

Communication Mechanisms
and Social Integration in
the Black Spider Monkey,
Ateles fusciceps robustus,
and Related Species

JOHN F. EISENBERG

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ABSTRACT

Eisenberg, John F. Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and Related Species. *Smithsonian Contributions to Zoology*, number 213, 108 pages, 63 figures, 40 tables, 1976.—The study describes the mechanisms of communication employed by the individuals of a captive colony of *Ateles fusciceps robustus* studied by the author for some ten years. The signal system is compared and contrasted with that of a free-ranging group of *A. geoffroyi panamensis*. The signal systems are discussed within the functional contexts in which they occur. Sexual, grooming, and grappling behaviors are given special quantitative treatment. Auditory signals are considered from the standpoint of syntactic description. A rigorous analysis of the vocalizations is presented together with a contextual description leading to a functional classification. The motivational basis for vocalizations is then explored. The development of vocalizations in the young *Ateles* is described together with the effects of auditory isolation on vocal development. The vocal repertoire of *Ateles* is compared with that of *Lagothrix*, the woolly monkey, and *Alouatta*, the howler monkey. Preliminary ethograms for *Alouatta* and *Lagothrix* are presented in the appendices. It is concluded that the vocal repertoire of *Ateles* can develop without imitative learning and that the signal system of *Ateles* shares homologous elements with that of *Alouatta* and *Lagothrix*. The degree of similarity is highest between *Ateles* and the woolly monkey.

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Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and Related Species

John F. Eisenberg

Introduction

This report concerns the behavior patterns of two species of spider monkeys, *Ateles fusciceps* and *Ateles geoffroyi*. The major portion of the material consists of observations on a captive group of *A. fusciceps robustus* maintained for some 14 years at the National Zoological Park. The history of this group through 1972 has been reviewed (Eisenberg, 1973). Except for some notes made by C. O. Handley in 1964, field data are lacking for this species. In order to expand our knowledge of communication in free-ranging *Ateles*, I conducted observations on an introduced group of *A. geoffroyi panamensis* on Barro Colorado Island, Canal Zone. The early history of this group has been described by Eisenberg and Kuehn (1966) and R. Dare (1974).

The vocalizations, gestures, and maintenance behavior patterns of these two species are quite similar and, for this reason, I have chosen to use the *Ateles geoffroyi* field data as a means of inferring the functional role in the field for some of the forms of communication shown by the captive *A. fusciceps* group. Appendix I contains a comparison of the physical characteristics of selected vocaliza-

tions for *A. geoffroyi*, *A. fusciceps*, *A. belzebuth*, and *A. paniscus*. Great similarities are indicated. That the first three species are closely related was already evident in the taxonomic review by Kellogg and Goldman (1944). Recently Hershkowitz (1972:353) has suggested that only one specific name for *Ateles* is valid, i.e., *Ateles paniscus*. I do not wish to take sides in any taxonomic controversy; however, in my opinion the four species show great behavioral homogeneity, although minor differences can be discerned. Thus, it seems fair to utilize the field data from the *A. geoffroyi* study to clarify the function of the homologous vocalizations displayed by *A. fusciceps* in captivity.

Captive Research

Four *Ateles fusciceps robustus* were received on 17 May 1961 at the National Zoological Park. This served as the founder stock for our colony, which has been maintained until the present time. The reproductive history of the group was reviewed in the publication by Eisenberg (1973). To date (September, 1974), 13 live births have occurred and of these 4 young were taken for hand rearing and the study of their behavioral development.

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The results of these developmental studies are reviewed on pages 52–58 (“Ontogeny of Behavior”).

The *Ateles fusciceps* group was studied intensively in the autumn of 1964 and 1965 and during the summers of 1966 and 1967. During the winter of 1967, observations were continued, but detailed behavioral studies were not initiated again until the spring and summer of 1972 and 1973. The composition of the study groups is summarized in Appendix II.

Most of the quantitative data referred to in this paper were taken during the summers of 1972 and 1973, and in the fall and winter of 1974–1975. During 1972–1973, the captive group of *Ateles fusciceps* consisted of an adult male, 3 adult females, and a juvenile male born in August of 1970. In 1974 the main study group included an adult male, 2 adult females, one juvenile female and 2 infant males. During the summers, the animals were housed in an outdoor enclosure measuring 5 × 3 × 3 meters. The enclosure was equipped with benches and a series of vertical poles. The bars of the cage permitted overhead brachiation. Food consisted of bread, carrots, sweet potatoes, kale, apples, oranges, bananas, and a prepared supplement (Zupreem Marmoset Diet). Water was obtainable at all times.

Data concerning the behavior patterns of these captive spider monkeys were recorded by direct observation and written notes in a semi-coded form on prepared checksheets. Alternatively, the behavior was described by speaking into a tape recorder and later transcribed onto prepared data sheets with the appropriate time intervals inserted.

During 1964 and 1965, adult and juvenile vocalizations were recorded and analyzed. In 1966 and 1967 hand rearing, behavioral ontogeny, and the development of vocalizations in isolation were described and analyzed. Over 300 hours of observations and recordings were logged in these years.

Observation periods involving transcribed recordings were conducted by a balanced series of 30-minute sessions in 1973 and 15-minute sessions in 1972. Over 50 hours of quantified observations were made during these two summers. Total hours of observation with hand notes or recordings exceeded 100 hours. Observation periods were balanced during various parts of the day to avoid bias induced by such activities as cage cleaning and feeding. In the interval 1974–1975, observations were again divided into 30-minute sessions for a

total of 40 hours of data.

Vocalizations, for the most part, were recorded on Uher 4000 Report-L tape recorders at $3\frac{3}{4}$ or $7\frac{1}{2}$ inches per second. Since most of the energy in *Ateles* vocalizations lies below 5000 Hz, the Uher microphone-tape recorder combination served as an adequate recording system. Some recordings during the last year of the study were made with a Nagra IV SJ. Vocalizations were analyzed utilizing a Kay Electric Company Missilyzer No. 675. Most of the analyses were carried out with 5000 Hz as the maximum setting. Within this range, the frequency band width is 20 Hz for narrow band analyses or 200 Hz for wide band analyses. When using the wide band setting, the frequency of the sound so reproduced was estimated at the midpoint or darkest portion of the sonographic display. Many of the sounds produced by *Ateles* do not exhibit a single frequency but, upon sonographic analysis, display side bands. These may be true harmonics or may be artifacts inherent in the functioning of the Kay Missilyzer (Watkins, 1967).

In order to check on the actual energy distributions in the recordings of some *Ateles* sounds that showed little discrete harmonic structure, the sounds were passed through a Tektronix Type 323 oscilloscope. The overall energy distribution in complex sounds could thus be assessed with respect to the dominant frequency. Clearly, some of the *Ateles* calls are truly harmonic in structure, others are definitely not—regardless of the sonographic portrayal. Thus, when referring to sonographs, the term side bands will be used uniformly, but in those cases where the sounds are purely harmonic it will be so indicated in the text (see also Appendix I).

Field Research

Ateles geoffroyi panamensis on Barro Colorado Island were studied by Eisenberg in 1964, 1965, 1966, 1970, and 1974. Altogether some 14 weeks were spent in observing these monkeys. A total of some 105 hours were spent recording behavior. Appendix II contains a synopsis of the history of this group. I am indebted to Dr. N. Smythe, Dr. M. Hladik, Dr. R. Dare, Dr. G. G. Montgomery, and Dr. A. Richard (1970) for filling in the gaps concerning the history of this group during the long

intervals when I was not present on the island. The main thrust of the observations on the group of *A. geoffroyi* concerned (1) the identification of the contexts in which vocalizations were produced,

and (2) an attempt to understand the development of social relationships among group members as the colony grew through births to the founding females from 5 to 15 individuals.

Natural History of *Ateles*

The genus *Ateles* ranges in tropical evergreen or semi-evergreen forests from southern Mexico to southeastern Brazil (Kellogg and Goldman, 1944). Field observations on *A. geoffroyi* in Mexico are described by Wagner (1956) and Eisenberg and Kuehn (1966). *Ateles geoffroyi* in Panama was studied by Carpenter (1935). Additional data for an introduced but free-ranging, breeding population of *A. geoffroyi* on Barro Colorado Island, Panama, have been collected by Eisenberg and Kuehn (1966), Richard (1970), Hladik and Hladik (1969), and Dare (1974). Klein (1972) has completed an extensive field study of *A. belzebuth* in Columbia, and Durham (1971, 1975) has reported preliminary results on *A. paniscus* in Peru.

It is generally agreed that *Ateles* is primarily frugivorous and feeds selectively at moderate to extreme heights in mature forests (Carpenter, 1935; Hladik and Hladik, 1969). Diurnally active, the bands tend to feed intensely in the early morning only to renew feeding in the afternoon. Carpenter (1935) noted that the troops of *A. geoffroyi panamensis* frequently broke up into subgroups during their feeding cycle. Indeed, such subgroups did not necessarily reconstitute themselves into the same social unit in sleeping trees at the end of the day's activity. Especially noticeable was a tendency for adult, unisexual subgroup formation and all-male groups were commonly censused. Eisenberg and Kuehn (1966:35-38) noted the tendency for independence in male activity in both a field and a captive population. Klein (1972) made similar observations on *A. belzebuth* and concluded that the all-male subgroups were composed of males who offered mutual support to one another during both intratrop conflicts and intertrop encounters. Based on further observations of the *A. geoffroyi* group in Panama, Eisenberg, Muckenhirn, and Rudran (1972) suggested that such all-male subgroups may be composed of related individuals and age-graded in the sense that mutual tolerance among such males has an orderly developmental succession based on continually renewed contact

over many years.

Wagner (1956) had noted that under some circumstances an *Ateles* troop could exhibit a unimale structure; that is, only one adult male associated with a female subgroup and their progeny. Eisenberg and Kuehn (1966:56-57), on the basis of a brief censusing operation in Chiapas, suggested that such unimale troops could be shown in areas of reduced carrying capacity. Freese (1975) noted similar troop structures during censusing in Costa Rica. Klein (1972) suggested that such unimale troops recorded in the literature may well have been the result of incomplete censusing, especially since adult males are very independent of the females in their movements. In Klein's study, the troops of *A. belzebuth* each had two or more adult males periodically in association with the females. Recently Durham (1975) has offered evidence for both unimale and multimale troops in *A. paniscus* from Peru. The unimale condition is typically shown in the smaller troops at high elevation habitats, which presumably have a reduced carrying capacity.

Thus, there is some disagreement concerning the typical form of the social organization shown by *Ateles*. In part, the multimale versus unimale controversy is artificial (Eisenberg, Muckenhirn, and Rudran, 1972), but only long term studies in the future will clarify the genesis of the so-called multimale troop. Further comparisons will be necessary before the relation between troop size and carrying capacity can be firmly established.

In spite of the uncertainties, there is agreement on the following points: (1) The home range of an *Ateles* troop is much larger than a comparably sized troop of howler monkeys (*Alouatta*) in a comparable habitat. (2) Compared to *Alouatta* and *Cebus*, the *Ateles* troop is less cohesive and subject to fractionation. (3) Males tend to be independent in their movements with respect of the rest of the troop. (4) Females with dependent infants and juveniles form the most cohesive subunit in a troop. (5) Adult males may be intolerant

of other males belonging to a distinct but neighboring troop. (6) A subgroup of age-graded males may act as a cooperative unit during offensive

and defensive behaviors. (For a definition of age-graded, see Eisenberg, Muckenhirn, and Rudran, 1972.)

Some Motor Patterns and Their Functional Contexts

Maintenance Behavior

The maintenance behavior patterns of *Ateles fusciceps* in captivity do not appreciably differ from those described for *Ateles geoffroyi* by Eisenberg and Kuehn (1966). Several points are worthy of comment, however, since in the intervening eight years we have had to modify earlier conclusions.

Locomotion is controversial, since *Ateles* has been considered a brachiator by Erikson (1963), on the one hand, and essentially quadrupedal by Napier and Napier (1967) at the other extreme. Recently Tuttle (1975) has described the long arms of *Ateles* as adaptation for feeding by hanging vertically and performing vertical lifts and drops during terminal branch feeding, as originally described for *Hylobates* (Grand, 1972). While it is true that *Ateles* feeds in a manner reminiscent of *Hylobates*, it is also true that *Ateles* locomotes by brachiation. The form of brachiation by *Ateles* differs from that of *Hylobates* in that *Ateles* uses its tail as an "assist" with each or one arm in a given two-arm cycle of brachiation (see Grand, 1975, for a complete discussion).

Leaping by *Ateles geoffroyi* is awesome and often involves considerable vertical descent, especially when it is part of the male display sequence (see "Male Agonistic Display," p. 20). Adult females carrying young (see "Infant-2," p. 55) will attempt leaps across gaps of 2 meters. At the moment of leaping the arms are generally extended to maximize the reach (Figure 1).

Activity is not strictly confined to daylight. As noted earlier (Eisenberg and Kuehn, 1966:55), some social interaction can and does take place after dark, and Handley (in litt.) comments that *Ateles fusciceps* has been noted to move a considerable distance as a troop on a moonlit night.

Concerning feeding patterns, Hladik and Hladik (1969) report that *Ateles geoffroyi* can consume up to 20 percent of its diet in the form of young leaves. This is somewhat higher than the

values obtained by Carpenter (1935), but still considerably less than the 40 percent value computed for *Alouatta* by the Hladiks. While it is still reasonable to consider *Ateles geoffroyi* primarily a frugivore, no doubt further studies of its foraging behavior are warranted.

It is worth mentioning that, as in *A. geoffroyi*, self-grooming (autogrooming) in *A. fusciceps* occupies a very small percentage of their time (Eisenberg and Kuehn, 1966:33). In 72 separate 30-minute observation periods, autogrooming accounted for only 0.64 percent of the total observation time (Table 1). These data are quite comparable with the earlier data obtained for *A. geoffroyi*.

TABLE 1.—Autogrooming frequencies and durations for individual *Ateles fusciceps*, 1973

Subjects	Σf	Σd	%
V	0	0	0
B	13	393	47.4
M	0	0	0
S	6	234	28.3
J	8	201	24.3

Σf = total frequency of grooming shown; Σd = total duration (sec) of grooming shown; % = percentage of summed durations of all autogrooming for all observation periods.

Total percent of observation time spent in autogrooming was 0.64%. The average duration of an autogrooming bout was 30.6 seconds.

Patterns of Interaction

REPRODUCTIVE BIOLOGY

During the course of our preliminary studies (Eisenberg and Kuehn, 1966), we had difficulty determining the receptivity of females and had no knowledge of the unique posture assumed during copulation. Indeed, we witnessed copulation once but did not interpret the behavior correctly (Eisenberg and Kuehn, 1966:19-20). The situation was clarified for us through subsequent observations from 1970 to 1972. Klein (1971) had correctly in-



FIGURE 1.—A leap by an *Ateles geoffroyi* female while carrying her infant dorsally. Note the extension of the forearms. (Photo by N. Smythe.)

terpreted the significance of the copulatory posture and he further called attention to the role that urine may play in coordinating the activities of adult males and females (Klein, 1971).

Although spider monkeys have been studied off and on for the last 50 years, the details of their reproduction have remained obscure. Goodman and Wislocki (1935) described cyclical uterine bleeding, which occurred every 26 to 27 days in adult females. Blood could be obtained through a vaginal lavage procedure for roughly 3 to 4 days. From time to time, we have noted what appeared to be dark secretions present on the sulcus of the pendulous clitoris but in no case were we ever able to determine on a regular basis by visual inspection when a female spider monkey was undergoing menstruation. The experience has been similar for other workers. The opening of the vagina itself and the clitoral structure may appear moist and somewhat tumescent around the time of estrus; however, precise criteria remain to be developed

for a visual determination of estrus in the female spider monkey.

Behaviorally, female spider monkeys show an increased tendency to manipulate, inspect, and lick the clitoris prior to maximum sexual receptivity. In addition, females approaching estrus tend to groom other group members with a greater frequency and will approach the adult male and present their genitalia or posteriors for his inspection. The male becomes more active in his own grooming activity when a female in the group is approaching estrus (Table 2).

In an established group, there are very few preliminaries which can be noted that indicate that a couple intends to copulate. We observed that the pair may move away from the main group to a point of seclusion and that juvenile animals may sometimes interfere with the copulation by the parents, especially the offspring of the copulating female (see "Sexual Behavior," p. 8).

The male may often sit or recline slightly with

or without an erection and be approached by the female who will sit in his lap, whereupon he will assume the copulatory position by clamping his hind legs firmly over hers. On the other hand, this locking of the male's legs over the female's, as described by Klein (1971), may occur outside the mating context (see "Role Summary," p. 15).

The copulations we have observed with *Ateles fusciceps* differ little from those described by Klein (1971) for *A. belzebuth*. Some thrusting movements are made by the male throughout the course of intromission, which may last in excess of 35 minutes. The male may mate with a given female over a 48-hour period; we have noted two such copulation sequences (see "Patterns," p. 9).

Gestation has been calculated at 226 and 232 days. This does not differ from the figure (7½ months) quoted for *Lagothrix* by Williams (1967). In the captive group of *Ateles fusciceps*, the interval between births is a function of the duration of lactation. If the young were taken at birth or were stillborn, the interval ranged from 8 months to 11 months 28 days (N=5). If lactation occurred, the interbirth interval was in part a function of the duration of lactation. Intervals ranged from 15 months 13 days to 29 months 28 days (N=8) (Eisenberg, 1973).

Our observations on the *Ateles fusciceps* colony suggest that youngsters may actively suckle from their mothers until at least 16 months of age, although they have begun to eat solid food some 8 months earlier. It would appear that the period of dependency on the part of the newborn is prolonged when compared with that of the macaque and baboon. Furthermore, the data suggest that mothers should produce a youngster every 22 to 36 months. Data concerning the long period of infant dependency are confirmed by field observations on *Ateles geoffroyi panamensis* on Barro Colorado Island. From 1966 to 1974, 14 births were recorded from 4 adult reproducing females (Appendix II). Klein (1971) also remarks upon the prolonged period of infant and juvenile dependency in his field study of *Ateles belzebuth* in Colombia.

Klein (1971) suggests that *Ateles geoffroyi* in the captive colony at San Francisco and *Ateles belzebuth* in Colombia exhibit no birth season. I am inclined to agree that *Ateles* can mate throughout most of the year, but the 19 births occurring at the National Zoological Park during the last 11 years

show a tendency toward two peaks, since 11 of the 19 full term births occurred in April, May, or June, and 5 births occurred during November, December-January. If the gestation is 7½ months, then we have the suggestion of an optimal breeding period for this captive group of *A. fusciceps* during the months of July, August, and September, and March and April. Perhaps mating in Washington, D. C., is in part regulated by a shift in the amount of light, since optimal breeding periods seem to occur around the periods following the spring and autumnal equinoxes. It is impossible at the present time to determine whether birth peaks are a result of male spermatogenic activity or female cycling. It is noteworthy, however, that estrus synchrony is suggested in our captive group of *Ateles fusciceps*, since 4 out of 19 births were within 5 days of each other and 8 births were less than or equal to 28 days apart (Appendix II).

SEXUAL BEHAVIOR OF *Ateles*

In an earlier publication (Eisenberg and Kuehn, 1966), an attempt was made to discuss some aspects of the sexual behavior of *Ateles belzebuth*, even though complete sexual behavior had not been observed. Eisenberg and Kuehn reproduced a protocol from 17 March 1964, which was based on an encounter between an adult male and an adult female. That particular set of observations was made during the course of an encounter series where adults were kept separated and allowed to come together in a large exercise cage. Because of the method of holding the animals in separate cages unless they were being studied in the encounter situation, certain aspects of contact-promoting behavior were exaggerated. Furthermore, grappling bouts occurred in an encounter situation at an exaggerated frequency than when compared with the field data (see "Grappling," p. 12). In such an encounter situation, grappling should resolve itself in the re-establishment of a dominance relationship between the pair but, as I have noted previously, grappling can terminate either with mixed elements of sexual behavior or terminate in aggressive arousal. This is especially true if the grappling bout involves individuals that have an imperfectly established dominance relationship. I agree with Klein (1971), however, that the sounds often associated with grappling, "ook-

ook," and the appeasement sounds or slightly frightened sounds of "squeaking" need not necessarily be associated with sexual receptivity or sexual motivation.

An encounter previously reported (Eisenberg and Kuehn, 1966:19) involved the assumption of the copulatory posture on two occasions. The first bout of interaction following upon grappling involved the male sitting on the swing with which the cage was provided. This swing had a baseboard approximately 8 inches wide and 3 feet long, which provided a rather secure resting place. As the male sat upright looking at the female, she approached him brachiating and hung above him; then she sat in his lap for about 1½ minutes. During this time there was some movement on the part of the male and she turned to embrace him face to face while remaining seated in his lap. Prior to sitting in his lap, she made low squeak vocalizations and he intermittently uttered low ooh-ooh sounds with a long interval between each emission. The vocalizations probably do not have anything to do with sexual receptivity but reflected a general ambivalence on the part of both animals. Upon rising from the male's lap, it was noted that the female's vaginal opening was somewhat dilated and moist, but no trace of an erection could be seen for the male. In retrospect now, we realize that the couple had assumed the copulatory posture, although our old notes do not permit us to say whether or not intromission took place.

After an interval of approximately 15 minutes, the animals began to interact heavily again. At this time it was noted that the male had an erection. He approached the female facing her while hanging up; the female was braced upright in a corner of the cage. He made a pelvic movement and then moved away. This we termed a "thrusting movement." He then sat and the female approached following him and sat in his lap. This again was the second assumption of the copulatory posture. She moved away after about 2 minutes followed by the male. They then hung up by the arms facing one another and showed alternate bouts of moving away by the male with following by the female; eventually the male remained hanging and manipulated his genitalia with his hind foot. The female was hanging opposite him, facing him, and once again he made a thrusting movement toward her.

She moved away and he remained hanging where he was.

Upon approaching him again, the female manipulated his genitals whereupon the male moved away followed by the female. Upon facing one another again, the male exhibited another thrusting movement and then moved to the swing and sat. The female followed, hanging over him, whereupon the male manipulated her clitoris; then he assumed a suspended position hanging behind her and, reaching out with his hind legs, he grasped at one of her hind legs and made a thrusting movement. This we termed "mounting," but we now realize that this was an attempt on the part of the male to lock his hind legs over her thighs and pull her into a copulatory position. "Mounting" in the fashion of macaques is not part of the normal mating sequence in *Ateles* (see "Patterns," p. 61). Hence, Eisenberg and Kuehn (1966:19) stated that intromission was not actually seen; rather it should have been stated that intromission was uncertain and that the "copulatory position" was assumed.

I agree with Klein (1971) that the attainment of an erection by the male prior to copulation and hanging up while making pelvic thrusts at the female is not necessarily a standard part of the precopulatory repertoire. The fifth element of sexual behavior that Eisenberg and Kuehn (1966) mentioned, sitting in the lap, is definitely part of the sexual pattern since this is in fact an element of the copulatory position. What was termed "mounting" now turns out to be a movement preparatory to intromission shown in a slightly novel context (see also "Complex Interactions," p. 14).

A certain amount of variation is shown in the mating behavior of spider monkeys. Here follow three abbreviated protocols of copulation for *Ateles fusciceps* in our captive colony.

Copulation 1, 1330 hours, 6 July 1972 (observer, L. McLanahan): Female approaches male who is sitting alone. She places an arm around his neck and he leans forward to sniff at her pectoral region. He then bends down and sniffs at her genital area. As he does so, the female assumes a quadrupedal stance with her genital area facing the male. The male continues to sniff and lick at her clitoris, being somewhat impeded by interruptions from subadult female B and the juvenile male who is the offspring of the interacting pair. Approximately 2½ minutes later, the female again approached the male and presented her anogenital area to him. The male immediately began to sniff and rub her pectoral

area with his hands and manipulated her clitoris and hind legs. The female was now directly in front of the male and, turning to face him, would stroke his head and arms only to turn around again and allow him to continue manipulating her clitoris and rub her pectoral region.

Thus, aside from turning around, for most of the initial interaction, the female was standing quadrupedally with her back to the male who was standing over her.

Then the male grasped the female with his forearms around her chest and, while sitting, pulled her down on him into the copulatory position. While pulling her down, he made an upward thrust. As he did so, the female stretched her body forward as the male hooked his hind legs over her thighs. The thrusting movements by the male subsided and he made a growling noise toward the juvenile male who attempted to insert himself between his father and mother. The next time the juvenile attempted this interruption, the male pushed him and he went to the other side of the cage squeaking and twittering.

The subadult female B would approach the copulating pair and occasionally allogroom the male. To this, the male did not particularly object. Throughout the copulation, the adult female would turn to stroke the male's head and neck. At 4 or 5 minute intervals, the male would resume active thrusting. The subadult female groomed the male less throughout and, at one time, grasped the copulating female and embraced her. Eventually the subadult female withdrew and curled up sitting to one side. Duration of copulation was slightly less than 25 minutes. At the end of the period of intromission, the male made three or four violent thrusts in which he raised his posterior from the ground.

This copulation occurred in a group context. Some interference occurred when the juvenile male and subadult female attempted to become involved. The subadult female was in estrus at the same time and the male copulated with her on the following day.

Copulation 2, 7 July 1972, 0950 (in this instance intromission was already in progress at the time the observer took notes) (observer, L. McLanahan): The male's legs were hooked over the female's thighs in the typical copulatory position. During this copulation the male was mating with the so-called subadult female B. The female with whom he had copulated previously was now sitting next to the male occasionally embracing his torso with her arms. He would respond to this by putting one arm on the old female's shoulder and extending his head toward her. [The significance of these interactions will be discussed under "Embracing and Hugging," p. 13]. The amount of interference was considerable from both the adult female and the juvenile. Once again, at the termination of the intromission, the male thrust 5 or 6 times and then appeared to withdraw his penis from the vagina of the female.

Copulation 3 (observer, J. F. Eisenberg): The male left the main group of animals at about 1335 and moved to a se-

cluded spot in the cage, namely the doorway giving access from the outer cage to the inside cage. The female approached him extending her hand, touched him on the head, entered the doorway, and turning and standing above him presented her genitals to his face, and then sat in his lap. The male immediately assumed the copulatory posture and they remained intromitted for 3 minutes 40 seconds. Thrusting movements were difficult to discern. During the time of intromission, the female turned around and looked at the male several times and touched him on the shoulder. Intromission terminated when the female began to rise and then turned and began grooming the male's neck and face. The female continued to groom the male on the chest and sniffed his genitalia. Since patrons began to initiate feeding, the female came to the front of the cage and the male followed after momentary inspection of his genitalia.

Eisenberg and Kuehn (1966:19) listed six aspects of primary sexual behavior. These included: (1) initial contact including embrace, followed by (2) genital manipulation, erection and pelvic thrusts by the male, sitting in the lap by the female, and (3) mounting by the male. Since it was incorrectly assumed that mounting by the male was in a conventional macaque pattern, sitting in the lap was not assumed to be a copulatory posture. Extension of the male's legs to grasp the female's hindlegs and lock his legs firmly over her thighs was interpreted as an attempted mount.

Following "contact" by the animals, I would now list as the primary elements of sexual behavior: (1) presentation of the genitals on the part of the female, followed by (2) sitting in the lap. Erection for some time prior to intromission on the part of the male, thrusting at the female as she approaches with an erect penis, and genital manipulation are not invariant components leading up to the copulatory position. In this, I concur with Klein (1971).

It is noteworthy that in all the copulations I have observed, the female plays an active role in approaching the male, touching, and eventually sitting in his lap. The male also may be active in initiating the copulatory position by extending toward her with his hindlegs and attempting to lock them around her torso (p. 7). We agree that copulation can take place in a group situation, but it would appear that the pair attempts to seek out seclusion since some interference from juveniles and subadults can occur in a confined captive situation. In the field, pairing off separately may occur more often than is suspected.

I no longer feel that grappling (play fighting) is

tied to primary sexual behavior, rather it is recognized that grappling is an interactional system whereby animals reinforce dominance status in ambivalent situations and is a play syndrome in juveniles. Induction of abnormal amounts of grappling as a result of Eisenberg and Kuehn's (1966) original encounter techniques, as suggested by Klein (1971), would appear to be the case. Excessive grappling between the male and the females of the *Ateles geoffroyi panamensis* group on Barro Colorado Island in the summers of 1964 and 1965 was undoubtedly associated with an imperfect dominance situation existing between the male and at least one of the four females. Nevertheless, during the latter period of field observations in Panama (Eisenberg and Kuehn, 1966:48), copulation did indeed take place, since the first infant was born in early January of 1966. Klein (1971) himself described a grappling bout that occurred in two free-ranging *Ateles belzebuth* prior to mating, but the grappling bout occurred some 7 hours prior to the first observed copulation.

Klein (1971) has implied that Eisenberg and Kuehn (1966) considered ook-ook, squeaking, and grappling as primary elements of sexual behavior. At no time in that paper were the ook-ook and squeak vocalizations referred to as being motivated primarily by sexual tendencies; rather, it was noted (Eisenberg and Kuehn, 1966:19) that, although the squeak may be given during the initial phases of primary sexual behavior, it would appear that the sound is given during a contact-seeking situation after the animal has been repulsed. In other words, the squeaking animal produces the sound as an appeasement signal and it is given with some overtones of fear. The ook-ook vocalization, although associated with grappling, is produced with many subvariants and may grade into aggressive growling or be produced in a low intensity variant, which may accompany certain aspects of sexual behavior. At no time was it inferred that ook-ook and squeak vocalizations were entirely sexually motivated or occurred entirely in a sexual context. In the same vein, it was not asserted that grappling was entirely motivated by sexual behavior, but rather only noted that it may sometimes have sexual "overtones" and occur prior to the expression of sexual behavior.

In the 1966 description of grappling, Eisenberg and Kuehn indicated that it involved elements of

embracing, pushing, pulling toward, mock biting, and slapping. Further, it was indicated that it may grade into agonistic behaviors, including a chase, and that sometimes it may occur prior to a sexual interaction. I do concur with Klein (1971) completely, however, that the encounter situation that was employed distorts the frequency of many of the behavior patterns in adult *Ateles*, and I certainly agree that sexual behavior may take place during the day and need not be confined to the evening.

Eisenberg and Kuehn (1966:18) erroneously assumed that copulation may often occur in the evening, since at this time much grappling occurred in the *Ateles geoffroyi* group on Barro Colorado Island. I now feel that this grappling was induced by the unstable dominance situation, the age of the animals, and the fact that interaction intensified in the early evening when the animals assembled at the sleeping trees. Copulations that were observed in captive *A. fusciceps* had occurred at 0830, 0950, 1330, 1335, and 1400.

AGONISTIC BEHAVIOR

Agonistic behavior in the captive colony of *Ateles fusciceps* was extremely rare. The adult male very often could cause two fighting animals to separate merely by approaching them rapidly; often progressing quadrupedally while showing pilo erection. Upon coming close to the fighting animals, the adult male would often show a partially opened mouth with the corners retracted thus exposing his teeth. This was not invariant, however, since a rapid approach by the male often sufficed to separate the combatants. Behavior on the part of the adult male directed toward an observer or keeper often assumed a threatening aspect. Frequently he would brachiate rapidly around the cage, flinging himself suddenly at the bars while staring directly at the object of his hostility. If the observer stared back at the male, he would frequently turn away, or, if the male attempted to maintain his gaze, he would retract the corners of his mouth while raising his lips slightly thus exposing his teeth. Very often shaking the bars could accompany this display (see "Male Agonistic Display," p. 20).

When they occur, aggressive interactions in the group are generally very swift. A rapid approach

TABLE 2.—Allogrooming bouts recorded for *Ateles fusciceps* through estrus, 1972

Subjects	27 Jun	28 Jun	29 Jun	30 Jun	1 Jul	2 Jul	5 Jul	6 Jul	7 Jul*	8 Jul	9 Jul	10 Jul	11 Jul	12 Jul
M → V	-	-	-	2	-	-	-	-	-	-	-	-	-	-
M → B	-	-	3	7	-	1	-	-	-	-	-	-	-	-
B → V	-	-	6	1	-	-	-	5	5	-	-	2	-	-
B → M	-	-	-	1	-	-	-	4	-	1	-	-	-	-
V → M	-	-	-	-	-	1	5	-	1	-	-	-	-	-
V → B	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Total	0	0	9	11	0	2	5	9	6	1	0	3	0	0

* Dates of copulation for females B and V. Data based on two 30-minute samples per day (see text).

may resolve itself into a chase with the approached animal fleeing. Sudden aggression may be displayed when an animal slaps another. Rarely does biting occur, but when it does, it is often swift with the bitten animal fleeing immediately, screaming, and remaining as far away from the attacking animal as possible. The attacked animal often shows extreme avoidance for some time after and may withdraw sitting crouched with his head buried between his knees. An animal so attacked may begin to utter twitter calls and screeches until it is approached by another group member, embraced, and held. Such behaviors of withdrawal and protest sounds were frequently shown by the juvenile male J upon being punished by his mother. Frequently it was the adult male that approached and embraced.

Recently the agonistic patterns of *Ateles* have been reviewed in depth by Klein (1974). Klein draws on both captive studies of *A. geoffroyi* and his field study of *A. belzebuth*. Klein emphasizes that in strong aggression there is relatively little active submission and generally an attack ends with one animal fleeing. Yet, if I define agonistic behavior broadly to include the numerous intragroup "spats" observed between mothers and young and between siblings, then the distress calls and solicitation of contact by an attached animal certainly qualify as an alternative to active submission. Sitting alone while hunching and lowering the head is to my mind a form of active submission, although this occurs after an intragroup altercation. Interspecific aggression and intertroop agonistic displays are carefully summarized by Klein.

ALLOGROOMING

Grooming relationships among 16 members of

an *Ateles geoffroyi* colony were analyzed by Eisenberg and Kuehn in the 1966 publication. Grooming interactions among the colony members were summarized for the entire observation period and discrete relationships were not analyzed for restricted periods of time. In the small colony of *Ateles fusciceps*, it was possible during 1972, 1973, and 1974 to analyze grooming relationships in much greater detail, with special reference to the exact relationship of the members of the group to one another. This has allowed me to extend our discussion beyond that of the conclusions drawn in 1966. In the 1966 study, Eisenberg and Kuehn concluded that the adult male received very little grooming, but dispensed grooming to a great many lower ranking individuals. The most grooming activity appeared to be shown by sexually mature females with dependent young. Indeed, these

TABLE 3.—Allogrooming frequencies and durations in *Ateles fusciceps*, 1973

Initiator	Recipient	Σf	Σd	%
M	V	1	4	0.1
M	J	7	135.5	2.4
M	B	2	222	3.9
V	B	2	79	1.4
V	M	3	70	1.2
V	J	14	527	9.3
B	V	33	4319	76.3
B	J	3	159	2.8
B	M	4	63	1.1
J	V	1	7	0.1
J	B	1	11	0.2
S	B	1	66	1.2

Σf = total frequency of grooming shown; Σd = total duration of grooming shown (sec); % = percentage of total duration of all allogrooming for all observation periods.

Total percent of observation time spent in allogrooming was 4.4%. The average duration of an allogrooming bout was 78.6 seconds.



FIGURE 2.—Allogrooming between two adult female *Ateles geoffroyi*. Female spider monkeys can form persistent grooming relationships that may involve mother-daughter dyads in captivity. (Photo by C. M. Hladik.)

“mothers” tended to give more grooming than they actually received (Figure 2).

In the small *Ateles fusciceps* group, once again the male appeared to receive little grooming and donated quite a bit of grooming to animals subordinate to him, including females S and B and young male J (Figure 3). Interestingly enough, the grooming relationships of J to other members of the colony changed significantly from 1972 to 1973 as he became more mature. In 1972 he received little attention from the male, but received a dramatic increase in attention in 1973 (Table 3).

One peculiarity of the *Ateles fusciceps* data concerns the tendency of female B to groom her mother, V. This tendency for B to show grooming toward her mother was consistent in both 1972 and 1973. The subordinate female S showed very poorly developed grooming relationships to all members of the colony, although she groomed male J in

1972. Female S had been hand raised and reintroduced to the group as a juvenile (Appendix II). Female V showed a pronounced grooming tendency with respect to her offspring J in 1972 and, although this trend persisted in 1973, its duration decreased (Table 4). One aspect of allogrooming, which was not evident when all data were summarized in the *Ateles geoffroyi* group, concerned the shift in grooming through a female's estrous cycle. An estrous female tends to groom more during her period of receptivity than at other times. The male's tendency to groom a given female shifts one week prior to her period of receptivity, showing an increase (Table 2). Finally, the amount of grooming shown by the *Ateles fusciceps* colony amounted to less than 5 percent of total observation time, which is comparable to that of the *Ateles geoffroyi* colony described by Eisenberg and Kuehn (1966).

TABLE 4.—Allogrooming shifts as the juvenile male matures

Initiator	Recipient	1972		1973	
		f	%	f	%
M	V	2	1.6	1	1.3
M	B	16	12.6*	2	2.7
M	J	—	0**	7	9.7
V	B	3	2.3	2	2.7
V	M	7	5.5	3	4.1
V	S	1	0.7	—	0
V	J	22	17.3	14	19.4
B	V	42	33.0	33	45.8
B	J	5	3.9	3	4.1
B	M	6	4.7	4	5.6
B	S	—	0	—	0
S	J	5	3.9	—	0
S	V	3	2.3	—	0
S	M	2	1.6	—	0
S	B	2	1.6	1	1.3
J	V	3	2.3	1	1.3
J	S	1	0.7	1	1.3
J	M	3	2.3	—	0
J	B	4	3.1	—	0
Totals		127		72	

* Includes estrus grooming shifts.

** Italic figures are discussed in text.

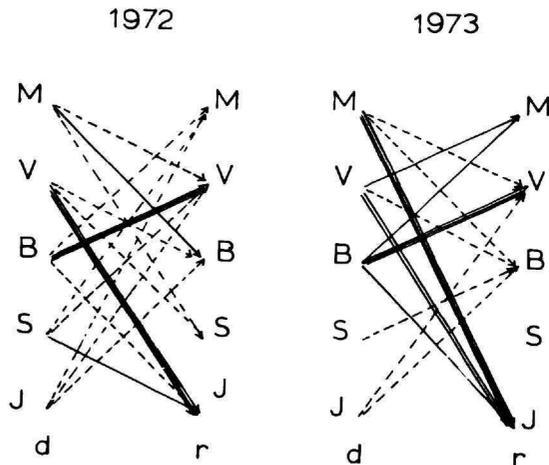


FIGURE 3.—Sociogram indicating allogrooming shifts as young male J matures (1972-1973). Animals are ranked (top to bottom) in order of decreasing age. (d=donor; r=recipient, see Table 3 for numerical values; M=adult male; V=adult female; B=daughter of V; J=son of V; S=subordinate adult female—note the tendency for S to be excluded from grooming dyads.)

GRAPPLING

This behavior pattern (Eisenberg and Kuehn, 1966; see also "Sexual Behavior," p. 6) is most frequently shown by juvenile and subadult animals, although adults may participate with them in the exhibition of this behavior (Figure 4).

An invitation to grapple often involves approaching a partner and either standing near or hanging above him. The initiator then extends a hand, often shaking its head slightly, while uttering the low ooh-oo vocalization. The interaction then takes the form of a wrestling match including mock biting and occasional genital manipulation.

During intensive observation of the *Ateles fusciceps* group in 1972 and 1973, the juvenile male initiated almost all of the grappling. Most of it was directed toward subordinate females or to the adult male and, altogether, it accounted for 4.5 percent of the total observation time (36 hours) (Table 5).

Grappling in the maturing juvenile appears to serve as a form of mock fighting. No doubt the relative strengths of the interactants can be tested without any serious harm coming to either of the participants. In previous studies (Eisenberg and Kuehn, 1966), grappling could be induced in

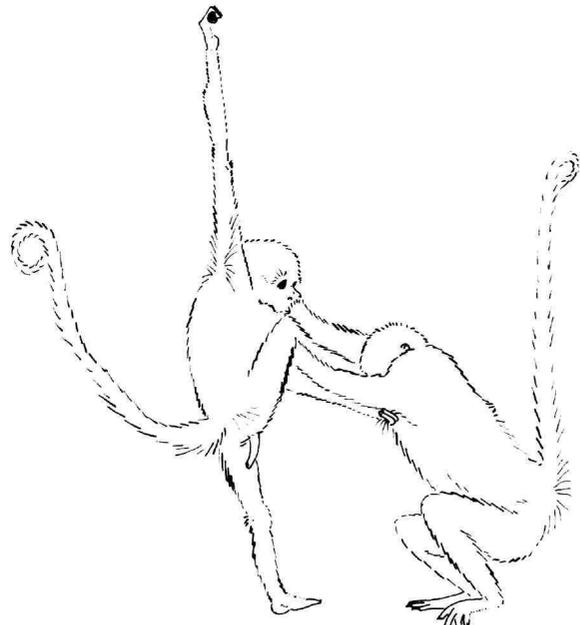


FIGURE 4.—Grappling bout between a male and a female *Ateles*. Kicking, pushing, and grasping are employed in a complex pattern of "mock fighting."

TABLE 5.—*Grappling*

Initiator	Recipient	Σf	Σd	%
J	V	16	574	9.7
J	B	19	1827	31
J	S	26	1097	18.6
J	M	9	1108	18.7
M	J	1	12	0.2
M	S	1	1.5	0
BV	J	1	20	0.3
MUTUAL:				
	S & B & J	2	17	0.3
	S & B	1	66	1.2
	J & S	3	397	15
	J & B	2	501	8.5
	J & M	2	74	1.2
	J & V	1	222	3.8

Σf = total frequency of grappling shown; Σd = total duration of grappling shown (sec); % = percentage of total duration of all grappling for all observation periods.

Grappling involved 4.57% of total observation; the average duration for a grappling bout was 6.96 seconds. J (juvenile male) initiated almost all grappling and the greatest percentage of it involved female B.

adults that were kept apart and allowed to encounter in a neutral arena. While such activities are not shown with such frequency and intensity in normal adult encounters in the wild, it no doubt serves the same purpose; namely, achieving contact and testing the relative strengths of the participants. The exact motivation of grappling is difficult to evaluate. At times it seems to have aggressive overtones, while at other times it seems to have some sexual significance. It should not, however, be thought of as a necessary prelude to sexual behavior (see "Sexual Behavior," p. 6).

EMBRACING AND HUGGING

Embracing, leading to hugging or clasping one another, is a form of contact behavior shown frequently in the captive group (Table 6). A juvenile initiating an embrace with its mother accounts for an extremely high percentage of all embracing activities. Juvenile males frequently embrace adult males as part of their development of a social bond with the adult male (see "Male Group," p. 68).

The form of the embrace very often depends upon previous actions. An animal that is insecure or frightened may approach an older dominant while exhibiting pursed lips and perhaps trilling.

An embrace will follow, whereupon the initiator buries its face in the neck or breast region of the adult. This brings the nose of the initiator in contact with the region of the pectoral gland or the axilla. Brief embracing following genital sniffing or accompanied by sniffing the pectoral regions is analyzed in Table 7. An exchange of olfactory information is strongly implied (see "Olfactory Communication," p. 18).

When an adult male initiates an embrace with a juvenile male, he may often continue on in the

TABLE 6.—*Embracing leading to hugging in Ateles fusciceps*

Initiator	Recipient	Σf	Σd	%
M	J	1	20	0.2
J	B	8	1656	19.9
J	M	10	1276	15.4
J	S	10	634	7.6
J	V	13	3059	37
V	M	1	353	4.3
V	B	1	17	0.2
S	B	1	65	0.7
S	M	1	550	6.6
S	V	2	659	7.9
S	J	1	8	0.1

Σf = total frequency of embracing shown; Σd = total duration of embracing and hugging shown; % = percentage of total duration of all embracing for all observation periods.

Embracing accounts for 6.4% of total observation time; the average duration of a hugging bout is 169.3 seconds. J to V (J's mother) embracing accounts for the highest percentage of all embracing. No quantitative rises or decreases were noted throughout the study period. J to M (J's father) embracing accounts for the third highest percentage.

TABLE 7.—*Sniff-embrace frequency analysis*

Subject	Mutual sniff	Individual sniff		Total
		I	R	
PECTORAL SNIFF-EMBRACE				
V	10	5	3	15
B	4	9	5	13
S	6	7	3	13
J	17	8	8	25
M	23	11	21	34
GENITALIA SNIFF-EMBRACE				
V	0			0
B	0			0
S	0			0
J	9			9
M	9			9

direction of his progression and step over the young animal. At the point of stepping over, a genital display may occur.

GENITAL DISPLAY AND GENITAL SNIFFING (MALE-MALE)

Aside from attentions paid to the external genitalia between a male and female during sexual behavior (see "Sexual Behavior," p. 6), a form of genital display seems to occur between an adult male and a juvenile or subadult male. The adult male will approach the juvenile, who may be sitting on a perch. As he approaches quadrupedally, the adult may emit the slow, guttural whinny while cocking his head to one side. He may then pause and either touch the younger male or embrace him, and then step over him. While stepping over he may pause again and raise one of his hindlegs so that adult male's genitalia are presented directly to the face of the younger male, whereupon the young male sniffs. The adult then proceeds in the original direction. A variation on the preceding consists of a mutual quadrupedal approach, often times with both animals pursing their lips and emitting low, guttural whinnies. This may be followed by a mutual embrace and sniffing of the pectoral region, then the adult male may step over the younger male and again permit an opportunity for the genital sniff.

Genital sniffing can also occur in a slightly different context. For example, the adult male may hang up from an overhead support, clinging with both hindlegs and arms to form a hammock in front of the juvenile male. The juvenile male then may groom the adult, followed by sniffing the adult male's genitals. Very often after sniffing, a grappling bout can occur.

SOME COMPLEX INTERACTIONS

Looking into Mouths

A juvenile may, during a feeding bout, approach a subordinate adult and by retracting its lips attempt to see into its mouth and extract food. This same behavior may be shown by an adult female to one of her full-grown offspring. Looking into a partner's mouth has also been observed in a non-

feeding context, but its exact significance cannot be ascertained.

