Very rare.	s – Play and alarm. p – All.	m – Playful and conflict from alarm. May be aggressive (*pigra*). f – Play releasing and displacement activity. r – Play and undetected.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Passing by and avoiding (Fig. 12) *A. seniculus*	d – Walking performer avoids receiver by passing below or behind at a fast pace. f – Rare.	s – When receiver seated in performer's walking trajectory. p – Mainly juveniles and adult females (rarely female carrying infant).	m – Submissive. f – Avoiding dominant animal. r – Undetected.
Lip puckering *A. caraya*	d – Lips puckered into "0" followed by yawn. f – Unknown.	s – Aggressive threat. p – Adult males.	m – Aggressive threat? f – Threaten? r – Undetected.
Vulval display *A. caraya*	d – Rear present, tail-up, body immobile. f – Infrequent.	s – Agonistic interactions, possibly also sexual. p – Adult and subadult females.	m – Inhibit aggression. f – Prevent escalation. r – Move apart.
Clitoral display *A. caraya*	d – Rear present, erect clitoris. f – Infrequent.	s – Subordinates to dominants in tense situations. p – Adult and subadults to males and females.	m – Fear? f – Prevent aggression. r – Move apart.
Scrotal display *A. palliata* *A. caraya*	d – Rear present, tail-up, testicles descended, body immobile.	s – Agonistic interactions. p – Males to males.	m – Inhibit aggression. f – Prevent escalation. r – Move apart.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Approaching and Stooping (Fig. 11) *A. seniculus*	d – Approaching receiver slowly with forequarters stooped. f – Very rare.	s – While approaching dominant conspecifics. p – Only observed in females.	m – Submissive. f – Avoiding aggression. r – Undetected, sometimes receiver touches performer with hand.
Crouching (Fig. 9) *A. seniculus* *A. fusca*	d – Seated or lying with arched back and lowered head, tail between legs and over back or on one side. f – Very rare.	s – While other subject walks over or after being threatened. p – Juveniles and adult females.	m – Submissive. f – Showing lower status. r – Undetected.
Lying on back *A. seniculus* *A. caraya*	d – Lying on back, sometimes one arm stretched forward. f – Rare.	s – During siesta time. When conspecific approaches performer sometimes stretches arm showing fur of flank. p – Adults of both sexes.	m – Friendly. f – Invitation to allogrooming. r – Allogrooming.
Extending leg (Fig. 9) *A. seniculus*	d – Seated subject extends leg and scratches its proximal end with fingers. Perhaps an incipient genital display as in *Saimiri*. f – Common.	s – Dominant conspecific at short distance. p – Adults and juveniles of both sexes.	m – Conflict from short distance to more dominant animals. f – Undetected. r – Undetected.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Approaching danger *A. seniculus* *A. fusca*	d – Subject approaches source of danger either by hanging by tail or by descending to lower branches. Accompanied frequently by staring, defecating, woof sounds and strutting (exaggerated lateral movements of hips and shoulders). f – Common.	s – External alarm (by observer, birds of prey, etc.). p – Mainly adult male.	m – Alarmed and curious toward alarm source. f – Group protection. r – Rest of groups retreats to core area.
Yawning *A. seniculus* *A. caraya*	d – Slowly opening mouth completely showing teeth and gums while raising head. f – Common.	s – When external alarm, when conspecific approaches, after sleeping and while being groomed. Sometimes when conspecifics mark branches near by and when group companions fight. p – Adult males.	m – Alarmed and as result of immobility. f – Threat and respiration. r – Undetected.
Sitting showing back *A. seniculus*	d – Subject crouches while facing opposite direction of receiver. f – Rare.	s – After moving away from threatening conspecific or from observer. p – All.	m – Alarmed and submissive. f – Avoiding continuation of aggression. r – Aggression stops.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Invitation to mount *A. seniculus* *A. palliata*	d – Subject waits for infant, lowers hindquarter and looks back at infant. Also presenting of neck. f – Very rare.	s – When mother and infant apart and before crossing branch junction. p – Adult females with infant.	m – Maternal. f – Infant protection. r – Infant approaches and mounts over mother's hindquarters.
Lip smacking *A. palliata* *A. caraya* *A. fusca*	d – Rhythmic in and out and up and down tongue movements. f – Very rare.	s – Male-female consorting p – Adults of both sexes.	m – Sexual. f – Copulatory invitation. r – Releases same pattern, copulation and sometimes no response.
Sexual presentation *A. palliata* *A. caraya* *A. fusca*	d – Showing hindquarters to receiver. Accompanied with lip smacking. f – Very rare.	s – Male-female consorting. p – Adult females.	m – Sexual. f – Invitation to copulation. r – Copulation.
VOCALIZATIONS [2]			
Roar or howl (Altmann's type A$_1$) *A. seniculus* *A. palliata*	d – Loud, deep roar, either maintained or rapid series of syllables. f – Very common.	s – General disturbance: terrestrial and avian predators, other howler groups, wind, rain, thunderstorms, etc. ... p – Adult males.	m – Disturbed and aggressive. f – Communication of alarm, territoriality. r – Group members either approach performer and emit sounds or retire and conceal in core area.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Incipient roar (Altmann's type A_2) *A. seniculus* *A. palliata*	d – Short popping roars, previous to and grading into full roar, also during roaring pauses. f – Common.	s – Mild general disturbance. p – Adult males.	m – Disturbed and aggressive. f – Communication of alarm, territoriality. r – Undetected.
High roar coda (Altmann's type A_3) *A. seniculus* *A. palliata*	d – High tone sustained roar. Common roar switches near its end into this sound. f – Rare.	s – At dawn and when alarm is maintained for some time. p – Adult males.	m – Disturbed and aggressive. f – Not known. r – Undetected.
Roar accompaniment (Altmann's type B and Baldwins' type B_1 and B_2) *A. seniculus* *A. palliata*	d – High pitched wailing or short syllables sound, while performers move about roaring male. f – Common.	s – While male roaring. Often when alarm is maintained. p – Older juveniles and adult females.	m – Disturbed and aggressive. f – Not known. r – Perhaps inciting the male to roar.
Male woof or bark (Carpenter's type 9, Altmann's type C_1 and Baldwins's "male woof or bark") *A. seniculus* *A. palliata* *A. caraya*	d – Loud, deep barking that tends to be given in clusters of 1-4 repetitions or in long sequences. f – Common.	s – Same as for roar, when the stimuli are less intense. p – Adult males.	m – Disturbed. f – Communication of alarm. r – Other males approach performer and emit same sound, rest of group retires and conceals in core area.

(cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Female woof or bark (Carpenter's type 1, Altmann's type D_1 and Baldwins' "female woof or bark") *A. seniculus* *A. palliata* *A. caraya*	d – Barking sound, higher in pitch than that of males. f – Rare.	s – Sudden presence of human close to group. p – Adult females.	m – Disturbed. f – Not known. r – Undetected.
Incipient male woof or bark. (Altmann's type C_2) *A. seniculus* *A. palliata*	d – Muffled male woof (uh-uh-uh-uh). f – Common.	s – Mild general disturbance and during group progression. p – Adult males.	m – Slightly disturbed. f – Communication of alarm. r – Other group members retreat to core area.
Incipient female woof or bark (Altmann's type D_2) *A. seniculus* *A. palliata*	d – Muffled female woof of higher pitch than incipient male woof (uh-uh-uh-uh). f – Common.	s – Mild general disturbance and when exploring. p – Adult females and in: *A. seniculus*, also juveniles.	m – Slightly disturbed. f – Unknown. r – Undetected.
Oodle (Altmann's type E) *A. seniculus* *A. palliata*	d – Rhythmically repeated in-out pulses of air ("oodloodlood"...). f – Common.	s – Intergroup confrontation, intense disturbance and during roaring pauses. p – Adult males.	m – Disturbed and aggressive. f – Threatening other howlers and communication of alarm to other group members. r – Companions and other groups' members display agonistic behavior.

(cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Whimper (Altmann's type G; perhaps Baldwins' "Squeak", type M) *A. seniculus* *A. palliata*	d – Continuous not too loud vocalization that sounds like a high whimper. Emitted with mouth corners backwards. f – Common.	s – General disturbance, especially from other group members. p – Infants, juveniles and adult females (doubtful for adult males).	m – Frustrated. f – Not known. r – Undetected.
EH (Altmann's type F) *A. seniculus* *A. palliata* *A. caraya*	d – A soft, expirant vocalization repeated every few second (eh, eh, eh). f – Unknown.	s – While exploring environment, play. p – Infants.	m – f – Maintaining contact. r – Undetected.
Cackle (Altmann's type I) *A. palliata*	d – A high, repeated cackling laugh (heh, heh, heh). f – Rare.	s – During agonistic social interactions. p – Infants, juveniles and adult females.	m – Threatened. f – Not known. r – Undetected.
Caws (Carpenter's type V) *A. palliata*	d – Series of three crying notes (caw, caw, caw). f – Unknown.	s – Lost or separated from mother. p – Infants.	m – Frightened. f – Not known. r – Undetected.
Wrah-ha (Baldwins' type K and perhaps Carpenter's type IV). *A. palliata*	d – Two (sometimes three) syllables, the first one louder and the second inhaled. f – Unknown.	s – Mother separated from infant or adult females separated from troop. p – Adult females.	m – Distressed from isolation or from absence of infant. f – Perhaps aiding infant locating mother. r – Undetected.
Yelp (Baldwins's type L) *A. palliata*	d – Like yelp of dog when suddenly hurt. f – Rare.	s – Sudden, intense disturbance. p – Infants 3, juveniles and adult females.	m – Highly frightened. f – Not known. r – Undetected.
Screech (Baldwins' type L) *A. palliata*	d – Loud high "EEEeee". f – Rare.	s – Sudden, intense disturbance. p – Infants 3, juveniles and adult females.	m – Highly frightened. f – Not known. r – Undetected.
Infant Bark (Baldwins' "Bark", type M) *A. seniculus* *A. palliata*	d – Explosive high bark. f – Very rare.	s – Startled by other animals and when in rough play. p – Infants.	m – Distressed. f – Communicating distress. r – Sometimes mother retrieves infant.
Purring (Carpenter's type VI) *A. seniculus* *A. palliata*	d – Low intensity tremulous sound produced with the mouth closed that sounded like a purr. f – Unknown.	s – When starting close body contact with mother. p – Infants.	m – Affection towards mother. f – Not known. r – Undetected.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
OLFACTORY PATTERNS			
Rubbing back (Fig. 6) *A. seniculus* *A. palliata* *A. pigra*	d – From bipedal position or while lying on back, the animal rubs its back laterally against substrate. f – Very common.	s – Before entering and after leaving sleeping site, during social and non-social stress and after rain. p – Adults of both sexes.	m – f – Perhaps marking. r – Releases same pattern in group companions in same point as performer. Sometimes approaching performer and sniffing rubbing site.
Rubbing muzzle (Fig. 6) *A. seniculus*	d – Rubbs muzzle repeatedly, salivating while protruding tongue, against certain branches. f – Common.	s – While moving in feeding area, when passing by certain selected point. Also when displaying towards observer. p – Mainly adult males, also adult females and juveniles.	m – f – Perhaps marking. r – Releases same pattern by group companions at same point. Group members often sniff at area rubbed on branch.
Chest rubbing *A. seniculus* *A. palliata* *A. pigra*	d – Rubs chest on branch f – Rare.	s – Unknown. Post-copulatory *(palliata).* p – Adult males.	m – f – Perhaps marking. r –
Throat rubbing *A. seniculus* *A. palliata* *A. pigra*	d – Throat rubbed on underside of branch for 1-2 minutes Accompanied by howling and/or piloerection.	s – During disturbance by conspecifics or humans. After copulation *(palliata)*.	m – Hostility, high arousal. f – Perhaps marking.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
A. caraya *A. fusca*	f – Common.	p – Adults and subadults, males more than females. Infrequently juveniles.	r –
Urine-rubbing *A. palliata*	d – Rubbing urine on soles of feet, palms of hands, ventral surface of tail and, occasionally, on throat. f – Common.	s – Following group rest, before or during troop travel and during social stress. p – Adult males, adult females and immature animals.	m – Distressed in social situations. Unknown motivation in other situations. f – Perhaps path marking. r – Not known.
Rubbing anal area (Fig. 6) *A. seniculus* *A. palliata* *A. pigra*	d – From sitting position, hands and feet close and on branch; performer rubs anal area back and forth against substrate. f – Common.	s – Before entering sleeping sites, following group rest and during social stress. p – All.	m – f – Perhaps marking certain sites in home range. r – Releases same pattern by other group members at same point as performer, sniffing by others.
Sniffing *A. seniculus* *A. palliata* *A. pigra* *A. fusca*	d – Performer sniffs genitals or flank of receiver. Males towards females and females towards males. f – Unknown.	s – During allogrooming and in sexual context. p – Adult males and females.	m – Exploratory while grooming partners hair and when sexually aroused. f – Perhaps releasing sexual behavior and detecting female estrus. r – Undetected.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Urine sniffing *A. seniculus* *A. palliata* *A. pigra*	d – Sniffing urine on branch or may place nose directly in urine stream. f – Unknown.	s – Related to estrus. p – Adult males for urine of females.	m – Sexual. f – Detect estrus? r – May curl lip *(palliata)* or show chewing *(pigra)*.
TACTILE PATTERNS			
Slapping *A. seniculus* *A. palliata* *A. fusca*	d – Slapping receiver on head or tail. f – Rare.	s – Before and during agonistic and rough playing encounters. p – All.	m – Aggressive or playful. f – Unknown. r – Undetected.
Biting *A. seniculus* *A. palliata* *A. fusca*	d – Biting conspecific. f – Very rare.	s – During agonistic encounters. p – All.	m – Aggressive. f – Repelling receiver. r – Whimpering, fighting or moving away.
Restraining (Fig. 11) *A. seniculus*	d – Sitting for a few seconds over receiver. f – Very rare.	s – When performer is fighting with conspecific or rather disturbed by other animals fighting or playing near by. p – Adults of both sexes.	m – Disturbed. f – Ending disturbing situations. r – Receiver crouches when performer sits over it and moves away when dismounting.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
Fighting *A. palliata* *A. seniculus*	d – Two individuals bite and slap at each other. f – Rare.	s – Proximity to conspecific during feeding or group progression. p – Adults and juveniles.	m – Aggressive. f – Unknown. r – Usually one of the participants moves away after the fight.
Pushing away (Fig. 9) *A. seniculus*	d – Pushing receiver away with hand. f – Very rare.	s – Conspecific near by and during play. p – All.	m – Not wishing contact and playful. f – Keeping conspecifics away and inciting to play. r – Moving away or playing.
Getting between *A. seniculus* *A. pigra*	d – While two animals are sitting in contact, the performer makes its way between them by pressing with arms and shoulders. f – Unknown.	s – Before sleeping. p – All except the oldest male of the group.	m – f – Not known. r – Undetected.
Mouth to mouth (Fig. 9) *A. seniculus* *A. palliata*	d – Two individuals sitting nearby embrace each other and join their muzzles together. f – Very rare.	s – Animals sitting together in relaxed situations. p – All.	m – Friendly. f – Group cohesion. r – Undetected.
Allogrooming (Fig. 10) *A. seniculus* *A. palliata*	d – From a sitting position, the performer inspects fur of receiver, sometimes	s – Mainly during siesta time.	m – Friendly. f – Group cohesion.

(Cont.)

Table XVI (Cont.)

Name of pattern and species	Description (d) and frequency of use (f)	Situations of use (s) and performer (p)	Motivation (m), function (f) and response (r)
A. pigra *A. caraya* *A. fusca*	approaching mouth to skin. f – Common, rare in *pigra* and *palliata*.	p – Adults and juveniles.	r – Remaining still and sometimes displaying area to be groomed.
Wrestling *A. seniculus* *A. palliata* *A. caraya* *A. fusca*	d – While facing partner, either on all fours or hanging by tail, the performers paw, tug or push at each other with hands or feet. f – Common.	s – Group together in relaxed situations. p – Adult females and juveniles.	m – Playful. f – Play functions. r – Observers often try to participate in play.
Copulation (Fig. 10) *A. seniculus* *A. palliata* *A. pigra* *A. caraya* *A. fusca*	d – Male mounts female either completely (his hands on her shoulders, his feet grabbing her heels while anchoring himself with tail to a branch), or making contact with substrate with tail and feet, only grabbing with hands the female's waist. f – Very rare.	s – When female in estrus. p – Adults.	m – Sexually motivated. f – Sexual functions. r – Sometimes female looks back at male and performs lip smacking.

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[1] Principal sources: Carpenter (1934), Altmann (1959), Moynihan (1967, 1976), Neville (1972b, 1979), Glander (1974), Milton (1975), Baldwin and Baldwin (1976, 1978), Braza (1978, 1981), Jones (1978, 1979, 1980a, 1983a, 1985), Shoemaker (1978), Young (1981a, 1981b, 1982a), Crockett and Sekulic (1982), Horwich (1983a), Sekulic and Eisenberg (1983), Young (1983), Thorington *et al.* (1984), Mendes (1985). Note: if a species is not listed as performing a certain behavior, this does not imply that it is not included in its behavioral repertoire.

[2] Vocalizations after Carpenter (1934), Altmann (1959) and Baldwin and Baldwin (1976). Others only cited if the description is related to the schemes of these authors.