Rough Grooming and Normal Allogrooming

It has been frequently observed that an adult may approach a subordinate or juvenile individual and force it down with its hands, while grooming its fur in an agitated fashion. This category is now recognized as "rough grooming" and should be separated from normal allogrooming, which is of a more deliberate nature and often solicited by the recipient. Such rough grooming, when tabulated with otherwise relaxed grooming, may give rise to a correlation of grooming frequency with dominance status (Eisenberg and Kuehn, 1966: 38-41). It is now thought desirable in future allogrooming analyses to distinguish carefully between these two categories for, when this separation is done, it is apparent that the grooming relationships do not always reflect a strictly hierarchical pattern (see "Agonistic Behavior," p. 9).

Riding

As is well known from previous descriptions, the infant *Ateles* rides on the ventrum of the mother for approximately the first 4 to 5 months of life, thereupon transferring to her dorsum and continuing to be carried with decreasing frequency until almost 1½ years of age (Carpenter, 1935; Eisenberg and Kuehn, 1966). What was not noted before, however, is the tendency for adult males to permit juvenile males to ride on their backs during the transition phase from mother transport to independent locomotion. Although this is not a frequently exhibited behavior pattern in captivity, our adult male *A. fusciceps* frequently allowed juvenile males, less than 2 years of age, to ride on his back for brief periods. These "rides" were often accompanied by grappling interaction and an increased attention on the part of the male toward his juvenile sons.

Tail Wrapping

As mentioned earlier (Eisenberg and Kuehn, 1966:4), an agitated *Ateles*, while pacing in the cage, may wrap its tail around its own body. The

same type of behavior has been noted with the *A. geoffroyi* group in the field. Occasionally two *Ateles* may wrap their tails around each other's body while locomoting together either quadrupedally or bipedally. This frequently occurs when the two animals have embraced and are seeking to approach a stimulus situation which has frightened one or both of them (Klein and Klein, 1971). It would appear that this is a mutually reinforcing behavior pattern.

ROLE SUMMARY

• In this section, I wish to briefly comment on the relationships in the captive *Ateles fusciceps* group and contrast them with the relationships as we now understand them in the free-ranging group of *Ateles geoffroyi* on Barro Colorado Island.

The adult male *A. fusciceps* is rather independent of the females in his movements. A considerable portion of his time is spent in active locomotion around the cage. When new visitors approach, it is the adult male who takes notice of the fact and increases his brachiation rate. He may display aggressively to noisy patrons in the zoo and has his own special aggressive relationships with certain members of the keeper staff. It is he that participates in leaping displays, bar shaking, and marking behavior with his pectoral gland (see "Olfactory Communication," p. 18, and "Male Agonistic Display," p. 20).

In the caged situation, it is the adult male who exclusively initiates long calls. The adult male shows increasing attention to juvenile males as they become independent of their mothers. He actively encourages interaction with them and shows protective responses toward them. During ambivalent interactions, the adult male may solicit participation of a juvenile male by approaching, embracing with a low, guttural whinny, and mutual pectoral sniffing. Then continuing to keep an arm around the young male, the adult male can lead him to the front of the cage to participate in threatening calls or can lead him to a corner of the cage whereupon the adult male will initiate a series of long calls. Thus, the adult male actively solicits participation in the performance of the long call acts or in the performance of mutual trilling to a potentially hostile stimulus source (see also "Male Group," p. 68).

Because of a special relationship between the adult male and myself, I was able to induce a variety of behavioral responses, most of which were quite predictable. When I attempted to interact with adult female V, the male would always approach me and generally his first act would be to hang up behind female V and grasp her about the waist with his hindlegs in a movement reminiscent of hindleg grasping and locking during copulation. The gesture with the hindlegs would be shown only for less than 5 seconds, whereupon he would generally brachiate away after touching the female. His rate of brachiation around the cage would vastly increase when I would approach without food.

Such behavior patterns by the captive male *Ateles fusciceps* were reminiscent of those shown by the free-ranging *Ateles geoffroyi* in Panama. It is the adult male who directs attention toward maturing juvenile and subadult male offspring. Through his efforts and the young male's efforts to remain near him, a subgroup of males is formed which ranges quite independently of the core group of females and their dependent offspring. Table 8 gives some indication of these subgrouping tendencies during 1970 and 1974.

It is the adult and subadult males, with supporting participation from juveniles, who respond to an intruder coming in upon them while resting in the trees. Rapid brachiation with descents of over 15 feet to land with a crash, branch shaking, and brachiation with branch breaking over the head

TABLE 8.—Subgrouping* tendencies for *Ateles geoffroyi*

Subgroups	Number of sightings	
	1970	1974
Adult ♂ (alone)	—	3
**Adult ♂ + 2 or more ♂	3	7
Adult ♀ (alone)	2	1
≥ 2 Adult ♀	1	—
Adult ♀ + J or I	5	1
2 Adult ♀ + J or I	2	1
≥ 2 Adult ♀ + J or I	—	3
Total	13	16

* Subgroup is less than half of total troop and found moving or resting at a distance > 100 m from other individuals.

** All male subgroup.

The male subgroup was seen resting near or moving with the females three times in 1970 and eight times in 1972.



FIGURE 5.—Typical subgrouping of two female *Ateles geoffroyi* and their dependent offspring. Note the enlarged mammae of the female on the left. (Photo by C. M. Hladik.)

of an observer are often initiated by the male group (Carpenter, 1935). In the confines of captivity, the male *A. fusciceps* cannot display the full range of behavior shown in the field; nevertheless,

his interest in juvenile males and their mutual participation in activities reflect the same sorts of processes manifested in the free-ranging group of *Ateles geoffroyi*.

Adult females, on the other hand, form their own subgroup. Affiliations among females are apparently based on long-term processes. Mothers and daughters often show a special affiliation with attendant grooming relationships. Females with offspring of a similar age class often form play groups, which permit the young to interact (Figure 5). As reported by Eisenberg and Kuehn (1966:45) adult females with young appear to be group promoters. Females with nearly mature young, how-

ever, may become much less bound to mothers with young of an equivalent age. In brief, then, females tend to segregate into subgroups based upon their particular phase in the infant rearing cycle. It is safe to say that any female can act independently of others and does so. Thus, even temporary subgrouping of mothers with young of an equivalent age can break up with females moving independently, accompanied only by their infant or dependent juvenile.

Signal Systems in *Ateles*

Problem of Communication Analysis

Marler in his theoretical article of 1961 adopts Morris' (1946) model for the study of semiotics. The three aspects of semiotic analysis include semantics, syntactics, and pragmatics. Syntactics involves the study of signs or signals and included in such a study are efforts to give a physical description of the signal itself and to compare such descriptions with other signals in order to formulate a classification of signal types. Such an effort eventually leads to the formulation of a "vocabulary" for the channel of communication under investigation. The study of syntactics can be extended in an ontogenetic or phylogenetic sense by comparison and by outlining criteria for discrimination between homologous and analogous signals.

Pragmatics involves the determination of the function of the signal. In other words, you attempt to infer the significance to the communicant by noting the nature of the response to the signal. There are four categories noted by Marler for the function of sounds: (1) Identifiers are signals that give spatio-temporal information. (2) Designators are signals that dispose the communicant to do something because the performance of that act will lead to a goal. (3) Appraisers are signals which communicate a preferential status concerning the sender. (4) Prescriptors are category signals that predispose an animal to choose to do (a) rather than (b), (c), (d), etc., because the performance of (a) leads to a goal more desirable than any of the alternatives. In a sense, then, prescriptors are tied to designators. Marler concluded that the semantic aspect of communication was more or less closed to the biologist.

A divergence in approach arose because Hockett (1960) listed "semanticity" as one of the attributes of a true communication system. Semanticity for Hockett evidently involves the relationship between the signal and a designata or referent in the environment. This theme of semantic analysis has in turn been expanded and developed as an approach by Smith (1965, 1968). It would appear to me, however, that this excursion into the semantic aspects of animal communication is fraught with certain difficulties. The "meaning of meaning" in terms of Ogden and Richards (1949) involves a triadic relationship between the symbol, the referent, and the thought in the mind of the communicant. In other words, the signal from a sender, upon being perceived by the receiver (given a defined external environment), involves both the perception of the signal and an association with the designata through memories. The cognitive act then leads to a selection of a response, which may involve the production of other signals or physical responses. But thought and selection of a response, when taken from a subjective standpoint of the receiver of information, leads us too far into unverifiable realms. We may be disposed to return to pragmatics (which, of course, implies semantics) as a more rigorous approach to the analysis of animal communication.

Semantics is the study of the relationship between the signal and the meaning, and meaning itself involves two aspects: connotation and denotation. Denotation refers to the object for which the signal (symbol) stands. Connotation involves the relationship between the referent for the symbol and what memories and recollections the receiver conjures up. Meaning, in the semantic sense, is

applicable to both the sender and receiver and, as such, involves the establishment of connections between the features of the signal and the corresponding mental processes in the act of signaling itself. In the broadest sense, the analysis of human language involves a consideration of the "meaning of meaning" and can do so only because we as humans have the capacity to introspect and relate our introspections to one another. This possibility is denied us when we stand as external observers describing the communication processes of animals via some metalinguistic system. As Cherry (1961: 222) points out, semantics and syntactics are indeed contained within the realm of the field of pragmatics, but pragmatics relies in the end on the description of the ongoing process rather than on inferences of what is internal to the animal itself.

Language for a human is used not only to express thought, but also shapes our categories of thinking (Whorf, 1959), and human language is not completely tied to emotional state, but in fact is a learned system albeit that the learning involves the shaping of an innate substrate (Chomsky, 1957; Count, 1973).

Thus, if I am an observer watching a troop of spider monkeys feeding and a man is approaching on the ground, I may note that the adult male near the terminal end of a branch indicates he has perceived the man by his attentive posture. The adult male may then show some pilo-erection, tensing of the muscles, rising to a more upright position, fixation of the man, and may commence uttering a barking vocalization. While continuing to vocalize, he may then shake the branches, bound down to a lower branch and shake again, continuing to utter the cry. Since I have observed similar behavior under conditions where attack or flight could be shown with equal probability, I can infer, on the basis of pilo-erection and branch shaking, that the male is highly aroused and that his mood implies a tendency to attack, as well as a tendency to flee. Meanwhile, the result of his vocalization causes a feeding subadult male to turn, assume similar postures, and utter barking cries while tending to move backward toward the trunk of the tree and away from the direction of the man. Furthermore, going back in time to the beginning of signal production by the adult male, I had noted that an adult female gathered a young to herself and moved away without making a sound.

By describing the whole contexts, I can ascribe a function to the call. The function may be phrased as a prescriptive category disposing the subadult male to perform action (a) and the adult female to perform action (b). I can also associate the sending of the signal with a specific mood of the adult male and with a certain set of physical circumstances. I do not think that I am justified in ascribing to the barking sound a denotative characteristic; that is, I do not think it necessarily means "man close," rather, if it means anything, it may mean that the male is highly aroused, and in a state of ambivalence between attack and flight. If this be denotative, it has the prescriptive function of inducing a response on the part of the receivers appropriate to their age and sex class.

It is possible to speak of the presumptive information content of the signal. Once again, without making a full excursion into semantics, if I confine the presumptive information content to be that information allowing the receiver to choose among several possible actions, I have still not entered the domain of the unknown mental processes of the sender and receiver.

Such excursions into semantics may have great heuristic value for workers following the theoretical structure developed by W. J. Smith, but for the purposes of this study I will confine myself in the main to contextual analyses inferring two types of information: (1) the mood of the sender and (2) its effect upon the receiver. From this may be derived a presumptive function and an inferred information content in the prescriptive sense. In no way, however, will there be any implication concerning the mental processes, other than the fact that some learning may be involved in the selection shown by the receiver with respect to the host of responses it may make upon perceiving the signal itself.

Olfactory Communication

Aspects of olfactory communication in *Ateles belzebuth* have been considered by Klein (1972) and Klein and Klein (1971). The Kleins (1971) point out that urine very probably conveys information concerning the estrous state of the female. Sniffing urine is predominantly a male activity. The Kleins further point out that the pendulous clitoris of the female with its median groove could serve

as a urine-retaining organ, thus allowing the scent of urine to be spread wherever the female sits. Similar behaviors have been noted with *A. fusciceps*. The male tends to sniff the urine spots of females, especially throughout the course of an estrous cycle (Table 9). Furthermore the clitoris of the female may frequently be touched by the male and the hands subsequently sniffed. The data from observing captive *A. fusciceps* have tended to confirm the Kleins' hypotheses.

Eisenberg and Kuehn (1966:18) mentioned the pectoral gland of *Ateles* and considered that during the embrace, secretions from the pectoral gland could be sniffed by the contacting animal. Very often during the embrace, the sniff is directed at the junction of the neck and chest or perhaps toward the axillary region. Thus, direct sniffing of the pectoral gland appears to be unnecessary. This may well be a result of the fact that the animals have a tendency to rub their pectoral area with their hands thus serving to spread the scent over the hairs of the venter and chest. Epple and Lorenz (1967) have reviewed the structure and placement of sternal glands in the Platyrrhine monkeys. They have called attention to the fact that adult male spider monkeys frequently rub the gland during aggressive arousal.

My observations on *Ateles fusciceps* suggest that several processes may be at work in the spreading

TABLE 9.—Urine sniffing and marking behaviors in captive *Ateles fusciceps*

Subject	Σf	Σd	%	Activity
M	6	239		Sniffing urine
B	2	6	83.6	Sniffing urine
M	1	8		Sniffing marked artifacts
J	1	11	6.4	Sniffing marked artifacts
M	3	10	3.4	Food sniff and chest rub
M	8	19	6.2	Ventral rub
V	1	2.5	0.5	Anal rub

Σf = total frequency of urine sniffing and related behaviors shown; Σd = total duration of urine sniffing and related behaviors shown; % = percentage of total duration of all urine sniffing and related behaviors for all observation periods.

Sniffing involved 0.23% of total observation time. M's (adult male) urine-sniffing accounts for the highest percentage of all olfaction-related activities. A quantitative rise in urine-sniffing is noted in connection with estrus and copulation since a 232-second bout of M's urine sniffing occurred after his first copulation with female B.

of scent by adult males and females, although marking frequency seems to be higher among adult males. During aggressive arousal, the male *A. fusciceps* may salivate greatly while brachiating around the cage. Saliva may be wiped from the chin and then the forepaw rubbed on the chest. In addition, without noticeable aggressive arousal, the male *A. fusciceps* would often rub strong smelling substances in his pectoral area.

Example: The male *Ateles fusciceps*, M, was noted to rub some food objects upon his chest after taking them from my hand and before biting into them to commence feeding. This movement was rather interesting, but somewhat puzzling with respect to interpretation. Initially I thought that because I had given him the food and since he regarded me as a rival, he may have found it necessary to mark the food with his chest gland thus making it familiar to him. However, it appeared that not all foodstuffs were marked in this way. He seemed particularly prone to rub his chest with slices of orange, thus it may be that the aromatic scent of orange helps lower the threshold for marking and the fact that I had given it to him had further raised his level of uncertainty to the point where marking has a reassurance function. He did not exhibit this rubbing behavior when he was handed string beans or apples.

The adult male *Ateles fusciceps* would also mark by rubbing his pectoral gland either on branches in the cage or on the vertical upright bars. This was done on four successive days immediately after my approach to the cage after I had been absent for some time. This same adult male would also mark during periods of aggressive arousal. Often a marking bout would be followed by a leap to the front of the cage and shaking the bars. Two forms of marking behavior were shown: (1) where the male would stand upright and wipe his chest up and down on a vertical support in the cage, or (2) alternatively, he would mark quadrupedally. Quadrupedal marking often occurred while the animal was in motion. As he depressed the forequarters, he would slide his chest for perhaps some 5 centimeters and then lift up his chest by increasing the foreleg extension phase as he continued walking. Preferred rubbing spots were shown on plane surfaces of the bench at the rear of the indoor cage. During successive marking bouts, the same spot would be marked. On two occasions, one of the females, upon approaching the spot, would sniff and mark in a corresponding fashion.

Not only is the pectoral region and the vicinity

of the sternum a target for sniffing during an embrace, but spider monkeys frequently sniff the genital and anal areas of each other during other forms of encounter behavior. The juvenile male frequently contacted the adult male when he was reclining by sniffing in the inguinal region or sniffing at the adult male's genitalia (see "Genital Display," p. 14). Finally, it should be mentioned that both males and females occasionally depress the anogenital region to a branch and slide forward, thus performing an anogenital rub. While some of these movements seem to be related to a comfort movement or relieving some irritation, at other times it would appear to be an incipient marking movement. Both males and females have been noted to rub their anogenital regions after copulation.

Clearly, then, chemical traces involving the use of urine or glandular secretions from such an area as the sternal gland are involved in the coordination and integration of spider monkey behavior patterns. Experiments have not been performed to elucidate clearly the functional aspects of marking behavior, but the association of sternal gland rubbing and aggressive display on the part of the male strongly implies that impregnating his immediate surroundings with his own scent may serve to communicate his individual and sexual identity to newcomers or intruders in his living space.

Visual Communication

Obviously the movement patterns of an individual monkey can, in and of themselves, impart information of intent to a potential receiver. Approaches, movements away from, reaching out to touch, reaching out to slap, are all aspects of a communicatory situation. In this section, I hope to discuss certain outstanding features of visual communication removed from the context in which they normally appear.

MALE AGONISTIC DISPLAY

Adult males characteristically perform a movement sequence towards intruders which may be termed a threat display. In captivity it may be shown toward handlers; in the field situation, it has been observed by adult males responding to human observers on foot. Aspects of the male dis-

play may also be shown toward potential predators, such as the tayra (*Eira barbara*). The male may run along a limb or bench in a cage with a crossed extension quadrupedal gait. During the quadrupedal gait, the back may be arched slightly in a manner reminiscent of the "arch display" by *Aotus*, but it is in no way ritualized and may in fact be a mechanical adjunct of forward, quadrupedal locomotion on a tree limb. The tail is held up and curled at the tip approximating a question-mark in form. Typically the male shows pilo-erection. He may stoop during his quadrupedal run, flex his forelimbs, and touch his sternal gland or chest region to the substrate. At the termination of a quadrupedal run, the male will exhibit rapid brachiation while looking toward the offending object, still showing pilo-erection, and, at some point while hanging by his tail, swing toward the offending object and grasping nearby branches (or in captivity, cage bars) shake the branches. At the time of shaking and while orientating toward the intruder, the adult male often shows an open mouth with full tooth exposure.

FACIAL EXPRESSIONS

Facial expressions may be given in the absence of vocalizations or associated with certain vocalization types. Vocalizations are described on page 23 ("Vocalizations"), but will be referred to in this section where appropriate. The lips of the spider monkey are rather mobile, thus the teeth and, in particular, the canines may be displayed conspicuously. Tooth exposure does not always accompany the opening of the mouth; indeed, the animal can yawn with little tooth exposure.

Van Hooff (1967) has outlined a scheme of facial expressions for higher primates. Most of his work was based upon an analysis of facial expressions in *Macaca* and *Pan*, but it would appear that his overall scheme is applicable to a wide variety of primates. Recently Chevalier-Skolnikoff (1973) has reviewed primate facial expressions building upon the analyses of Van Hooff. Van Hooff distinguished 8 major facial expressions involving variations in ear position, eye closure, and retraction or extension of the lips. Partial squinting, ears forward, and lips contracted but not exposing the teeth was termed the "tense mouth," and was associated by Van Hooff (1967) with attack tend-

encies. Varying degrees of staring with open mouth, with or without bared teeth, appeared to involve a balance between attack and flight tendencies. Often these expressions were accompanied by vocalizations. A silent expression with squinted eyes and retraction of mouth corners with tooth exposure, termed the "silent bared teeth," was associated with a weak flight tendency and seemed to have an appeasement function. Extension of the lips in the "pout face" appeared to accompany a desire to approach an object or express, in the case of a young animal, a wish to be with the mother. An open mouth with relaxed lips accompanied a so-called "play face" expression and was often involved in ludic behavior.

In Eisenberg and Kuehn (1966), the facial expressions of *Ateles* were broken down into categories: open mouth with no canine exposure, open mouth with canine exposure, the grimace which was similar to the preceding but the corners of the mouth more retracted, and pursed lips similar to the pout face or protruded lip face defined by Van Hooff. Eisenberg and Kuehn (1966:25) remarked that expressions of *Ateles* corresponded roughly to the series proposed by Van Hooff and suggested an evolutionary parallelism in the development of facial expression in the Cebidae, when compared to the Old World macaques.

The 1966 work was based primarily on *Ateles geoffroyi*. Current analysis of *Ateles fusciceps* and further consideration of expressions and their use in *A. geoffroyi* leads me to make the following additional comments. The term "grimace" as applied to an expression showing extreme retraction of the lips and full tooth exposure is best not treated as a separate expressive type, but rather it should be considered as part of the class of expressions involving tooth exposure. Partially open mouths with the corners of the mouth retracted and exposure of the teeth are seen to occur in "tense" contexts such as: (1) when a juvenile is frightened by a sudden movement, or (2) when an animal has been teased by another member by having its tail or hair pulled, or (3) when another



FIGURE 6.—Contrasting facial expressions by *Ateles belzebuth*: a, pursed lips with half closed eyes during approach to a dominant social partner; b, open mouth with no tooth exposure; c, open mouth with slight lip retraction and moderate tooth exposure. (Drawings by C. Dorsey from the author's photographs.)

individual approaches too closely towards an animal having a desired food item. There may be no accompanying vocalization with this expression.

Staring at a partner with a partially opened mouth and little tooth exposure often involves the production of a twitter or trill-awk call. An animal may produce this call and expression when a social partner moves away and the communicator wishes contact; as, for example, when a mother withdraws from a suckling juvenile. A similar face and the trill-awk phase of vocalization may be produced by a juvenile after being slapped, but, during high intensity expressions of trilling, the facial expression may involve an open mouth and some tooth exposure. The same expression and vocalization may be produced when an individual is frightened by a sudden movement.

On the other hand, protruding the lips and the production of a slow, growling whinny sound may be involved with approach and embrace. The same facial expression can be employed while the animal is trilling when an approach-retreat game is being played involving role reversal between a male and a female. Protruded lips may also be shown during initial approaches at the onset of a grappling bout, again seeming to indicate contact receptivity. It should be pointed out, however, that during a grappling bout or mock fighting the animals may show open mouth with retracted corners thus exposing the teeth. Tooth exposure in this context appears to imply "mock agonistic behavior."

Exhibiting a chin-up often accompanies a greeting call of the tee-tee or whinny. Production of whinnies and tee-tees is often done with a virtually closed mouth and the vocalization seems to be produced through the nose. However, during slow whinnies which often accompany an approach and embrace, pursed lips may be shown (Figure 6).

It seems fair to say that facial expressions of the spider monkey parallel those of the macaque, but I have been unable to subdivide the expressive forms as finely as that accomplished by Van Hooff. It is true that an open mouth with no canine exposure or an open mouth with some canine exposure appears to accompany frightening situa-

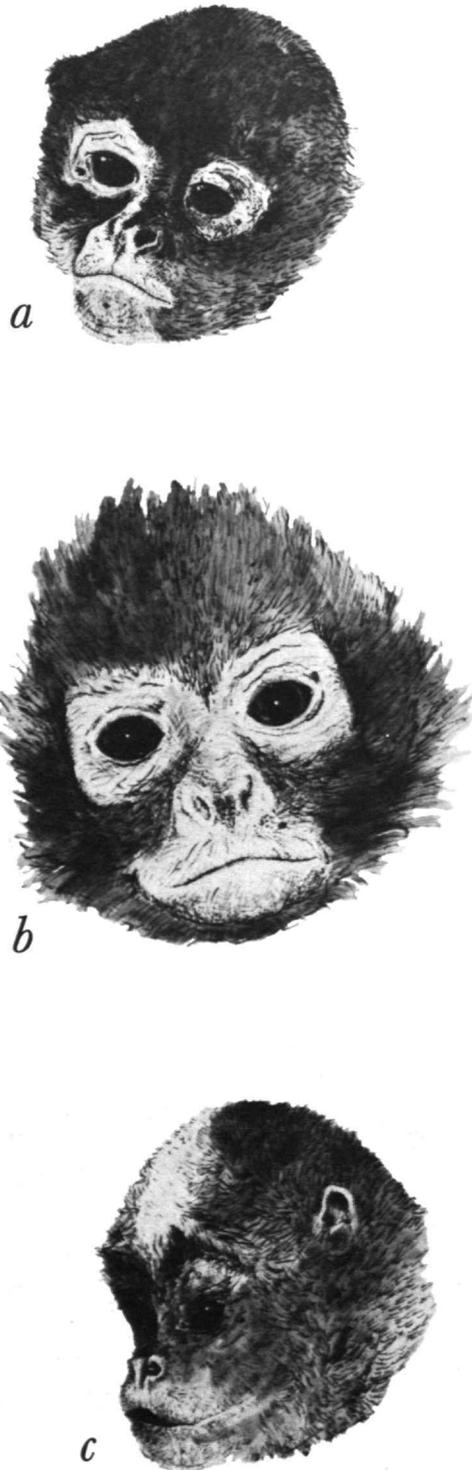


FIGURE 7.—Facial expressions by *Ateles*: a, relaxed face prior to sleep, *A. geoffroyi*; b, direct stare (nonhostile), *A. paniscus*; c, expression during whinny, *A. belzebuth*. (Drawings by C. Dorsey from the author's photographs.)

tions. Extreme tooth exposure may be involved in a threat context. Lifting the chin appears to accompany the production of greeting sounds, but the lips are generally kept closed. Protruding the lips does appear to correlate with a contact receptivity, although the vocalization accompanying lip protrusion may vary and include the ook-ook and grappling receptivity all the way to slow, growling whinnies and embraces. Protruded lips may be shown even while the animal squeaks, if the animal is both withdrawing from a dominant, yet exhibiting aspects of contact receptivity.

Aside from the play contexts which will be elaborated on later, it is fair to say that canine exposure accompanies situations that suggest propensity to attack with perhaps a balanced tendency to withdraw. Pursued lips seem to be associated with friendly sounds and contact receptivity. The chin-up, which often accompanies the production of tee-tees, whinnies, and slow whinnies, may be involved in the production of the sound itself, but I am inclined to think that it has in part a ritualized function that decreases tension in the recipient.

Direct eye contact can be a threatening expression depending on the receiver. In my relationship with the adult male *A. fusciceps*, staring at him directly could cause him to avoid and then immediately respond with an aggressive display (see "Male Agonistic Display," p. 20). On the other hand, direct eye contact with the females generally caused them to lift their chins and produce one of the whinny variants. (For diagrammatic clarification, see Figures 6 and 7.)

Vocalizations of *Ateles fusciceps* and *A. geoffroyi*

SYNTACTIC ANALYSIS

Utilizing the Missilyzer (Kay Electric Co., Model 675), selected tapes were analyzed to prepare sonograms of representative vocalizations (see "Captive Research," pp. 1-2). Tracings on the sonograph paper were analyzed with respect to frequencies emphasized, duration, and interval. Vocalizations showing numerous side bands indicative of pulse modulation were also analyzed on a Tectronix Oscilloscope (Type 323) for a more refined frequency analysis.

The following definitions are employed through-

out the text (adapted from Struhsaker, 1967): A syllable is an uninterrupted tracing by the sonograph. A phrase is a group of syllables separated from another group by an interval longer than any intersyllabic interval. A call is a phrase or group of phrases which is distinctive in form. Calls are generally referred to by a descriptive or onomatopoeic name. A bout is a group of calls which forms a temporally distinct unit.

Syllabic transformation is common in the production of sounds by spider monkeys. Some simple forms of intergrading were discussed by Eisenberg and Kuehn (1966), but in general this topic was unexplored. While it is true that certain calls can be defined with respect to context and structure, the existence of intergrading syllables makes it now possible to describe the vocalization system of *Ateles* as a graded system. As will become apparent the syllabic transformations involved in the genesis of calls include the following mechanisms: (1) prolonging the duration of the syllable while shortening the interval between syllables in a phrase or shortening the interval greatly, which may result in (2) fusion of syllables to form a longer syllable of the same structure, and (3) frequencies may be modulated between individual syllables to achieve a different tonal quality.

Before proceeding to a discussion of the calls, the syllabic structure will be considered in some detail. For convenience, syllables, as displayed on the sonograph, can be broken into four "morphological" classes (Figure 8): (1) Clucks: short sound <0.05 seconds in duration with little harmonic structure. (2) Clear, harmonic calls: syllables which emphasize a single frequency band with true harmonics present. The syllable may be brief, <0.05 seconds, or quite long, >2.0 seconds, and may show either little or a great deal of frequency modulation. (3) Syllables with a vibrato form: On the sonograph numerous side bands are evident. The energy is not displayed in a single narrow frequency range. Some or all of these syllables may result from rapid pulsing of extremely short emissions (Watkins, 1967). (4) Syllables that show little structuring and approximate noise.

Utilizing syllable structure as displayed on a sonograph (Missilyzer), the following key can be designed which specifies the call types formed from the syllable variants. Two keys are offered. The first key considers calls composed of relatively uniform syllable types; the second key considers calls composed of two or more syllable types.

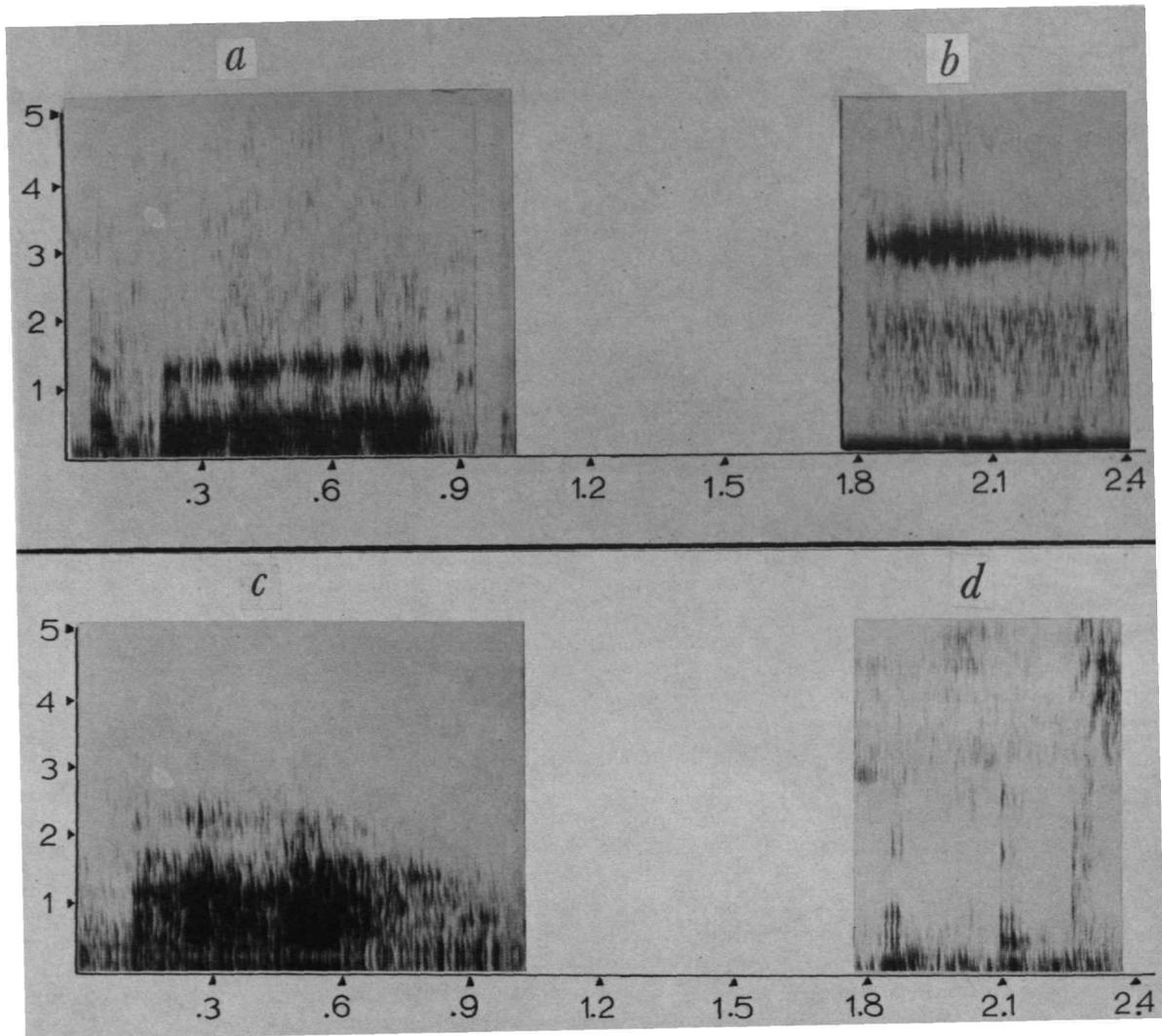


FIGURE 8.—The four basic syllable types: *a*, syllables with a vibrato form, side bands are evident; *b*, clear, harmonic syllables; *c*, syllables that show little structuring, side bands, and approximate white noise; *d*, short syllables, "clicks or clucks," showing little structure and side bands. (Ordinate in Khz, abscissa in seconds.)

Syllabic Key to Some Calls of Ateles fusciceps

Syllables of Calls That Are Uniform in Structure

I. Low Intensity Calls.

- A. Unvoiced: Syllable consists of rather uniform energy distribution; results from an exhalation termed a hiss (Eisenberg and Kuehn, 1966).
- B. Voiced.
 1. Syllables are brief pulses (<0.03 sec) of sound almost click-like. An infant sound and a precursor to several adult sounds (see "Ontogeny," p. 52), clucks or chuckles.
 2. Syllables are short in duration (≥ 0.07 and <0.2 sec) and grunt-like, termed "ook-ook"

(Eisenberg and Kuehn, 1966), each syllable when analyzed on a missilyzer shows numerous side bands, i.e., the energy may be pulse modulated. The lower frequencies are emphasized with most energy lying below 1.5 KHz. The syllables are repetitive and rhythmic. The call may vary in its intensity.

II. Variable Intensity Calls.

A. High pitched calls (much energy >2 kc) with a relatively strong emphasis on a narrow frequency range with true harmonics.

1. Calls composed of syllables which are short (<0.5 sec) in duration, but show little frequency modulation from one syllable to the next.

a. Each syllable shows considerable frequency modulation (over a range of ~ 0.5 KHz).

(1) Calls which are composed of extremely short syllables (<0.07 sec) separated by short intervals (<0.19 sec): trills and twitters.

(a) Syllables chervon in form with long intervals (0.08–0.19 sec): trill.

(b) Syllables with complex modulation but in other respects comparable to the above: trill.

(c) Syllables with complex modulation but with very short durations (<0.05 sec) and brief intervals (<0.08 sec): twitter.

(2) Calls which are composed of short syllables (>0.07 – ≤ 0.20 sec) separated by short intervals (<0.3 sec). Syllables are complex generally beginning with a frequency modulated pulse which ascends over a range of 1 KHz: yip-yip or pulsed trill. At low intensity with intersyllabic modulation, it may grade to a slow whinny (II.A.2.a(1)), or it may show fusion of syllables to a pulsed chitter (II.A.1.b(2)).

b. Each syllable shows some frequency modulation. High frequencies are emphasized (~ 3 KHz).

(1) Duration of syllable exceeds 0.4 seconds; may be uttered in bursts with short intervals: squeak (Eisenberg and Kuehn, 1966), can grade to chitter.

(2) Duration of syllable between 0.16 and 0.38 seconds, intervals between syllables are short; energy as high as 5.4 KHz may be emphasized: pulsed trill or pulsed chitter. (Eisenberg and Kuehn, 1966). This call may grade by fusion of syllables to a longer call, e.g., pulsed chitter.

2. Calls composed of short syllables but some are lengthened in duration (>0.5 but <1.0 sec).

a. Inter- or intra-syllabic modulation over a range of around 1 KHz.

(1) Syllables may range from 0.03–0.92 seconds in duration. A given syllable may differ in pitch from the preceding syllable by as much as 1 KHz. Intervals between syllables are variable from <0.04 to 0.3 seconds. Fusion of syllables converts to a true whinny. In its present form, the call is referred to as a yip-yip or slow whinny variant (Eisenberg and Kuehn, 1966).

(2) Syllables typically long from around 0.5 to 0.8 second.

(a) Highly modulated syllable with frequencies rising and falling three to four times over a range of 0.8 KHz during a period <0.9 seconds. Pitch may range from 3.0 to 5.0 KHz: tee-tee (Eisenberg and Kuehn, 1966).

b. Syllables relatively unmodulated from one to the other, duration of syllable ~ 0.7 seconds. Several harmonics may be present: chitter.

3. Calls containing long syllables which exceed 0.8 seconds in duration.

a. High pitched syllables which show frequency modulation over a wide range. The duration may be 2.0 to 2.3 seconds with energy emphasized at 1.4 to 4.8 KHz: whinny (Eisenberg and Kuehn, 1966).

b. Syllables of intermediate pitch (~ 1.5 KHz) with some modulation.

(1) Descending call with energy concentrated from 1.8 to 1.5 KHz: eecaw (I'.B.2).

(2) Ascending (1.8 to 2.2 KHz), often ends in a screech; about 1.0 seconds in duration and repetitive: grunt-trill (Eisenberg and Kuehn, 1966) äh eëë.

c. Syllables of intermediate pitch with little modulation (see III. Loud Calls).

B. Calls which may emphasize low frequencies (<1.5 KHz) or high frequencies (>1.5 KHz) but have an imperfect harmonic structure. Each syllable is composed of many brief pulses which upon sonographic analysis display numerous side bands.

1. Low frequencies (<1.0 KHz) emphasized.

a. Each syllable within a phrase is brief (<0.5 sec).

- (1) Syllables within a phrase exhibit relatively uniform frequencies.
 - (a) Syllables >0.15 but <0.5 seconds in duration; the intervals range from 0.17 to 0.60 seconds. A repetitive sound with energy emphasized between 0.6 and 1.4 KHz: bark or yap (Eisenberg and Kuehn, 1966; see also III. Loud Calls).
 - (b) Syllables average between 0.6 and 0.14 seconds in duration. They are rhythmic and repetitive. Intervals range from 0.06 to 0.22 seconds: ook-ook; ak-ak (Eisenberg and Kuehn, 1966); panting (Klein, 1972).
 - (2) Syllables within a phrase show frequency shifts from one syllable to another. Each syllable may be <0.05 seconds with an equal interval. The phrase or call may be 1.8 seconds in duration with energy emphasized at 0.5 and 0.2 KHz: guttural whinny or sobs (see slow whinny, p. 39).
 - b. Syllables may be long (>0.6 sec) and intermittent in their utterance. Energy is typically concentrated below 1.0 KHz.
 - (1) Syllable 0.6 to 0.9 seconds: growl (Eisenberg and Kuehn, 1966:13).
 - (2) Syllable >1.2 seconds: caw (Eisenberg and Kuehn, 1966:15). (See also III. Loud Calls.)
 - 2. Higher frequencies emphasized.
 - a. Each syllable is very brief (0.03 to 0.12 sec); frequency emphasized can vary within a call from 2.0 to 3.0 KHz. Intervals between elements can be from 0.04 to 0.13 seconds. Phrase duration may exceed 2.0 seconds: slow guttural whinny (Eisenberg and Kuehn, 1966); sobs (Klein, 1972).
 - b. Syllables longer in duration: >0.20 second: screams (juvenile) or >1.0 second: scream (adult).
 - C. Calls with little harmonic structure or poorly defined side bands.
 - 1. Frequencies <0.7 KHz emphasized.
 - a. Short (<0.3 sec): cough (Eisenberg and Kuehn, 1966:14).
 - b. Very short (<0.09 sec): terminal notes (see I'. Intermediate Intensity Calls).
 - c. Long (>0.5 sec): growl and roar (Eisenberg and Kuehn, 1966).
- III. Loud Intensity, Repetitive Calls.
- A. Short syllables.
 - 1. Short, repetitive syllables, low frequency (see II.B.1.a(1)(a)).
 - 2. Short, repetitive syllables emphasizing high frequencies (see II.A.1.b(2)).
 - B. Intermediate length syllables ($\geq 1.0 \leq 1.5$ sec).
 - 1. Complex modulation, single frequency emphasized. Includes the grunt-trill or ceeaw (two subtypes described in II.A.3.b(1) and (2)).
 - 2. Little modulation, not repeated, no single frequency emphasized: caw (II.B.1.b(2)).
 - C. Long calls (>1.5 sec) often complex with terminal syllables (II.C.1.b).
 - 1. Rather uniform energy distribution confined to a single frequency band at about 0.7 KHz but harmonics are present. Terminal notes may be present (see also II'. Loud Intensity Calls): wail (Klein, 1972).
 - 2. Pulsed phrasing with subsequent side band production when sonographed. Maximum energy at ~ 0.6 to 0.9 KHz: caw (Eisenberg and Kuehn, 1966:15); whoop (Klein, 1972) roar (Oppenheimer, 1968) (see also II'. Variable Intensity Calls).

Compound Calls

- I'. Intermediate Intensity Calls.
 - A. High pitched elements in call (much energy >2 KHz); calls containing long syllables which exceed 0.7 seconds in duration. Ascending (1.8 to 2.2 KHz), often ends in a screech; about 1.0 second in duration and repetitive: grunt-trill (Eisenberg and Kuehn, 1966).
 - B. Calls that begin with a relatively narrow frequency range but end with a noisy sound: compound call.
 - 1. Descending pitch from 3.0 to 0.16 KHz. Duration 0.10 to 0.20 seconds: awk (juvenile sound).
 - 2. Ascending from 1.6 to 2.0 KHz. Duration 0.20 to 0.8 seconds: uh eek (juvenile sound).
- II'. Loud Intensity, Repetitive Calls.

Rather uniform energy distribution confined to a single frequency band at about 0.7 KHz but harmonics are present. Short, terminal notes may be present: wail, caw or roar (III.C.1 and III.C.2).

Syllabic Transformations and the Genesis of Calls

Given the key based on syllabic structure, the manner in which syllables can be transformed will be best understood by a systematic description of each major call type. The call types intergrade according to the chart in Figure 22. In spite of the intergrades, certain call forms are distinctive with respect to form and general context. Their existence leads the investigator in a first order analysis to describe what appears to be a "particulate" or discrete system. The existence of intergrades does not negate the older more typological approach (see "Influences," p. 49).

Since the naming of calls in a dynamic system is only a convenience for written communication, Table 10 offers a portrayal of phonetic equivalents for the more mundane names applied by the author in earlier publications (Eisenberg and

Kuehn, 1966). Appendix 1 includes a summary of the physical measurements for all call types.

Call Types Named and Defined

LOUD, SHORT CALLS WITH A REPETITIVE PATTERN AND AN EMPHASIS ON LOWER FREQUENCIES.—This call form is often termed "barking" (Eisenberg and Kuehn, 1966:13) or yapping (Key II.B.1.a(1)(a)). The syllables vary with respect to the frequencies emphasized. The syllable may sonograph showing a harmonic structure with energy at ~ 800 and 1400 Hz. When higher frequencies are emphasized, it may have a pealing quality with a longer duration. It would appear that intervals between syllables and syllable length itself can vary as a function of mood shifts on the part of the sender. Figure 9 illustrates this principle with five forms

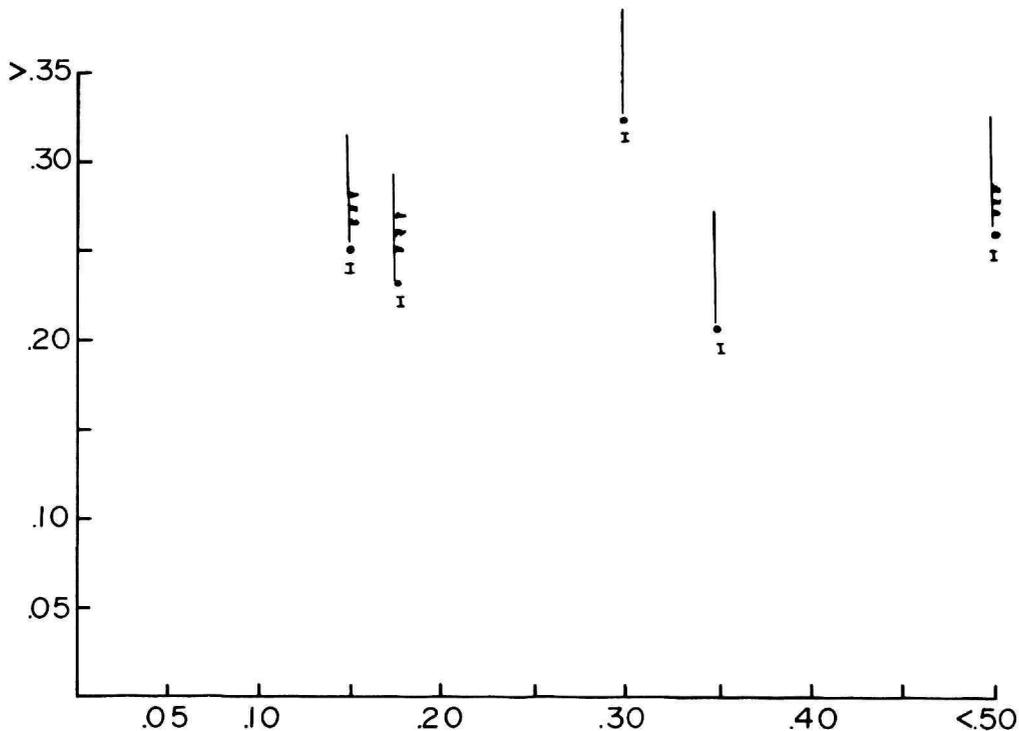


FIGURE 9.—Temporal patterning of barks. Intervals separating consecutive syllables are plotted on the ordinate in seconds. The abscissa indicates the average syllable duration in seconds. Each sample point includes the average of at least five entries. The points represent numerical values; however, the sonographic display properties of a bark syllable are drawn for several points as visual reference only (Appendix I).

TABLE 10.—Syllable type and call forms for Ateles

Call reference no.*	Syllable type		Transformation form	Name	Resultant call type		Form of phrasing	Characteristic (age class)
	Primary key reference	Secondary key reference			Descriptive name	Form of phrasing		
DISCRETE ENERGY DISTRIBUTION OR SIMPLE HARMONICS								
III	II.A.1.a(1)(a)		Repetitive	Trill		iiiii ih	Repeated phrases	Nonspecific (adult or juvenile)
III	II.A.1.a(1)(b)		Repetitive	Trill		iiiii ih	Repeated phrases	Nonspecific (adult or juvenile)
IV	II.A.1.a(1)(c)		Repetitive/or	Twitter		ē ē ē ē	Repeated phrases	Nonspecific (adult or juvenile)
X	II.A.1.a(1)(c)		Fusion	Squeak	II.A.1.b(1)	ēēēk	Repeated bursts	Nonspecific (adult or juvenile)
V, IX	II.A.1.a(2)		Repetitive/or fusion combined with terminal	Yip-yip	II.A.2.a(1)	ih ih ih	Repeated phrases	Nonspecific (adult or juvenile)
			awk (noise)	Chitter	II.A.1.b(2)	ēē ēē	Repeated phrases	Nonspecific (adult or juvenile)
Via	II.A.1.a(2)		Frequency modulated within or between syllables	Chitter-awk		ēē ē āawk	Repeated phrases	Nonspecific (adult or juvenile)
			within or between syllables	Yip whinny	II.A.2.a(1)	ih ēh ih ēh	Usually a single call	Nonspecific (adult or juvenile)
XIb	II.A.2.a(2)		A single frequency modulated syllable or call	Tee-tee		twē twē twētcē	Usually a single call	Nonspecific (adult or subadult)
Vic, XIIa	II.A.3.a		"	Whinny		ih ēēh ih ēēh	"	Nonspecific (adult or subadult)
IX	II.A.3.b(1) or III.B.1		"	E-awk		ēēē aw	Repeated calls	Nonspecific (adult or subadult)
XIII	II.A.3.b(2) or III.B.2		"	Grunt-trill		āāāēēh	"	Nonspecific (adult or subadult)
Ic	III.C.1		A single note	Wail; clear long call		ō ō ō ō ē	May be repeated or combined with terminal note (II')	Nonspecific (adult or subadult)
TENDENCY FOR BLURRED HARMONICS (SIDE BANDS)								
I	II.B.1.a(1)(a)		Repetitive	Bark		ārk ārk ārk	Repeated in long chains	Nonspecific (adult or subadult)
VIII	II.B.1.a(1)(b)		Repetitive, shortened	Ak-ak; ooch-ooch		oo oo oo	"	Nonspecific (adult or juvenile)
VId	II.B.1.a(2)		Repetitive; frequency modulated between syllables/or shift to higher frequency	Guttural whinny sobs	II.B.2a	ā ē ē ā ē ē	Usually a single note	Nonspecific (adult or juvenile)
VII	II.B.1.b(1)		Nonrepetitive	Growl		ā ā h	May be repeated	Specific (adult male)
IIa, IIb	II.B.1.b(2)		Repetitive, long	Caw or roar		āāāāh; oo-oo-rah	Not structured	Nonspecific
	II.B.2.b		Long, single utterance	Scream		ā ā ech		

IIa	III.C.2	Long, single utterance	Long call caw	ää ää rah	May be compound call with terminal note	(adult or subadult male)
Infant	I.B.1	Repeated	Clucks	üh üh	Bursts	(infant)
VIII	II.B.1.a(1)(b)	Repeated	Ak-ak	äh äh	Bursts	(juvenile-adult)
VIa, b	II.B.2.a	Repeated with pitch shift	Slow whinny	ih eh ih	Usually a single phrase	(juvenile-adult)
CLICK-LIKE SYLLABLES						
UNSTRUCTURED, NOISY SYLLABLES						
VII	II.B.1.b(1)		Growl	äääh	Not structured	(juvenile-adult)
	I.A.		Hiss		Not structured	(juvenile-adult)

• Roman numerals as used in Figures 9, 10, 15, 17 and 22.

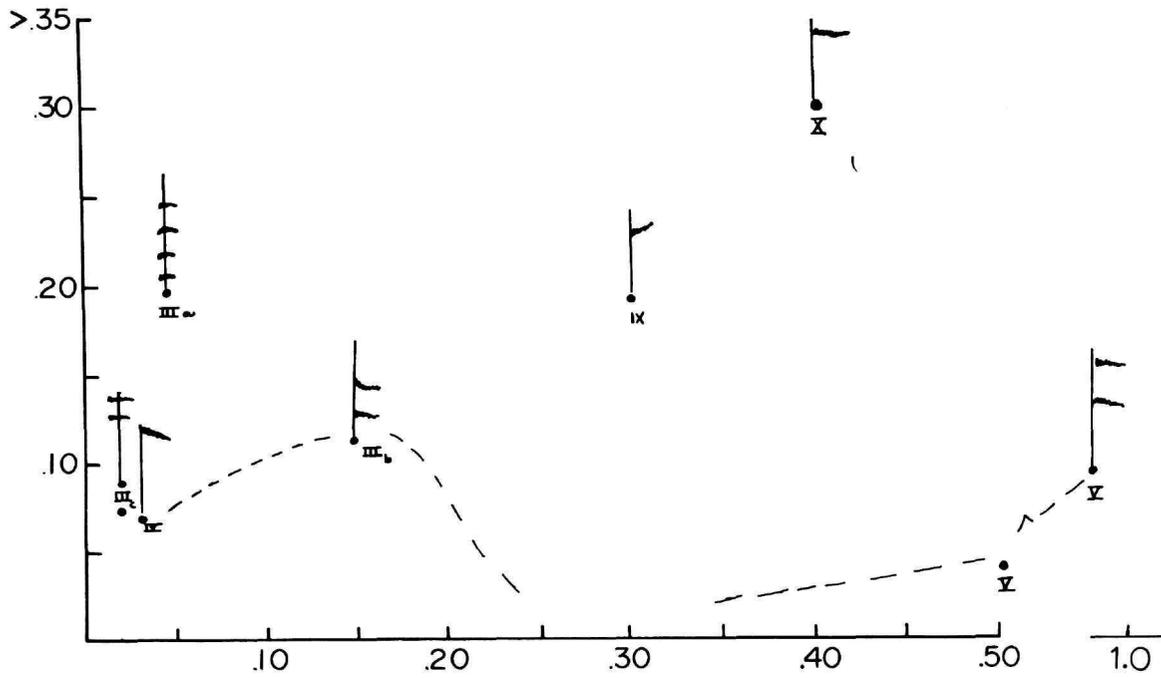


FIGURE 10.—Trill, twitter, squeak, and chitter temporal relationships. (Syllabic transformation is indicated by the broken line; scales as in Figure 9; syllable types are assigned a roman numeral corresponding to the call form as designated in Table 10.)

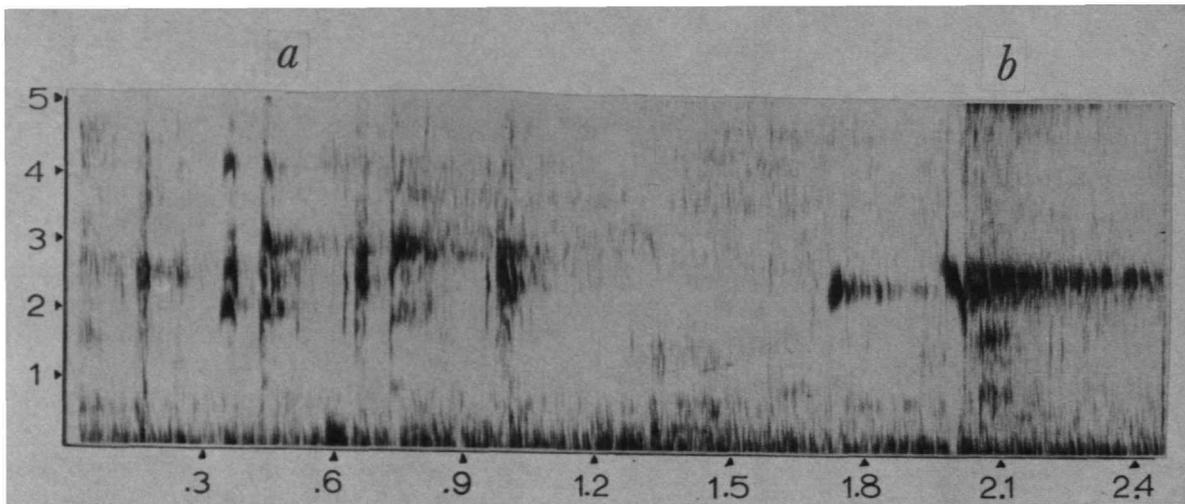


FIGURE 11.—Sonographs of trill variants: *a*, trill to chirp series; *b*, fusion of trill to chitter. (Ordinate in Khz, abscissa in seconds.)

of the bark portrayed. Syllable duration ranges from 0.15 to 0.46 seconds with intervals from 0.16 to 0.59 seconds. The longer, peeling barks with emphasis on higher frequencies are characteristic of an animal in distress ("Contexts," p. 38). Bouts of barking may persist for over 30 minutes.

This analysis of the bark illustrates well the importance of temporal patterning as an indicator of arousal level. The question can be raised as to whether we are justified in treating this as one type of call. I believe we can, for the following reasons: (1) the syllable is relatively uniform in structure for all forms, and (2) the context appears

to be functionally similar ("Influences," p. 49). The call can be heard at a considerable distance and is easily localized by a human observer. It would appear to function as a "mobbing" call as will be described later.

INTENSE, HIGH FREQUENCY SOUNDS AND THEIR DERIVATIVES.—Two call forms are involved, one in which the syllables are incompletely fused, giving a pulsed quality; the second type demonstrating syllabic fusion and a smooth emission of sound.

Pulsed phrases: Trills and twitters (Key II.A. 1.a(1)). These high pitched calls include syllables which are brief (<0.05 sec) in a twitter or 0.20

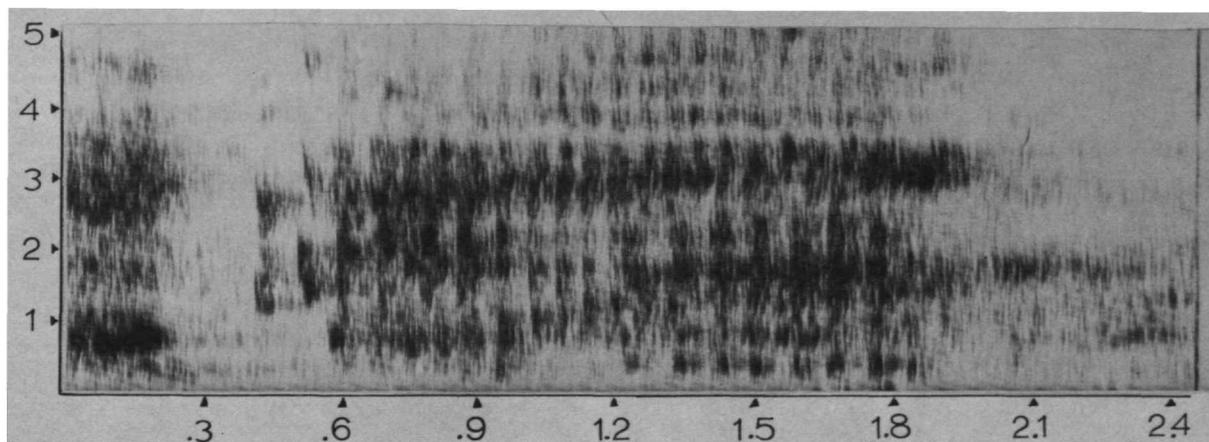


FIGURE 12.—Sonographs of trill to chitter transforms: fused trill or harsh "metallic" chitter. (Ordinate in Khz, abscissa in seconds.)

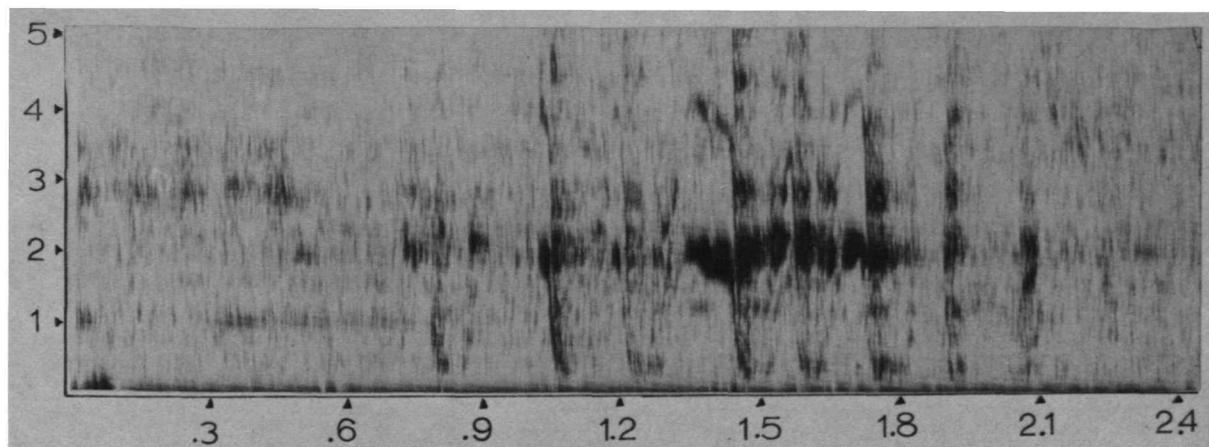


FIGURE 13.—Sonographs of the whinny. Note extreme frequency modulation. See Appendix I. (Ordinate in Khz, abscissa in seconds.)

seconds in the trill. The form of the syllable is variable but high frequencies 3 to 5 KHz are emphasized. Syllabic elements may be separated by intervals as short as 0.05 seconds and ultimately the syllables may fuse to form the pulsed chitter (Key II.A.1.a (2)) (Figure 10). The figure illustrates a fundamental rule for syllabic transformation, namely fusion of elements by shortening the interval between syllables. Figure 11 illustrates the trill variants.

Continuous emissions: The squeak is a high pitched call with little modulation and of moderately high pitch; it may grade into the chitter form (Key II.A.1.b (1) and (2)). Chitters of long duration (>0.7 sec) may transform to an ee awk form by ending with a noisy syllable (Key I'.B). These sounds seem to be related functionally and form a graded series. Some call forms, such as the squeak, are relatively distinct to the human ear, but the other call forms more or less intergrade. This complex of intergrading sounds illustrates the "rule of fusion" in syllabic transformation (Figure 12).

HIGH FREQUENCY CALLS EXHIBITING EXTENSIVE FREQUENCY MODULATION.—The tee-tee call is brief and nonrepetitive, generally <0.9 seconds in duration. It appears to function as a greeting. Frequencies are modulated over a range of 800 Hz. The whinny is similar in structure but longer (may

exceed 2 seconds). The whinny has variable intervals separating the phrases and its elicitation depends on variable external input (see "Mood," p. 46, and Key II.A.3.a). The whinny is related to the slow whinny or chirp series and appears to be formed from syllabic fusion (Figure 13).

CALLS WITH VARIABLE FREQUENCIES EMPHASIZED.—These calls are rhythmic and their frequency is modulated from one syllable to the next. These calls are formed from brief syllables (<0.1 sec), but the syllabic structure is variable (Figure 14).

Highly modulated syllables may grade to the true whinny. The syllables emphasizing lower frequencies can grade to a long call form (Figure 15).

The uniting feature for this class of syllables appears to be the rhythmic shift of pitch from one syllable to the next; however, classifying low, guttural whinnies (Key II.B.1.a (2)) with the chirp series (Key II.A.2.a (1)) may in effect be artificial since two moods may be confounded (see "Mood," p. 46). Nevertheless, there is a functional continuity for this class of vocalizations (see "Influences," p. 49).

REPETITIVE, RHYTHMIC, LOW FREQUENCY SOUNDS (Key II.B.1.a (1) (b)).—These calls are composed of brief (<0.1 sec) syllables having a relatively unmodulated energy distribution. Intensity shifts and shifts in the frequencies emphasized correlate

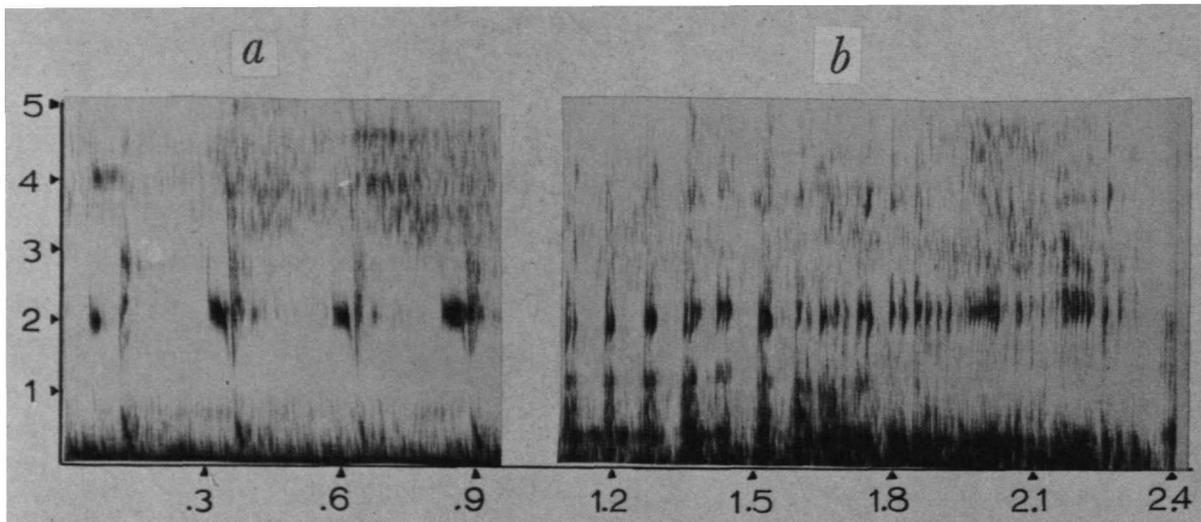


FIGURE 14.—Sonographs of two whinny variants: *a*, slow whinny note, modulation from one syllable to the next; *b*, guttural whinny, modulation from one syllable to the next but low fundamental. (Ordinate in KHz, abscissa in seconds.)

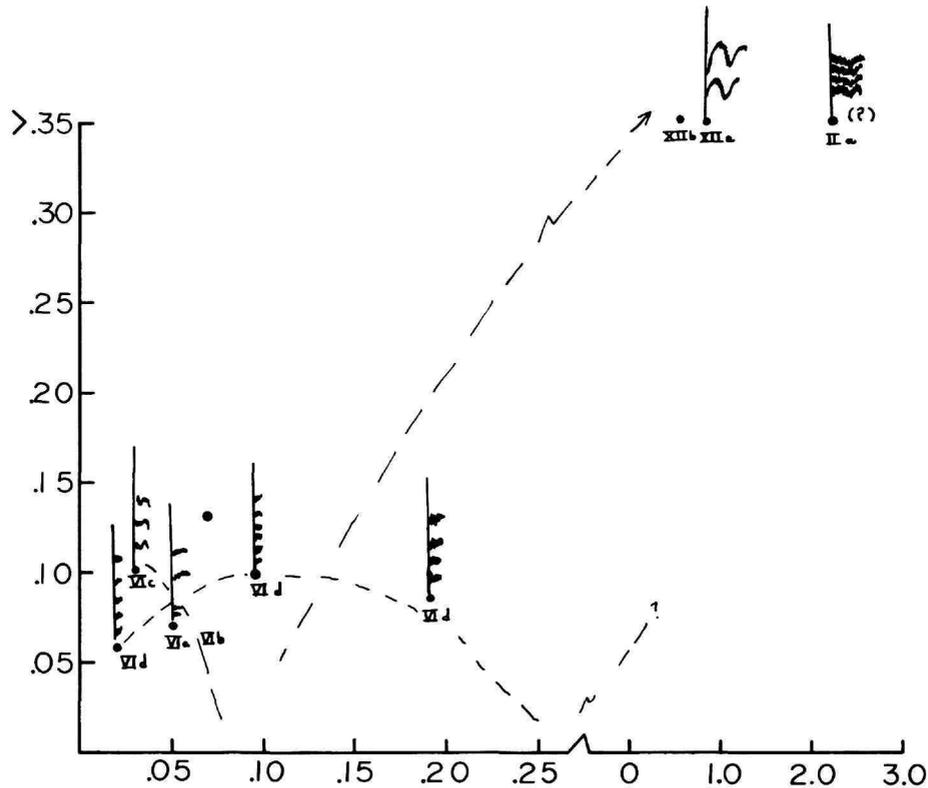


FIGURE 15.—Temporal patterning and transformation within the whinny series. (Scales as in Figure 9; roman numerals refer to call form as described in Table 10; broken lines indicate known syllabic transformations.)

with different levels of excitation. The calls sound like ook-ook or ak-ak. Context and function appear to be well defined (see "Grappling," p. 12; Figure 16).

HARSH, ATONAL SOUNDS (Key II.B.1.b (1)).—May be low in intensity (low growl) or extremely loud (roar). Characteristically frequencies <1.0 KHz are emphasized. These calls are not to be confused with the long, loud calls (Figures 16, 17).

INTERMEDIATE LENGTH LOUD CALLS (Key III.B.).—These calls are difficult to classify. Some types appear to be transitions to the long loud calls, others appear to be high intensity variants of other call forms. This category may be somewhat artificial. In Eisenberg and Kuehn's earlier work (1966: 12), the grunt-trill was described for *A. belzebuth*, which now appears to be two call types: (1) either a preface note or a low intensity precursor to long,

loud calls showing little pulse modulation (see below), or (2) an ascending trill often ending in noise. In the 1966 paper, the former variant was termed the grunt-trill plus the caw; it is not to be confused with the caw (see p. 34).

The grunt-trill is typically from 0.7 to 1.3 seconds in duration. It may be relatively pure in tone and ascend in frequency from 2 to 3 KHz. It may be described as: äh ēē ēē ēē ääh or ēē ēē ooch, and be quite repetitive; except for the modulation, the call resembles the chitter. On the other hand, these calls may descend from ~2.0 to 1.6 KHz during 0.7 seconds and sound like ääh üuh or ih äaah äaah. This latter variant has not been described before (Figures 11, 18 and Appendix I).

LONG, LOUD CALLS (Key III.C.1 and Key II').—Call types in this category are often uttered in a

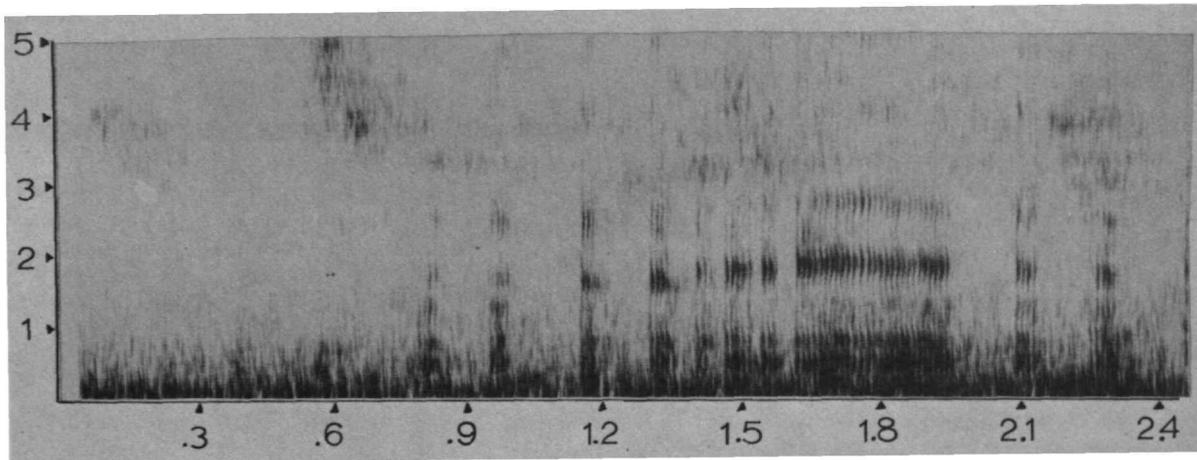


FIGURE 16.—Ook-ook to growl series showing syllabic transformation. (Ordinate in Khz, abscissa in seconds.)

compound phrase. The syllables contained in a phrase are long in duration, often exceeding 2.7 seconds in duration, but within a phrase terminal syllables may be as short as 0.03 seconds. These terminal syllables follow upon a longer syllable by an interval of some 0.1 to 0.3 seconds and are separated from each other by short intervals of around 0.04 seconds. In the field the terminal notes may be missed by an observer at ranges of several hundred meters, but the long syllables carry up to 0.5 km. Referred to for *A. geoffroyi* as the "caw" (Eisenberg and Kuehn, 1966:15) and as a "roar" by Oppenheimer (1968). In the *A. belzebuth* population studied by Klein (1972), these call variations were referred to as "whoops."

Ateles fusciceps: Two syllable types are noted: The short terminal notes have a duration from 0.02 to 0.04 seconds. The long syllables range from 1.5 to 2.7 seconds. Energy distributions average from 0.87 to 3.3 Khz (a range of 2.4 Khz). The average frequency is about 2.0 Khz, but the average energy emphasized lies at 1.16 Khz (N=19). Some three to four harmonics are involved (Figure 19).

At least two main subtypes can be distinguished: (1) the clear form, and (2) the vibrato or harsh form; both types can occur in the same series of phrases. The clear form shows little frequency modulation whereas the vibrato form is pulsed in its delivery with slight modulations over some 50 Hz within each pulse (Appendix I).

Syllables in a phrase are separated by intervals

≥ 0.3 seconds. The terminal syllables when present are separated from each other by intervals of less than 0.3 seconds. Phrases average some five syllables of which three are generally the short terminal form (Appendix I). Bouts of calling may last up to 30 minutes. Ten minutes thirty-five seconds of continuous recording showed that the calling male emitted phrases during 53 percent of the total time. He produced 36 phrases with an average duration of 9.4 seconds. The average number of syllables per phrase exceeding 1.5 seconds in duration equaled to 3.9 (N=15), range = 2 to 6 (Appendix I).

In the captive situation, this call is given by the adult male. Juvenile males may also be included in a chorusing behavior. Females approximate the call when in captivity, confined alone and visually separated from the group.

Ateles geoffroyi: In the field, *A. g. panamensis* males may show long, loud calls as a chorus. In addition long, loud calls may be uttered by either males or females when alone. Several variants have been distinguished. Oppenheimer (1975) has described a series of roars uttered in phrases of three calls, which are given by an adult male and apparently promote assembly by the females. This is the "caw" described by Eisenberg and Kuehn (1966). Calls by females are discussed on page 39. Male chorusing may occur after assembly through the use of intermediate length loud calls or chitters (see "Signals," p. 69).

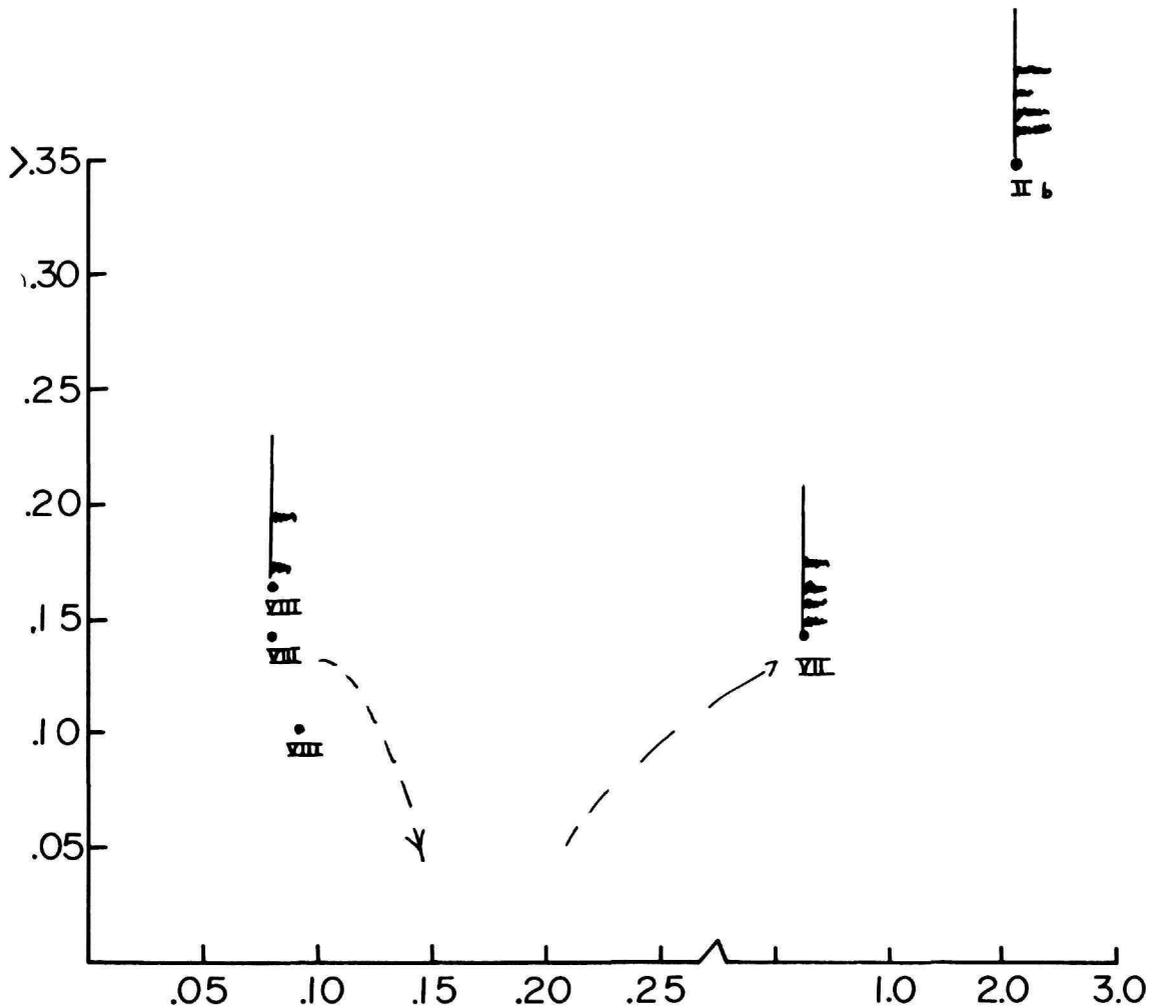


FIGURE 17.—Temporal patterning and transformation within the ook-ook to growl series. (Scales as in Figure 9; roman numerals refer to call form as described in Table 10.)

Compound Calls and Their Genesis

Thus far the main thrust of the discussion has been concerned with calls that appear to be derived from a single syllable type, which is transformed by alterations in the rate of utterance (fusion) or a rhythmic shift of pitch (the whinny series). A number of calls, however, involve two or more syllable types. For example, the eeeaw (trill-awk) when repeated, seems to involve a possible alternation between a "clear" syllable and

a "noisy" syllable. This may indicate a simple shift between two motivational states (see "Mood," p. 46) or it may imply a more simplistic explanation. For example, if we consider rising excitation as accompanied by increasing energy output during excitation, then during the delivery of a trill the glottis may become more open allowing a greater volume of air to escape, but causing a definite shift in pitch to a lower frequency.

In the case of the long calls, the inclusion of terminal syllables which appear to differ in syl-

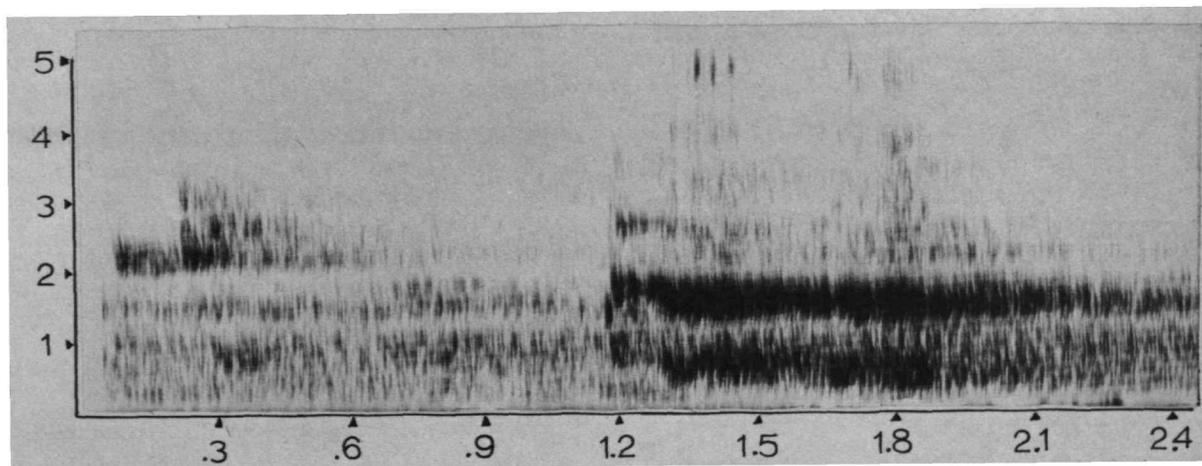


FIGURE 18.—Intermediate length long calls; ascending trill descending to a noisy syllable e aaah-
aah. (Ordinate in Khz, abscissa in seconds.)

labic structure from the preceding longer syllables may not imply a motivational shift. If the terminal notes convey information concerning the precise location of the sender, then we must assume selection has favored this call form as an entity. The terminal syllables are thus best considered as part of a call that has resulted from long term evolutionary processes, which may have "fixed" the neuromuscular complex responsible for its genesis.

CONTEXTUAL ANALYSIS OF ADULT AND JUVENILE SOUNDS

In analyzing the function of a signal, one must designate a presumptive sender and receiver (the roles are interchangeable) for each dyad that is examined. In his essay concerning the biology of expression and impression, Leyhausen (1967) notes that the innate propensity to express patterns of presumptive communicatory value, such as vocalizations, gestures, facial expressions, and postures, may in fact take place in situations where a definite response upon the part of a presumptive receiver is not evoked. Expressive movements and sounds to a large extent are shaped by the social situation in which they are performed. As will be seen (see "Ontogeny," p. 52), expressive movements can develop in young *Ateles fusciceps* without imitative learning and in the absence of a "normal" social environment. To quote Leyhausen (Lorenz and Leyhausen, 1973:304), "An animal

with a fair amount of learning ability and a fixed set of innate mechanisms for expression and impression, with the help of which it stimulates specific behavior in a conspecific and reacts itself to the other's expressive behavior, naturally cannot with time help noticing that this is so." In my work with hand-raised *Ateles*, I was not prepared to take data in a fashion which would allow precise discrimination of what effects the artificial rearing situation had with respect to the frequency of certain forms of expressive behavior. Nevertheless, the conclusion is inescapable, that most of the expressive movements and vocalizations of *Ateles* do not require imitative learning for their initial performance. It is also evident that the utilization of vocalizations and expressive movements on the part of *Ateles* can be specific to certain situations and presumably have an influence on the activities of some of the presumptive receivers. If the signal in question is to carry information from the sender to the receiver, we must infer the information content from a contextual analysis. In short, what happens during the signal exchange, and what happens after?

Obviously one primary function of a signal is to pass on information concerning the mood of the sender. A motivational analysis is thus a necessary step, which can yield a motivational classification. It should also be possible to relate syllabic transformation to motivational shifts.

It seems intuitively obvious that as an animal

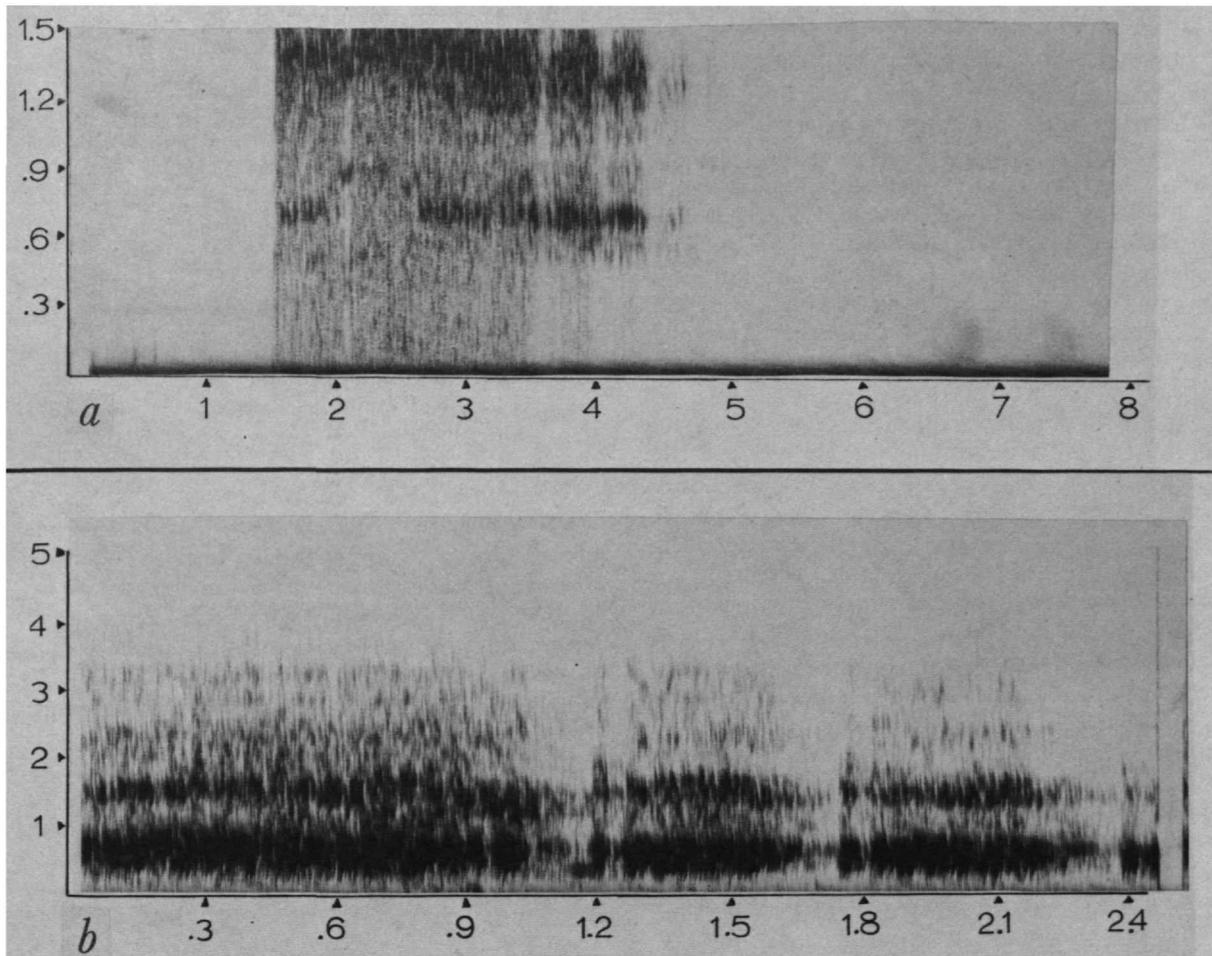


FIGURE 19.—Long call variants for *Ateles fusciceps*: *a*, undulating long call, possible derivative from guttural whinny; *b*, harsh long call series showing variation in syllable length (wide band analysis 200 Hz increments). (Ordinate in KHz, abscissa in seconds.)

becomes more aroused, a signal may vary in intensity by increasing the amplitude and/or syllabic frequency as for example during barking (see "Mood of Sender," p. 46). Can we then distinguish between intensity changes within a single mood and shifts in mood as evidenced by a change in syllable form? This question will be dealt with under "Alternation" (p. 48).

Considerations of Caste Differences

As will be shown (see "Ontogeny," p. 52), the vocalizations of *Ateles* are developed in their basic

form without imitative learning. Basic syllable formation and temporal patterning develop with a minimum of environmental influence. Nevertheless, there may be subtle learning involved in the full maturation of long call temporal patterning. In general, the two adult sexes have equivalent vocal repertoires, but females do not produce loud, long calls in the presence of an adult male. Juvenile males are actively sought out by adult males and allowed to participate in long call bouts. What effect this has on their adult repertoire has not been adequately assessed.

Contexts of Sound Production

BARKING.—*Ateles fusciceps* display this behavior rarely in captivity. They have barked at a stray dog wandering in the park and often bark after initial confinement in a shift cage. During the latter context, the barks are often of the "pealing" form.

Ateles geoffroyi in the field bark at human observers if the troop is unhabituated. Where spider monkeys are hunted, barking and mobbing will not be shown to humans (Wagner, 1956; K. Green, pers. comm.). The *A. g. panamensis* group has been noted to bark at the tayra, *Eira barbara* (see Eisenberg and Kuehn, 1966:53).

While barking the animal may show varying degrees of pilo-erection and when a group begins barking, urination and defecation may be noticeable during the initial barking response. When group members bark at a tayra, they may remain in the vicinity for 20 to 30 minutes peering at the intruding animal. Under these circumstances, one may speak of a "mobbing behavior." Tendencies to approach and withdraw are noticeable.

From a contextual analysis, it appears that barks are delivered in response to a novel stimulus from which the animals can escape or when the animal is confined but unharmed and within hearing range of its group. The pilo-erection, urination, and defecation suggest high autonomic arousal with simultaneous tendencies to defend itself and avoid the stimulus object (s). The intensity of the response is somewhat graded.

TRILLS AND TWITTERS AND THEIR DERIVATIVES FOR *Ateles fusciceps*.—These high pitched intergrading calls are involved in situations where the animal is excited (as evinced by some pilo-erection), socially attracted to the stimulus object, and at the same time ambivalent or actually fearful, since it avoids a close approach. It is given by a subordinate avoiding a dominant and appears also in play situations where a dominant reverses roles with a subordinate.

Slow twitter: Given by juvenile male as he slips during climbing.

Twitter to trill: Performed by adult female to a patron who has a noise-maker; performed by adult female V to daughter B as V chases B away from the vicinity of adult male.

Twitter with half open mouth, no tooth exposure: Given by female V to me when food is with-

held from her; juvenile male to adult male as adult male persistently follows him.

Twitter to eek-eek (squeak): Given with partially open mouth, incisors showing, lips lifted, by M and J. Open mouth, no tooth exposure: J after V slaps him.

Metallic trill (chitter): Given with chin up, lips parted to lips pursed, by adult male to me as I leave the Monkey House. An awk syllable may be incorporated on the end of the metallic chitter to make it approximate an eēē awk.

Squeaks: Contexts are similar to the preceding but a more definite avoidance is shown by the sender. This call may also be given if the animal slips and falls, thus lending support to the idea that this is a "fear" sound.

Squeak, which is low in volume and almost "crooning": Appears to be less than 1.0 second, not recorded. Given by adult female to infant when the infant is off the mother playing just prior to a shift in locus by the mother. The mother will reach out to the infant while uttering the call, thereby focusing the infant's attention on the mother. Cannot be heard at a distance exceeding 3 meters in captivity.

Trill-awk (ēē-awk): Expressed by juveniles when isolated or when companion moves away. A similar sound is given by adults at the departure of a familiar attendant. Will be shown by adults when isolated from a group and confined (captivity).

Example of trill and trill-awk production by *Ateles fusciceps* (J = juvenile male, M = adult male): J sniffs M's genitalia; they break apart, then M starts to follow as J moves away, mutual emission of trilling awk calls continues. Lips are pursed during the call. M catches J, they embrace. J moves away with trill calls. As M catches J, he gives a low growling whinny (sobs). M trills following J. J trilling. They embrace. M low whinny (sobs); J moves away. They come together, M and J embrace as they do so, M gives a low whinny, they break apart, M to the bars and gives a low bark (cough) to the patrons. J hangs trilling and twittering, trill-awk to patron. Then they come together and renew following on the part of M, moving away on the part of J.

TRILLS, TWITTERS, SQUEAKS AND THEIR DERIVATIVES FOR *Ateles geoffroyi*.—As with *A. fusciceps*, the contents exhibit high degrees of excitement and ambivalence.

Example of scream: Juvenile female roughly 7 to 8 months of age screams and flees at approach of adult female (who has no baby), while retreating to her mother. If male ap-

proaches, juvenile female will squeak to trill and move away, but does not flee.

Example of low squeak: As an animal attempts to effect crossing on a sapling that bends under its weight in the direction of the next tree. Second animal in tree reaches out to the animal on the bending sapling; they join hands and the animal on the sapling effects the crossing, whereupon they embrace and sniff their pectoral regions (similar to mother-infant call).

Example of rapid twittering-squeak series: Given by an infant when it slipped and fell; later female approached and carried the infant on her back.

Example of twitter series: Given by adult female as she notices me in blind and drops down to lower branches to observe more closely.

CHITTER.—A high intensity derivative of the trill series. Appears to derive from a thwarting context where the sender is somewhat intimidated but threatening. It may be followed by branch shaking and violent brachiation (for further examples, see "Signals," p. 69).

TEE-TEE; WHINNY AND SLOW WHINNY.—This frequency modulated class of vocalizations can actually be broken into three categories: (1) A high intensity, rapid, nonrepetitive form, termed the "tee-tee-tee," is used as a greeting call to persons that the monkeys have associated with feeding. Example: Tee-tee-tee given with chin up and pursed lips or nonpursed lips, but mouth closed; appears to be a greeting to persons associated with feeding. (2) A shrill quick call, often repeated several times, is given by several members of the group when all foraging for an abundant and desirable food item on the floor of the cage. The variant is termed the "whinny" and is often given with chin up and lips closed. (3) As feeding progresses, the animals may from time to time give a slow, harsh whinny, which is the third variant. If another animal approaches closely while feeding, the slow harsh whinny form may grade into an awk sound.