IX. LOCOMOTOR AND POSTURAL BEHAVIOR

Descriptions of the locomotor-related anatomy of howler monkeys can be found in such publications as Bodini (1963), Bodini *et al.* (1971), Erickson (1963), Grand (1968a, 1968b), Schön (1968; see also Schön Ybarra, 1982, 1984) and Stern (1971). The key aspects are as follows: (1) Limb lengths are roughly equal in trees; the monkey is either quadrupedal or hanging by some combination of limbs and tail or tail alone. It is not a brachiator. The rare instance, photographed in Carpenter's 1960 film, of a howler using upside-down quadrupedal locomotion was mislabelled as brachiation. (2) The hands have the generalized aspect of the New World monkeys. The thumb is not distinguished from the other fingers to form a truly opposable digit, as with the catarrhines, and grasps of branches may most often occur between the second and third of the five digits. (3) Its prehensile tail is an important security device in locomotion, but its main use may be to enable the howler to dangle (usually using one or more of its limbs as well) from small branches while feeding below its support.

It is interesting that the anatomy of *Alouatta* is often used as a model for the generalized aspects of the early Hominoidea and anthropoids (for example, Cartmill and Milton, 1977; Mendel, 1975; Fleagle and Simons, 1978; Schön Ybarra, 1982, 1984), although without losing sight of the fact that the prehensile tail represents a major specialization.

A number of studies have examined the locomotor patterns of *Alouatta* in the wild. Mendel (1976) established that, at BCI, *palliata* was most frequently active on small, flexible, nearly horizontal supports on the periphery of tree crowns, which is corroborated by Smith (1977) and others. Slow, deliberate locomotion was the norm. The howlers were walking in 70% of observations, with the weight being supported by diagonally opposite limbs. The monkeys climbed to gain altitude. Dropping or leaping were about equally frequent. Mendel (1976) saw no brachiating, and feeding postures were usually suspensory using various combinations of limbs and tail involving a number of anatomical traits which had hitherto been suggested as related to brachiation or forearm suspension. Large males were more likely to use large supports. "Resting was the predominant activity and was most often done in a sitting or lying posture".

Fleagle and Mittermeier (1980) compared locomotor anatomy and behavior among seven species of sympatric Surinam monkeys. They found a strong relation between body size and locomotion style: increasing size led to increasing climbing, decreased leaping, and the use of larger supports. Walking made up 80% of the observations of travelling howlers (*seniculus*), and leaping only 4%. During feeding, climbing (as opposed to quadrupedal walking) increased, as did the use of smaller supports.

Some aspects of the locomotion of *fusca* were studied by Young *et al.* (1983). They distinguished four categories: quadrupedal walking and running, suspensory locomotion, climbing and leaping (see Mittermeier, 1978). As for *palliata* and *seniculus*, quadrupedal walking and running was the most frequently used, even on branches only a few centimeters thick. Armswinging and upside-down quadrupedalism were used occasionally, the latter especially during play, but never brachiation. The category climbing is subdivided into quadrupedal ascent and descent, horizontal climbing, bridging, supported bipedal walking and lowering (descending to the extremity of a support and adopting a suspensory posture at the tip; frequently to obtain a food item). Lowering was very rare and supported bipedal walking was never seen. Otherwise, these modes of locomotion were usually seen either when manoeuvreing to obtain access to food or when moving to a horizontal branch to initiate quadrupedal progression. They very rarely leap more than a few meters.

Howlers on the ground appear relatively awkward. The fingers are loosely spread in front of them, their elbow and knee joints remain slightly flexed, and they are relatively slow, although Glander (pers. obs) asserts that they can outrun humans. Despite the dangers of being on the ground, they may cover relatively long distances between food trees in the *llanos* (Neville, 1972a), and to gain access to a water source or "salado site" (Izawa, 1975). Schön Ybarra (1982, 1984) found that about 28% of the travelling time of a *seniculus* group at HMG was terrestrial (107 hours of observation).

Young *et al.* (1983) divided their analysis of postures of *fusca* into those adopted during feeding, short rests and long rests. This species is most frequently sitting while feeding, but may also do so while suspended or standing. Bipedal, tripedal and quadrupedal standing accounted for 23% of the feeding postures recorded. They were never observed reclining while feeding. Most feeding was carried out while on twigs and small branches, and only infrequently while on boughs. The most common suspensory posture while feeding involved three limbs, followed by those using four limbs. Five-limb and one-limb suspension was rare. *A. fusca* usually sits during short rests, most frequently on branches and boughs and infrequently on twigs. Long rests were also usually seated. Only 8% recorded involved a reclining posture and during long rests they usually sat on larger branches and boughs more than during short rests.

Generally, limited use of the hands in feeding is suggested by the lack of specialization of the thumb. Smith (1977) described *palliata* feeding as follows: "Usually they grab a branch about 30 cm from its tip and bend it back to bring fruit, leaves, buds or flowers close to their mouth and pick the food with their lips or teeth. The food is manipulated in the mouth, usually without the aid of hands, and may be rejected by spitting it out of the mouth".

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