Ateles fusciceps: When soliciting food, they may give a whinny to a bystander in the slow, low intensity form. When this is done, the lips may be pursed but almost closed. This is termed the "yip-yip whinny" or "slow whinny." The chin is held up in most cases, but occasionally no lift of the chin is shown. It is given as a greeting to an attendant or observer or to a cage mate. A lower pitched variant, the growling whinny, can almost

grade to an ook-ook. It is often given with pursed lips, but may also be given with closed mouth. Chin up is a common association. It is demonstrated when feeding is well under way or may be given as a greeting, or during embrace (see "Slow Guttural whinny or sobs," p. 39).

Ateles geoffroyi panamensis: Although the whinny is associated with feeding, it appears to involve contact maintenance and can involve group movements.

Example 1: While sitting as skies darken and wind increases, animals whinny to each other. Whinny calls at rate of 3 in 4 minutes. After the rain begins, it seems to promote whinnying back and forth among assembled females. Three whinnies are then recorded in 4 minutes. By now all females have assembled and huddled in the same tree throughout the rain.

Example 2: Female gives whinny as male approaches. Male replies with whinny. They join and move together into the lower part of the canopy.

Example 3: Whinny call given twice in one minute following upon thunder. Calls from one of three females who are sitting near each other in the same tree. Whinny again after a 2-minute pause, fourth animal joins other three. Whinny. At onset of rain, again the animals whinny to one another. Ten whinny calls in period of 12 minutes.

SLOW GUTTERAL WHINNY OR SOBS FOR *Ateles fusciceps*.—This is prominent during embracing as well as during feeding.

Example 1: Animal J performing the trill grading to eek sound at roughly 1 per second. Animal delivers the call with an open mouth and no tooth exposure. M approaches juvenile who is sitting alone vocalizing (call this the distress call), male embraces juvenile, as he does so gives a low, guttural whinny.

The slow, guttural sobbing can grade to a long call intermediate form (see "Mood," p. 46).

Example 2: M and J embrace. As they do so, M gives a low, guttural whinny, they break apart; M to bars and gives a single, low bark (cough) to patrons. J hangs trilling and twittering. Then M gives a rolling ooo-ooo-aah-aah call or whoop; J approaches and again they initiate following and moving away; trill-awk by M; awk-awk-trill by J. The interaction breaks off. J hanging, extends his hand to M; M reaches out; J jumps at M; they embrace, M gives a slow whinny; they break apart, trilling by J as he moves away; he hangs and reaches out; M reaches toward J.

OOK-OOK OR AK-AK SERIES.—Soft ook-ooks are correlated with play fighting or grappling; this activity may precede sexual play in newly encoun-

tering individuals (see "Grappling," p. 12). As play becomes more aggressive, the sound grades to the ak-ak form. At high intensity, the call can grade into growls (see below).

GROWL-ROAR COMPLEX FOR *Ateles geoffroyi*.—The growl may terminate aggressive play and lead into the roar often with a chase by the dominant animal.

Example 1, growl: Two animals in a tree grappling, ook-ook sounds grading to growls, finally ending in a roar. They break apart, a slight chase; one being chased utters low squeals. Grappling between females or between male and females often accompanied by low ook-ook sound which may grade to growl.

Example 2, roar: Accompanying a three-way grappling bout which breaks up. Male approaches group of females. As he does so, he gives a loud roar.

Example 3: Long roar from male at approach of *Cebus*. Another aggressive roar produced by the male *Ateles* while chasing a *Cebus* monkey.

COUGH.—This appears to be a warning sound, the function of which is poorly understood (Eisenberg and Kuehn, 1966:14). Structurally the cough resembles a single syllable of a bark. It is produced in what appears to be conflict situations but it is of rare occurrence and little data are available to elucidate its function.

INTERMEDIATE LENGTH LONG CALLS.—The grunt-trill or rolling grunt-trill, as defined in Eisenberg and Kuehn (1966), is much too broad in its original definition and included at least two distinct vocalization types: (1) the ascending intermediate call, and (2) the grunt-trill-caw combination which is in reality one possible form of the long call series. The ascending call or eeah appears to be given by an animal either at the departure of a companion or by an isolated animal. The descending form oah or aah may be a precursor to a fully developed long call.

LONG, LOUD CALLS.—Several forms of the long call can be distinguished. They share in common the fact that they are relatively harmonic in tonal structure, generally exceed 2 seconds in duration, are quite loud, and often repeated. In *Ateles fusciceps* a long call phrase typically has a terminal series of grunts termed the "coda." The following variants are classified on the basis of physical form. Although the call shows a relatively constant frequency, it may have two subforms: (1) clear, monotonic where the energy bands are relatively

"pure" in a sonograph, and (2) harsh, monotonic which shows less tonal purity and superimposition of more noise. This latter variant of the long call was referred to in 1966 (Eisenberg and Kuehn, 1966:15) as the caw. Generally only an adult male or satellite subadult males call when they are with females. Females do call in the absence of the male.

***Ateles fusciceps* (captive contexts):** The male *A. fusciceps* generally gives long calls while highly aroused. He may brachiate between bouts. He called frequently when the juvenile male and one female were isolated from his group, but also called on the day they were returned (see "Calling Frequencies," p. 43).

Example 1: When the male was held alone in a cage, a long call undulating aa-aaa-awk given as a single call was given during high excitement.

Example 2: A series of long calls were given at the onset of rain. It was a prolonged series lasting some 30 minutes and given in phrases of 4 or 5 syllables. The total duration of a phrase often exceeded 6 seconds and was given without reference to any specific stimulation.

***Ateles geoffroyi* (field contexts):** For further details of contexts for *A. geoffroyi* long calls, see "Signals," p. 69.

Example 1, male calling: Male calls with a prolonged aawk-aawk-aawk, generally given as a triad, may be given singly, often while brachiating (Oppenheimer, 1975).

Example 2, female calling: One adult female in B canyon alone uttering a call: aawk, eeaawk, eeawk, awk, etc., repetitive and harsh sounding (similar to the caw, as well as the ending of a roar given during a grappling bout that turns aggressive). Called for about 7 minutes, then crossed to A canyon; no reply.

Example 3, female calling: Rain appears to be imminent; sky darkens, wind rises. One female is somewhat isolated from the group and begins to call: ooo-ooo-ooo in rhythm of the whinny, ooo-ooo-ooo ooo-ooo-ooo, it has a low plaintive quality, then the ooo's are terminated with an awk rising at the end very similar to the intermediate length ascending call (grunt-trill), then pure aawk calls are given alternating with eeaawk calls as on a previously noted occasion. (I propose that the ooo portion has a rhythmic quality like the whinny that can grade into a grunt-trill type call that may have a terminal awk and then grade into pure aawks that have a roar quality.) This roaring whoop continues for some time.

Example 4: The eëë-ööök call, long, moderately high pitched, caw-like quality, repeated; sound produced by adult female sitting alone. Others assemble from rest spots and they move off together.

TABLE 11.—Call types and contexts of occurrence

Situation	IV to																					
	Ia	Ib	Ic	VIIIa	VIIIb	VII	IIb	XIV	VIIb	VId	VId	VIIc	XII	IIa	IIIa-b	XI	IX IIIc-d	V	X	IX	XIII	
Approach of—	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
familiar friend	-	-	-	-	-	-	-	-	-	-	-	-	XXXXX	-	-	-	-	-	-	-	-	-
rival	-	-	-	-	-	-	-	-	-	-	-	-	-	XXX	-	-	-	-	-	-	-	-
While feeding or	-	-	-	-	-	-	-	-	XX	XX	XX	XX	-	-	-	-	-	-	-	-	-	-
While feeding or	-	-	-	-	-	-	-	-	XX	-	XX	-	-	-	-	-	-	-	-	-	-	-
to a partner	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Approaching a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'crying'	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
juvenile	-	-	-	-	-	-	-	-	-	XX	XX	-	-	-	-	-	-	-	-	-	-	-
Isolated animal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	XX
Approach or avoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
superior	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
While threatening	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	XX
Play, mock fight	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Play, mock fight	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	XX
Aggressive play	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prior to	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
copulation	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
copulation	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ground predator	XXX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ground predator	XXX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Novel stimuli	XXX	XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Novel stimuli	XXX	XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caught (netted)	-	-	XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caught (netted)	-	-	XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prior to attack	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prior to attack	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Approach to rival	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Approach to rival	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
During threat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
During threat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
display	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
display	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Injured	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Injured	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fleeing	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fleeing	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Departure of—	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
a rival	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
a rival	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
a friend	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
a friend	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Avoiding	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Avoiding	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
dominant	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
dominant	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Play avoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Play avoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

X = occurs in the context noted; XX = occurs frequently; XXX = occurs very frequently; XXXX = occurs exclusively and frequently in the context noted.

TABLE 12.—Calls and associated circumstances for *Ateles geoffroyi* in the field

Call type	Sight human	Initial movement	Chase	Grapple	Move away	Feeding	Prior to or during a move	Onset of rain	Settling down	Afraid to cross a gap	After separation	Before moving as a group	Sight of a rival	When threatening			Sitting alone
														Female	Sloth	Eira	
XI Screech-whinny	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
XIIb Tee-tec	3	-	-	-	-	8	4	-	-	-	-	-	-	-	-	-	-
XIIa or VI Whinny	1	-	-	-	-	45	22	2	1	-	1	-	-	-	-	-	-
X Squeak	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-
IIIc Shriek	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
VII Growl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IIa Long call-harsh	-	-	3	-	-	-	-	-	-	-	-	1	-	-	-	-	1
IIb Roar	-	-	2	1	-	-	-	-	-	-	-	-	-	1	-	-	-
IIb Aah aah aah	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1
IIb Ooah (caw)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
VIII Ook-ook	-	-	-	-	13	-	-	-	-	-	-	-	-	-	-	-	-
I Barking	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1*
Cough	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
V Chitter	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-
XII or IX Eeaw	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
IIc Long call-pulsed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1*	-	-

* Performed as a chorus.

Klein (1972), in his study of *A. belzebuth*, implicates whoops in intertroop encounters and wails (long call—clear form) as a means of facilitating subgroup mergers.

The foregoing outline of contexts for the various calls can be summarized in tabular form (Tables 11, 12). For comparative purposes, I have utilized in Table 11 contexts similar to those employed by Winter, Ploog, and Latta (1966) for *Saimiri*. Although I agree with the preceding authors that a given call type tends to occur in several contexts, I feel that certain syllabic forms and certain types of temporal patterning can be associated with moods or intentions on the part of the sender. Within any mood the calls show variations in intensity and rhythm, which suggest that a range of arousal patterns can be discerned; that is to say, a series of "excitation indicators" is discernable within a mood. Transitional call forms then connect or serve as "bridges" between two motivational tendencies (see "Mood," p. 46).

Frequency of Calling and the Contexts for Free-ranging Ateles

As indicated previously, the vocalizations for *Ateles geoffroyi* were very similar to those produced by *Ateles fusciceps*. In order to elucidate the functional significance of the vocalizations for the captive *A. fusciceps*, reference is made to homologous vocalizations and their cotexts for *A. geoffroyi*.

For the purposes of this analysis, I have selected 13 hours of continuous recording of interactions broken down into 52 15-minute blocks. Each 15-minute observation period was balanced with respect to time of day, so that samples were drawn throughout the entire activity period of the animals. Ten hours of data were taken during 1964 with an average of 3 animals visible at any one time. Three hours of data were taken in 1974 with an average of 7 animals visible at any given time. Thus, 51 "animal-hours" of data were taken for 183,600 "animal-seconds." During these sample periods, an attempt was made to record every bout of vocalizations heard. Since the average observer-animal distance exceeded 20 meters, low amplitude vocalizations were undoubtedly missed, thus this sample is biased toward louder vocalizations. Nevertheless, the data are instructive.

The data can be reported in two ways, either with respect to the frequency of vocalization types uttered or the summed durations. Durations were calculated by multiplying average frequency of vocalization times average duration as determined by recording and sonographic techniques. Two classes of vocalizations required an additional calculation; these were barking and the chorusing long calls, since both of these types involved the participation of several animals. In each case, calculations of duration were based on the number of animals participating in the chorusing behavior.

Whinnies were the most frequently heard vocalizations as indicated in Figure 20; the least frequently heard vocalizations in terms of bouts were barking and the long call. Agonistic calls were of infrequent occurrence. The tee-tee and ook-ook calls were of moderately frequent occurrence. When we consider, however, the duration of the calls emitted in terms of animal units, then we see that one bout of barking occupied more time than all of the other vocalizations taken together. Similarly, the participation of several animals in long calls results in a great deal of energy expended when these calls are given; however, they are given infrequently. Thus, group calls such as barking or the long calls of males, although of infrequent occurrence, involve considerable expenditure of time when they are given. On the other hand, whinny calls and tee-tee, although very brief, are given frequently, but do not account for a very great percentage of time involved in emission of calls.

To summarize then, out of the 51 animal-hours of observation, only 568 seconds of vocalization were noted, or only three-tenths of 1 percent of the time did the animals indulge in vocalizations that were audible to the observer over the range so noted. This analysis supports the notion that calls promoting contact in the forest while feeding (whinny calls) are frequent but do not carry far. Sounds which carry far (barking and long, loud calls) are infrequent but of great significance. The former (barks) are utilized as part of the anti-predator mobbing response. The long-loud calls are distinctive and are related to intertroop encounters and troop assembly (Klein, 1972). They may be considered as partial analogs of gibbon calls or the long calls of *Alouatta* (see "Comparisons," p. 62).

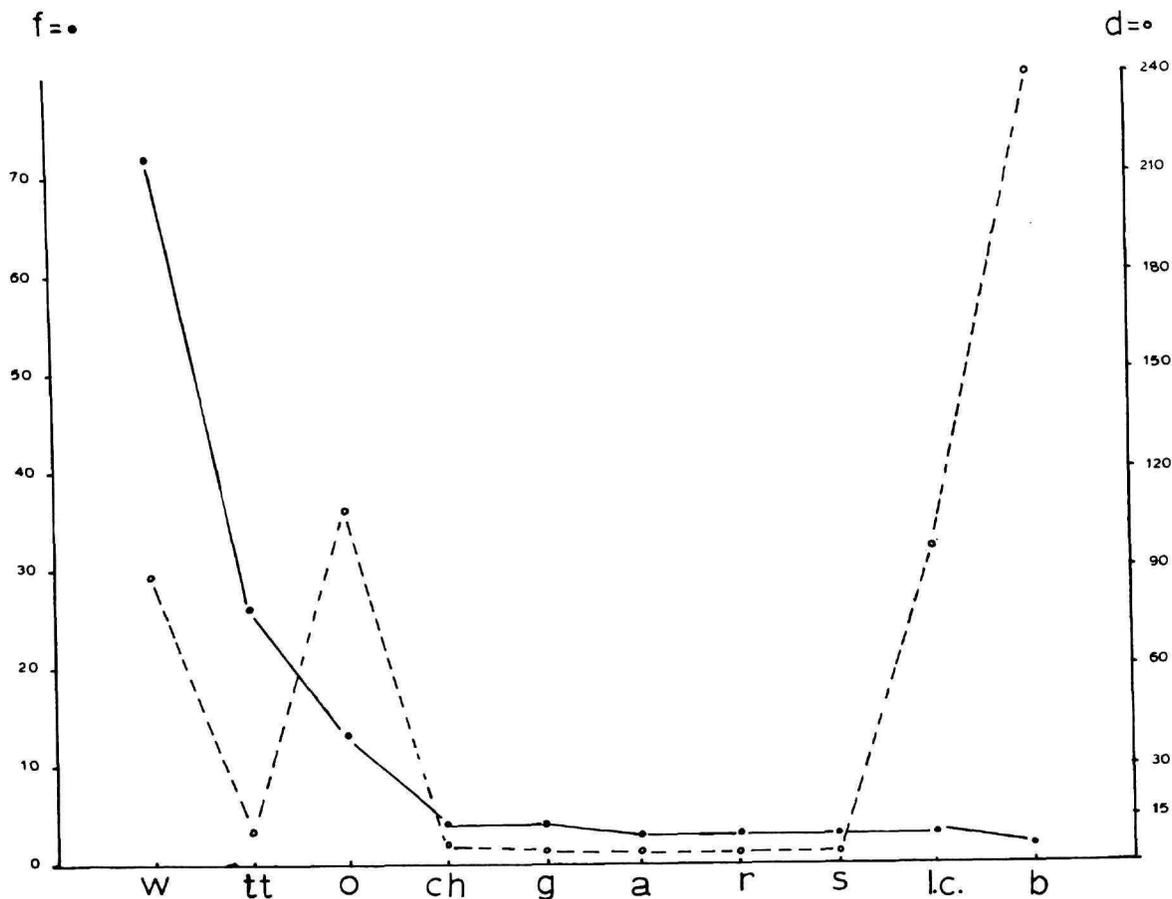


FIGURE 20.—Frequency and duration of vocalization forms for free-ranging *Ateles geoffroyi* (solid line=frequency (f) of vocalization bouts, left ordinate; dotted line=total duration (d) in seconds of each vocalization type as recorded during the entire sample interval, right ordinate; w=whinny; tt=tee-tee; o=ook-ook; ch=cough; g=growl; a=long call intermediate length; r=roar; s=scream; l.c.=long call; b=bark).

Some Calling Frequencies for Captive *Ateles fusciceps*

The type of analysis presented in the previous section for free-ranging *Ateles geoffroyi* is difficult to perform in a captive situation, since there is uncontrolled external disturbance; however, Table 11 presents an indication of the relative frequencies of various vocalization forms shown throughout a series of set observation periods. Perhaps of greater interest will be a consideration of the form and context of vocalizations shown when the captive group of *Ateles* had to be separated during June of 1973. At this time the group consisted of the

founding father "M," a female of his age class "V," her son "J" and daughter "B" and an adult female hand-reared in 1966 and reintroduced to the group in 1967, "S." During testing for tuberculosis, subadult female B and J were isolated from the main group, which was on exhibit in an outside cage. B and J were placed in an inside cage in auditory contact with the family group, but visually isolated from them. Upon separation on 13 June, J proceeded to give a repetitive series of eee-awk calls interspersed with trills fusing to chitters. During a sample period of 330 seconds recording, calls were given by J during 18 percent

TABLE 13.—Call analysis of separation and reuniting series of *Ateles fusciceps*

	Energy (Khz)	D (sec)	I (sec)	Rate (calls/sec)	Average % of time calling
Calls after separation of B and J from Group VI/13/73; recorded sample 330 sec					
Call forms for J					
Eee-awk (or eēēt-āāht)	(1.3-2.4)-1.1	0.29	Var.	0.75	18
Trill—chitter (or twi twi twi ēēē-ē)	0.1-1.8, 2.7-3.8	0.23	0.20		
Calls on VI/14/73 during long call series by Father "M"—recorded sample 229 sec					
Call forms for M					
Long call type II āāāā h r̄ vi- bratto (see appendix I) Number of phrases: 4; duration of phrases 1.5-5.5 sec; range of interphrase intervals 2.5-3.5 sec	-	-	-	-	-
Call forms for B					
Intermediate length long calls (frequency of calls 21, summed duration 13 sec) ūkāūāākk h r̄	0.2-1.0, 1.2-1.8	0.90	Var.	-	-
Call form for J					
Trill-chitter	0.1-1.8, 2.7-3.8	0.20	Var.	0.19	5.6
Calls on VI/16/73 during reuniting; recorded sample 270 sec					
Call forms for M					
Slow whinny, guttural (sobs) āāh āāh ih ih during embrace	1.3-2.5	0.19	0.07	0.41	50
Call forms for J					
Metallic chitter kkk ēēē ēt	0.7, 1.6, 3.0	0.06	0.02	0.77	58
āh āch āā ēēē k	1.2-3.6	0.17	0.05		

of the time. B was relatively silent. On the following day, the father, M, initiated a long call series. The exact amount of calling by the male was imperfectly quantified, because the calls of subadult female B and juvenile male J were studied intensively. B tended to respond to the calls of her father with an intermediate length long call having a frequency similar to the calls of the male, but a far shorter temporal patterning. J responded by an excited series of trills grading to chitters, but his percentage of time calling during the male's long call bouts dropped to 5.6 percent. On 16 June 1973, B and J were reunited with the family and their vocal behavior recorded for 270 seconds. The adult and subadult females, after greeting one another with whinnies, settled down immedi-

ately; however, the interaction between the adult male and his son was intense. Essentially, it consisted of repeated approaches on the part of the adult male, while uttering the slow guttural whinny (sobs) and embracing the young male while the young male alternated between withdrawal and approach to the male, giving intermediate length calls including a metallic pulsed chitter alternating with an aah aah ee. During the entire recording session, the adult male was calling 50 percent of the time and the juvenile 58 percent. These data are summarized in Table 13.

The interpretation of this would be as follows: Separation induced an extreme anxiety situation in the juvenile male, who responded by repeatedly calling in the eee-awk or trill-chitter variant. On

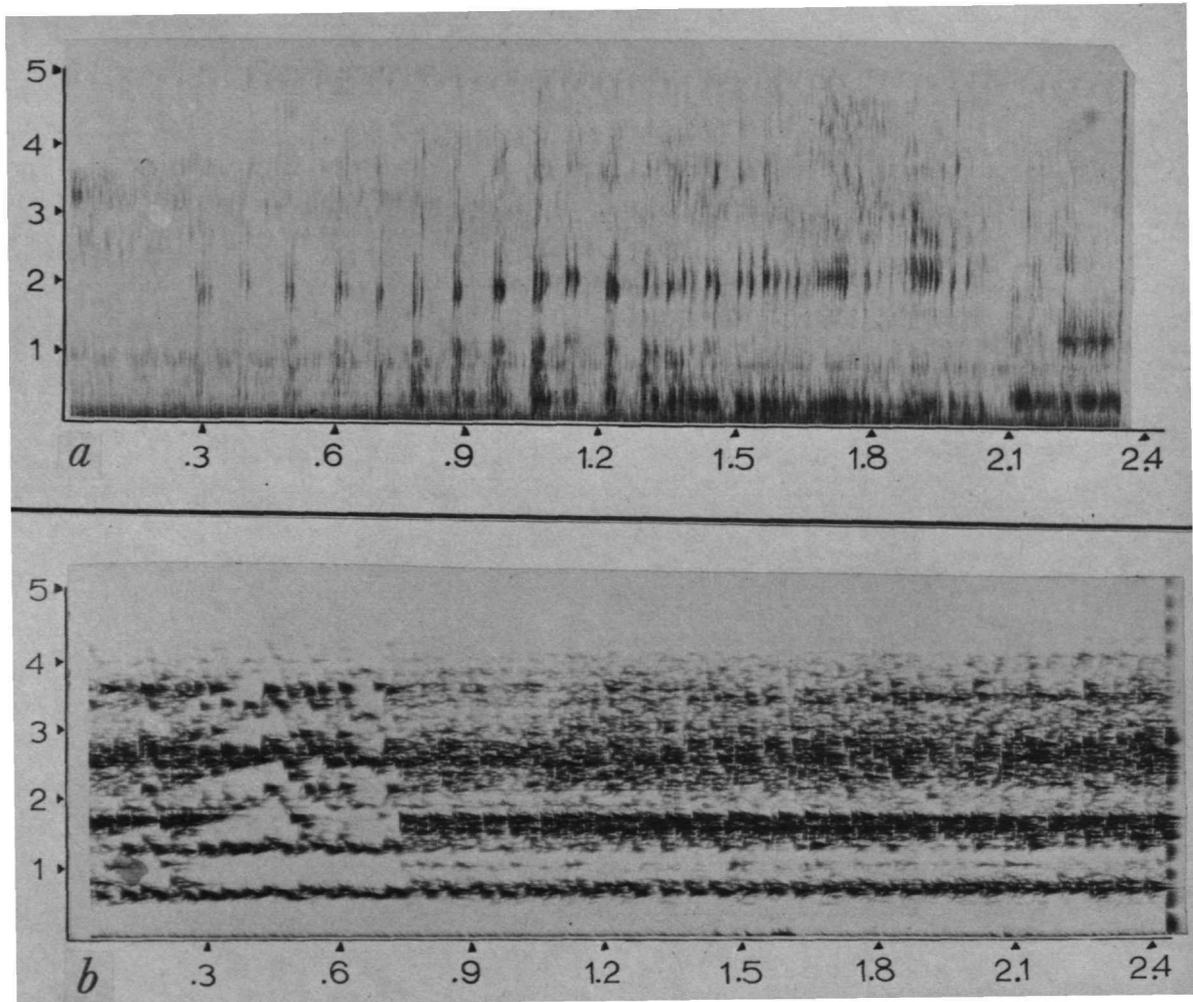


FIGURE 21.—Transformation of sobs (guttural whinny) into a long call by adult male *Ateles fusciceps*: *a*, sobs (slow guttural whinny), wide band; *b*, undulating long call derived from *a*, narrow band analysis. (Ordinate in Khz, abscissa in seconds).

the following day, the adult male responded to the absence of part of the group by emitting a long call series, which was responded to on the part of the subadult female with intermediate length long calls. At a lower level of arousal, the juvenile male exhibited the anxiety separation call. During reuniting the most intense interaction took place between the adult male and the juvenile male. The adult male showing embracing and "sobbing;" the juvenile male alternating between extreme withdrawal and anxiety and approach touched

with anxiety. This leads us then to the question of motivation.

MOOD OF THE SENDER

Dynamics

Referring to Table 11, it can be seen that the true whinny and slow whinny variants are often tied to feeding and made with reference to group members. The slow, guttural whinny (sobs) is made

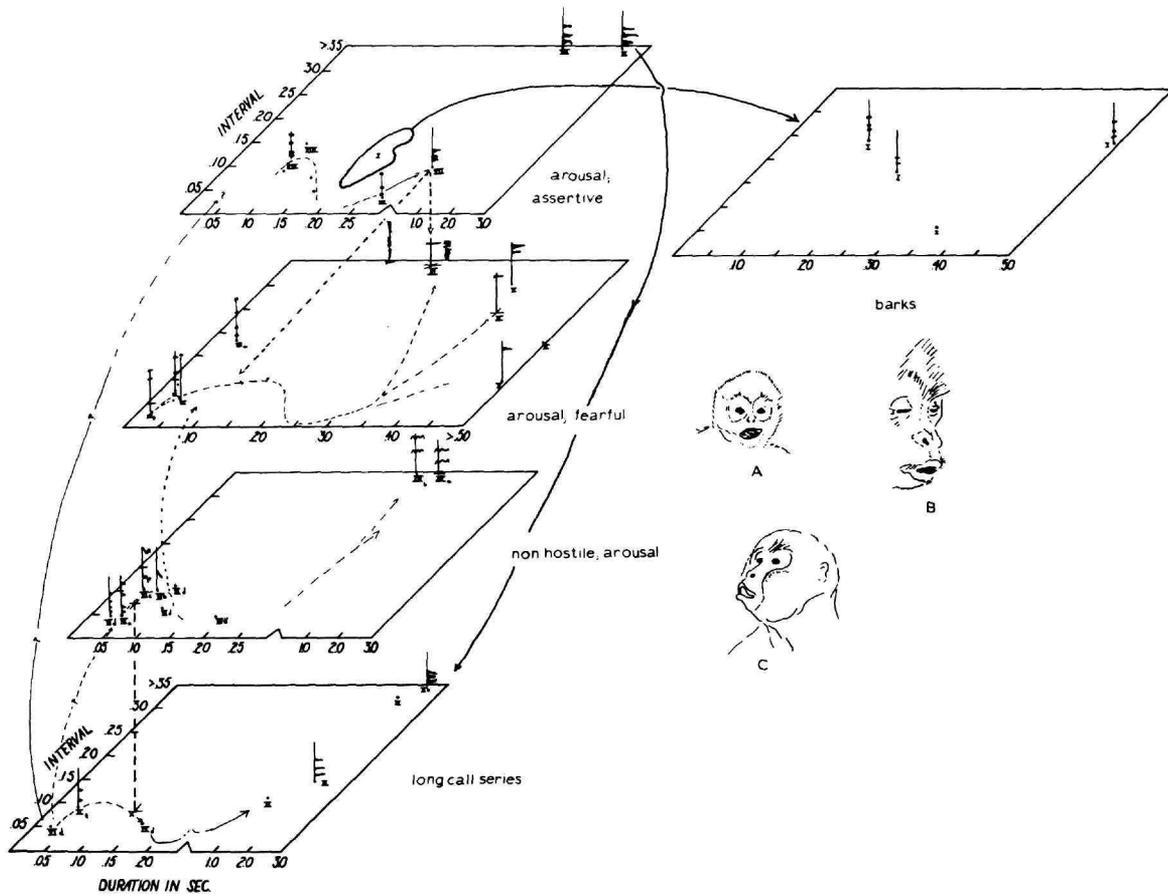


FIGURE 22.—Call transformations and syllabic similarity, a composite diagram derived from Figures 9, 10, 15, and 17. The discrete call forms (roman numerals, Table 10) are shown with transitional syllables. Calls believed to be indicative of the same general mood are portrayed on the same plane (p. 46). Broken lines indicate pathways of syllabic transformation. The three faces include: A, expression during a growl; B, expression during a squeak; C, expression during a long call.

during friendly approach to a group member. The tee-tee-tee is made to an approaching group member. It would appear that such highly modulated sounds reflect a nonhostile mood and function in greeting and location. Slow whinnies can grade to long calls, which may be employed in distance communication of location and facilitate subgroup encounters in the dense forest (Figure 21).

The twitter, trill, squeaks, and chitter involve varying degrees of withdrawal or anxiety. They are associated with the approach of a dominant, loss of physical support, separation from a partner, withdrawal of a familiar attendant, and, in the

highest form, may accompany an ambivalent threat display. Glottal tension produces high frequencies, but little rhythmic modulation as in the preceding class of sounds. At low intensity, the slow whinny series ties the two moods. During extreme fright a noisy scream can be produced.

Low frequency, loud, unmodulated sounds appear to be involved in an aggressive, approach-prone mood. Ook-ook is a low intensity ritualized signal, which is rhythmic and tied to play fighting but, through intergrades, growls or roars agonistic in character can be produced.

Barks form a graded series, which appear to be

TABLE 14.—Some common syllabic transitions*

Call types	I	II	IIIa	IIIb	IIIc	IV	V	VIa	VIb	VIc	VIId	VII	VIII	XII
I	88	—	—	—	—	—	—	—	—	—	—	—	—	—
II	—	31	—	—	—	—	—	—	—	—	—	—	—	—
IIIa	—	—	36	—	2	1	6	2	—	—	—	—	1	—
IIIb	—	—	—	2	—	—	—	—	—	—	—	—	—	—
IIIc	—	—	21	—	30	—	—	—	—	2	—	—	—	—
IV	—	—	2	—	—	42	—	—	—	—	—	—	—	—
V	—	—	3	—	—	—	5	—	—	1	—	—	—	—
VIa	—	—	—	—	—	—	—	31	7	—	—	—	—	—
VIb	—	3	—	—	—	—	—	—	22	—	—	—	—	—
VIc	—	—	1	—	2	—	—	—	—	18	—	—	—	—
VIId	—	5	—	—	—	—	—	—	—	—	78	—	—	—
VII	—	—	—	—	—	—	—	—	—	—	—	3	—	—
VIII	—	—	1	—	—	—	—	—	—	—	—	16	42	—
XII	—	—	—	—	—	—	—	—	—	—	—	—	—	**

* Roman numerals refer to call numbers as used in Table 10; sample is drawn from tabulated summaries in Appendix I.

** Defining interval too long to be described as sequential.

related to the growl series, but may be a highly ritualized call form indicative of extreme ambivalence coupled with moderately high arousal. Barks can rarely grade to roars or screams.

The long calls and intermediate long calls are motivationally puzzling. They may represent high intensity variants within one of the previously defined moods. For example, the ascending ee-awk or grunt-trill may be motivationally related to the trill series. The loud long calls, however, may be phylogenetically derived from roars or slow guttural whinnies (vibrato form and clear form, respectively), but presently they are ritualized and seem to have taken on a distance communication function that could help unite subgroups and repel neighboring troops (see "Comparisons," p. 62).

The 10 calls as defined on pages 38–42 ("Contexts") are arranged in Figure 22 to portray mood similarities, transitionals, and excitation changes. The conceptual scheme parallels that developed for caviomorph rodents (Eisenberg, 1974), marsupials (Eisenberg, Collins, and Wemmer, 1975), and insectivores (Gould, 1971).

The existence of syllabic transforms is readily evident from an inspection of the sonographs in Figures 15, 17, and 21. The slow guttural whinny can serve as preface notes and be converted by lengthening and maintaining the frequency constant into a long call. The ak-ak variant during play can be converted to a growl by decreasing the interval separating the syllables. Growls can convert to loud roars by increasing amplitude and

prolonging the duration of each individual utterance. Slow chirping whinnies can convert to the true whinny by fusion of the syllables to form a continual utterance. These syllabic transformations, which do not include drastic changes in the form of the syllable, would appear to indicate excitation extremes within the same mood.

On the other hand, call forms consisting of several syllable types may in fact reflect alternations in mood. There is no reason to assume that an animal's prevailing mood is subject to no shift at all. It is a truism to say that, given the utterance of a certain syllable type, there is a high probability that the same syllable will follow it. Table 14 illustrates that syllable type IIIa is most often followed by itself, as is the case with syllable type IIIc and syllable type V. On the other hand, IIIa can convert to syllable form IIIc or even to V through fusion. Syllable type VIII, through fusion, can convert to syllable type VII. Syllable type VIId can convert to II. These do not involve a necessary alternation in basic mood.

Alternation, Insertion, and Ambivalence

We have now come to the problem of considering an actual shift in mood during the course of a session of intense expression. The simplest case may be taken from the following example: A group of *Ateles geoffroyi* is barking at an *Eira*. The barking response of three of the members of *Ateles* causes a fourth to approach the tree in which the

action is taking place. As the fourth animal approaches, one of the barking animals looks up, sights it, and immediately gives a tee-tee-tee call, only to return to barking. This is clearly a case of mood shift (insertion) and a return to a previous motivational state.

A second example might be taken from the *Ateles fusciceps* interaction between the adult male and the juvenile male in the summer of 1972. Many of their interactions took on a play-like quality, which made it difficult to ascribe a specific mood to the participants. For example, the young male may show extreme avoidance behavior toward the adult, uttering trill-awks and trills to chitters. The adult male would approach and look away, would approach and extend his hand. The young male would eventually allow himself to be touched and embraced, and the adult male would utter slow guttural whinnies (sobs). Whereupon the adult male would move rapidly away from the juvenile male, trilling, giving extended trills, ascending in tone, whereupon the young male would begin to follow him. This type of mood alternation has a play-like quality in that the adult male would begin to exhibit mock "anxiety" behavior toward the juvenile, apparently reinforcing the juvenile to take upon the role of a pursuer.

Perhaps the best examples of mood shift and ambivalence during interaction come from my own experience in handling the adult male *Ateles fusciceps*. I could induce him to grapple with me through the bars of his cage by shaking my head laterally and uttering soft ook-ook sounds. He would extend a hand and attempt to grasp mine, whereupon we would begin a grappling bout. Nevertheless, he would often alternate between two tendencies. If I stared directly at him, he might open his mouth exposing all of his teeth, squeak, and try to withdraw his hand. At other times, if I pretended to be weak and allowed him to draw my arm into the cage, he might change from the ook-ook to rapid ak-ak and growl and actually slap at my hand. Clearly I was participating with him in a shift from anxiety on the one hand to agonistic behavior on the other. In fact, I could modulate the situation by controlling my own tendencies to look directly at him while exerting great pressure on his arm or look away and exhibit weakness in my grip. The same sorts of interaction could be seen time and again at a

lower intensity level during the "mock fighting" or grappling session between the adult male and juvenile male or the juvenile male and subadult females. These three examples suffice to clarify the reality of alternation in mood, insertion of an expressive form within the context of a prevalent mood, and out-and-out ambivalence resulting from a conflicting set of motivational tendencies. The reality of such mood-shifts greatly complicates the interpretation of the function of various expressive movements and ultimately an understanding of prevailing mood and the form of expression associated with it must rely upon the actual responses of the receiver within the social context to clarify the function of the expression system for the social context in question.

FUNCTION AND INFLUENCES ON THE RECEIVER

It should be obvious from the preceding section that auditory signals can impart considerable information to a presumptive receiver. Roars reinforced with a rush promote withdrawal. Trills by a juvenile stimulate approach and embrace by a dominant. Whinnies during a rain storm promote clumping; barks stimulate mobbing; ook-ook plus a head-shake facilitate grappling (Table 15).

It should also be evident that most close contact vocalizations involve facial expressions, gestures, touching, and odors. Obviously a functional analysis of vocalizations requires that the entire "gestalt" for the receiver be taken into consideration. Table 16 attempts to integrate the sound form with other signals and specify the functional aspects.

STRUCTURE AND FUNCTIONS OF CALLS

The classical work of Richard Andrew (1963) demonstrates the possibility of describing the origins of signal systems in higher mammals, such as primates, from a consideration of sound production in morphologically conservative species, such as tree shrews, lorisooids, and lemurs. The key contribution in Andrew's papers concerns the recognition of a graded series of signal types accompanying mood change or alternation of mood in a sender. Further, Andrew links a graded series of sound types to rather simple stimulus input changes, which induce the motivational shift in

TABLE 15.—Overt responses to vocalizations*

Call type	Actions by receiver							Vocalizations by receiver			
	Move away	Change position	Approach and join	Assume	Look at	Turn to and "assist"	Head- shake	Tee-tee	Whinny	Ook-ook	Eee-awk
				attentive posture							
<i>Ateles geoffroyi</i> (field)											
Tee-tee	-	-	5	-	1	-	-	3	2	-	-
Whinny	-	-	2	-	-	-	-	-	4	-	-
Ook-ook	-	-	-	-	-	-	3	-	-	4	-
Low squeak	-	-	-	1	2	2	-	-	-	-	-
Growl	3	-	-	-	-	-	-	-	-	-	-
Caw (ooo ah-ah) ...	-	-	3	-	-	-	-	-	-	-	-
<i>Ateles fusciceps</i> (captive)											
Tee-tee	-	-	-	-	-	-	-	3	-	-	-
Whinny	-	-	-	-	-	-	-	-	2	-	-
Ook-ook	-	-	-	1	1	-	2	-	-	4	-
Low squeak (mother)	-	-	-	-	1	-	-	-	-	-	-
Squeak or screech (infant)	-	-	-	-	-	3	-	-	-	-	-
Twitter	-	1	-	-	-	-	-	-	-	-	-
Chitter	1	-	-	-	-	-	-	-	-	-	-
Growl	2	-	-	-	-	-	-	-	-	-	-
Ascending trill (juvenile)	-	-	-	-	1	5	-	-	-	-	-
Long call	-	-	1	-	-	-	-	-	2	-	1

* Low numbers result because only responses which were clearly subsequent to a vocalization without accompanying movements are included; ambiguous cases are not enumerated. All notes used and only frequencies tabulated; data in Table 13 not included.

the presumptive sender. The simplest stimulus input is the "stimulus contrast situation," where, regardless of the many qualitative aspects that might be considered in the stimulus source, attention of the investigator is focused on the shift in the intensity of the stimulus input, which can be reflected in the shift of intensity of mood in the animal by a corresponding shift in the intensity of signal output. Andrew goes beyond a simple motivational classification. He departs from the classical approach where animal behavior patterns are related to three fundamental moods: sexual, aggressive, and fearful. In attempting to describe the origin of signal systems in mammals, Andrew (1964) expands the motivational analysis to cover a wide range of categories including contact-seeking, greeting, avoidance, appeasement, feeding. (For a reevaluation of this earlier theoretical position, see Andrew, in Hinde, 1972:179-204). To my way of thinking the impact of Andrew's

papers includes two fundamental postulates: (1) Primate vocalizations have resulted from natural selection to promote effective indicators of mood shift or changes in arousal within a mood, and (2) the diversity of syllable types has resulted from selection on a finite number of basic syllable forms.

An underlying similarity in the structure of sound types produced by neotropical primates has been pointed out by Moynihan (1967). It would appear that the repertoires of different primate species can be expanded or contracted within any given functional or motivational class of syllables. The vocal repertoires of the woolly monkey, howler monkey, and spider monkey are closely compared on page 63 (see also Appendix IV). However, for this section we must only recognize that it is possible to arrange the vocalizations of several species of neotropical primates within the same classification scheme that I have developed for the spider monkey.

TABLE 16.—Some calls and associated movements for *Ateles*

Call type	Frequently associated expression	Head position or movements	Other signal elements	Function
Long call (harsh) ..	Various, open mouth with little tooth exposure	No special head movement; tendency to locomote	Sounds of shrubbery or branch movements	Position indicator and identifier; mood is confident to assertive
Long call (clear)	No tooth exposure; open mouth	Little locomotor movements	No special movements	Position indicator and potential identifier may promote assembly
Bark	Little or no tooth exposure; mouth open	No special movements, or head position	May involve branch-shaking and/or jumps	Position indicator, promotes assembly; can serve as a warning signal
Chitter	May be extensive tooth exposure by lip retraction; mouth often partially open	No special head position	May involve branch-shaking and/or leaps	Not specifically a position indicator; focuses attention of potential receiver on disturbances in the environment; can serve as a warning to conspecifics
Tee-tee	Mouth may be closed	Head often lifted vertically	No special movements unless signaler is preparing to depart	Position indicator; nonhostile greeting
Whinny	Mouth may be closed	Head often lifted vertically	No special movements unless signaler is preparing to depart	Position indicator; nonhostile greeting; accompanies feeding, may serve to indicate availability of food
Ook-ook-ak-ak	Mouth may be open with pursed lips; no tooth exposure or may show pronounced lip retraction	Head is often shaken horizontally	Accompanies grappling or mock fighting	Indicator of arousal level; may function as an invitation to play
Guttural whinny ... or sobs	Lips may be pursed	Head is lifted vertically	Often accompanies slow approach to receiver	Signifies nonhostile approach, may accompany an embrace
Growl	Mouth may be open; lip retraction may not be pronounced; direct stare is noticeable	Gaze is fixated	No special signal elements, but sender is often approaching	Signal indicates a hostile approach

If we turn to the woolly monkey, *Lagothrix*, as described by Williams (1968), then in a contextual sense and in a morphological sense, the "eeolk" series of *Lagothrix* is directly comparable to the whinny series of *Ateles*. Tuff-tuff, oo, and hu-hu are comparable to the ook-ook, ak-ak growl series. Nyonk, argh, yook-yook are comparable to the *Ateles* bark series. Squeaks and screams are comparable to the twitter, chitter, scream series of *Ateles*.

A small species, such as *Saimiri sciureus*, has a rapid temporal patterning in the delivery of its syllables. In addition, the pitch of most syllables is higher than that shown by *Ateles* or *Lagothrix*. Yet if we slow the vocalization down by half speed during playback on a tape recorder, many calls sound very much like the calls of *Ateles*. With

this compensation in mind, then in the Winter, Ploog, and Latta (1966) classification for *Saimiri*, the peep, twitter, trill, and chirp are comparable to the *Ateles* whinny series; the play peep, err-arr, are comparable to the ook-ook, ak-ak series; the yap series is functionally equivalent to the bark. Cackle, arr, and kecker are comparable to the growl-roar series of *Ateles*.

The comparison of *Ateles*, *Saimiri*, and *Lagothrix* suggests that similar physiological mechanisms underlie the expression of these calls and that the calls reflect a common evolutionary history, but the form of a call not only reflects its evolutionary history, but also the selective influences that have shaped the call in the species micro-environment. Marler (1957) has pointed out that the warning cries of many Passeriform birds have a

remarkable structural similarity. Without attempting to investigate the question of similarity in structure as a function of relatedness or homology, Marler approaches the structure of sounds from a functional standpoint. Obviously the warning cries of Passeriform birds are functional analogs, indeed the sound form allows an individual to give a warning cry to conspecifics, but minimizes its vulnerability to predation since the sound can be localized only with great difficulty. Similarly, sounds that are repetitive, low frequency pulses having a clear onset and ending permit a maximum possibility for localization on the part of a receiver; such sounds are employed in mobbing vocalizations by birds. By a similar application of logic, one can also conclude that barks and short grunts may be used to indicate the position of a sender and thus, in mobbing responses in primates, the bark is a functional analog across species (Marler, 1973).

Morton (1970) presents some evidence from the analysis of bird song suggesting that the environment in which the vocalization is produced and the function for which it is intended put constraints on the form of vocalization which the animal may exhibit. Following on early suggestions

by Moynihan (1964:51-52), Morton points out that the transmission of sound differs significantly when forest conditions are compared with those of the savanna. Obviously within the physical limitations of the animal, the lower the frequency sound produced in the forest the better its propagation will be, since the foliage and trunks act as absorbers of high frequency sound energy. Morton's research suggests that birds which call in the lower parts of the forest call with a narrow range of frequencies with an average of 2.2 Khz. This can be contrasted with grassland singing birds, which sing with an average frequency of 4.5 Khz and a much wider frequency range. It would seem, then, that loud, long calls of primates in the forest, which function to either communicate with conspecifics over a great distance to promote contact or are used to repel close approach by neighboring troops, tend to emphasize lower frequencies. In the case of the loud, long calls of *Ateles*, the frequencies emphasized conform to the model proposed by Morton. Further consideration of these factors are taken up on pp. 62-64 ("Comparisons").

Ontogeny of Behavior in Spider Monkeys

Since 1966, four (1 male and 3 females) *A. fusciceps* infants were hand-reared. Three of these specimens were studied in some detail with special attention given to growth and motor development. Of these, two (one male and one female) were selected for special recording of vocalizations at selected intervals during their maturation. Details concerning hand rearing are included in Appendix II. Of the four specimens hand-raised, one was removed from the mother after an interval of less than 8 hours, two specimens were removed at intervals less than 48 hours following birth, while the fourth animal was removed after some 7 days

with the mother. Two subjects were raised alone and the other two raised together.

During hand-rearing the young animals were unable to hear or see adult animals. They were not deprived of sensory input, however, and interacted with the individuals rearing them. Thus, any inferences concerning the development of vocalizations and expressive movements do not refer to animals in any way deprived of sensory input; however, we feel that three of the individuals studied certainly had a minimal exposure to the vocalizations of adults and the associated expressive movements. It seems reasonable to assume that

TABLE 17.—Ages when removed from mother

Subject*	Date born	Date removed	Age at removal
1 ♀	26 Apr 1966	28 Apr 1966	<48 hours
2 ♂	6 Aug 1966	8 Aug 1966	<48 hours
3 ♀	25 Nov 1969	25 Nov 1969	8 hours
4 ♀	25 Feb 1973	13 Mar 1973	16 days

* Animals 1 and 2 raised together from 8 August 1966; Animals 3 and 4 raised alone.

imitative learning is ruled out as a possible source of information to these hand-reared individuals. Table 17 summarizes the foregoing information.

As a control, the maturation of behavior was studied by observing two (one male and one female) young who were mother-raised in the captive group. These data, where appropriate, will be compared with observations on hand-reared animals. In addition, data obtained from observing mother-reared young of *Ateles geoffroyi* on Barro Colorado Island will be introduced.

Condition at Birth and during First Weeks of Life

At birth, the young of *A. fusciceps* weigh slightly less than 500 grams, incisors are present and the first premolars in both the upper and lower jaw are visible through the gums. The grasping reflex is well developed and the tail shows some prehensile ability. The face and ears are pink and this flesh coloring is retained until over 14 months of age. The face gradually becomes pigmented, but the skin around the eyes can still be pink at 19 months of age. They are covered with black hair, especially prominent on the dorsum. The ventrum is only sparsely haired. The ventrum of the torso shows pink skin with little evidence of pigment as does the underside of the tail. The mid-dorsum of the back likewise shows little pigment in the skin, however, the lateral aspects of the dorsum, as well as the dorsal parts of the hind and fore limbs, are pigmented with black. The dorsum of the tail is sparsely haired and the skin is visible. The clitoris in the infant female may be 40 mm in length. The testes are undescended in the young male. The neonate can produce soft cluck-like chuckles when lightly tickled and a loud squawk in response to sudden stimulus contrast.

At two weeks of age, the young animal will try to avoid noxious stimuli by turning its head away. It will push objects away from its vicinity using its hand; its tail will readily support its entire weight. Vocalizations include a well-defined chuckle, cluck-awk, and squawk. The chuckle seems to be produced when the animal is attempting to obtain something (e.g., food) that is being withheld from it. The squawk vocalization is produced when the

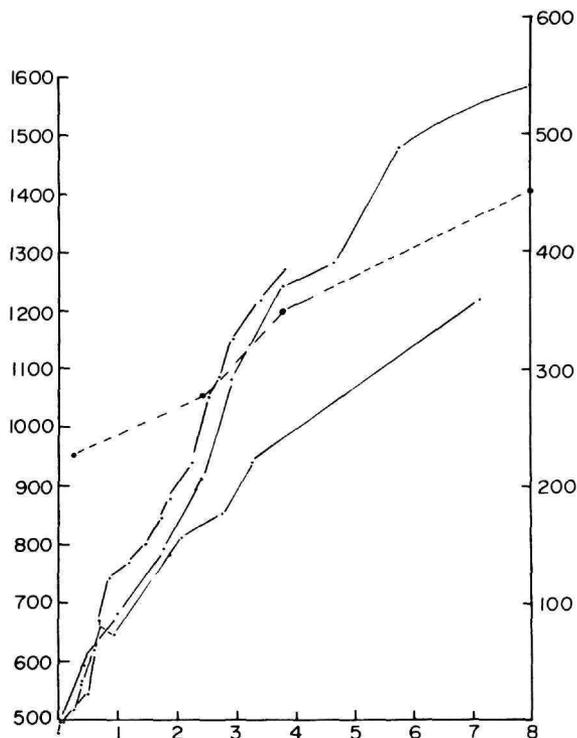


FIGURE 23.—Growth of infant *Ateles fusciceps* during the first eight months of life. (Ordinate, left, weight in grams, solid line; ordinate, right, tail length in millimeters, dashed line; lower growth curve represents growth of *A. paniscus* as reported by Gensch, 1965.)

TABLE 18.—Physical data of infant *Ateles fusciceps*

Subject	Sex	Age* (day)	<i>i</i> ₁ <i>i</i> ₂	<i>Pm</i> ₁	Arm span (mm)	Tail (mm)	Skull diameter (mm)	Torso (mm)	Weight (gm)
1	♂	18	erupted	subcutaneous	369	258	220	150	720
2	♀	17	erupted	subcutaneous	481	245	190	160	534**

* When first measured.

** Dehydrated.

Note: Clitoris may be 40 mm at birth.

i = incisor; *Pm* = premolar.

animal is disturbed or when it is removed from the handler. The premolars have still not emerged from the gums.

In mother-reared animals, the young at this age clings almost exclusively to the mother's ventrum. The mother will support the infant with one hand while climbing, although the infant is able to cling to the mother without any support. Measurements of young between 2 and 3 weeks of age are presented in Table 18, and a growth curve during the first 8 months of development is presented in Figure 23.

Between 8 and 9 weeks of age, the animals will begin to show a chin-up with pursed lips toward the handler. The whinny vocalization (or precursor of the whinny) is uttered at this time. Interest in the environment around the infant increases. It begins to pick up objects and sniff them. At roughly 10 weeks of age, the animals can hang independently by their tails while manipulating objects and they begin to show increasing self care; scratching with the hindleg begins to be demonstrated at 9 weeks of age. At 3 months of age, the animals are hanging by their tails, playing with one another, demonstrating the head-shake to one another, and the vocal repertoire has expanded greatly. High-pitched trills may be given during thwarting situations.

The common vocal repertoire developed at 3 months of age and accompanying expressive movements may be summarized as follows: When held by an attendant and tickled or stroked, the animal may emit short grunts or brief grunts in a series (chuckles) with the lips either tightly closed or slightly open (see Figure 24). If the animal is handed to an unfamiliar person or approached by a stranger, it may show a slightly open mouth and emit a squawk or a high-pitched chirp, which grades to a squeak. These vocalizations may be repetitive. If the young animal has something forcibly removed from it, such as food or a blanket, then with an open mouth it may give a loud ee aw, which shows a slight shift in pitch, and we believe this to be a precursor to the chitter in the adult. Continued deprivation of a desired object can lead to a shriek or a series of grunts which fuse to rise to a shrieking cry (Figure 25).

During the fourth and fifth months, interactive play increases. A rhythmic grunting or precursor of the adult ook-ook with head-shakes may be demonstrated. In mother-reared animals, the youngster now may move several feet away from the mother, climbing alone. There is an increased tendency to climb on the mother's back. Most of the adult vocalizations can be recognized at 5 to 7 months of age.

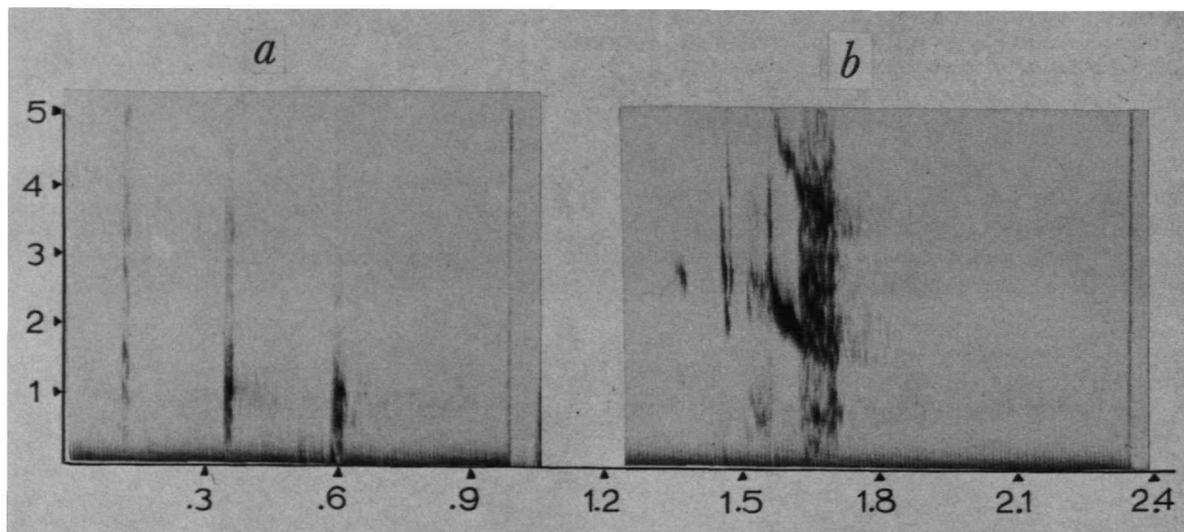


FIGURE 24.—Some infant calls for *Ateles fusciceps*: a, chuckle series or ook-ook precursor, 14 days of age; b, ee ah call, 14 days of age. (Ordinate in Khz, abscissa in seconds.)

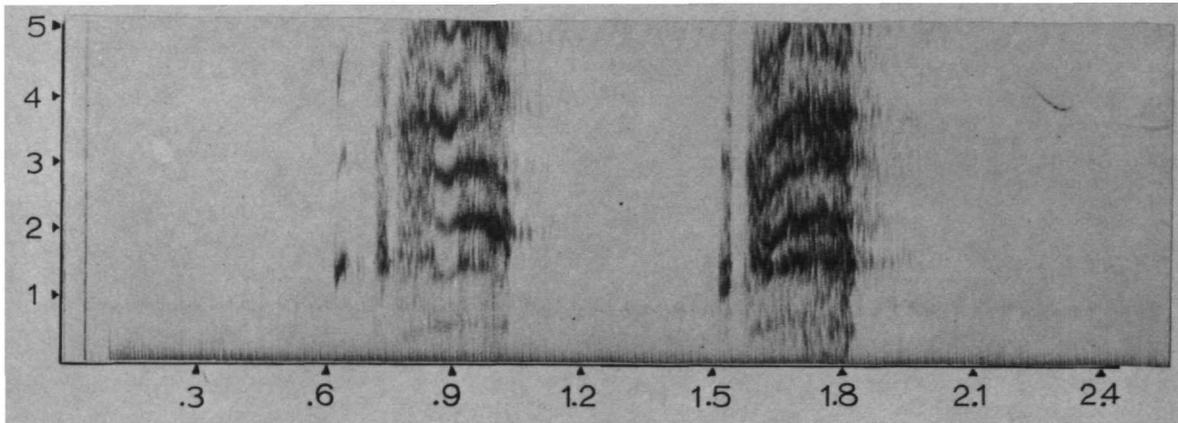


FIGURE 25.—Some ee-aw variants (squawks) by infant *Ateles fusciceps*. (Ordinate in Khz, abscissa in seconds.)

Later Stages of Development

Figure 26 indicates a growth curve for *Ateles fusciceps*. This is based on the growth of two females through the seventh year of age and one male up to 4½ years of age. As can be seen the growth of males and females remain quite similar until 3½ years of age, when the male shows an increased rate of growth relative to the female. *Ateles fusciceps* is a dimorphic species, the male averaging 1½ kg greater in weight than the female and being somewhat longer. Head and body measurements of one male exceeded the largest adult

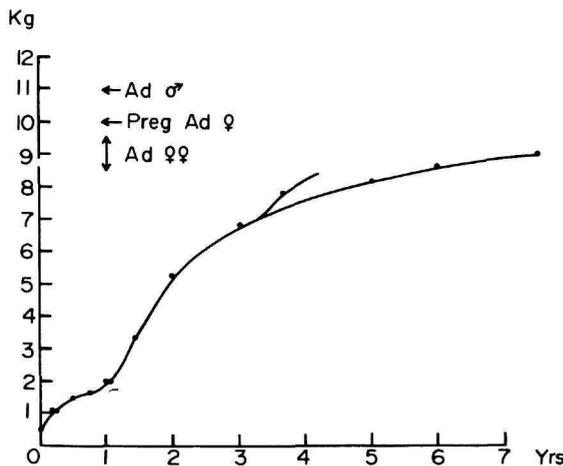


FIGURE 26.—Growth records over a seven year period for one male and two female *Ateles fusciceps*.

female by 40 mm (Kellogg and Goldman, 1944).

Ateles fusciceps development may be broken down into the following age classes: Infant-1, 1 to 4 months of age. Almost all nutrition derived from the mother, tendency to hang to the mother's ventrum, little tendency to leave mother or break contact.

Infant-2, approximately 5 to 12 months of age. At the end of this period, the youngster weighs approximately 2 kg. During this time interactive play with like-aged animals and increasing inde-

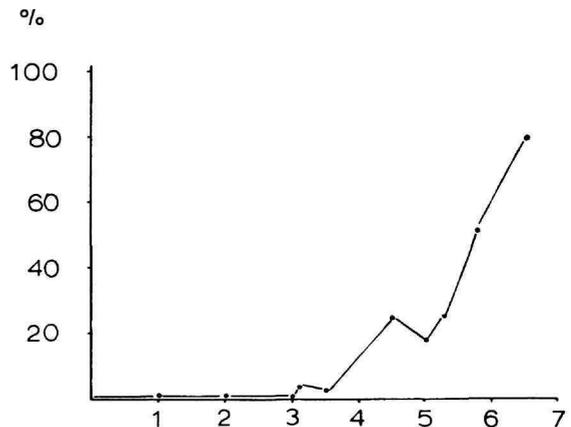


FIGURE 27.—Changing amount of time the infant *Ateles fusciceps* spends clinging to the mother. Data averaged only for daylight hours; infants and juveniles sleep with the mother until over one year of age. (Ordinate is percent of time infant is off the mother—infant is almost always near the mother; abscissa is age in months.)



FIGURE 28.—The mother-infant unit in *Ateles geoffroyi*. (Photo by C. M. Hladik.)

pendent movement from the mother manifest themselves. Most of the expressive movements and vocalizations are employed at this time in social interactions. Youngster still returns to female for nursing, tends to ride on the back of the female (see Figures 27, 28).

Juvenile-1, 12 to 24 months of age. Growth is

very rapid and the young animal may reach one-half of the adult weight. It is much more independent in its movements from the female. During this period weaning takes place, perhaps as early as 14 months, but intermittent suckling may continue until 18 months of age. Youngster tends to sleep with the mother.

Juvenile-2, approximately 24 to 36 months of age. Growth begins to slow down. Females and males still growing at approximately the same rate. At the end of the 3-year period, the animal may be three-fourths the weight of the adult. Behavioral differences between males and females are evident during this life phase. Males begin to show increasing affiliation with the adult male and other subadult males. The young male may participate in "male activities." It will join the adult male in his movements and may participate in the long calls. Females, on the other hand, within the Juvenile-2 age class remain bound into the core mother group, although they may tend to move independently.

Subadult female, 3 to 4 years of age. Females still show some juvenile characteristics including participation in grappling bouts with each other and with males. First estrous cycles may perhaps be shown at the middle of this phase. Earliest conception in captivity by *A. fusciceps* was at 4½ years of age.

Subadult male, 4 to 5 years of age. Males begin to show an increased rate of growth relative to females. Earliest age of successful insemination for a subadult male was at 4 years, 9 months. The subadult male is as large as an adult female at the end of the fifth year, and may be almost indistinguishable from the adult male, but apparently continues to grow well into the fifth year of age.

Although I do not have a growth curve for *A. geoffroyi panamensis* on Barro Colorado Island, its chronology of development is very similar to that for *Ateles fusciceps* and the major difference concerns the condition of the young at birth. Young *A. geoffroyi* are born entirely black and the reddish pattern on the dorsum does not begin to manifest itself until about 5 months of age. This feature then defines a transition to the Infant-2 class. Infant-2 animals from about 6 to 12 months of age show the adult color pattern. The young now ride on the back of the mother and only go to her venter to nurse. At approximately 12 months of age, the youngster may move as much as 17 meters away from the mother. Youngsters from 6 to 12 months of age show a great deal of interactive play with one another and feeding on solids increases.

During the Juvenile-1 age class, young males are singled out for special attention on the part of

subadult and adult males; thus, the transition to Juvenile-2 is facilitated by the increasing attention on the part of males toward juvenile males.

Subadult females, from about 3 to 4½ years of age, still show some juvenile behaviors; they grapple and their first estrous cycles may be shown at the end of this phase. Females of *A. geoffroyi* appear to conceive in Panama at about 4 to 4½ years of age. An adult female generally has her first infant during the early part of her fifth year.

Subadult *A. geoffroyi* males are almost fully grown at 5 years of age. At this time they show participation in all the male activities; they are part of a male subgroup. They may subtly challenge the Alpha male for a dominance position and may be increasingly involved in dominance contests with some of the subadult or adult females. The adult male at 5 years of age generally exhibits features of male behavior including initiation of long call choruses and some leadership role with respect to extended group movements. At this age, he may display frequently, including chest rubbing. The secretory activity of the pectoral glands is markedly increased during the last year and a half. Although capable of fertilizing females, he may not be sociologically dominant unless he achieves ascendancy over the current male leader.

Development of Expressive Movements and Vocalizations

Expressive movements, such as chin-up, pursed lips, relaxed open mouth, open mouth with tooth exposure, and retracted mouth corners, all appear to develop without imitative practice and to be displayed in appropriate contexts. Although the vocalizations of infants and juveniles differ from those of adults with respect to intensity and distribution of frequencies, they show great similarities in their morphology. In their temporal patterning, the sounds suggest homologs with adult calls. Such vocalizations appear to develop without imitative practice, and once again be displayed in appropriate contexts.

Vocalizations for infants, between 5 and 6 months of age, show the following relationships to the vocalizations of adults: (1) Series of repetitive grunts with varying emphasis on frequencies that are basically derived from a click form are homologous with adult ook-ook and specific to a

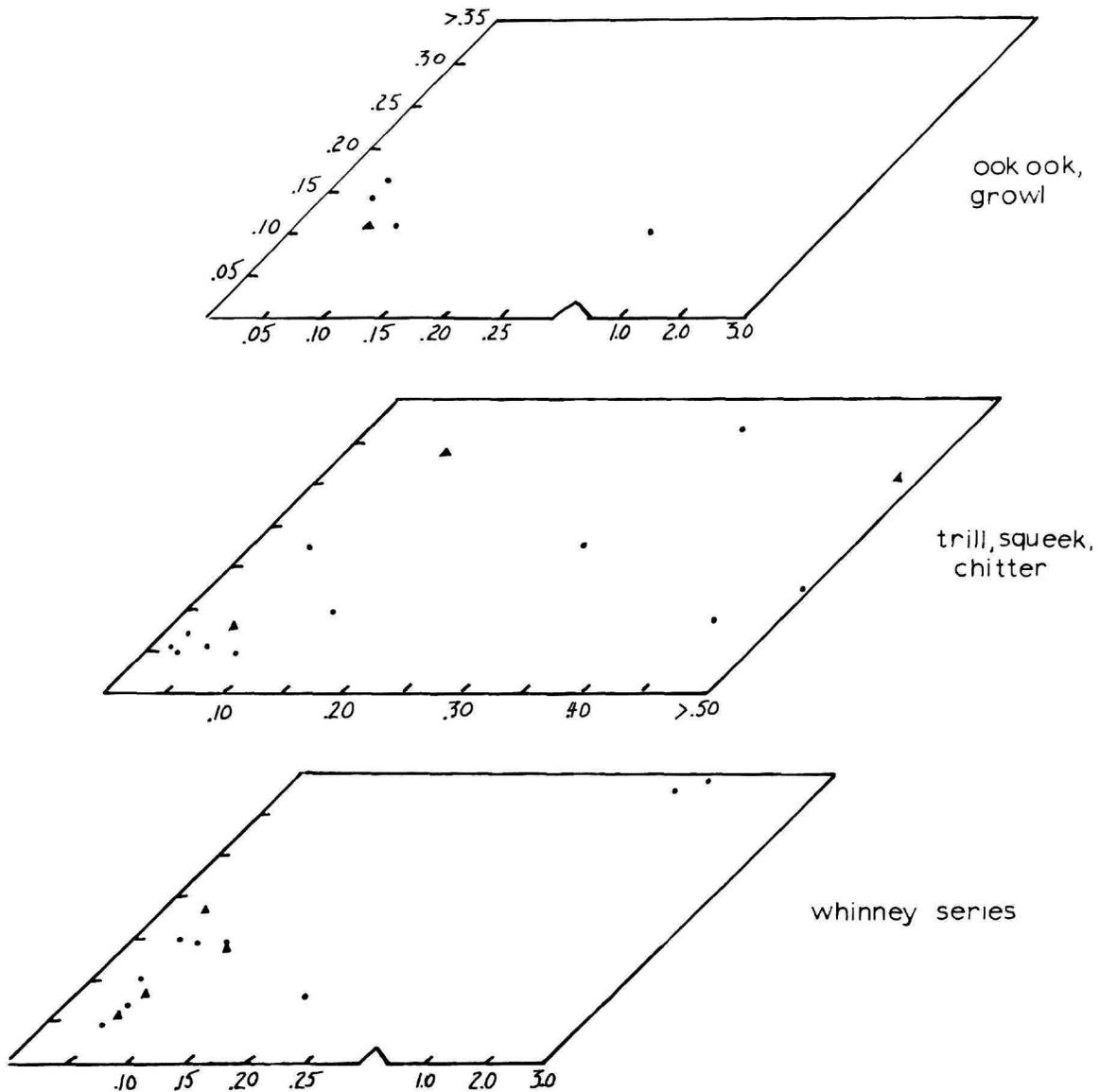


FIGURE 29.—Temporal patterning of young *Ateles* vocalizations. Three vocalization forms are portrayed for isolate reared *Ateles* at 8–11 months of age. The values for the young animals are contrasted with a sample from group-raised adults and juveniles.

▲ isolate-raised ● group-raised

grappling context. (2) Chirp-like calls composed of different syllable types may be a sliding chirp or a whistle, but invariably they are given as a series and in situations where the animal is insecure and is perhaps seeking contact; they are

related to twitter-trill series of adults. (3) Squawk, with two variants, is a high pitched or low pitched call, noisy and loud, sounding like an aak or awk, given in frustrating situations. It may be higher pitched when the animal is somewhat frightened

and thwarted. The syllables are similar to those produced by adults when emitting the intermediate length calls. (4) Separation call of young, eee-awk, which is produced when seeking contact after forcible separation from partner or handler. It is an ascending long loud call. Frequencies are concentrated around 1 KHz and it exceeds 0.5 seconds in duration. Perhaps it is related to ee-awk of the adult. (5) Chirrup call, repetitive; homologous to the whinny series of adults.

The calls of the young appear to differentiate out of fundamental elements demonstrated by the infants within their first 2 weeks of life. Frequency and amplitude modulation appear to develop without imitative practice. Homologous calls for isolation-reared infants and group-reared infants are compared in Appendix III with respect to various physical parameters. These infant and juvenile calls are then again compared with adult homologs in Figure 29. It would appear that with a minimum of environmental feed-back, young spider monkeys can develop a vocal repertoire similar to that of group-raised counterparts. Un-

fortunately, analyses of the long loud calls produced by adults have not been made on isolate-reared animals, since all hand-reared animals were eventually returned to mother-reared animals or to their original mother after 12 to 14 months of separation. It is entirely possible that some modulation and context specificity is learned from older adults, especially by young males when they participate in chorusing behavior with adult males (see "Contexts," p. 69).

Winter, et al., (1973) studied the development of vocalizations in *Saimiri* under conditions of extreme acoustic isolation including the deafening of one subject. The vocal repertoires of the experimental animals were virtually identical to the normal subjects. His evidence is supportive of our findings. Newman and Symes (1974) found that *Macaca mulatta* infants raised in acoustic isolation showed some structural modification in their clear calls, but most other calls appeared structurally normal. The conclusion then that many primate species develop species typical calls without imitative learning seems unavoidable.

Comparisons of Ceboid Communication Systems

Introduction

The Callithricidae and Cebidae comprise the two living families of neotropical primates which underwent an adaptive radiation in the neotropics in isolation from similar radiations of continental Old World primate stock giving rise to the families Cercopithecidae, Pongidae, and Hylobatidae. The existence of the Ceboidea allows for fruitful comparisons with their Old World counterparts in order to elucidate questions concerning convergent and parallel evolution. Andrew (1963, 1964) pioneered in the analysis of primate vocalizations and expressions. He proposed an evolutionary sequence for vocalizations and defined fundamental syllable types.

Moynihan (1967) and Oppenheimer (1975) have called attention to the fundamental unity of the New World primates with respect to certain communication mechanisms. In this section, I would like to expand on Moynihan's earlier ideas by comparing some displays and, in particular,

closely comparing vocalization forms. The author regrets that he was unable to include the excellent analysis of *Miopithecus* vocalization by J.-P. Gautier (1974) in this discussion. The publication arrived after submission of this study to the press.

In any comparison, the question of homology immediately arises. The determination of homologies has been given a rigorous theoretical treatment by Wickler (1961). The special difficulties encountered in establishing homologies among vocalizations of closely related species are reviewed for marsupials (Eisenberg, Collins, and Wemmer, 1975) and caviomorph rodents (Eisenberg, 1974). There are several examples of sound types produced by closely related forms which are nonhomologous. For example, click sounds produced by tooth-chattering may sound almost identical to clicks produced by short expirations. Yet clearly, because different physiological mechanisms underlie their production, these sounds must be considered nonhomologous, but, if functionally similar then they are *functional analogs* (Eisenberg, Collins,

and Wemmer, 1975). On the other hand, it is probably safe to assume that two sound forms are homologs when they are nearly identical structurally or, if they differ, intermediate forms can be found linking the two sounds. Overall pitch of the sound may not be an indicator of homology, but rather similarities in discrete syllable structure and temporal patterning may reflect homologous neuromuscular mechanisms employed in the production of the sound type. For this section, the question of behavioral homologs is of less interest than the description of functional analogs and, thus, the question of homology will not be stressed. Rather, we will discuss behavior patterns that seem to have identical functions, highlighting those behavior patterns that appear to be homologs.

In order to expand the discussion in this section, comparisons will be made relying heavily on previous studies. The display repertoires for *Callicebus*, *Aotus*, and *Saguinus oedipus geoffroyi* were described in the series of publications by Moynihan (1964, 1966, 1970). *Alouatta* has been described by Carpenter (1934) and Altmann (1959). *Cebus capucinus* was treated by Oppenheimer (1968) and *C. nigrivittatus* by Oppenheimer in 1974. *Saimiri sciureus* has been rigorously studied by Winter, Ploog, and Latta (1966), Winter (1972), Ploog, Hopf, and Winter (1967), and others (e.g., Rosenblum and Cooper, editors, 1968). Epple (1967, 1968, 1975) has summarized the displays of the Callithricidae. In the remainder of the discussion, I will draw upon the series of observations presented by the preceding authors and include previously unpublished data from observations on ceboids at the National Zoological Park. These data include observations on *Alouatta palliata*, *Lagothrix lagotricha*, and *Saguinus oedipus geoffroyi* (Muckenhirn, 1966, 1967). These first two species were studied intensively in captivity by Ms. L. McLanahan (see Appendix IV).

Nonauditory Signal Systems

POSTURES, EXPRESSIONS, AND MOVEMENTS

The arch back posture assumed in a quadrupedal stance has been carefully described for *Aotus trivirgatus* (Moynihan, 1964) and for *Cebuella pygmaea* (Christen, 1964). As Moynihan mentions, this posture is also shown in a similar form by

Callicebus torquatus and several of the marmoset species, including *Callithrix geoffroyi* (Muckenhirn, 1967, Moynihan, 1970). Moynihan (1967) also notes the occurrence of the quadrupedal arch posture in *Alouatta palliata*. Our observations at the National Zoological Park confirm the scheme as outlined by Moynihan. A modified form of the arch may be shown while the animals are bipedal. These arch postures are not shown in a ritualized form by either *Lagothrix* or *Ateles* (Appendix IV).

Tongue protrusion, during male-female interaction, is commonly displayed by *Saguinus*, *Callithrix*, *Leontopithecus*, *Aotus*, and *Alouatta*, but ritualized tongue protrusion is not demonstrable in *Lagothrix* and *Ateles*. *Lagothrix* has a unique expression during sexual behavior, which involves lip retraction, rapid jaw movements, and some tongue movements. This so-called lip smacking is reminiscent of a similar expression shown by the genus *Macaca* (Appendix IV).

Table 19 summarizes the foregoing, as well as aspects of display and movement patterns shown by the better studied species of ceboids. It is evident that *Alouatta* shares some aspects of display with *Aotus*, *Saguinus*, *Callicebus*, and *Callithrix*. *Lagothrix* and *Ateles*, on the other hand, appear to be somewhat distinct by the absence of tongue protrusion and the arch posture.

MARKING BEHAVIORS

Most of the ceboids possess specialized glands in association with the genitalia, as well as a chest gland. The morphology of the so-called sternal gland has been reviewed by Epple and Lorenz (1967). Although the movement patterns involved in scent deposition vary within the Ceboidea, the deposition of secretions from the chest gland on various objects in the environment is common to all members. *Ateles* and *Lagothrix* appear to have reduced gland fields in association with the genitalia and do not exhibit anogenital rubbing movements in as ritualized a fashion as those movements shown by *Aotus*, *Saguinus*, and *Callithrix* (Oppenheimer, 1975).

PENILE DISPLAYS

The penile display of *Saimiri sciureus* has been described by Ploog and MacLean (1963). Although

TABLE 19.—*Expressive movements or postures for the Ceboidea*

Species	Quad- rumped arch	Bipedal arch	Chin up & stare	Chest rub (object)	Chest rub (self)	Jaw move- ment & lip smack	Tongue protrusion
<i>Callithrix geoffroyi</i>	+	+	-	+	+	-	+
<i>Saguinus oedipus</i>	-	+	-	+	+	-	+
<i>Alouatta palliata</i>	+	+	+	+	+	-	+
<i>Lagothrix lagotricha</i>	m	-	+	+	+	+	-
<i>Ateles fusciceps</i>	m	-	+	+	+	-	-

m = modified and no longer comparable with other species; + = behavioral pattern demonstrated; - = behavioral pattern not noted.

no comparable ritualization has been described for other species of ceboids, certainly the presence of an erection excites great interest on the part of females and juveniles in *Ateles*. Although genital display in *Ateles* is not comparable in its degree of ritualization to that shown in *Saimiri*, the behavior is noteworthy (see "Genital Display," p. 14, for a more complete discussion).

GROOMING

Patterns of grooming, as we understand them for the Ceboidea, are summarized by Oppenheimer (1975). Compared with cercopithecoid primates, the proportion of allogrooming displayed by ceboids appears to be somewhat lower. Grooming in *Lagothrix* and *Ateles* appears to be strongly associated with estrus in the female and also in mother-infant dyads.

EMBRACING

Embracing as a mechanism of bond reinforcement is frequently shown in all the ceboids, but the degree of embracing and mutual sternal gland sniffing seems to reach a high frequency in *Lagothrix* and *Ateles*. Special vocalizations accompanying embracing, such as sobbing, or the slow whinny, are characteristic for *Lagothrix* and *Ateles*.

PATTERNS OF SEXUAL BEHAVIOR

Data concerning mating behavior in ceboid primates is sparse, but what data we have would indicate some interesting divergences. The temporal patterning of copulation has been only sporadically studied. Carpenter (1934, 1965) found

that the howler monkey, *Alouatta palliata*, is characterized by short copulations with continuous thrusting during intromission. A copulation bout averages some 22 seconds in duration. Similarly, the squirrel monkey, *Saimiri sciureus*, exhibits a series of mounts with intromission and thrusting. Multiple ejaculations can occur, and the duration of intromission is comparable to that of *Alouatta* (Clewe, 1969; Latta, Hopf, and Ploog, 1967). Copulation in *Saguinus oedipus* and *Leontopithecus rosalis* again appears to involve multiple mounts with intromission and a brief mount duration (Epple, 1975; Kleiman, pers. comm.). Mounting, intromission, and duration of copulation in *Lagothrix* involves postures similar to those of *Ateles*. The male hooks his hindlegs over the thighs of the female while she reclines forward or upright on a branch or bench. Intromission can exceed 4 minutes (Appendix IV). *Ateles* is characterized by a long intromission with thrusting, but no multiple intromissions. It is as if *Ateles* achieves the same amount of female stimulation by a single long intromission as is accomplished by the other species with a multiple intromission system. Details on the temporal patterning of copulation in *Ateles* have been published by Klein (1971) and Eisenberg (1973).

The peculiar copulation posture of *Ateles* and *Lagothrix* with the male sitting down may be an adaptation to prolonged intromissions in an arboreal situation. More conventional mounting with the female standing quadrupedally as in *Saguinus* or *Cebus* may be possible arboreally if the male's mount is brief. The long mount of *Ateles* and *Lagothrix* may in some manner correlate with an anatomical peculiarity of the Atelinae, namely the absence of an *os penis* (Hill, 1962: 163). In this respect the Atelinae resemble the

perissodactylans, which have no baculum and exhibit prolonged foreplay and mount durations when they are contrasted with the Artiodactyla.

Comparisons of Vocalizations

Although the smaller ceboid primates tend to have a great many high pitched vocalizations and, further, their rhythm of delivery often is somewhat faster than that of the larger ceboids, the overall temporal patterning appears to show remarkable similarities (Oppenheimer, 1975). This similarity can be enhanced by playing back tape recordings of the smaller species at one-half or one-fourth

the normal recording speed. It is as if the whole temporal patterning of *Saguinus* or *Saimiri* is from four to five times faster than the patterning shown by *Ateles*, *Alouatta*, and *Lagothrix*. This evidence is strongly indicative of underlying, homologous neuromuscular mechanisms. Table 20 compares those species of ceboid primates for which we have data with respect to the form of vocalizations occurring in selected functional contexts. As can be seen from an inspection of the table, play-fighting tends to be accompanied by rhythmic vocalizations exhibiting a blurred harmonic structure. Anti-predator calls leading to mobbing generally involve the production of rhythmic calls; the syl-

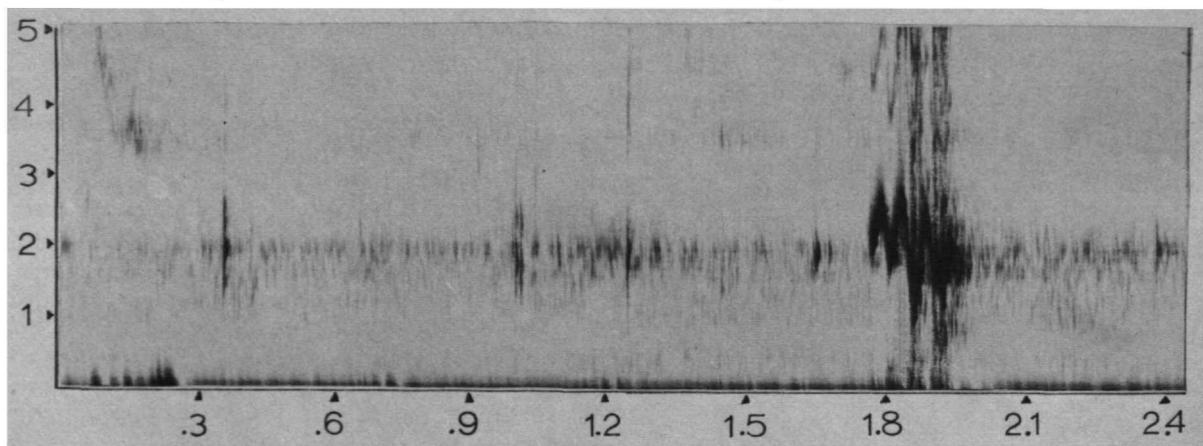


FIGURE 30.—Classic E-olk! call by *Lagothrix lagotricha*. Note modulation similar to tee-tee of *Ateles*. (Ordinate in KHz, abscissa in seconds.)

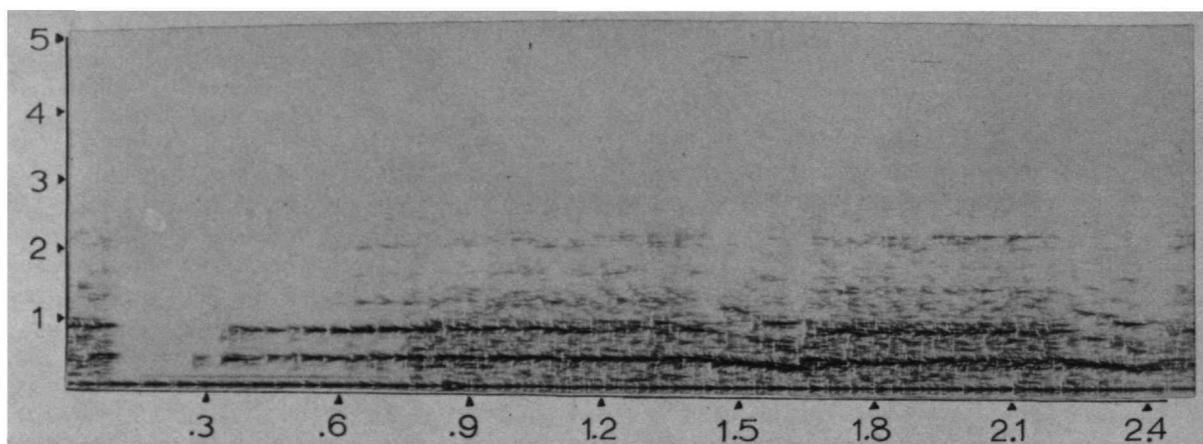


FIGURE 31.—Some vocalizations of *Alouatta palliata* (narrow band analysis). Undulating roar or long call by male *Alouatta palliata*. Fundamental energy is 0.4 KHz (apparent fundamental is background noise). Note the slight modulation at around 1.65 seconds. (Ordinate in KHz, abscissa in seconds.)

TABLE 20.—*Functional analogues for some cebid calls*

<i>Cebus capucinus</i>	<i>Ateles fusciceps</i>	<i>Lagothrix lagotricha</i>	<i>Alouatta palliata</i>	<i>Saimiri sciureus</i>	<i>Callicebus moloch</i>	<i>Saguinus Geoffroyi</i>
Oppenheimer 1968	Present study	Williams 1968 Present study	Carpenter 1934 Altmann 1959 Present study	Winter et al. 1966	Moynihan 1966	Muckenhiem 1967 Moynihan 1970
1. Guttural chatter	1. Ook-ook	1. Ooh-oooh	1. E uh-uh	1. Play peeps	1. -	1. -
2. Yip-moan	2. Tee-tee	2. Eeolk	2. ?	2. ?	2. ?	2. -
3. Cohesion call	3. Whinny	3. Eeoolk	3. ?	3. Twitter	3. ?	3. Single slide
3'. -	3'. Guttural whinny	3'. Sobs, puffing	3'. ?	4. Yapping	4. Chuck notes	4. Narrow range bursts
4. Gyrrah	4. Bark	4. Nyonkh-nyonkh	4. Bark	5. ?	5. ?	5. Mrou
5. ?	5. Ascending trill	5. Yoohk-yoohk	5. ?	6. Alarm squeak	6. ?	6. Strong chirp
6. Scream	6. Chitter	6. Scream (frust)	6. His-scream	7. Isolation squeaks	7. Various dawn calls	7. Long calls
7. Arrawk	7. Long call	7. Call cries	7. Roar	a. ?	a. Gobbling	a. Chorusing
	a. With coda- harsh	a. E eeoolk-awk	a. Roar A ₂	b. Isolation squeaks	b. ?	b. Long call
	b. Clear	b. E eeoolk	b. Roar A ₁	8. Peep-alarm squeak	8. Squeaks-trill-whistle	8. Trills-whines
8. Chirp-trill	8. Twitters and trills	8. Squeaks	8. Soft chirp-trill	9. Cackling	9. Low moan	9. Growl
9. -	9. Growl	9. Argck-argck	9. Growl			

? = homology of call uncertain; - = call form unreported.

lables are uttered in long sequences with a clear onset and termination of each individual syllable. These mobbing calls tend to be loud. Sounds produced in situations involving submission or slight withdrawal tend to be high pitched twitters. A graded series is shown under conditions of extreme fright; such sounds fuse to produce noisy screams with emphasis on higher frequencies. Feeding calls tend to be clear in their harmonic structure and show a great deal of frequency modulation (Figure 30). Agonistic sounds tend to be unharmonic and loud.

Long calls involved in contact over a great distance tend to be loud with long duration syllables; such calls involved in maintaining contact among troop members tend to be clearer in syllable structure. Those long calls involved in intertroop encounters and displays tend to show a more blurred harmonic structure (Figure 31).

Clearly some of these similarities may indicate homologous neuromuscular mechanisms in the production of the sound itself. However, it is important to point out that structural similarities in calls may equally well be the result of environmental pressures setting limits on variability in the call form whenever the specific function of the call necessitates clarity in transmission. The long loud calls of primates used to communicate location and identity over reasonable distances in the forest are a case in point (Oppenheimer, 1975). Propagation of sound in the forest is severely interfered with by the presence of trees, which serve as sound absorbers. A low frequency sound, all things being equal, has the best propagation over distance, but in the forest the physical structure of the forest itself may force primate species to a more restricted frequency band than would be the case in more open environments. Such an hypothesis was explored by Morton (1975) in an analysis of the calls of Panamanian passeriform birds. By comparing the frequencies employed in the songs of various bird species, Morton concluded that forest birds were under more environmental restriction in that they produced songs having a narrower range of frequency distribution than did their grassland and forest-edge counterparts.

Figure 32 portrays the frequencies emphasized in the syllables produced by seven primate species. The graph has been prepared in such a way that the size of the species is taken into consideration.

The question may well be raised, if a smaller primate species such as *Saguinus* might not be incapable of producing low frequency sounds. An inspection of the figure will indicate that *Saguinus geoffroyi* does in fact produce higher pitched sounds than does the larger *Ateles fusciceps*. Nevertheless, the range of frequencies emphasized is very broad for *Saguinus*; so it is evident that this species is quite capable of producing low frequency sounds. The correlation that emerges from an inspection of the graph is that the larger primate species have a more restricted range of sound production or, in general, tend to produce syllables that emphasize lower frequencies than do the smaller ceboid species. The long distance calls for all of the forest dwelling primate species, with the exception of *Saguinus* and *Cebuella*, appear to fall within the range of 0.4 to 1.5 KHz. *Lagothrix* is somewhat exceptional in that its complex long call repertoire tends to emphasize frequencies up to 2.5 KHz as well as at 1.5 (Appendix IV).

Although *Saguinus geoffroyi* shows the greatest range of frequencies emitted in its syllables, its long calls consistently show emphasis of energies at 3.5 KHz. In Morton's study of avian song, he found that forest-edge birds and grassland birds sang with average frequencies at 4 to 4.3 KHz. If *Saguinus geoffroyi* is a forest-edge or second growth adapted form, as suggested by Moynihan (1970:2-3), then perhaps its higher pitched, long calls show a relaxation of selective pressure when compared with mature forest dwellers, such as *Callicebus*, *Aotus*, *Cebus*, *Lagothrix*, *Ateles*, and *Alouatta*. On the other hand, the use of higher frequencies for long loud calls in *Saguinus* may be related to its small size, in that, it is more difficult to produce the requisite amplitude in a low frequency loud call. The series of long loud calls discussed here for the Cebidae may not reflect true homologs in all cases, but, if they do, they surely also reflect a similarity in environmental selection, producing call types having frequencies consistent with long distance communication.

In spite of the similarity in the frequencies utilized for long ranging calls, the temporal patterning of such calls renders them completely distinct and species specificity is retained by making use of such temporal parameters. *Callicebus* calls tend to resemble the gobbling of turkeys. The hooting call of *Aotus* is distinct from the ara call

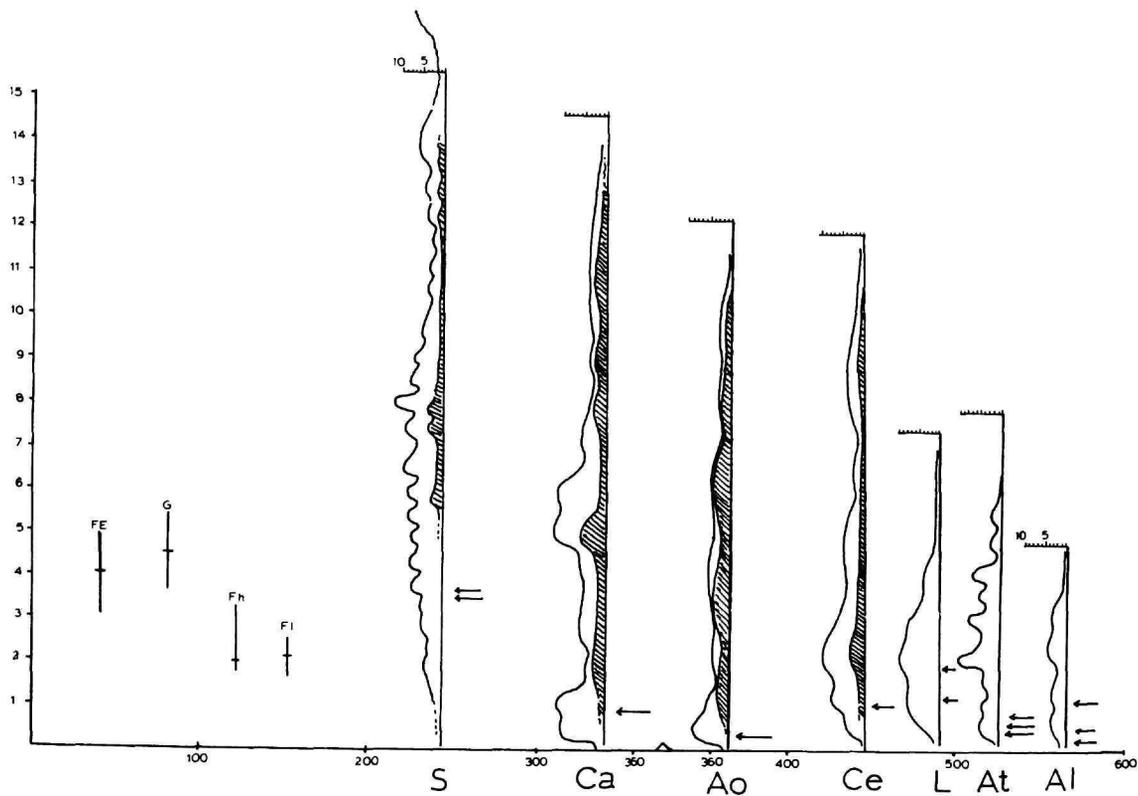


FIGURE 32.—Correlation of body size and frequencies employed in ceboid vocalizations (analyzed to 15 KHz only). (Shaded portion=infant and juvenile calls; ←=frequencies emphasized in long, loud calls; ordinate in KHz, abscissa in average mm of head-body length; small scale at the top of each species' axis=number of calls utilizing a given frequency; S=*Saguinus oedipus geoffroyi* (Muckenhirn, 1967; Moynihan, 1970), Ca=*Callicebus* (Moynihan, 1966), Ao=*Aotus* (Moynihan, 1964), Ce=*Cebus* (Oppenheimer, 1968), L=*Lagothrix* (see Appendix IV), At=*Ateles* (see Appendix I), Al=*Alouatta* (see Appendix IV); avian singing ranges (from Morton, 1970): Fe=forest edge, G=grassland, Fh=high in forest, Fl=low in forest.)

of *Cebus*. *Lagothrix* has an exceedingly complex long call employing a wide range of syllable types, but having a patterning similar to barking mixed with long syllables. *Ateles* employs long syllables

with terminals and *Alouatta* resembles *Ateles* in its temporal patterning, but the sound quality is entirely different and the amplitude is much greater in the howler monkey.

The Signal Systems and Social Structure of *Ateles*

Dimorphism

In a recent review it has been suggested that the female of *Ateles* is larger than the male (Crook, 1972). Unfortunately, the data published in the sources consulted by Crook represent samples in which the absolute age of the specimens was im-

perfectly known. As indicated on page 52 ("Ontogeny"), the weight of subadult males of *A. fusciceps* begins to surpass that of females toward the end of their third year of life. The reason that some of the published summaries of data seem to indicate that females are larger may be attrib-

uted to two causes: (1) Total lengths are often given rather than head and body lengths. The tail of *Ateles* is quite variable in its length relative to the head and body and, as a result, a long-tailed female may give the misleading impression that she is larger than is actually the case. (2) Most preserved specimens in museums are the result of rather unselective shooting on the part of museum collectors. Since subadult and juvenile males form a subgroup and the number of fully adult males relative to subadults and juveniles may be rather small, one can anticipate that a "male" sample would be somewhat biased toward the younger age classes.

Table 21 contains some measurements of adult *Ateles* (probably in excess of 7 years of age) with respect to linear measurements. It can be clearly seen that, although the species is not greatly dimorphic, the male tends to be heavier and its torso is somewhat longer than that of the female. What is noteworthy, however, is that the degree of dimorphism is not nearly as great as that shown by many species of the Old World genera, *Macaca*, *Cercocebus*, and *Papio*. The demorphism shown by the latter genera no doubt arises from complex processes of sexual selection. The morphological differences derive from a combination of (1)

competition among males for consortships when females are in estrus, and (2) actual selection on the part of females for males possessing certain characteristics, among which may be a larger size. On the other hand, differences in size alone may also be related to nonsexual selection where the roles of the two sexes are differentiated so that they come under different types of environmental pressures. These factors will be dealt with in subsequent sections.

Parental Investment

Trivers (1972), in a provocative essay, points out that some dimorphism between the sexes may be in fact related to different reproductive strategies. In brief, if a male wishes to increase his individual fitness and at the same time has little involvement in parental care, then his reproductive strategy would involve an attempt to mate with as many females as possible; such a polygynous system would of necessity put the male in a competitive position with respect to other males in the troop. Such male-male competition could account for sexual selection leading to a size dimorphism when the two sexes are compared. The female in such a system increases her own fitness by concentrating her care on an infant born to her while at the same time attempting to mate with males having a high potential fitness; thus, influencing to some extent by their own selection the same and other characteristics of the observed dimorphism (see also Crook, 1972).

On the other hand, males of species that show a great deal of parental investment—approximating that of the female—may be disposed to concentrate their reproductive efforts with only one female, thus insuring their own fitness by increasing the survivorship of the offspring of a given mate. In most mammals, the degree of initial parental investment by the male is low. This results from the fact that the early nutrition of the young by means of mammary gland secretions generally precludes the participation of the male (Figure 33). Exceptions have occurred, however, in some Carnivora (Kleiman and Eisenberg, 1973), and in the primates of the family Callithricidae (Eisenberg, 1966; Epple, 1975). There is some evidence to indicate that male participation in the early phases of parental care is high in some cebid primates,

TABLE 21.—Maximum external measurements (mm) for *Ateles**

Species	Sex	TL	HB**	T
<i>A. paniscus paniscus</i>	♀	1450	570	880
	♀	1413	660(?)	753
<i>A. paniscus chamek</i>	♂	1270	450	820
	♀	1380	500	880
<i>A. belzebuth belzebuth</i>	♂	1450	640	810
	♀	1330	635	695
<i>A. belzebuth marginatus</i>	♂	1250	500	750
	♀	1245	475	770
<i>A. belzebuth hybridus</i>	♂	1248	498	750
	♀	1330	474	856
<i>A. fusciceps robustus</i>	♂	1220	590	630
	♀	1260	510	750
<i>A. geoffroyi gucatanensis</i>	♂	1141	397	744
	♀	1176	420	756
<i>A. geoffroyi panamensis</i>	♂	1280	594	786
	♀	1225	440	785

* All records from Kellogg and Goldman, 1944, except for ♂ *Ateles belzebuth belzebuth* from Museo Ciencias Naturales, Caracas, Venezuela.

** HB derived by subtracting T from TL.



FIGURE 33.—Even temporary contact between an adult male *Ateles* and its juvenile offspring can be a powerful socializing influence as affiliation develops in the years ahead.

including the genera *Aotus*, *Callicebus*, and some species of *Pithecia* (Moynihan, 1967; Mason, 1971). All of the foregoing genera are not conspicuously dimorphic in size, although some species of *Pithecia* show a pronounced color dimorphism.

Considering that the degree of parental investment is in some way reflected in the degree of size dimorphism is a useful concept. Nevertheless, when species are compared the correlations are not consistent, no doubt a result of the additional selective pressures which were outlined (p. 66; see also Kleiman, 1976). It is worth noting, however, that parental investment by males may be influential at different stages of the development of the young animal than is the case with the female. Whereas the female's parental investment may be initially very high, in some species male parental investment may be significant as

the young become more mature (Eisenberg, 1966: 18, 65). In addition, it is important to concentrate on the fact that the degree of parental investment by an adult may not be equally directed toward juvenile animals; in short, males may in fact direct more parental investment toward their juvenile male offspring than toward their daughters (Dittus, 1974, 1975). The affiliations manifested by adult males toward juvenile males are profoundly developed in both *Ateles geoffroyi* and in *Ateles fusciceps*. These behavior patterns no doubt contribute to the early survivorship of young males born into a troop. Indeed, these attentions on the part of adult males probably contribute in no small manner to the formation of the unisexual sub-groupings which are characteristic of *Ateles*. These groups ultimately may lead to a differential use of the home range on the part of the two sexes.

females remains to be demonstrated, but the data suggest that a more efficient utilization of dispersed resources in a home range could be achieved thereby. The necessity for young males to disperse and join a male subgroup is probably not only adaptive but essential for the normal maturation processes of young males. Evidence from captive studies would suggest that, if young males cannot form an affiliation with older males, independent of the influence of females, they may be severely persecuted.

Social Pathologies

Eisenberg and Kuehn (1966) observed that the young males maturing in the captive colony at Vancouver appeared to suffer a significantly higher mortality than was the case with young females. At first we assumed that this could possibly be due to the fact that young males were stressed considerably during their maturation phases through continual conflict with subadult females. Although this may be the case in certain captive groups, it is also possible that young males are more susceptible to calcium deficiency; this suggestion was raised by Du Boulay and Crawford (1968:230). Nutritional deficiencies induced by low levels of vitamin D₃ may have been responsible for the low survivorship of young males in the colony at Vancouver; however, it is undeniable that in close confinement young males may be subjected to abnormal amounts of social stress (Appendix II).

Since sexual maturation in the spider monkey precedes sociological maturation (see "Sexual Behavior," p. 6), I suggest that the maintenance of a successful dominance relationship over females may be a necessary prerequisite before a male can mate. It would appear that grappling or mock fighting is a means of establishing and maintaining dominance relationships among troop members. It would appear then that under close confinement, some zoo colonies may show abnormal stressing of young males on the part of an increase in intensity of grappling which can turn into an out-and-out aggressive encounter. As the young males attempt to dominate females, unnecessary stressing of young males can occur. I still cling to the conviction that the formation of an all-male subgroup and its capacity to spatially separate from the core,

mother-rearing group is an important attribute for social health in groups of spider monkeys.

In crowded zoo colonies, direct conflict among males of an equivalent age grade can also occur, especially at the time that females are in estrus. Recently Ms. Eve Mitchell reported to me an increased mortality among young male spider monkeys in the zoo colony at Birmingham, Alabama. According to her data, the male mortality is so pronounced that out of a colony of 44 monkeys, there are only 5 males 2 years of age or older (2 adults, 1 juvenile-2, 2 juvenile-1).

At Birmingham some of the aggressive behavior toward maturing males derives from the two adult males, but this may in part be an artifact of the close confinement of adult males in the presence of reproductive females. Once again, the inference is clear that the ability of a subgroup of young males to form spatially separate groups from the females is essential. Of course, a great deal depends on the structure of the cage and the history of the group itself. No such excessive male mortality has been observed in the colony of *Ateles geoffroyi* in San Francisco (Klein and Klein, 1971). Thus, social pathologies in captivity are far from being understood completely. The genesis of social pathology no doubt is a function of the individual history of the colony founders, the structure of the cage, and the total area in which the group can develop (see also Klein and Klein, 1971).

Signals in Context

It seems necessary to conclude this monograph with some attempt to place the signaling system of the *Ateles* troop into an environmental context. I have attempted to avoid imputing a semantic content to the signals expressed by interacting *Ateles*. Indeed, I personally lean toward the view that the signals tend to reflect the immediate emotional state of the presumptive sender and, if they evoke responses from a presumptive receiver, they probably do so by inducing an empathetic mood rather than imparting discrete or quantifiable information (Langer, 1973:141-214).

Consider the *Ateles geoffroyi* troop on Barro Colorado Island. Upon awakening at dawn in the sleeping trees, the individual members will begin arousal, yawning, self-scratching; infants will begin to play with one another. Some individual

movements to get up and disperse commence. A 5-year old male may begin brachiating suddenly and emitting a long loud call type 2, perhaps with three phrases. There is no noticeable effect on other troop members. A 3-year old male may be following closely behind the 5-year old. Gradually, the younger males through following begin to move toward a feeding tree. A female with a 2-year old young may follow. A young male upon finding fruit in the tree will utter a twee-twee-twee call. This will be answered by a following animal; as each member of the male subgroup arrives at the tree or a neighboring tree, the call may be repeated.

In the meantime, a female with a dependent infant may reach down and grab her infant, which immediately settles upon her back, and initiate brachiation either toward the feeding spot where the twee-twee calls have come from or toward another spot, which may be nearer. This female will then be followed by a second female who has assembled her infant in a similar manner. Upon reaching the feeding tree, the infants may descend from the females and perhaps take food from the mother. The mother upon reaching the tree will have uttered the twee-twee call. This may be followed by a slower whinny as feeding proceeds, taken up perhaps by a third individual, a sub-adult female who has followed the mothers at some distance.

At the conclusion of a 15-minute feeding bout, one female may begin to move off, pausing to look back at her infant who will, upon perceiving her movement, attempt to follow her. The mother jumps to a branch, the infant utters a low squeaking call, the mother turns, extends her arms to the infant, the infant grasps the mother's arm and is pulled to her. The mother then proceeds with the infant riding and she may or may not be followed by the other two females.

The foregoing descriptions give some idea of the kinds of vocalizations performed during the normal maintenance activities of the animals. Certainly the twee-twee call serves to maintain contact. Its association with feeding would indicate that the call functionally serves to signal food, but the intent of the caller may only be guessed at. Squeaks of an infant unwilling to jump concentrate the mother's attention toward it and elicit an extension of herself to permit the infant to traverse a

gap. The long loud call of a seemingly boisterous young male could function as a territorial announcement call, although the intent of the signaler again remains unknown. Certainly it seems to accompany an exuberant display of initial activity in the morning.

The complex of calling during an unexpected encounter with a sloth will conclude this monograph. Here follows a description from field notes where agonistic, fearful, and chorusing behavior are combined. It was an unusual incident reminiscent of the kind of serious situation that might happen during an intertroop encounter (Klein, 1972), but instead resulted from the presence of a two-toed sloth (*Choloepus*) in a favorite resting tree, a place where the sloth was "unexpected."

Notes on *Ateles geoffroyi* taken 26 February 1974, 1250-1330, at the laboratory clearing on Barro Colorado Island. A most extraordinary series of events occurred with the *Ateles* troop. The situation was as follows:

A two-toed sloth was present in a tree near the edge of the clearing; this is the most recent afternoon resting area for the *Ateles* male subgroup. The adult male, Chumbo, was about 50 meters away in an entirely different tree. The male Class-5, Rico, encountered the sloth and began to scream and display. The display included brachiating and leaps, pilo-erection, roar; roar followed by a grimace, then approach and move away from the sloth. He then went into a shriek or pulsed chitter while shaking the branches, continued to chitter, ee-ee-ee-ee-ee-ee, continues to brachiate, roar to croon, then this croon approximates the old "grunt-trill," eoooch, ee-ee-oooch, awk, ee-awk, ee-awk, in short, a mixed display with aggression and fear alternating. He redirects display to the human observers. He recruits by this display two other males, a Class-4 and a Class-3; these three proceed to attack the sloth who fights back with clawing and open mouth. The *Ateles* slap at the sloth and alternate calls of ee-ee-ee, ee-ah-ah, ah-ah, this latter sound approximates aggressive transition growl heard in a grappling bout.

After arriving with the Class-5 male, the other males embrace, sniff pectoral, sniff arm-pit, and then "attacked" the sloth. They will break to re-embrace one another. This is a reassurance behavior. Ee-ee-awk, ee-ee-awk while approaching, slap, and pull away from the sloth. Then the 3, 4, and 5 males brachiate to Chumbo (the founder, adult male), each embraces and touches him, and Chumbo initiates a long call, the Class-4 and -5 males join in to form a chorus; it is the pulsed long call oo-oo-rah oo-oo-oo-rah oo-oo-oo-rah chorus for around 2 minutes. Chorus consists of the voices of Chumbo, the Class-5 male, the Class-4 male; then the males 4 and 3 return to the sloth tree; they are more relaxed. A second Class-3 male approaches, embraces, pectoral sniffs, and

the other Class-3 male chases the second away. Meanwhile male 5 returns to watch the sloth, the male 4 teases it occasionally. This persists for some 16 minutes.

This interaction clearly shows the chitter (eee-eee), roar, eee awk, and long loud calls in a context of high arousal, aggression, withdrawal, mutual reassurance, and finally a long call chorus reminiscent of a "triumph ceremony."

The description of these behaviors allows for a functional interpretation as outlined on page 38 ("Contexts). There may be alternative possibilities for functional interpretations but such hypotheses must await further study. The most fruitful pursuit would seem to lie with the analytical techniques as developed for *Macaca fuscata* by S. Green (1975).

Appendix I

Physical Measurements and Description of Measurement Techniques for the Sounds of *Ateles fusciceps* and Related Species

The vocalizations of *Ateles* form a graded system. Although it is possible to define and classify certain calls as discrete entities, any physical description must indicate the range of variation and display transitional forms. Seventeen calls and transitional forms are illustrated by photographs. The defining criteria for the measurements are portrayed on each figure (see Marler (1973) for a similar system of measurement). The measure-

ments are then included for each call form in a series of tables. Sample sizes are variable since only recordings of the best quality were utilized in the tabulations. Standard deviations were calculated when the sample sizes were sufficiently large. The syllable types are referred to in the figure legends according to the syllabic key outlined on pages 24-26. The call types are similarly referred to by numbers corresponding to the list in Table 10.

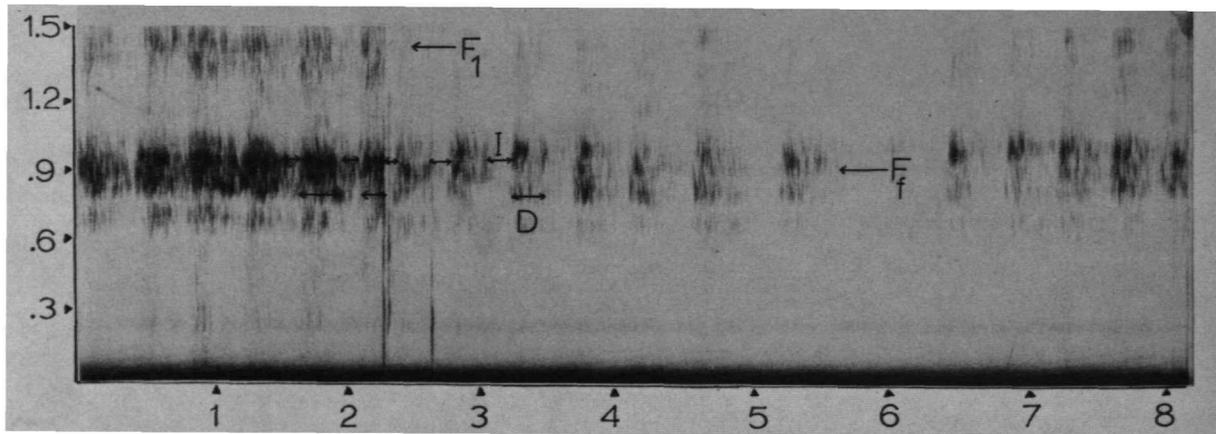


FIGURE I-1.—Bark, Call Number I [Key II.B.1.a (1) (a)]. Letter code refers to tabulation in Table I-A. Throughout the remainder of the figures, the letter codes define the measurements as recorded in the tables corresponding to each call type. (Ordinate in KHz, abscissa in seconds.)

TABLE I-A.—Bark, Call Number I

Call form	D (sec)			I (sec)			Frequencies (KHz)		
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F ₃
<i>A. fusciceps</i>									
Slow	11	0.5	—	10	0.25	—	0.8	1.2-1.8	2.2-2.8
<i>A. belzebuth</i>									
Rapid	20	0.23	—	19	0.17	—	0.9	—	—
All barks	72	0.15	±0.06	69	0.24	±0.14	0.8	1.1	—

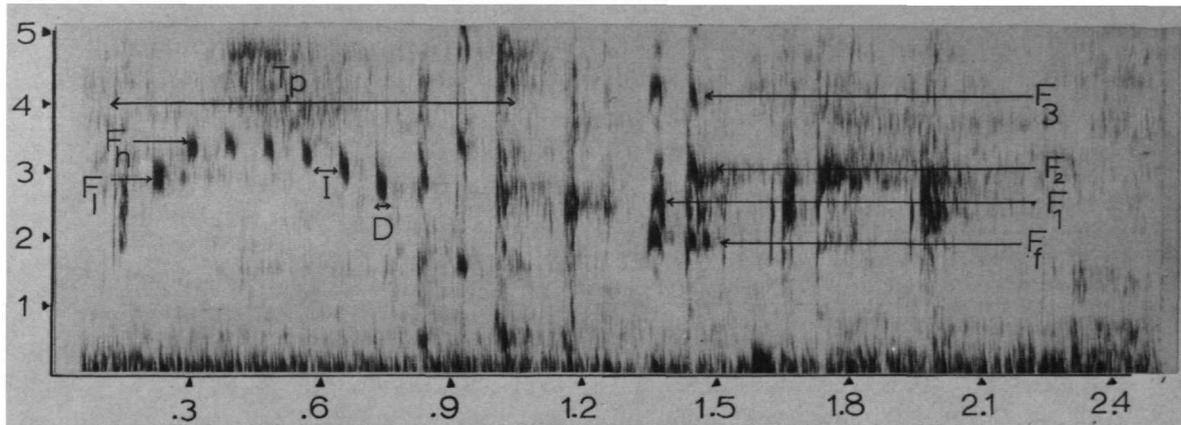


FIGURE I-2.—(left) Trill, Call Number IIIc [Key II.A.1.a(1)(c)] and (right) Call Number IIIa-IIIb [Key II.A.1.a(1)(a) or (b)]. (Ordinate in KHz, abscissa in seconds.)

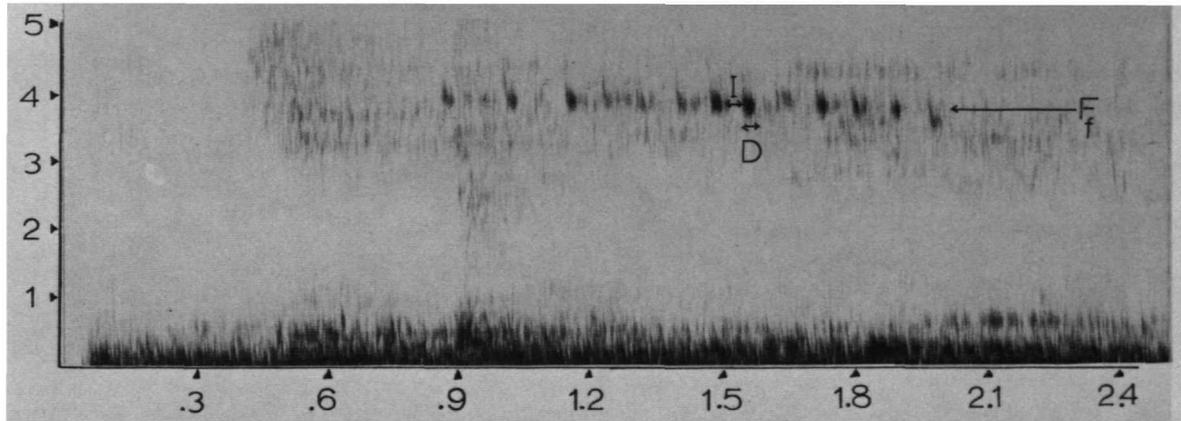


FIGURE I-3—Twitter, Call Number IV [Key II.A.1.a(1)(c)] (Ordinate in KHz, abscissa in seconds.)

TABLE I-B.—Trills and twitters of *Ateles fusciceps*, Call Numbers IIIa, b, c, and IV

Call form	D (sec)			I (sec)			Average frequencies (KHz)						
	n	Av.	S.D.	n	Av.	S.D.	F_H	F_1	F_f	F_1	F_2	F_3	T_p
IIIa	37	0.047	±0.053	32	0.198	±0.28	-	-	0.4-0.6	1.1-1.9	2.8-4.8	-	-
IIIb	2	0.03	-	-	-	-	4.2	3.6	-	-	-	-	-
IIIc	32	0.022	±0.009	30	0.091	±0.10	3.8	3.1	-	-	-	-	0.59-0.98
IIIc IIIa	50	0.027	±0.013	48	0.086	±0.08	3.4	1.8	-	-	-	-	-
IV	46	0.034	±0.04	42	0.069	±0.059	-	-	3.2-4	-	-	-	1.03

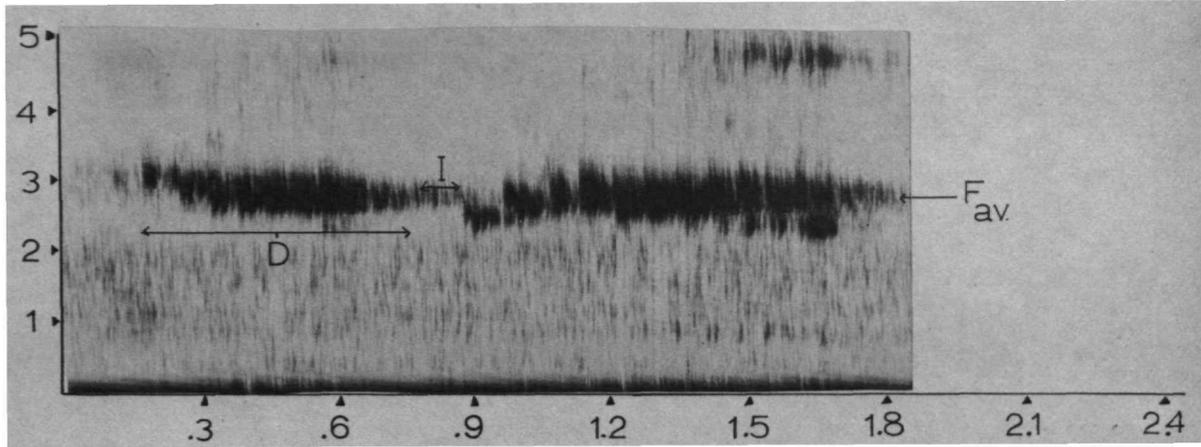


TABLE I-C.—Fused trill, squeak or chitter, Call Numbers X to V

Ateles species	D (sec)		I (sec)		Av. frequencies (Khz)
	n	Av.	n	Av.	F
<i>A. fusciceps</i>	3	0.53	2	0.23	2.9-3.1
<i>A. belzebuth</i>	10	0.40	Variable		3.6-4.1

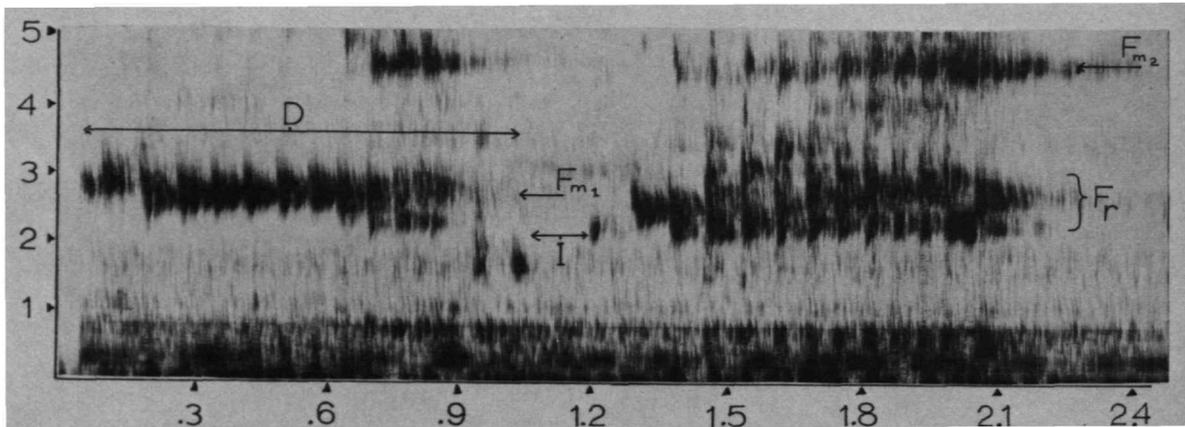


TABLE I-D.—Pulsed trill or chitter of *Ateles fusciceps*, Call Numbers IIIb to V

Series call	D (sec)			I (sec)			Av. frequencies (Khz)		
	n	Av.	S.D.	n	Av.	S.D.	Fm ₁	Fm ₂	Fr
Chitter Series 1	3	0.64	±0.22	2	0.3-0.05	-	2.7	-	-
Chitter Series 2	3	0.75	-	1	0.09	-	2.8	4.5	0.8
Pulsed trill Series 3	13	0.163	±0.13	11	0.110	±0.074	3.3	4.3	-

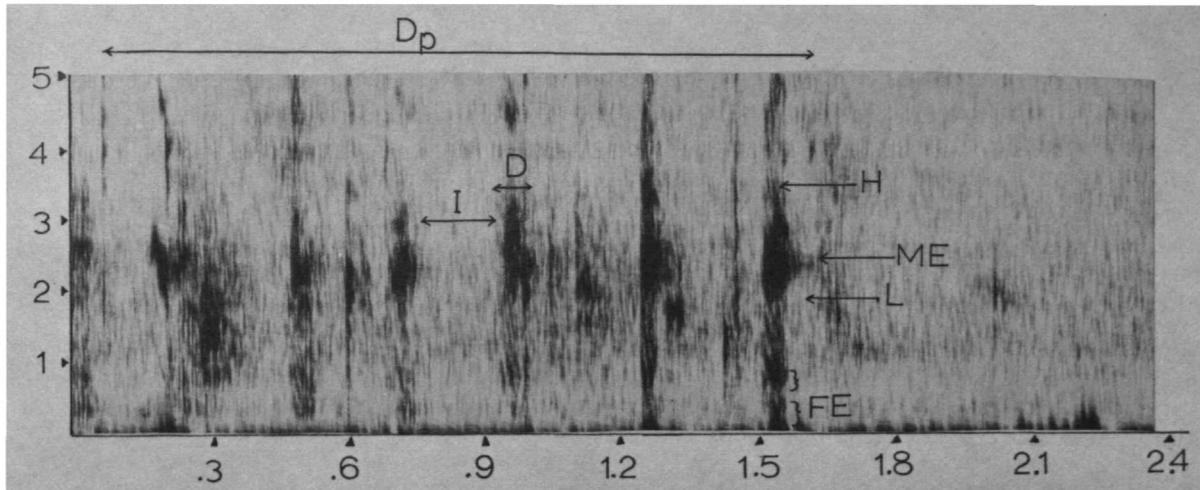


FIGURE I-6.—Slow whinny (chirp series or yip whinny), Call Number VIc [Key IIA.1.a (2), grades to IIA.2.a (1) or IIA.2.a (1)]. (Ordinate in Khz, abscissa in seconds.)

TABLE I-E.—Slow whinny (chirp or yip form), Call Number VIc

Ateles species	D (sec)			I (sec)		Frequencies (Khz)		
	n	Av.	Dp (sec)	n	Av.	FE	H	L
<i>A. fusciceps</i>	16	0.03	2.1-2.3	18	0.10	0.2-0.7	3	2.1

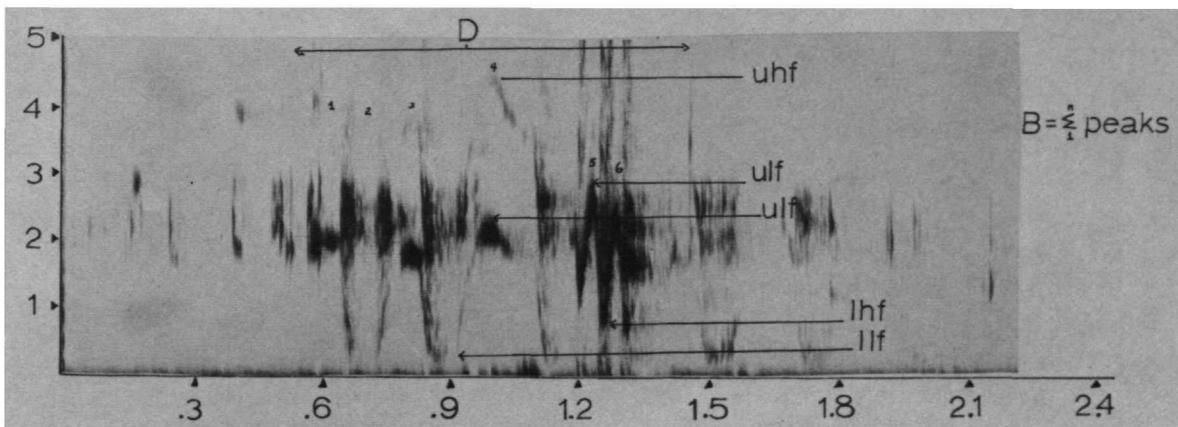


FIGURE I-7.—True whinny, Call Number XIIa [Key IIA.3.a]. (Ordinate in Khz, abscissa in seconds.)

TABLE I-F.—True whinny, Call Number XIIa

Ateles species	D (sec)		I (sec)		B	Frequencies (Khz)			
	n	Av.	n	Av.		LLF	LHF	ULF	UHF
<i>A. fusciceps</i>	2	0.96	-	-	7	0.9-1.8	1.4-2.9	1.9-3.4	4.4-4.8
<i>A. belzebuth</i>	7	0.98	-	-	6.9	1.8-3	2.4-4.2	3.5-3.8	4-5.2
<i>A. geoffroyi</i>	2	0.95	-	-	7-8	1.0-2	3-3.1	2.5-3.8	5.2

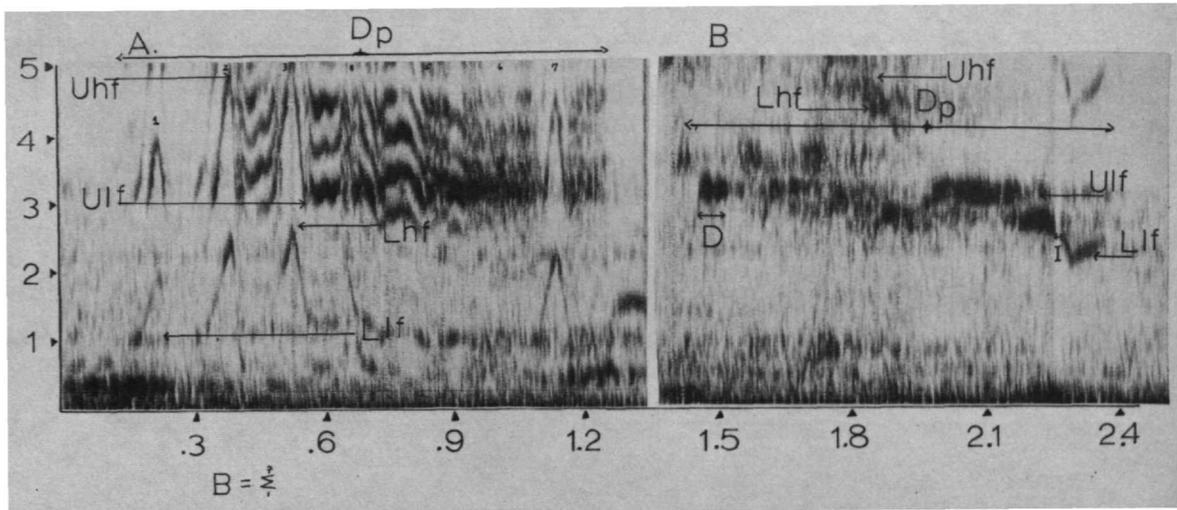


FIGURE I-8.—*a*, Tee-tee (twi-twi-twi), Call Number XIIb [Key II.A.2.a (2)]; *b*, slow whinny, Call Number VIa or VIb [Key II.A.2.a (1)] (Ordinate in Khz, abscissa in seconds.)

TABLE I-G.—*Tee-tee* (twi-twi-twi), Call Number XIIb

Ateles species	D (sec)		I (sec)		B	Frequencies (Khz)			
	n	Av.	n	Av.		LLF	LHF	ULF	UHF
<i>A. fusciceps</i>	1	0.69	1	—	7	2.2	3.8	3.3	5.4
<i>A. geoffroyi</i>	1	0.65	1	—	5	1.2	3.2	2.4	5

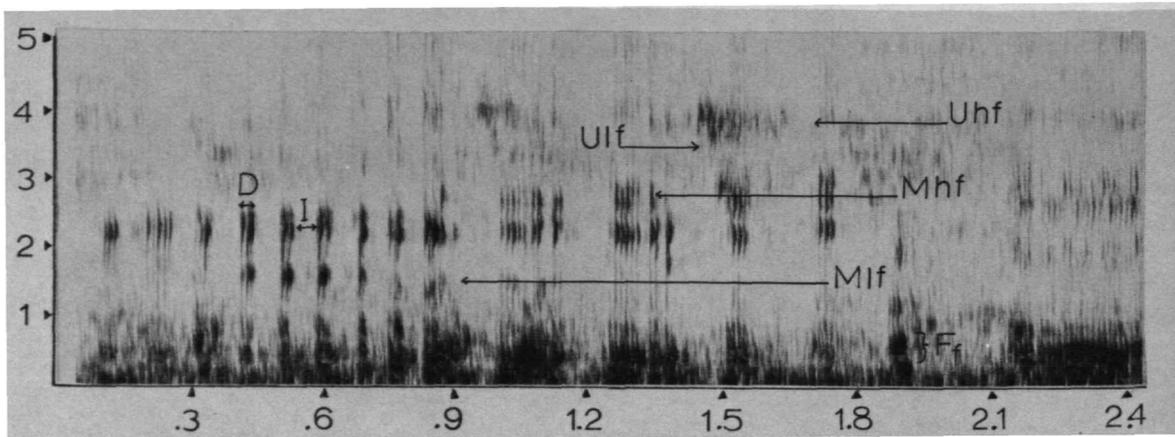


FIGURE I-9.—Slow, guttural whinny, Call Number VIc [Key II.B.2.a]. (Ordinate in Khz, abscissa in seconds.)

TABLE I-H.—*Slow whinny, Call Numbers VIa or VIb*

Ateles species	D (sec)			Dp (sec)	I (sec)			Av. frequencies (Khz)			
	n	Av.	S.D.		n	Av.	S.D.	UHF	LHF	ULF	LLF
<i>A. fusciceps</i>	65	0.05	±0.08	<2.4	60	0.07	±0.05	4.1	3.8	2.2	2.4

TABLE I-I.—*Slow, guttural whinny, Call Number VIId*

Ateles species	D (sec)			I (sec)			Frequencies (Khz)				
	n	Av.	S.D.	n	Av.	S.D.	UHF	ULF	MHF	MLF	F _f
<i>A. fusciceps</i>	11	0.02	-	11	0.06	-	3.8	3	2.2	1.8	0.8-1.2
	19	0.196	±0.06	17	0.07	±0.05	-	-	-	-	-
	6	0.092	±0.05	6	0.13	±0.08	-	-	2.5	1.3	-
	47	0.087	±0.15	44	0.07	±0.07	2.6	1.8	1.2	-	-

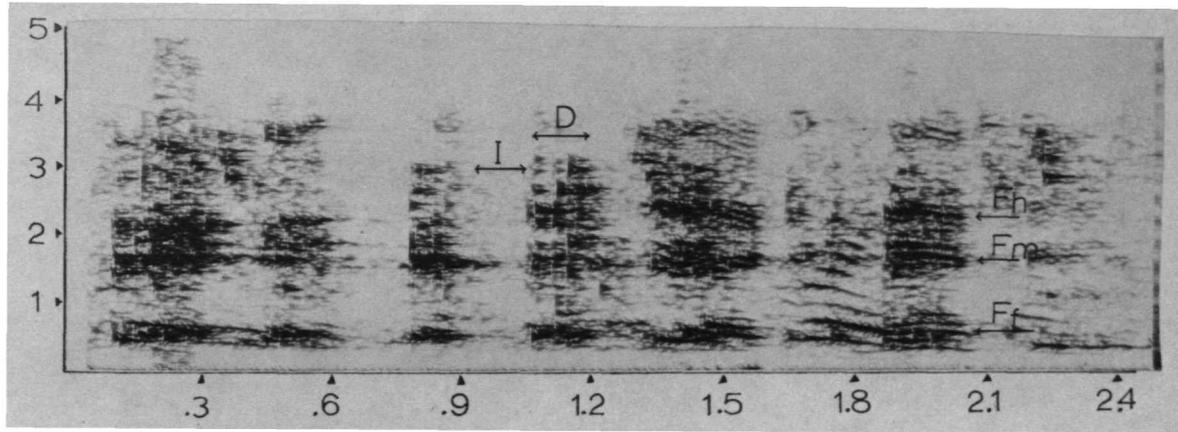


FIGURE I-10.—*Sobs* (slow, guttural whinny variant), Call Number VIId [Key II.B.1.a(2)], narrow band analysis. (Ordinate in KHz, abscissa in seconds)

TABLE I-J.—*Sobs* (slow, guttural whinny variant), Call Number VIId

Ateles species	D (sec)			I (sec)			Av. frequencies (Khz)		
	n	Av.	S.D.	n	Av.	S.D.	F _f	F _m	F _h
<i>A. fusciceps</i>	19	0.19	±0.06	17	0.07	±0.05	0.5	1.3	2.5

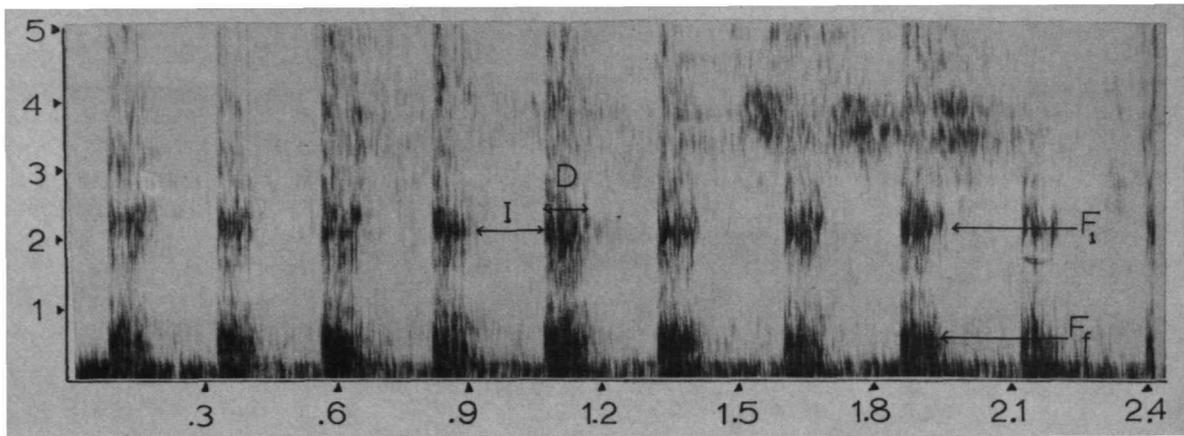


TABLE I-K.—*Ook-ook* or *ak-ak*, Call Number VIII

Call form	D (sec)			I (sec)			Frequencies (Khz)		
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F ₃
<i>A. fusciceps</i>									
Ak-ak	20	0.075	-	17	0.14	-	0.4	0.8	1.4
Ook-ook	10	0.09	-	6	0.1	-	0.2-0.8	2-3	-
Ak-ak	9	0.08	±0.008	8	0.162	±0.007	0.5	2.2	-
<i>A. belzebuth</i>									
Ook-ook	7	0.14	-	6	0.112	-	0.6-1.2	2-2.4	-
Ak-ak	4	0.07	-	5	0.16	-	0.6-0.8	2	-

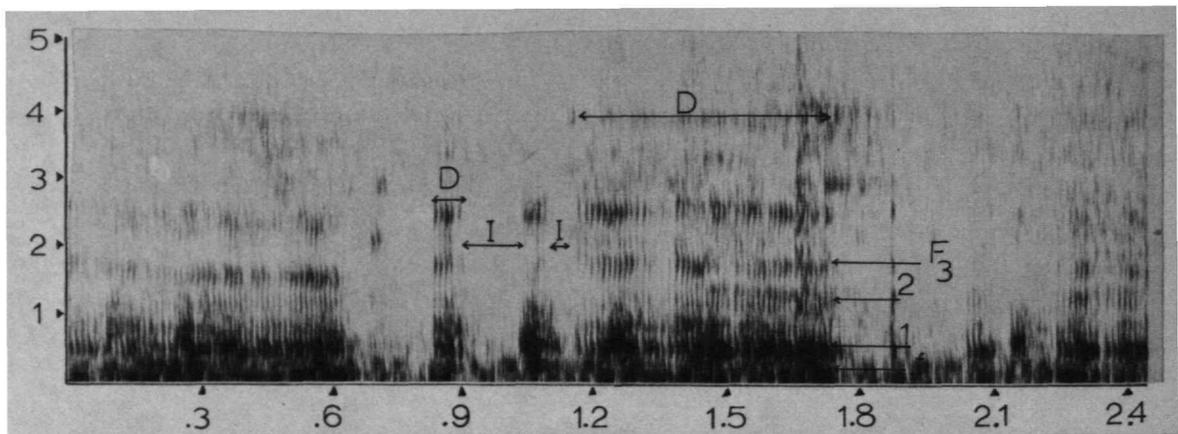


TABLE I-L.—*Growl* of *Ateles fusciceps*, Call Number VII

Call form	D (sec)			I (sec)			Frequencies (Khz)			
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F ₃	F ₄
Growl	13	0.67	±0.31	3	0.14	-	0.2,	0.5,	1.2-1.4,	2.6
							0.4-0.6	1.2	2-2.2	
Ak-ak to growl intergrades	49	0.152	±0.205	46	0.071	±0.056	0.5	1.6	2.5	-

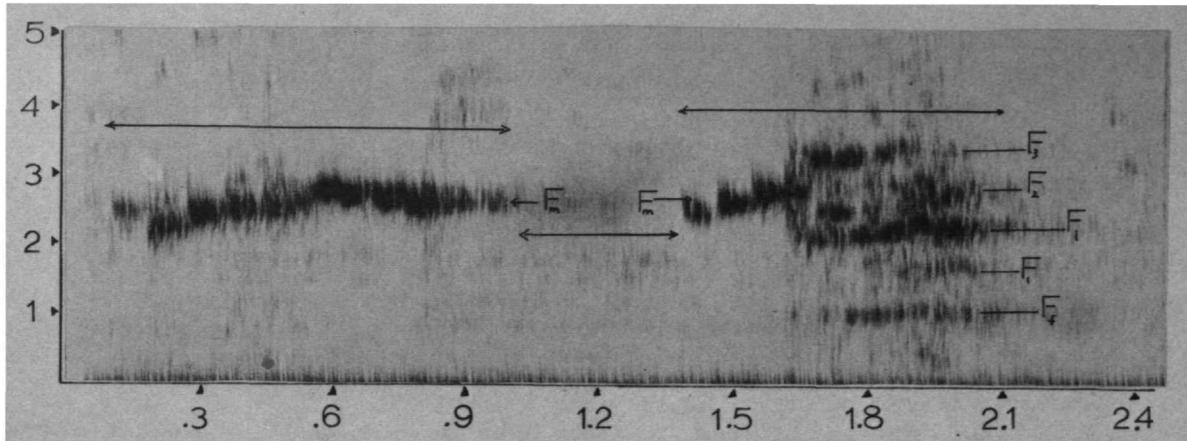


FIGURE I-13.—Intermediate length compound calls: ascending trill (grunt-trill of adult and eee-awk of juvenile), Call Number IX [Key I'.A]. (Ordinate in KHz, abscissa in seconds.)

TABLE I-M.—Intermediate length compound calls of *Ateles fusciceps*, Call Number XI [Key II.A.3.b (1) or I'.A]

Call form	D (sec)			I (sec)			Av. frequencies (KHz)					
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F _m	F ₁	F ₂	F ₃
Ascending trill	-	0.7	-	-	0.6	-	-	-	2.5	-	-	-
Eee-ah:												
Eee	4	0.26	-	}	<0.01		-	-	2.8	-	-	-
Aah	4	0.38	-				0.8	2.1	-	1	2	3

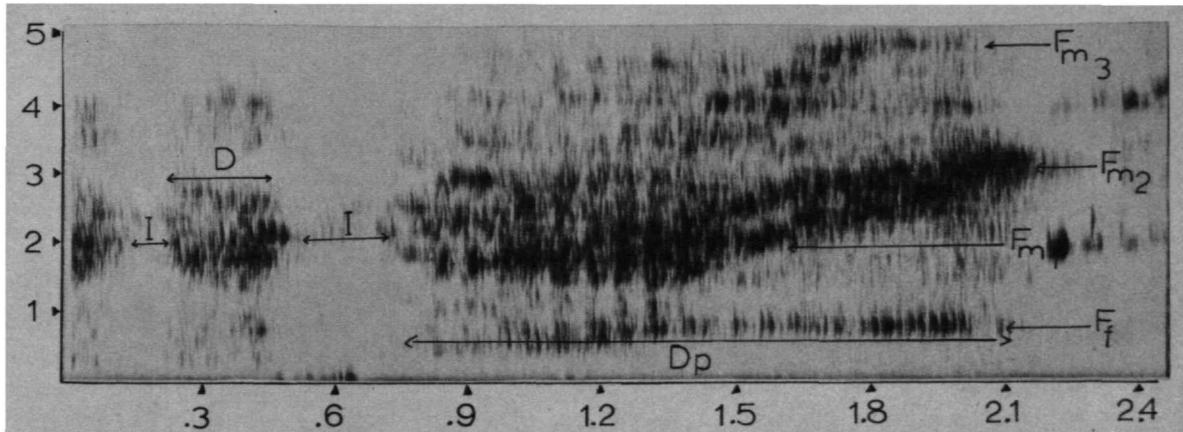


FIGURE I-14.—Intermediate length compound calls: variant of trill awk: ääh ääk aa-ëëee äh [Key II.A.3.b (1)]. (Ordinate in KHz, abscissa in seconds.)

TABLE I-N.—Intermediate length compound calls

Ateles species	D (sec)			Dp	I (sec)			Av. frequencies (KHz)		
	n	Av.	S.D.		n	Av.	S.D.	F ₁	F _{m1}	F _{m2}
<i>A. fusciceps</i>	9	0.16	±0.24	1.2	8	0.05	±0.10	0.8	1.4	3.4

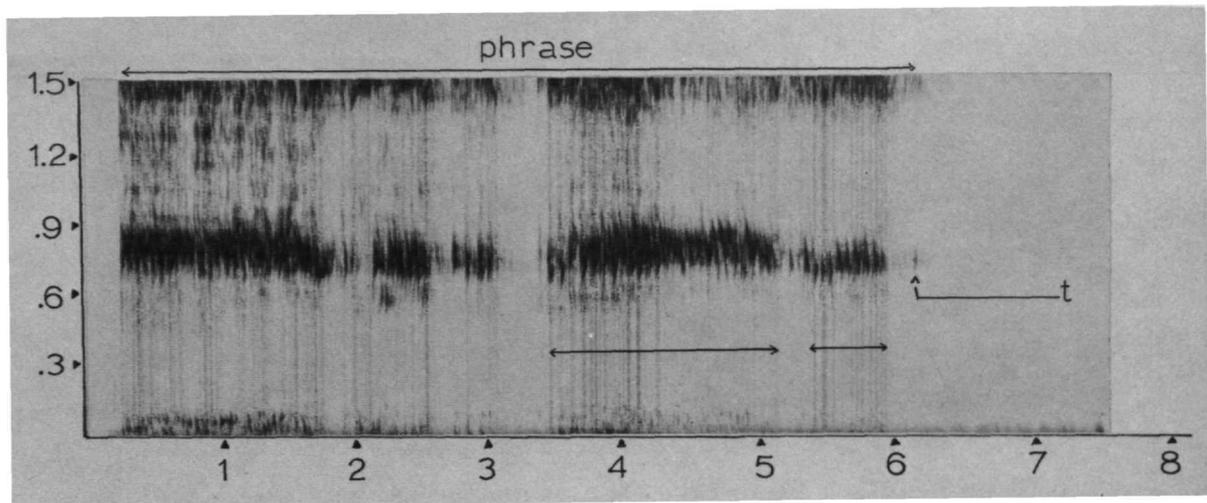


FIGURE I-15.—Long call phrasing of *Ateles fusciceps* short syllables, long syllables and terminal notes "t" are shown (see Tables I-O, I-P). (Ordinate in KHz, abscissa in seconds.)

TABLE I-O.—Long calls by *Ateles fusciceps* (narrow frequency modulation; emphasis on $E \leq 1$ KHz)

Series*	Long, loud syllable $\geq 2^{**}$	Intermediate length syllable $\geq 1.5 < 2$	Long terminal note $> 0.2 < 1$	Terminal note ~ 0.1	Comments
a	1	—	2	—	Wail form
b	1	—	2	—	Vibratto (harsh) form, caw
c	1	—	3	—	
d	1	—	8	—	Wail, v-syllables almost merge to vibratto form
e	—	1	2	—	Undulating wail
f	1	3	2	3	Harsh call, caw
g	—	3	2	2	Harsh call, caw

* Consecutive series of long calls on a single recording for *A. fusciceps*.

** Times defined in seconds.

Range 2.4 KHz; average frequency emphasized 1.15 KHz or 0.7 KHz; average frequency 2.04 KHz.

TABLE I-P.—Long call bout for *Ateles fusciceps M*

Frequencies emphasized (KHz)	No. of syllables/phrase	D (sec)	I (sec)	Average duration of phrase (sec)
0.58, 0.74, 1.6	1-6	1.02	0.11	9.4

Total time of recording = 635 seconds; % of time calling = 53%.

Appendix II

Reproductive Data, Medical Histories, Hand-rearing, and Genealogies

Reproductive Data

ATELES GEOFFROYI

Ateles geoffroyi panamensis was reintroduced on Barro Colorado Island (BCI) during the years 1959 to 1961. It is impossible now to ascertain the fate of all introduced animals, but by 1964 five subadult and adult individuals (1 ♂, 4 ♀) were established at the laboratory clearing. A juvenile-2 female was introduced in 1966 and successful reproduction by at least three of the females commenced in 1965 with three live births in 1966 (Eisenberg and Kuehn, 1966). From 1966-1970 the exact patterns of reproduction are imprecise, mainly because the individual identity of the founding four females was not maintained in the recording system, but birth dates were recorded and Eisenberg made a new census in 1970. Dare (1974) has documented the group composition during 1971 and 1972. In 1973 Ms. Carrie Thorington prepared a photographic record of all individuals named by Dare, and Eisenberg recensused the group in 1974.

In Table II-A, I present a possible genealogy, which is based on known birth dates and presumed identities of the mothers. This table differs from Dare's interpretation, but I present the table as a basis for my calculations concerning interbirth interval and population growth. In Table II-B, I have compared interbirth intervals from my probable genealogical tree with Dare's intervals from his own interpretation of the data. Since there is little difference in the range and the mean, I assume that for all practical purposes the population analyses derived from my life table are essentially correct.

For comparison the interbirth intervals for those zoo births where the mother raised her baby are included. The captive interbirth intervals are shorter (2 years 9 months versus 2 years 4 months)

and this is to be expected, considering the more predictable nutrition plane in captivity.

In my publication of 1973, I stated that the *Ateles geoffroyi* births appeared to have an interval of 22 to 36 months. With data through February of 1974 and given the errors inherent in the reconstruction of genealogies, the range according to Dare would be 17 to 45 months and for myself 22 to 45 months. The range for captive *A. fusciceps* is 22.8 to 31.5 months (including only cases where the mother reared her young to social weaning). With a gestation of 7½ months and milk dependency for 10 months in captive *A. fusciceps*, then 17.5 months may be taken as the theoretical minimum in captivity. In the wild it is surely longer and I now feel that 28 to 30 months is a reasonable mode.

Table II-C presents reproduction data for the BCI *Ateles*, which allows a calculation of r_1 . This value, based on a cohort of females, reflects the low reproductive rate of wild *Ateles*. It is almost one-half the value obtained by Dittus (1974) for *Macaca sinica*. The lesson is clear. Given the inherent errors in the interpretation of the BCI records between 1967 and 1970, both Dare and I agree that *Ateles geoffroyi* have a rather long interbirth interval. These conclusions are supported by the data from the captive *A. fusciceps*. The conclusion for management is quite clear. *Ateles* populations are slow to recover from any form of hunting or cropping. In terms of conservation then the genus *Ateles* is very sensitive to hunting and probably will be the first species to decline under severe hunting pressures.

ATELES FUSCICEPS

The reproductive history for our captive group of *A. fusciceps robustus* through 1972 has been published (Eisenberg, 1973). Table II-D includes

TABLE II-A.—Breeding records for *Ateles geoffroyi* (BCI) founding females through 1974*

Consecutive birth dates	Survivorship status of young	Mother-young association prior to next birth (days)	Interbirth interval (days)
FEMALE 1			
5 Jan 1966.....	Survived to weaning	—	—
3 Sep 1969.....	Survived to weaning	1340	1340
24 Jun 1972.....	Survived to weaning	1024	1024
FEMALE 2			
10 Apr 1966.....	Survived to weaning	—	—
4 Oct 1969.....	Survived to weaning	1272	1272
31 Jul 1972.....	Survived to weaning	1030	1030
FEMALE 3			
21 May 1966.....	Survived 19 months	—	—
30 Jan 1970.....	Survived to weaning	570	1313
5 Dec 1972.....	Survived to weaning	675	675
FEMALE 4			
2 Feb 1966.....	Did not survive	—	—
? Mar 1967.....	Survived to weaning	7	390
12 Dec 1969.....	Did not survive	1005	1005
17 Oct 1971.....	Survived to weaning	14	673
FEMALE 5			
? Oct–Nov 1968.....	Survived to weaning	—	—

* R. Dare discusses the difficulties in maintaining a consistent genealogy; this table should be taken as an approximation (see Dare, in litt.). Introductions on BCI extend from 1959 to 1961 and by 1964 1 male and 4 females were established in the vicinity of the laboratory clearing (see Dare, 1974; Eisenberg and Kuehn, 1966).

TABLE II-B.—Interbirth intervals for young that survived until social weaning

<i>Ateles fusciceps</i> (N.Z.P.)	<i>Ateles geoffroyi</i> (BCI)*
2 years 6.5 months	3 years 9 months
1 year 10.8 months	3 years 8 months
2 years 7.5 months	3 years 6 months
	2 years 10 months
	2 years 10 months
	2 years 9 months
	1 year 10 months
\bar{x} = 2 years 4.2 months	\bar{x} = 3 years

* Data concerning interbirth intervals taken by R. Dare (1974) equals 2 years 9 months for an average.

TABLE II-C.—Life table data for female *Ateles geoffroyi* (BCI)

Year	X	lx	mx	lxmx	xlxmx
1964.....	4-5	4	0	—	—
1965.....	5-6	4	0	—	—
1966.....	6-7	4	1	4	28
1967.....	7-8	4	0.25	1	8
1968.....	8-9	4	0.25	1	9
1969.....	9-10	4	0.75	3	30
1970.....	10-11	4	0.25	1	11
1971.....	11-12	4	0.25	1	12
1972.....	12-13	4	0.75	3	39
1973.....	13-14	4	0	0	0
1974.....	14-15	4	0.50	2	30
Total.....				16	167

$$R_0 = \frac{16}{4} = 4$$

$$T = \frac{167}{16} = 10.4 \text{ years of production}$$

$$*r_1 = \frac{\log_e R_0}{T} = \frac{\log_e 4}{10.4} = \frac{1.39}{10.4} = 0.133 \text{ young per female per year of a female's life}$$

* r_1 = approximate value since cohort has not ended its life span

the previous data and new data through 1974. A rash of premature deliveries in 1973 retarded reproduction in this colony. An unidentified virus infection was suspected. Reproduction returned to normal in 1974 concomitant with changes in the diet and treatment of the females.

Since young were removed for hand-rearing at various times in the history of the colony, we can say a few important things concerning lactation anestrus. When captive females raised their own young, the interbirth intervals ranged from 22.8 to 31.5 months. If the female gave birth to a pre-

TABLE II-D.—*Reproduction records of Ateles fusciceps robustus females through December 1974*

<i>Consecutive birth dates</i>	<i>Date young removed from mother</i>	<i>Mother-young association prior to next birth (days)</i>	<i>Interbirth interval (days)</i>
FEMALE V			
3 Jan 1962	22 Mar 1962 ^a	—	—
13 Apr 1963	9 May 1964 ^a	78	465
2 Nov 1964	3 Sep 1965	391	568
5 Aug 1966	5 Aug 1966 ^a (Max)	305	641
29 May 1967	Left in colony (Beatrice)	0	297
29 Nov 1969	4 Dec 1969	915	915
4 Aug 1970	Left in colony (Junior)	6	249
20 Jun 1972	20 Jun 1972 ^b	685	685
17 Sep 1973	17 Sep 1973 ^b	0	443
11 May 1974	Left in colony (David)	0	237
FEMALE H			
18 Apr 1962	18 Apr 1962 ^b	—	—
17 Apr 1963	5 Sep 1963	0	364
27 May 1964	11 Apr 1965	141	405
26 Apr 1966	26 Apr 1966 ^a (S or April) ^c	319	699
20 Apr 1967	29 Jan 1969	0	359
25 Nov 1969	25 Nov 1969 ^a (Binky)	649	949
8 Jun 1970	8 Jun 1970 ^b	0	196
FEMALE R			
27 Jun 1964	4 Jul 1964	—	—
13 Dec 1965	4 Jan 1966	7	544
FEMALE B (Beatrice)			
25 Feb 1973	11 Mar 1973 ^a (Princess) ^d	—	—
28 Oct 1973	28 Oct 1973 ^b	7	245
23 Jul 1974	Left in colony (Eddie)	0	269
FEMALE S			
19 Nov 1973	19 Nov 1973 ^b	—	—

^a Taken for hand-rearing.

^b Stillborn, premature.

^c Returned to group July 1967.

^d Reintroduced to group October 1973.

Arrived 17 May 1961: Male M (Macho) \geq 4 years; female V \geq 4 years; female H (Happy) \geq 3.5 years; female R \sim 2 years. Female R died 19 October 1966; female H sold in 1971 with Max. S and J formed as a pair separate from M, V, and B in September 1974. Females V, Happy, and R listed simply as A, B, and C, respectively, in Eisenberg, 1973.

TABLE II-E.—Compositions of study groups for *Ateles fusciceps*

Study year and grouping	Adult		Subadult		Juvenile II		Juvenile I		Infants		Σ	ΣΣ
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		
1964	M	V,H,R							1	1	6	
1965							1				4	6
Group 1	M	V,R									2	
Group 2		H						1				
1966	M	V,R,H							All young removed for hand-rearing			
1967											1	7
Group 1	M										4	
Group 2		V,R,H							Q	B	2	
Group 3							Max	S				
1968											5	7
Group 1	M	V,H						Q	B		2	
Group 2					Max	S						
1970	M	V,H				S		B	J		6	
1971	M	V		S		B	J				5	
1972	M	V		S	J	B					5	
1973	M	V,S		B	J						5	
1974												
Group 1	M	V,B				P			D,E		6	8
Group 2		S		J							2	

mature foetus and subsequently gave birth to a full term infant, the range of interbirth intervals was 7.9–14.7 months. Given a gestation of 7.7 months, it then seems conclusive that the female giving birth to a full term infant will pass into a lactation anestrus for a period of 15.3 to 24 months. On the other hand, if she does not sustain lactation, she can come into estrus within 8–10 days of losing her infant. Variability in interbirth interval for females losing their young at birth may result from a complex of possible factors, but some seasonality in conceptions is suggested from our records (Eisenberg, 1973).

The composition of study groups has varied from year to year. Table II-E includes a synopsis of study group compositions.

Medical Histories

NUTRITION

As noted in an earlier study (Eisenberg and Kuehn, 1966), the breeding colony of *Ateles geoffroyi* at the Vancouver Zoological Park was characterized by a certain amount of bone deformation developing in young animals born to the group.

Two out of seven subadult animals exhibited deformities suggestive of ricketts. Although this particular colony had access to an outdoor enclosure on almost every day of the year, the extreme overcast to which this area is subjected may have reduced the efficiency of vitamin D₃ synthesis by the animals when they were exposed to sunlight. Dietary deficiencies with respect to Ca and P levels may have accentuated the situation.

The colony of *Ateles fusciceps* in Washington, D. C., was allowed access to an outdoor enclosure for approximately 6 to 7 months of each year; during the remaining months the animals were held indoors. From 1962 through 1965, 7 young were born to the founding females. One young was stillborn and the other 6 were raised by their mothers for varying periods of time. No mother succeeded in rearing her young beyond the age of 12 months and all of the young surviving to an age of greater than 4 months began to exhibit signs of nutritional bone disease (for a review of the problems, see du Boulay and Crawford, 1968).

Encouraged by the Hamptons' research on marmosets (Hampton, Hampton, and Landwehr, 1966) Dr. C. W. Gray and myself instituted the following prophylactic procedures. Ultraviolet

lamps were installed over the indoor cages and the animals were subjected to UV radiation for 15 minutes during 2 periods of each day, one in the morning and the other in the afternoon. In addition, vitamin D₃ supplement was added to the food. This procedure was adopted not only for the spider monkeys, but also the woolly monkeys housed under the same conditions. In order to study the efficiency of this procedure, we agreed to take the first two young born to the colony for hand-rearing, using vitamin D₃ supplements in the feeding formula. These young were taken in April and August of 1966 and were successfully reared with the D₃ supplements, and no bone deformities resulted. In accordance with our plan, the next two young born were allowed to remain with the mothers. These were born in April and May of 1967. Both young were successfully reared to weaning.

Since our 1966 and 1967 efforts, diets have been improved and changed so that now the colony is fed on Zu-Preem Marmoset Diet, which contains adequate amounts of D₃ supplements. Ultraviolet radiation has been discontinued. Ten births have occurred from 1966 to 1973; 4 were stillborn and the factors underlying these stillbirths have yet to be determined. Three of the young were hand-reared and three were mother-raised.

We have concluded that successful rearing of spider monkeys demands either that the animals have continual access to outdoor cages and be exposed to sufficient sunlight so that requisite amounts of vitamin D₃ can be synthesized by the animals or the animals must be fed a diet which includes vitamin D₃ as a supplement. In addition, we recognize that the protein content of the diet must be reasonably high and that sufficient calcium and phosphorus be present in the food so that the D₃ can effectively promote recovery and deposition of these minerals from the dietary intake. Adequate amounts of vitamin D₃ must be provided in dietary supplements in the absence of direct sunlight, particularly for neotropical primates, which is confirmed in the review by du Boulay and Crawford (1968).

LEAD POISONING

Although lead-free paint has been used in the primate house for more than twenty years, certain

deaths in our primate collection were diagnosed as chronic lead toxicity by Drs. R. Sauer and B. Zook. The specimens were able to ingest lead-bearing material from old layers of paint which had been covered by new applications. In contrast to macaques and mangabeys, *Ateles* was not significantly affected by lead poisoning because of its low tendency to allogroom, manipulate artifacts, gnaw bars, and/or pick at the walls. (For details, see Zook, Eisenberg, and McLanahan, 1973.) The old primate house was completely renovated in 1972-1973.

Hand-rearing Procedures for *Ateles fusciceps robustus*

Initially for Max and April (= S), a basic milk formula, Bermol, was employed with the following supplements: Vitamin D₃ drops, one per day added to milk mixture at a specified feeding, and a calcium additive to the milk mixture in the proportion of one teaspoon of calcium for each two ounces of milk (Calcium DCP 340). The Bremol mixture was prepared in the ratio of 4 tablespoons of Bremol for each 8 ounces of water. At 85 days of age, the young animals were introduced to solid food. A commercial baby cereal, Pablum, thinned with the milk mixture, was offered in small quantities from a plastic spoon. Small slices of fresh pear were also offered, as were grapes and banana. At 110 days of age, Vitamin D₃ supplement in the milk was discontinued and the young animals were exposed to ultraviolet radiation for 10 minutes twice a day for about a month's time; after that, ultraviolet radiation was given for 20 minutes once a day. The lamp was maintained at approximately 2 meters distance from the floor of the cage. Bottle feeding was discontinued gradually and complete weaning was achieved by approximately 10 months of age.

A second spider monkey hand-rearing technique involved the preparation of Esbilac, 3 parts Esbilac to one part water. The newborn animal did not accept this mixture, and the formula was changed to one part Carnation evaporated milk to 2 parts water. This formula with vitamin additives appeared to work very well and steady weight gains were made as indicated in Figure 23.

In some cases the hand-reared specimens were

initially held in an incubator at approximately 80°F for maintaining their body temperature during the first months of life. However, in two cases the young animals were wrapped and kept with the handler even at the handlers' bedtime, thus insuring adequate warmth.

Yet a third hand-rearing technique included the following procedures. The animal was initially placed on a diet of Carnation milk mixed with water, one part milk to two parts water. Until about 10 days, between 2 and 2½ ounces of liquid were consumed in each 24-hour period. The amount consumed increased to 3½ ounces by 16 days of age. Baby formula custard (Gerbers) was introduced into the diet at 20 days of age in the

amount of 6 teaspoons per day. Milk intake was held at approximately 3½ ounces per day. At 27 days of age, milk intake was increased to 4¼ ounces; the custard intake was maintained at the same level. By 35 days of age, milk intake had increased to 4¾ ounces per day, given in three separate feedings, and custard intake had increased to 10 cc. Milk intake was increased to approximately 5 ounces thereafter and held constant, while the custard intake was raised to approximately 15 cc per day. Pieces of biscuit and banana were introduced at 45 days of age into the diet and gradually increased over the next three months. Weaning procedures were scheduled as in the first case.

Appendix III

Infant Vocalizations, Their Physical Measurements and Variation

As in Appendix I, the sonograms of vocalizations are prepared as figures indicating the manner in which the measurements of duration, frequency and intervals were performed. The tables corre-

sponding to the figures include the actual tabulations of the measurements. Refer to pages 90-91 ("Expressive Movements" and "Vocalizations") for a full discussion.

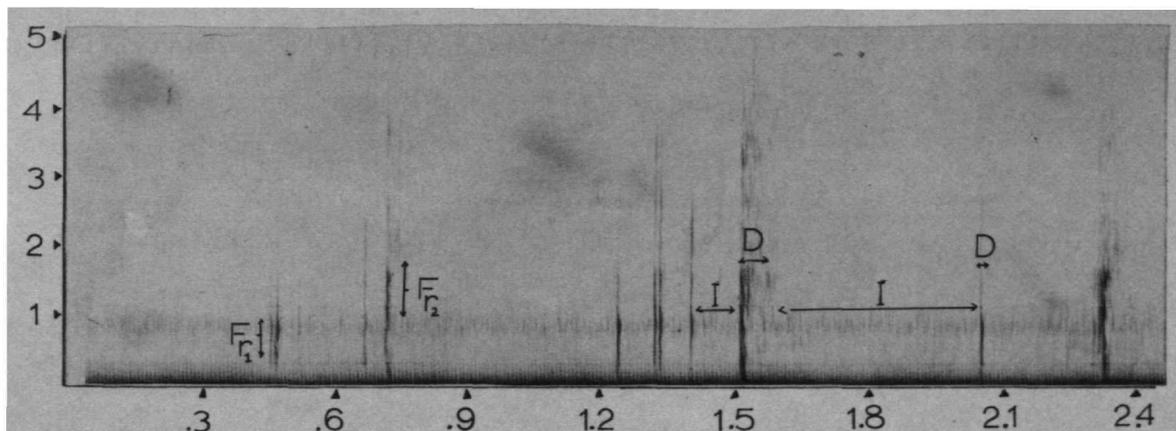


FIGURE III-1.—Chuckle series, ook-ook precursor, *Ateles fusciceps*, 14 days of age (letters define the measurements as portrayed in the tables of Appendix III; ordinate in Khz, abscissa in seconds).

TABLE III-A.—Chuckle series, ook-ook precursor, *Ateles fusciceps*, 14 days of age

Series	D (sec)			I (sec)			Av. frequencies (Khz)	
	n	Av.	S.D.	n	Av.	S.D.	Fr ₁	Fr ₂
I	13	0.027	-	14	0.176	-	0.75	1-1.6

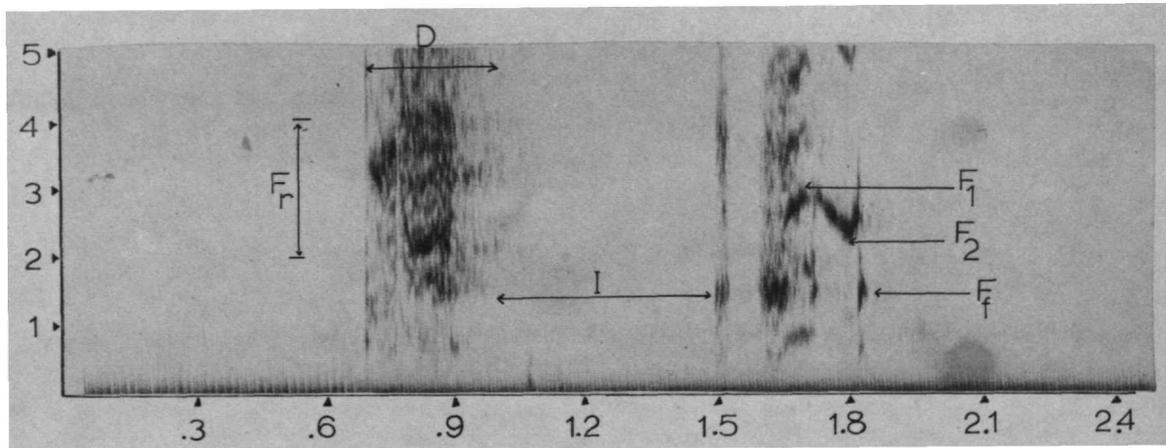


FIGURE III-2.—Screech (left) and ee-ah (right) call by 14 day old *Ateles fusciceps*.
(Ordinate in Khz, abscissa in seconds.)

TABLE III-B.—Screech and ee-ah by young *Ateles fusciceps*

Call type	D (sec)			I (sec)			Av. frequencies (Khz)			
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F ₃	F _f
Screech (14 days)	1	0.3	-	-	Variable	-	-	2.5	2	2.2-3.6
Ee-ah (14 days)	1	0.3	-	-	Variable	-	1.5	2.8	2	-
	4	0.25	-	2	0.49	-	-	2.6	1.2	-
Screech (5 months)	8	0.56	±0.19	6	0.25	±0.09	-	1.2	2.1	1.2-3.8

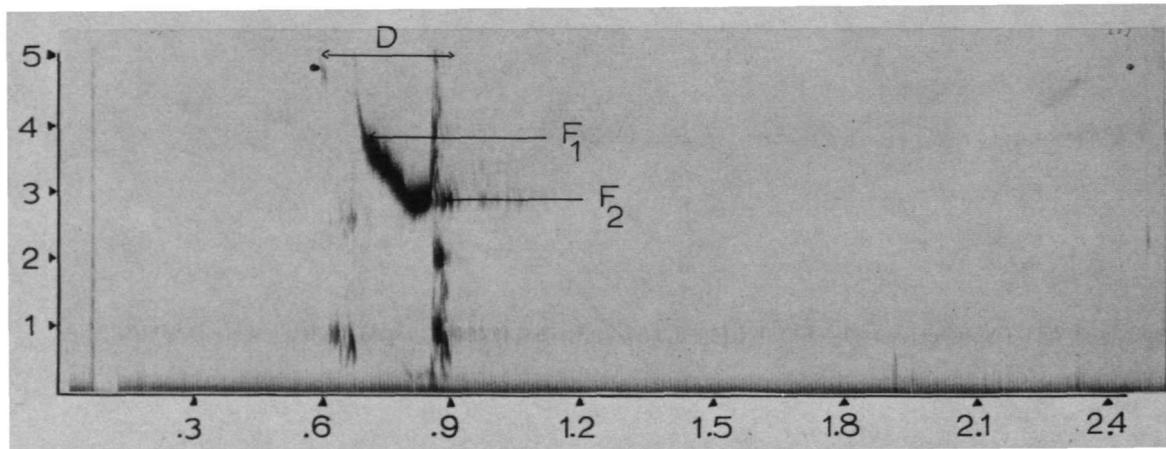


FIGURE III-3.—E-ak (awk) call by *Ateles fusciceps*, 14 days old.
(Ordinate in Khz, abscissa in seconds.)

TABLE III-C.—E-ak (awk) call by *Ateles fusciceps*, 14 days old

Series	D (sec)			I (sec)			Av. frequencies (Khz)	
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂
I	2	0.165	-	-	Variable	-	3	1.6

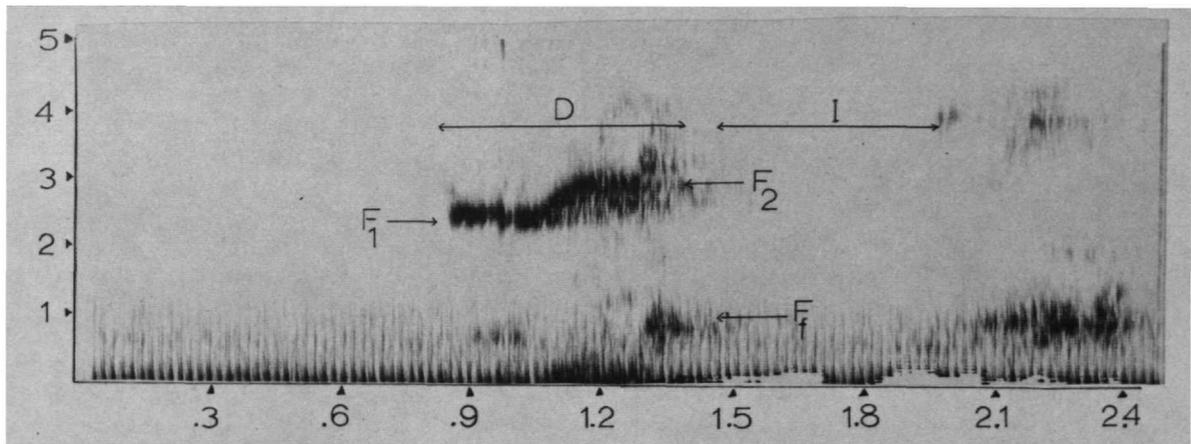


FIGURE III-4.—Eeeeah call by 5 month old *Ateles fusciceps*.
(Ordinate in Khz, abscissa in seconds.)

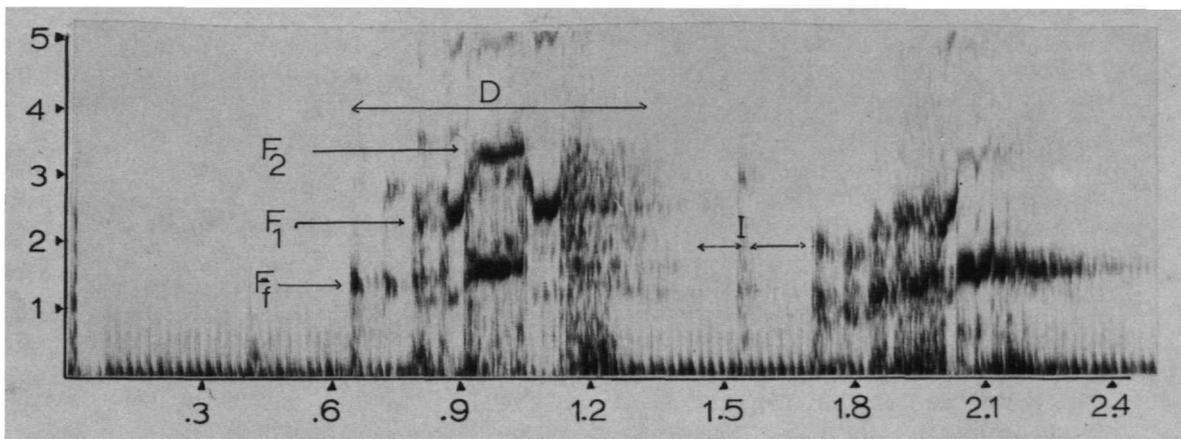


FIGURE III-5.—Ee ah to ah eē alternations, a separation call by 5 month old *Ateles fusciceps*.
(Ordinate in Khz, abscissa in seconds.)

TABLE III-D.—Eeeeah call at 5 months of age

Species	D (sec)			I (sec)			Av. frequencies (Khz)		
	n	Av.	S.D.	n	Av.	S.D.	F ₁	F ₂	F _f
<i>A. fusciceps</i>	2	0.58	-	1	0.63	-	0.9	2.3	3.4
	2	0.63	-	1	0.31	-	1.3	2.4	3.4

Appendix IV

Behavior Patterns for Captive *Lagothrix* and *Alouatta*

Within the body of the text, frequent comparisons of the repertoire of *Ateles* were made with the behavior patterns of the larger cebids, *Lagothrix* and *Alouatta*. Although these genera have been studied by a variety of workers, *Lagothrix* has not been the subject of an intensive field study and *Alouatta* has not been studied in detail under captive conditions. Williams (1965, 1968) has described the behavior of captive *Lagothrix* in detail, and Schifter (1968) has documented marking behavior, as well as the development of the young in the Zurich Zoo. *Alouatta palliata* was studied intensively on Barro Colorado Island by Carpenter (1934) and later by Altmann (1959), Collias and Southwick (1952), and Chivers (1969). In all these studies aspects of free-ranging behavior are described and interpreted. In spite of the preceding work, the sonographic analysis of vocalizations has not been performed.

Since the study of *Ateles fusciceps* in captivity necessitated the development of standardized data recording procedures, it was deemed desirable to extend the same procedures to captive groups of *Alouatta* and *Lagothrix*. The resulting data could then be used for base line comparisons of *Lagothrix* and *Alouatta* with *Ateles*. Thus this appendix presents the results of an observation series performed by L. McLanahan with our captive cebids, together with a preliminary analysis of vocalization patterns carried out by J. F. Eisenberg. These data should be considered in conjunction with the monographic material of Carpenter (1934) for *Alouatta* and Williams (1968) for *Lagothrix*.

Behavior Patterns in *Lagothrix lagotricha*

METHODS AND SUBJECTS

A group of three *Lagothrix lagotricha* was observed during June and July 1973. One adult male

≥9 years old, one adult female ≥8 years old, and their 10-month-old offspring comprised the group. For the month of June, the group was housed indoors in a small 3 × 2 × 3 meter cage of wire mesh to prevent the infant's having contact with lead-painted bars and artifacts (Zook, Eisenberg, and McLanahan, 1973). On 3 July the group was moved outdoors to a lead-free cage measuring 4 × 4 × 5 meters. Numerous branches and artifacts were provided for climbing and brachiation. The animals were fed and watered daily between the hours of 9:30 and 11:00 a.m.

The group was observed for 30 minutes twice daily. Observation periods were balanced so that significant activity samples from each of the daylight hours between 7:30 a.m. and 6:30 p.m. might be recorded within the two-month period. The total observation time was 30 hours.

Quantitative data was taken on all interaction and individual behaviors, such as displays and self-care. A frequency measure was taken for vocalizations. All observations were recorded manually and summarized weekly. For prolonged periods of interaction, such as copulation, a detailed description was made in addition to the recording of duration and frequency measures of the accompanying behaviors.

PATTERNS OF SOCIAL BEHAVIOR

Expressive Movements

HEAD-SHAKE.—While looking at partner, the animal moves its head from side to side rapidly. The head-shake can accompany grappling, vigorous playing in infants, and agonistic encounters.

GROOM SOLICITATION.—The body is turned to expose the pectoral area and one or both arms are extended to touch the partner.

GRIMACE.—A facial expression in which the lips are partially opened to expose the lower teeth

row and canines. It is seen most frequently in adult males during displays, long call sessions, and vigilant behavior. Adult animals tend to grimace during defecation.

BRANCH-SHAKING.—An arousal-related movement.

CAGE-SHAKING.—Performed by grasping a part of the cage with the hands and feet and alternately pushing against and pulling away from it rapidly.

LEAPING.—A series of springing movements. The movement is usually correlated with a high degree of arousal in the performer. It can be done in either a quadrupedal or bipedal posture.

ANAL DRAG.—A movement in which the animal, while sitting erect, drags its anus across a flat surface by pulling itself forward with the arms. The movement is usually 2 to 3 seconds in duration.

ANAL RUB.—A movement similar to the anal drag except that the animal remains in one place and moves its anus in a circular pattern over a flat surface for approximately 2 seconds.

CHEST RUB.—The animal drags its chest over a flat surface for anywhere from 1 to 175 seconds.

BACK ROLL.—The animal, lying on its back does a series of side to side rolls for approximately 5 seconds. Each bout is comprised of 5 to 7 rolls.

LIP SMACKING, TOOTH CHATTERING, AND RELATED MOVEMENTS.—While looking at the partner, the lips are retracted to expose the upper and lower teeth rows striking against each other repeatedly. This gesture is often accompanied by head-shaking when the animal is begging for food. It is interpreted as an appeasement and contact-promoting gesture when the mouth is pressed against one arm. Head-shaking may also accompany the latter variant.

HEAD ROLL.—The head is moved rapidly in a counterclockwise circle. The movement may occur in 3 or 4 bursts. It may accompany food-begging and also agonistic encounters. In the case of the latter, the grimace may also occur. The head roll has only been observed in the adult male.

Vocalizations

The following definitions apply to sounds produced by adults unless otherwise noted (terminology adapted from Williams, 1967) Tables IV-A, IV-C).

E-OLK.—A sound of approximately 0.05 seconds duration. The call is given prior to feeding and

can be an accompaniment to contact-promoting gestures. The vocalization is uttered most often by the adult female. The lips are slightly pursed in production of the sound (Figures IV-1, IV-2).

SLOW EOLK.—A sound of 1 to 2 seconds duration. It is correlated with feeding and may be uttered during mastication. Only the adult female has been heard to produce this sound (Figure IV-1).

UH-UH (tuff-tuff).—A broken series uttered by an animal that is grappling or is involved in a vigorous play bout. Adult and infant versions of this sound are similar. The head-shake frequently accompanies this vocalization (Figure IV-2).

LONG CALL BOUTS.—A high intensity call uttered by adult animals in a state of arousal. The vocalization has only been heard in the early morning and evening hours. The female and male long calls have the same pitch range and frequency modulation, but the male's call is louder.

LONG CALL SESSION.—Composed of long calls, this session may last for up to 20 minutes and involves one animal, most frequently the adult male. Exposure of the lower canines, excessive salivation, and displaying are components of this activity and indicate a high level of autonomic arousal in the animal (Figures IV-3, IV-4).

Contact and Contact-promoting Patterns

EXTEND.—The act of extending an arm, leg, or the tail to touch another animal.

TOUCH.—Contacting another animal by touching lightly with any part of the body.

EMBRACE.—A gesture which may be either mutual or unidirectional. It involves placing the arms and/or tail around a second animal's body.

ANAL-GENITAL INVESTIGATION.—A pattern whereby the mouth and/or nose are brought near the anal-genital area of another animal.

GROOMING.—This act may be preceded by soliciting. The groomer parts the fur of another individual with its fingers and then either licks or nips the dried skin or fur.

GRAPPLING.—A pattern accompanied by the uh-uh vocalization. Grappling is comprised of several components including wrestling, pushing, mock biting, slapping, and chasing. Grappling can be a prelude to an agonistic encounter.

MUZZLE SNIFFING.—A pattern that may be

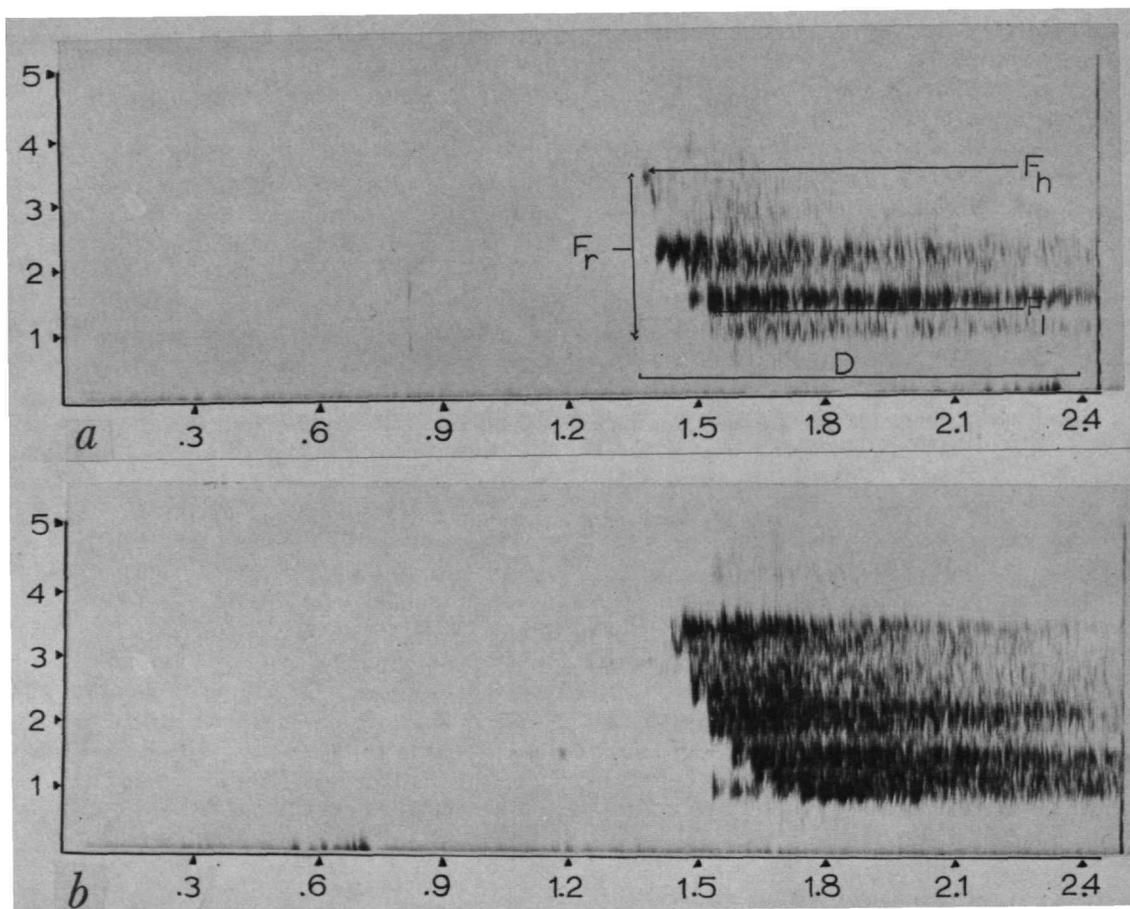


FIGURE IV-1.—Frequency modulated calls of *Lagothrix* (\bar{E} -olk series—nomenclature from Williams, 1967): *a*, slightly modulated form; *b*, modulated form with sidebands. (See also Figure 30.) (Ordinate in KHz, abscissa in seconds.)

TABLE IV-A.— \bar{E} -olk syllables

Syllable type	D (sec)			I (sec)			Frequencies (KHz)			
	n	Av.	S.D.	n	Av.	S.D.	F_h	F_i	F_{av}	F_r
Modulated form with sidebands	2	0.75	-	Variable			2.1	1.3	-	0.8-3.8
Slightly modulated form ..	5	0.21	± 0.08	Variable			-	-	2.4	-
Classic form	8	0.13	± 0.14	6	0.10	± 0.07	3.2	1.2	-	-
	5	0.24	-	Variable			3.4	0.9	-	-

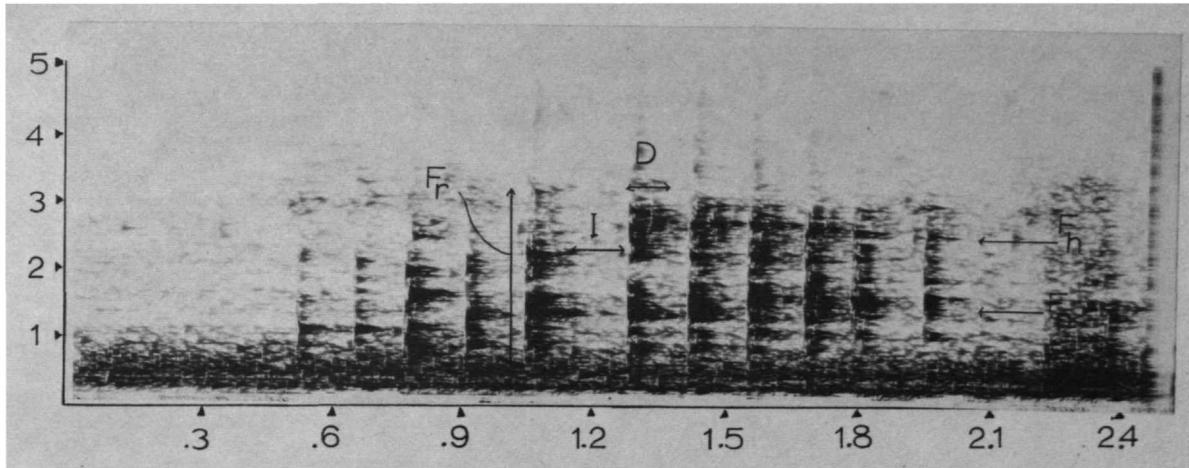


FIGURE IV-2.—Uh-uh or chuckles for *Lagothrix*. (Ordinate in Khz, abscissa in seconds.)

TABLE IV-B.—Uh-uh or chuckles

Species	D (sec)		I (sec)		Frequencies (Khz)		
	n	Av.	n	Av.	F _r	F ₁	F _r
<i>A. fusciceps</i>	11	0.08	10	0.05	2.6	1.5	0.1-3.4

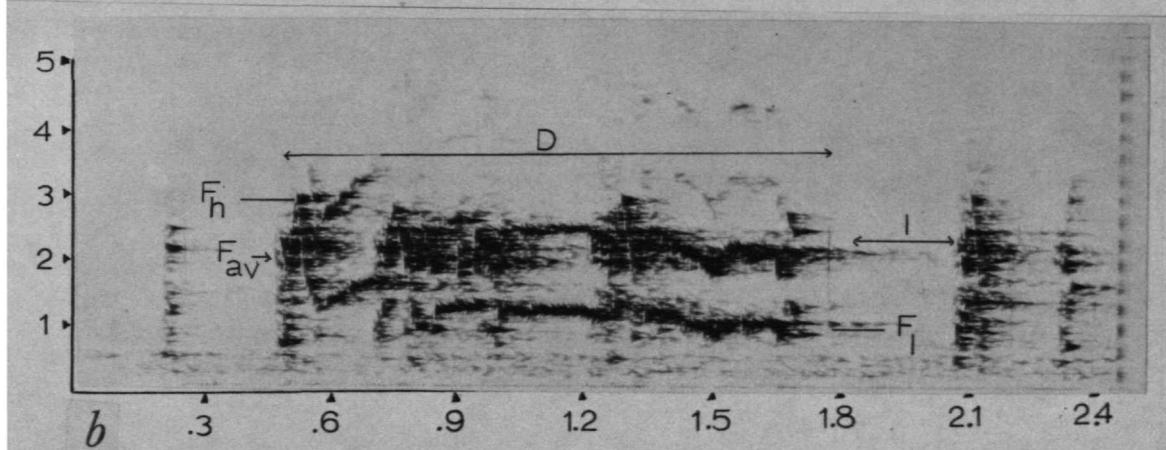
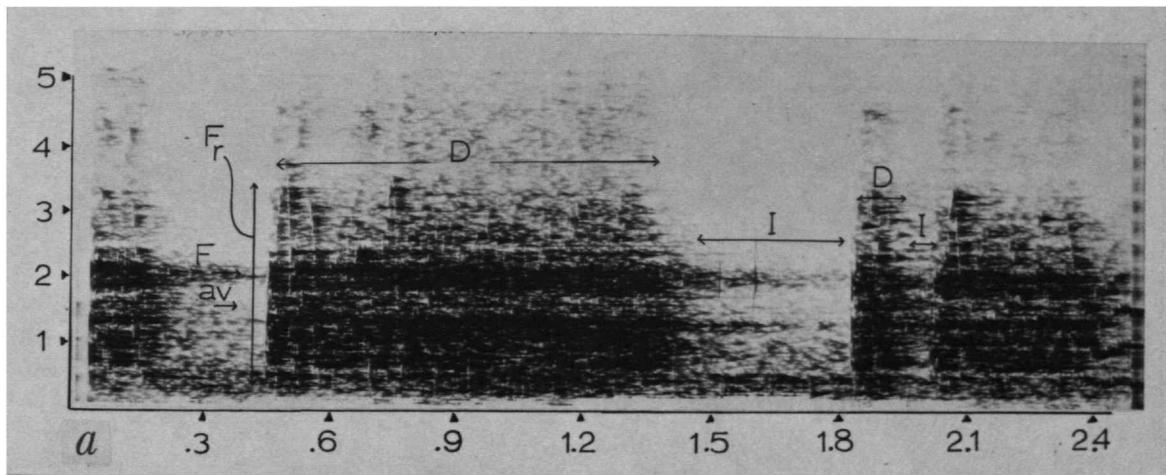


FIGURE IV-3.—Syllable forms employed in long call session by adult male *Lagothrix lagotricha*:
a, roar to bark; *b*, trills with side bands. (Ordinate in Khz, abscissa in seconds.)

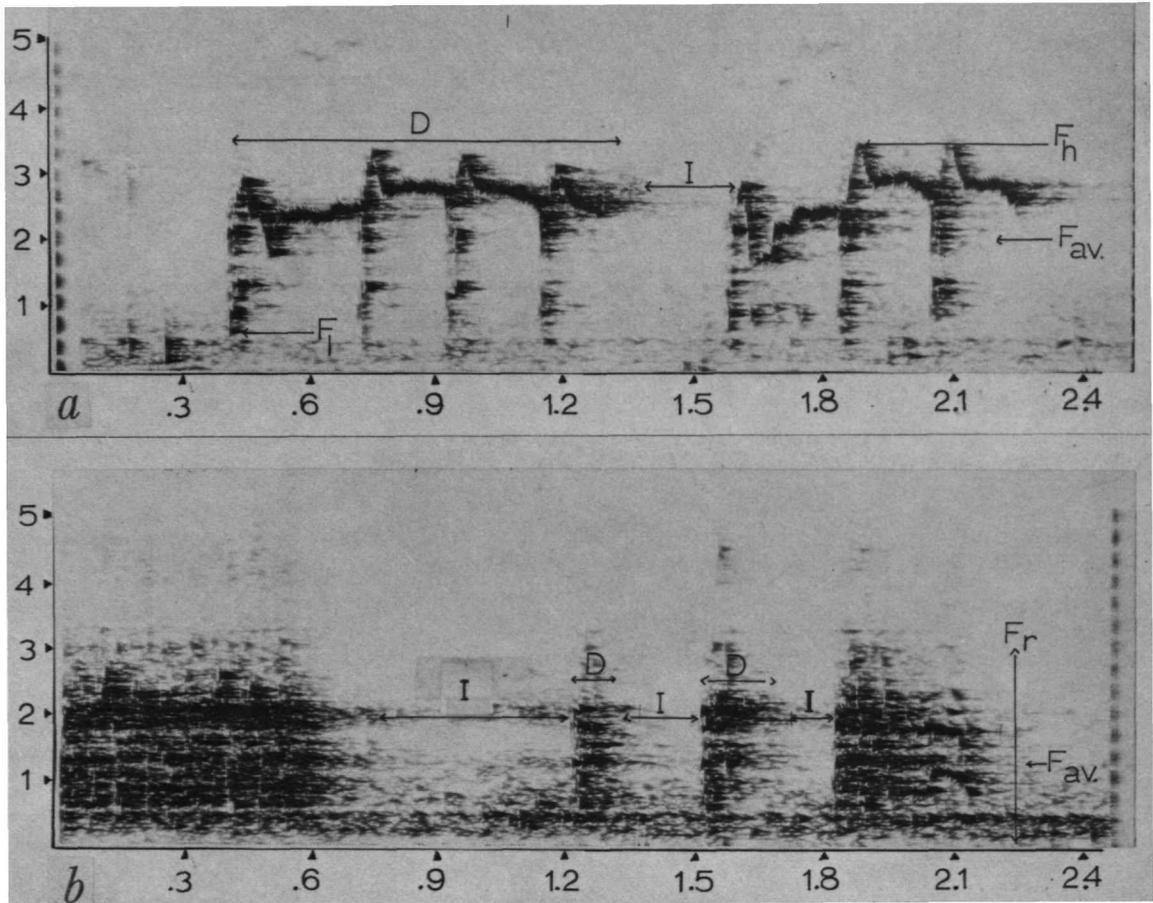


TABLE IV-C.—Long call analyses for *Lagothrix* male

Call type	ROAR-LIKE SYLLABLES (FIGURE IV-3a) AND BARK-LIKE SYLLABLES (FIGURE IV-3b)							
	D (sec)			I (sec)			Frequencies (Khz)	
	n	Av.	S.D.	n	Av.	S.D.	F _r	F(Av.)
Roar	32	0.33	—	27	0.13	—	0.2-3	1.46
Bark	15	0.13	—	12	0.22	—	0.2-3	1.59
	TRILL-LIKE SYLLABLES (CLEAR) WITH NOISE (FIGURE IV-4a)							
	D (sec)		I (sec)		Frequencies (Khz)			
	n	Av.	n	Av.	F _h	F _i	F(Av.)	
Clear	5	0.84	3	0.29	2.7	2.4	2.27	
With noise:								
Series 1	4	0.93	2	0.23	3	0.5	1.68	
Series 2	4	0.79	4	0.19	3.2	0.6	1.74	
Series 3	5	0.63	3	0.30	3.4	0.2	1.24	

either mutual or unidirectional and in which one animal sniffs or licks the muzzle of another. This pattern is frequently correlated with feeding and occurs between the infant and adult female.

Agonistic Patterns

BOUNCING.—A pattern in which one animal raises an arm to hit another, but instead places the arm on the partner's shoulder and leaps up and down two or three times. Frequently seen between the adult male and female.

BOXING.—A series of light blows directed at the head area. This pattern is correlated with food stealing.

Sexual Patterns

Primary sexual behavior in the genus *Lagothrix* is seldom observed in either the field or captive situations. The following three protocols offer a partial description of the sexual behavior of *Lagothrix lagotricha*.

Protocol 1, 28 June 1973, 1430–1440 hours (observer, L. McLanahan): Adult male and adult female. Observer approached and stood immediately outside the cage. Male moved toward observer and began to tooth-chatter. Three minutes later, female approached and extended her arm to observer. Male immediately moved behind female, hooked his legs over her legs and wrapped his arms very tightly around her abdomen. Approximately 5 seconds later, male exhibited a series of 7–10 pelvic thrusts. When female abruptly disengaged him from her; the male was observed to have an erection.

Protocol 2, 2 October 1974, 0905 hours (observer, J. F. Eisenberg): Subadult female around 3 years of age has been allowed to encounter with adult male and his son about 2 years of age. Before the animals are allowed together, an exchange of ee-olk-ee calls are given by the male, generally replied to by the female with an ah-olk or ee-och and finally a slow ee-olk. New female enters; the juvenile male is active, hanging upside down, shaking the bars, and pays a great deal of attention to the juvenile female. The adult male shows broadside quadrupedal standing and little movement. The adult male and juvenile male approach one another, hug. The juvenile male approaches the juvenile female twice. Then the female approaches the juvenile male who is hanging by his tail and sniffs his face. Juvenile male head-shakes. Then they begin to interact, mutually hanging upside down, head-shaking and tagging at each other, giving an uh-uh-uh grading to eek-eek-eek calls interchanged. This is homologous to grappling in *Ateles*. Occasionally, a low and inflected version of the ee-olk will be given. Expressions on the face

include half open mouth with teeth exposed. This expression may grade into a complete "grimace" with the mouth corners retracted on the part of the juvenile male. Suddenly the juvenile female screams, showing open mouth and teeth exposure. The juvenile male runs to the adult male and hugs him.

The two juveniles then ee-olk back and forth. Occasionally the adult male utters a loud and pronounced ee-olk! At the terminal part of the ee-olk there is a vibrato. Then the grappling interaction between the juvenile male and the juvenile female commences again. When grappling during this phase, the lips are often slack when they look at one another. The mouth may be open but only the lower teeth may be showing. Preparatory to grappling the animals may stand bipedally slightly hunched over, the back now assumes an arch; this may be homologous to the bipedal arch of *Alouatta*, but it is relatively unritualized. In this posture the tail often grips the branch of a tree.

During grappling, whichever member of the pair is showing defensive behavior lowers its head and appears to offer the crown of thick black hair, which is then nipped by the other. In this case, the juvenile male is doing most of the nipping. The juvenile female seems to solicit this biting behavior by lowering her body quadrupedally, resting on her arm, with her head facing the opponent, and her lips slack at the corners, with the lower lip drooping slightly. During the grappling that ensues, one partner may look away and, at the time that it looks away, the lips are drawn back and the teeth are displayed. Grappling breaks off.

The female has learned to turn on the drinking fountain and both animals drink while she holds the stream on. Then the female looks at the male and begins tooth-chattering. The juvenile male now has an erection and the juvenile female continues this chattering and lip smacking and extends a hand and touches the young male's genitalia. He moves behind the female and makes several pelvic thrusts at the base of her tail. She continues to remain quadrupedal, turns and looks at the juvenile male while tooth-chattering (lip smacking). He thrusts at the base of her tail. Both are now hanging up. They are not properly positioned but it is definitely play with strong sexual overtones.

The young male now sits to one side of the female. She sniffs at his erection. He manipulates his genitalia. She continues to tooth chatter. He begins rubbing on her thigh with his erection. She hangs up. He begins to show slow jaw champing movements and some tongue movements. She begins to play with his tail. This sexual interaction (it is now 0940) is persisting.

During chattering movements, there may be some lip retraction, thus showing the teeth. The young male *Lagothrix* mounts the female and begins thrusting rhythmically, orientation is nearly correct, but the penis is hitting high at the base of the tail. The juvenile male's legs are not hooked over the female's thighs; however, this is not necessarily a normal orientation. The adult male has been sitting alone and feeding. The amount of tooth exposure during chattering is not as extensive as that shown during a full lip retraction and grimace, but the teeth are definitely visible.

Protocol 3, 20 November 1974, 1235 hours, (observer, L. McLanahan), observations on *Lagothrix*: Adult male, subadult female, and juvenile male have been housed together since 2 October. This sequence involves sexual behavior on the part of the adult male toward the subadult female.

Female to the male, approaching 4 times, sniffs his genital area, and twice presents her genital area to him. Juvenile male approaches adult male and adult female attempting to grapple. Female tooth chatters (lip smacks) whenever in visual and/or physical contact with the adult male. The juvenile and adult male lip smack during their grappling bouts. The female's lip smacking appears to correlate with her sexual receptivity. 3:28* Female to adult male, contacts him, they embrace and huddle. 3:31 Male mounts female. Male is vigilant and lip smacks intensely as he looks at juvenile male who is around 4 feet away. The juvenile male approaches the couple and attempts to grapple with the adult male. All are now lip smacking. Male thrusts briefly and shallowly, but is interrupted by the activities of the juvenile male. 4:43 Two deep thrusts by male. 4:51 Two deep thrusts from a momentary bipedal stance. 4:58 Female leaves. Male was not observed to leg lock during this thrusting bout and intromission probably was not sustained. 5:00 Female follows male and sniffs his genitals approximately every 3 seconds. Female approaches male and presents her genital area to him 3 times. 5:27 to 5:46 Male mounts female, juvenile male disrupts the mount. 5:50 to 6:34 Female approaches male 3 times, attempts to mount him twice and once pectoral sniffs. Then female approaches male, male mounts female, juvenile disrupts mount, all huddle and lip smack. Male leaves. Female approaches male and anogenital sniffs him twice. Male sniffs female's genitalia once. Female follows male with frequent anogenital sniffing. Female presents her genitalia to male. 6:47 Female approaches male, female mounts, holds male and thrusts for about 8 seconds. Male mounts, holds female, female leaves. Male approaches female. Male mounts and holds female, female leaves. 7:06 to 7:23 Male approaches female, holds her in a mount for 17 seconds. Juvenile attempts grappling with male and female. 7:23 Male mounts female, distinguished from previous mounts in that he now locks his legs over her thighs. Juvenile approaches and attempts to grapple with male. 7:23 to 9:30 Male thrusts briefly and shallowly while attempting to grapple with juvenile simultaneously, all are lip smacking. Juvenile calms down

* Minutes and seconds elapsed.

and rests against male for the remainder of the mount. 9:30 Male thrusts deeply 3-4 times, female's lip smacking becomes louder and more rapid. 9:42 Two deep thrusts. 9:53 Male leaves. Copulation judged to have been complete, total intromission time around 150 seconds. 10:03 to 10:43 Female approaches male 6 times, 4 times anogenitally sniffs, and presents her genitalia once. 11:17 The animals are now being fed and all sexual activity subsides.

SOCIAL STRUCTURE IN A CAPTIVE GROUP

The following analyses of quantitative data taken on contactual, grouping, and individual behavior are drawn for purposes of clarifying existing roles and relationships within the observed group so that the processes of group social organization might be better understood.

Autogrooming Analysis

Only the adult female was observed to autogroom and this comprised 5.72 percent of the total time spent in all grooming for all observation periods. The frequency of autogrooming was approximately 25 percent that of the frequency of allogrooming.

Display Analysis

All observed displays were performed by the adult male and in three contexts: (1) during vocalization sessions, (2) in response to loud noises or public disturbance, and (3) just prior to feeding. Three separate displays were noted: cage-shaking, which occurred in response to noise and disturbance; leaping, which occurred prior to feeding; and head-rolling, which frequently occurred between long calls during vocalization sessions. Displaying accounted for only 0.28 percent of the total observation time (see Table IV-D).

TABLE IV-D.—*Display analysis*

Subject	<i>Cage-shake</i>			<i>Leaping</i>			<i>Head-roll</i>		
	<i>Tf</i>	<i>Pd</i>	<i>D</i>	<i>Tf</i>	<i>Pd</i>	<i>D</i>	<i>Tf</i>	<i>Pd</i>	<i>D</i>
Male	102	0.787	1.7	2	0.03	4	15	0.188	4

Tf = total number of times display occurred for all observation periods; *Pd* = proportion of the total duration of all displays for all observation periods; *D* = mean duration of seconds of display.

Marking Analysis

Marking behaviors were exhibited by both the adult male and the adult female and consisted of the anal drag or rub, and the chest rub. The chest rub occurred most often and was observed only in the male. The context in which marking behaviors occurred was not determined. These activities accounted for 0.24 percent of the total observation time (see Table IV-E).

TABLE IV-E.—*Marking analysis*

Subject	Chest rub			Anal drag or rub		
	Tf	Pd	D	Tf	Pd	D
Male	5	0.709	37.5	9	0.132	2
Female	0	0	0	31	0.203	2.6

Tf = total number of times display occurred for all observation periods; Pd = proportion of the total duration of all displays for all observation periods; D = mean duration of seconds of display.

Allogrooming Analysis

Allogrooming comprised 94.34 percent of all grooming observed and roughly 1.35 percent of all summed activity durations. Allogrooming was always observed to be initiated by the female and directed at the infant. It should be noted that the female allogroomed the infant only after he had initiated either an embrace or embrace/suckle. The average duration of an allogrooming bout was 52 seconds. These results indicate a cohesive bond between the mother and infant in spite of the fact that the infant was almost in the weaning stage. An analysis of grappling data provides additional information on parent-infant bonding.

Grappling Analysis

Grappling comprised 2.16 percent of the total observation time and was most frequently observed between the infant and the adult male. All observed grappling bouts were initiated by the infant. That grappling bouts were directed at the adult male roughly 4 times more than at the adult female indicates two possibilities as to its function: (1) a means by which male-male bonding is developed, and (2) a means by which male avoidance-flight,

threat, and agonistic behavior patterns are learned and exercised.

Grappling might also be considered to be instrumental in expanding the mother-infant and father-infant bonding into familial and three-way bonding. Evidence for this is the fact that grappling was the only contactual behavior, besides wrestling, in which all three animals were seen to participate simultaneously (see Table IV-F).

TABLE IV-F.—*Grappling analysis*

Initiator	Recipient	Tf	Pd	D
Infant	Male	14	0.729	162.2
Infant	Female	3	0.167	130
Infant	Male/Female	2	0.103	128.3

Tf = total number of times display occurred for all observation periods; Pd = proportion of the total duration of all displays for all observation periods; D = mean duration of seconds of display.

Embracing Analysis

Embracing comprised 8.02 percent of all observed activity, which is the largest percentage for any contactual behavior observed. That it was most frequently observed between the female and infant further supports the existence of a cohesive mother-infant bond. The activity was always observed to be initiated by the infant. Embracing usually occurred in one of two contexts: during rest or during adult male cage-shaking displays by which the infant was terrified.

DIFFERENT ROLES AND RELATIONSHIP
WITHIN THE CAPTIVE GROUP

The Maternal-Young Relationship

Mother and infant show a close bond. At this age (10–12 months), the infant frequently clings to the mother during rest, suckling, or when frightened. During suckling or embracing, the infant is usually groomed by the mother. The female dispenses more grooming to the infant than to either herself or the adult male. Contact between the mother and infant occurs more frequently and for longer periods of time than it does between either the male and female or the male and infant.

The Paternal-Young Relationship

The most frequent form of father-infant contact is grappling, and it is hypothesized that this grappling may be a means by which specifically father-infant and more generally male-male bonding is developed and also by which male avoidance-flight, threat, and agonistic movements are learned and exercised.

Role of Adult Male

As the grouping data indicates, the adult male is usually by himself at an average distance of 2.5 to 3 yards from either the female or infant. With the exception of occasional grappling and embracing bouts, the male devotes his energy to vigilant behavior. Lengthy morning and evening vocalization sessions and displays, which are correlated with a high degree of arousal, are often the outgrowths of this vigilant behavior.

Behavior Patterns in Alouatta palliata

METHODS AND SUBJECTS

A pair of *Alouatta palliata* was studied for two months for a total of 36 hours observation time. The animals, one adult male ≥ 5 years old and one adult female ≥ 5 years old, had been hand-raised from birth with two other animals and were later introduced to their captive setting.

Housing consisted of a 5 × 1 × 2 yard indoor enclosure equipped with branches, an overhead exercise pole, and two resting benches. The cage was divided into two areas, which were used respectively for feeding and activity. The animals were fed a daily ration of grapes, apples, oranges, bananas, cottage cheese, kale, bread, and strained meat. Water was provided through a push-lever dispenser.

Thirty-minute observation periods were conducted twice daily, during morning and late afternoon hours. Data were recorded manually and vocalizations were taped for sonograph analysis.

PATTERNS OF SOCIAL BEHAVIOR

Expressive Movements

TONGUE-FLICK.—(1) While the animal visually fixates on its partner, the tongue is extended

through pursed lips and rapidly flicked up and down for an average duration of 2.7 seconds. Dependent on context, the tongue-flick can be interpreted as a contact-promoting, greeting, or an appeasement gesture; (2) during auto-investigation, the flicking tongue may be brought into contact with that part of the body under examination; and (3) during contact, one animal may tongue-flick the genitalia, muzzle, or tail of another.

ARCH.—In fixating an animate object, the animal, most frequently the male, drops its head so that the chin is at ground level and arches its back. The movement is usually accompanied by tooth-grinding and eye-squinting and is interpreted to be an aggressive display.

EYE-SQUINT.—Associated only with male aggressive displays, this expression involves half-closure of the eyelids and scalp retraction.

TOOTH-GRIND.—This movement involves full exposure of the upper and lower teeth rows, which are grating against each other in a sideways motion. Tooth-grinding occurs in agonistic encounters and male displays.

BACK-ROLL.—The animal, lying on its back, does a series of side-to-side rolls for an average duration of 10.2 seconds. This movement may be an artifact of captivity.

LEAP AND REAR.—Always associated with the arch, the movement involves the animal's leaping straight up and, upon landing, sliding backwards on the hind limbs. It is an extremely aggressive gesture.

CHIN RUB.—A male behavior pattern comprised of moving the chin back and forth along a surface for the mean duration of 5.5 seconds. It is correlated with a high level of arousal in the animal.

CHIN AND CHEST RUB.—A male behavior in which the chest and chin are alternately rubbed against a flat surface in a circular-horizontal motion. The animal sits erect during this activity. The mean duration is 17.5 seconds.

ANOGENITAL RUB.—A female behavior in which the anus and vulva are rubbed on a flat surface in a sideways motion. Mean duration is 2.5 seconds.

ANOGENITAL DRAG.—A female behavior in which the anus and vulva are dragged across a flat surface for an average of 3 seconds. There is no specific context in which the latter two behaviors are performed.

URINE SNIFFING.—A male behavior in which

urine on the ground is sniffed or licked. An animal may dip its fingers in a urine puddle and lick them clean.

Vocalizations

BARK.—A short sound usually uttered by the male and in stimulation-related situations or prior to feeding. The sound is approximately 0.27 seconds in duration and may be repetitive (“chah”) (Figure IV-5, Table IV-G).

WHINE.—A drawn-out and high pitched vocalization only heard in the female. Approximately 1.0–1.5 seconds in duration, it is correlated with contact situations. The vocalization is uttered with no less than a 2-second interval between sounds.

GROWL.—A sound of approximately 0.5 seconds duration, which may be repeated, and is correlated with aggressive arousal in the male.

SHRIEK HISS.—A shrill sound of 1.5 seconds duration, which is uttered by the female in aggressive encounters with the male. The lips are retracted to expose the upper and lower teeth rows.

The mouth is usually closed, but may be slightly opened.

LONG CALL (Roar).—A drawn out, “legato” vocalization of anywhere from 2–5 seconds duration, which is uttered by both the male and female. It contains elements of the bark and growl and is correlated with an abundance of external stimuli, i.e., crowd noise and vocalizations of other animals. The female’s long call is more high-pitched than the male’s (Table IV-H, Figure IV-6).

E-UH-UH.—A series of sharp, low-intensity sounds averaging approximately 0.3 seconds with a small interval between. This vocalization is uttered by the female during grappling (Figure IV-7).

Ô-EH Ô-EH.—Brief repetitive syllables with great frequency modulation. Often given by the male when alert and in low stages of autonomic arousal. It can serve as a group warning sound (Figure IV-8).

SOFT CHIRP.—Brief high pitched notes given by animals in ambivalent contexts, not necessarily repetitive (Figure IV-9).

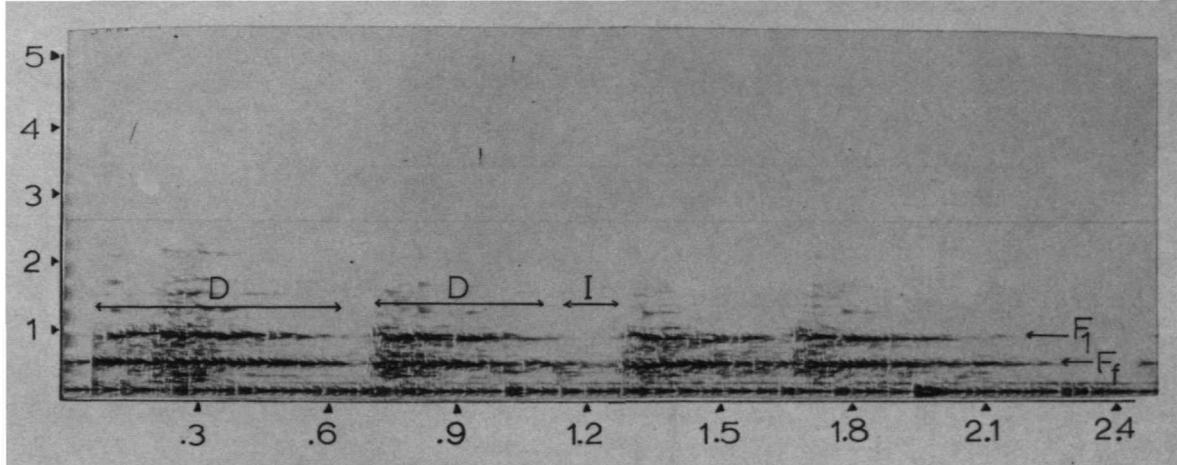


FIGURE IV-5.—Barking by *Alouatta palliata* male (narrow band analysis). (Ordinate in Khz, abscissa in seconds.)

TABLE IV-G.—Bark series preceding roar by adult male *Alouatta palliata*

Species	D (sec)		I (sec)		Dp (sec)		Frequencies (Khz)	
	n	Av.	n	Av.	n	Av.	F ₁	F ₂
<i>A. palliata</i>	10	0.27	6	0.07	3	3.6	0.42	0.84

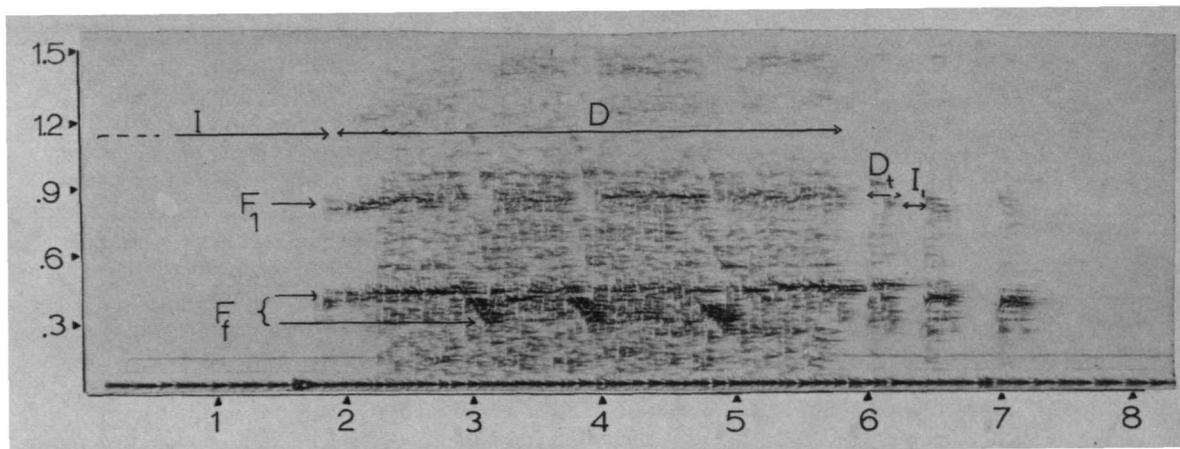


FIGURE IV-6.—Roar by *Alouatta palliata* male. Note modulation and terminal notes (see Table IV-H). (Ordinate in KHz, abscissa in seconds.)

TABLE IV-H.—Undulating roar or long call by male *Alouatta palliata* (fundamental energy is ~0.4 KHz)

Grouping	Terminals				Phrases				Frequencies (KHz)	
	D+		I ₁		D (sec)		I (sec)		F _f	F ₁
	n	Av.	n	Av.	n	Av.	n	Av.		
Single ♂	2	1.25	2	0.1	2	4.8	-	-	0.42-0.3 or 0.42-0.48	0.84-0.7
Chorus	-	-	-	-	4	3.7	4	9.8	0.42-0.3 or 0.42-0.48	0.84-0.7

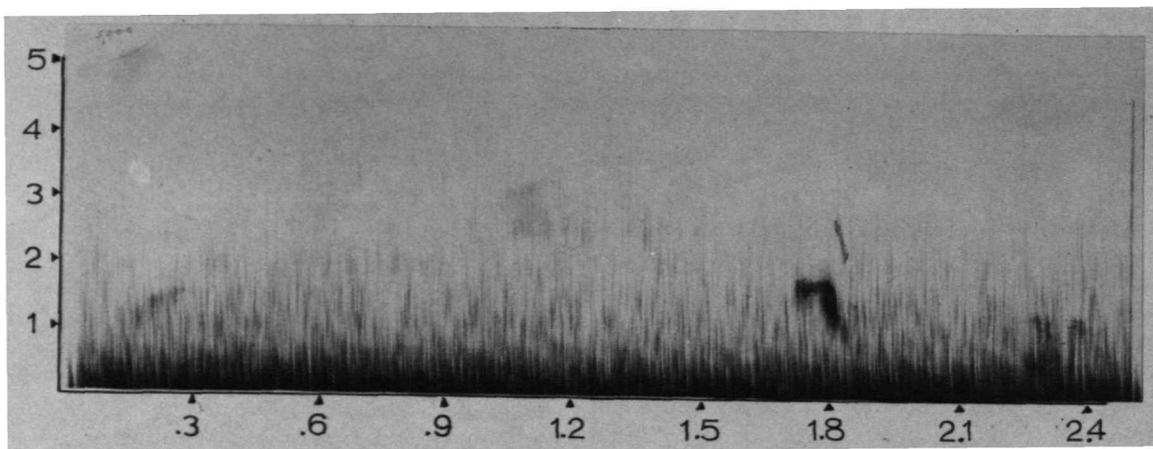


FIGURE IV-7.—E-uh call by *Alouatta* (chuck). (Ordinate in KHz, abscissa in seconds.)

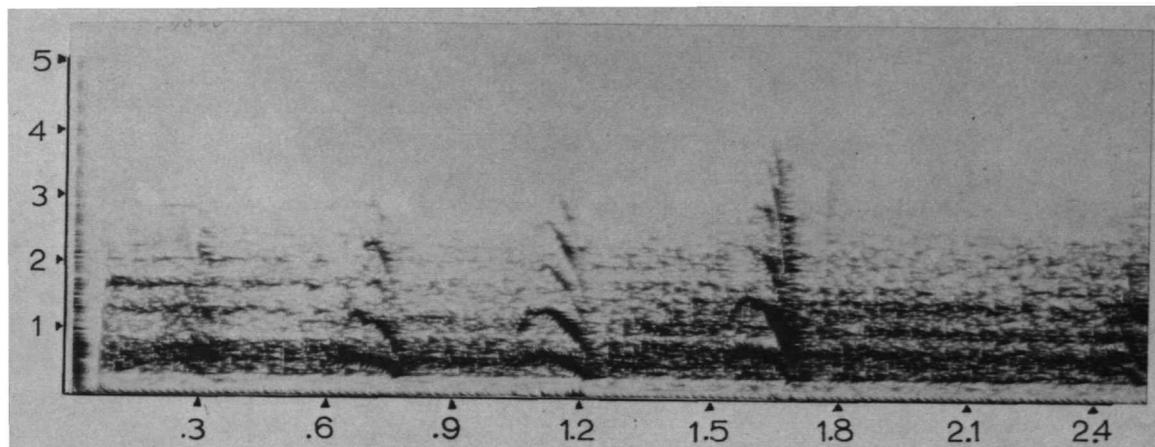


FIGURE IV-8.—Oh eh oh eh series by male *Aouatta*. (Ordinate in Khz, abscissa in seconds.)

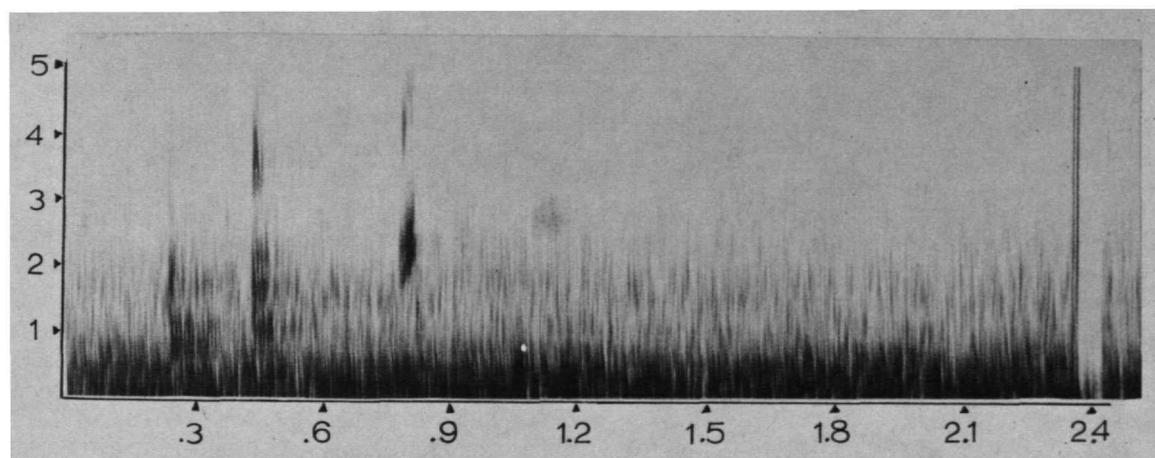


FIGURE IV-9.—Soft chirp series by *Aouatta* approximates a trill. (Ordinate in Khz, abscissa in seconds.)

Patterns of Interaction

Contact and Contact-promoting Patterns

APPROACH.—One animal moves toward another, meanwhile visually fixating on it. No particular facial expression or vocalization may accompany an approach.

TOUCH.—Intentionally contacting another animal with hands, tail, or feet.

TONGUE-FLICK.—Contacting the genitalia, muzzle or limb of another animal by means of a rapid tongue extension.

ANAL-GENITAL INVESTIGATION.—One animal investigates the anus and/or genitalia of another with mouth, nose, or hands.

MUZZLE TOUCHING.—Unidirectional or mutual mouth-to-mouth contact.

GRAPPLING.—A play behavior composed of “mock” agonistic and avoidance patterns and accompanied by the “uh-uh” vocalization in the female and the low “growls” in the male. Muzzling, genitalia nipping, poking, pushing, and tugging are components of grappling behavior.

HEAD-WRESTLING.—Two animals butt and push

each other with their heads.

RUMP-NUDGING.—A male to female wrestle, which is usually subsequent to a female anogenital presentation.

MUZZLE-POKE.—A female-initiated pattern, which involves the poking of a finger into either the mouth or nose of the male. This poke may lead to either grappling or sexual behavior.

LIMB-GRABBING.—A prelude to grappling.

Agonistic and Avoidance Patterns

BITE.—A rapid slash to any part of the body applied by the canines or incisors.

DUCK.—Behavior involving backing off from an encounter and cowering.

THREAT.—A female behavior involving extending the head towards the opponent and hiss shrieking.

Sexual Patterns

ANOGENITAL PRESENTATION.—An animal approaches its partner, turns, and directs its anal and genital areas at the partner for an average duration of 15 seconds.

SCROTAL TONGUE-FLICK.—During presentation, the female flicks her tongue against the male's genitalia. In performing this behavior, the female forms a half-circle around the male. The scrotal tongue-flick accompanies the majority of female presentations to the male.

VULVAL TONGUE-FLICK.—The male approaches the female from behind and flicks his tongue against her vulva.

INTERACTION ANALYSIS

Nonsexual Interaction Forms

Nonsexual interaction refers to behaviors that are initiated by one animal and directed towards another, which usually grade into grappling or sexual behavior and are far less complex patterns of interaction in themselves. They are analyzed under a separate heading. Rump-nudging and head-wrestling are usually sex-related and muzzling, muzzle-handling, and limb-grabbing are grapple-related (Table IV-I).

TABLE IV-I.—*Nonsexual interaction analysis*

Activity	Subjects*	Σf	Σd	Pd	D
Head-wrestle	♂-♀	4	177	0.558	44.2
Rump-nudge	♂-♀	2	28	0.088	14
Muzzle	♂-♀	4	7	0.023	1.8
Muzzle-handling	♀-♂	8	81	0.253	10.1
Limb-grabbing	♀-♂	3	24	0.076	8

* First sign initiates, second is recipient; Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; Pd = proportion of all allo-activity time spent in a given activity; D = mean duration of activity in seconds.

Anal-Genital Investigation Analysis

Anal-genital investigation accounted for 0.5 percent of total observation time and this was the largest percentage of any observed contactual behavior (Table IV-J). Further evidence for such an imbalanced participation in sexual behavior is exhibited in an analysis of the anogenital presentation (Table IV-K).

Anogenital presentations were most frequently observed subsequent to such allo-activities as muzzling, muzzle-handling, and limb-grabbing. As the compound behaviors analysis indicates (Table IV-L), the scrotal tongue-flick was often an accompaniment to these presentations.

"Compound Behaviors" (Table IV-L) refers to two or more separate activities, which are participated in sequentially during one interaction bout. They accounted for 0.21 percent of total observation time and were interpreted to be ambivalence related.

TABLE IV-J.—*Anal-genital investigation analysis*

Subjects*	Σf	Σd	Pd	D
♂-♀	10	62	0.095	6.2
♂	1	3	0.046	0.5
♀-♂	17	147	0.225	8.7
♀	68	442	0.675	6.5

* First sign initiator, second sign is the recipient.

Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; Pd = proportion of all allo-activity time spent in a given activity; D = mean duration of activity in seconds.

Note that the female spends roughly 600% more time in auto-investigation than the male and about 200% more time in allo-investigation.

TABLE IV-K.—*Anogenital presentation*

Subjects*	Σf	Σd	D
♀-♂	29	403	2.7

* First sign initiator, second sign is the recipient.
 Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; D = mean duration of activity in seconds.

TABLE IV-L.—*Compound behaviors analysis*

Subjects*	Σf	Σd	Pd	D	Activities
♀-♂	3	71	0.258	23.6	Presentation/scrotal tongue-flick
♀-♂	2	87	0.316	43.5	Presentation/grapple
♀-♂	5	117	0.425	23.4	Allogroom/grapple

* First sign initiator, second is the recipient.
 Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; Pd = proportion of all allo-activity time spent in a given activity; D = mean duration of activity in seconds.

Tongue-flick Analysis

For each of the three separate contexts in which it occurs, tongue-flicking is hypothesized to have a different function. It can be an appeasement or greeting gesture when it accompanies partner-fixation; it can have a cleaning and testing function when it is used against parts of the animal's own body; and it can be a method of ascertaining receptivity and promoting contact when it is used against parts of the partner's body. Table IV-M presents an analysis for all instances in which tongue-flicking can occur.

TABLE IV-M.—*Tongue-flick analysis*

Subjects*	Σf	Σd	Pd	D	Circumstance
♀-♂	19	156	0.389	8.2	Scrotal
♀-♂	36	165	0.412	4.6	Fixation
♂-♀	2	27	0.067	13.5	Vulvar
♂-♀	1	2	0.005	1	Fixation
♀	3	36	0.089	3	Vulvar
♂	7	15	0.037	2.1	Scrotal

* First sign initiator, second is the recipient.
 Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; Pd = proportion of all allo-activity time spent in a given activity; D = mean duration of activity in seconds.

Note that female to male scrotal and fixational tongue-flicks account for the largest percentages of total tongue-flick time.

Grappling Analysis

Second to anal-genital investigation, grappling accounted for the largest percentage of total observation time and was the only contactual behavior in which male and female participation was almost equal. It should be noted (Table IV-N) that sequential measures are very low in comparison with those of other contactual behaviors.

TABLE IV-N.—*Grappling analysis*

Subjects*	Σf	Σd	Pd	D
♂-♀	8	222	0.513	27.7
♀-♂	9	212	0.487	23.5

* First sign initiator, second is the recipient.
 Σf = total number of times activity occurred; Σd = total number of seconds for each activity class; Pd = proportion of all allo-activity time spent in a given activity; D = mean duration of activity in seconds.

INDIVIDUAL BEHAVIORS

Displays

Because these animals had been hand-raised, they were extremely responsive to keepers and sometimes to visitors, positive and negative reactions to a familiar face were registered in the form of frequent and vigorous displays, occasionally accompanied by specific vocalizations.

The inverted quadrupedal display was observed only in the male and occurred most frequently in the early morning and afternoon hours when he was involved in vigilant behavior. The display is labeled "inverted" because the animal would climb rapidly along an overhead pole in an upside-down posture.

Olfaction-related Behaviors

Olfaction-related behaviors were recorded on the basis of their possible connection with female receptivity. It was hypothesized that as the female became more solicitous and initiated more contact a quantitative rise in female anogenital marking and male urine-sniffing would occur. Table IV-O presents data on anogenital marking, urine-sniffing, and contact behaviors recorded during the same time spans.

Although significant conclusions cannot be drawn between contact- and olfaction-related behaviors on the basis of quantitative changes, differences in the intensity with which the animals participate in the separate behaviors can be determined. Table IV-O illustrates that the female initiates 89.3 percent of all contact, yet 37.2 percent of all olfaction-related behavior. Two hypoth-

eses can be drawn: (1) Since male olfaction-related behavior does not increase with solicitation behavior in the female, but rather remains relatively stable, it may have a territorial and not an investigative function, and (2) when the female is receptive, it may be that instead of the male initiating contact with her, she initiates contact with him on an even greater scale.

TABLE IV-O.—*Marking and contact behavior analysis*

4 Jun		11 Jun		20 Jun		28 Jun		10 Jul		18 Jul	
Tf	33 (♀)	AGI	134 (♀)	Tf	123 (♀)	Tf	20 (♀)	AGI	104 (♀)	AGI	56 (♂)
Tf	7 (♂)	CB	117 (♀)	AGI	161 (♀)	CB	103 (♀)	Tf	275 (♀)	AGI	29 (♀)
AGI	210 (♀)	AA	157 (♀)	CB	30 (♀)	AGI	23 (♀)	AA	40 (♀)	CB	76.5 (♀)
AA	188 (♀)	CC	52 (♂)	CC	174 (♂)	SU	8 (♂)	CC	118 (♂)	AA	52 (♀)
CC	98 (♂)					AD	2.5 (♀)	SU	0.5 (♂)	CC	22 (♂)
SU	7 (♂)					CC	26 (♂)	AD	2 (♀)	AD	12.5 (♀)

Tf = tongue-flick; AGI = anal-genital investigation and presentation; AA = allo-activities; CC = chin and chest mark; SU = sniffing urine; AD = anal drag; CB = compound behaviors; (♀) = female is initiator; (♂) = male is initiator.

Description: Contactual behaviors include grappling, compound behaviors, allo-activities, anal-genital investigation, anogenital presentation, and tongue-flicking. All figures represent directional measurements.

SUMMARY

A captive pair of *Alouatta palliata* was observed twice daily for two months. Expressive movements, postures, and vocalizations were described and interpreted. Patterns of interaction were analyzed quantitatively with the following conclusions being drawn concerning social roles and structure: (1) The male expends a large amount of time and energy in vigilant behavior and associated displays. (2) Male-female interaction is most often initi-

ated by the female. (3) Grooming is of reduced importance in social behavior. (4) Sexual activity is initiated by the female and most often in the form of the combination genital presentation and tongue-flick to scrotum. (5) Marking and other olfaction-related activities are performed regularly by the male and are not correlated with the female's estrous cycle. (6) Male domination in the form of ritualized mounting and supplanting is not present in *Alouatta*.

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In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

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