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THE BEHAVIOR OF
ATELES GEOFFROYI
AND RELATED SPECIES

(WITH SIX PLATES)

By

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THE BEHAVIOR OF
FATELLS GEOFFROY
AND RELATED SPECIES

W. H. S. RAY

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(WITH SIX PLATES)

INTRODUCTION

The study of primate behavior experienced a renaissance in the past ten years, and today a concerted effort is being made to study primates in both field and laboratory settings. The major focus of recent effort has been on the anthropoid apes and the Old World ground-dwelling macaques and baboons. The only monographic studies of Neotropical primates include the pioneer efforts of Carpenter (1934) on *Alouatta* and the recent study by Moynihan on *Aotes*. Although the howler monkey has been the subject of several recent publications the remainder of the New World primate genera have virtually escaped attention.

In order to extend the descriptions of primate behavior we undertook a preliminary study of the spider monkey, *Ateles*. We wished to approach this study in both a field and a captive setting in order to develop refined techniques for quantifying behavior and also to observe the effects that captivity had on the expressed behavior patterns of the animals. In the laboratory special emphasis was given to the forms of auditory and visual communication. The zoo setting allowed a quantitative description of the social structure and a determination of some of the mechanisms responsible for group coordination and cohesion. The field observations served as a control situation for testing the hypotheses generated by the captive studies.

The study of primate social behavior need not be an end in itself. In fact it is highly desirable to integrate the specific conclusions reached through the study of one primate species not only with the studies of social behavior in other primates but also with the studies of other orders of mammals. To this end the discussion sections have been used to integrate the observed trends in primate behavior with those trends discernible in other mammalian taxa.

THE BEHAVIOR PATTERNS OF *ATELES*

METHODS AND SPECIMENS

A colony of four *Ateles* was established in the laboratory at Vancouver on August 2, 1963. Judging by the descriptions in Kellogg and Goldman (1944) three species were represented: a male and a female *A. belzebuth*, designated A and C respectively; a male *A. paniscus*, designated B; and a female *A. geoffroyi pan*, designated D. These specimens were judged to be adult at the time of acquisition. Since they were purchased from a commercial dealer, no accurate information with respect to origins or past histories could be ascertained.

The animals were maintained in individual cages measuring 4 x 4 x 4 feet. Each cage was provided with an overhead exercise bar and a bench for resting and sleeping. The sides, top, and bottom of the cages were of wire. The specimens were fed and watered in the morning and late afternoon. Their food ration consisted of fresh fruits and vegetables, nuts, bread, and a liquid vitamin supplement. Cooked hamburger was offered once a week and three of the specimens accepted this meat supplement readily.

The animals were housed in a heated room, 15 x 18 feet. In this same room was the exercise cage, 5 x 10 x 8 feet, which contained a swing. Approximately every second day each subject was released into this large cage, giving him space and implements for exercise. The exercise cage was also utilized as an encounter arena. Two animals could be released into the cage simultaneously and the resultant interaction recorded.

The encounter series was initiated a week after the arrival of the animals. All combinations of male-female and female-female encounters were run once in order to formulate a description of the behavioral elements involved in their social interaction. From August 29, 1963, to January 1, 1964, a formal series of encounters was run according to the following plan. The observer sat in full view

of the animals and verbally recorded the interaction patterns with a tape recorder. The verbal descriptions were then transcribed on paper with a 10-second time interval signal. Thus a measure of the temporal patterning of the behaviors could be made. Any sustained behavioral unit was recorded as occurring once if it was less than or equal to 10 seconds in duration. Short-term activities of less than 5 seconds having a clear onset and termination could, however, be counted twice or more within a given interval of 10 seconds.

From January 3 to March 17, 1964, the subjects were observed from an adjoining room through a pane of one-way glass. In this way the bias induced by the observer was removed and certain aspects of the animals' sexual behavior could be noted.

The period of observation was not fixed and an encounter was sampled over intervals ranging from 10 to 40 minutes. During the weeks when the animals were allowed to encounter, not all encounters were recorded on tape. Photography, both still and moving, as well as handwritten notes of interaction patterns, and tape recordings of vocalizations were made during the encounter periods and supplemented the formal recordings. Altogether 52 encounters were studied and of these 34 were verbally recorded in detail. On April 10, 1964, the colony was disbanded.

To supplement the controlled observations in the laboratory we have also introduced data from observations and recordings made at the Vancouver Zoological Gardens (see pp. 29-31) and the U.S. National Zoological Park. At the National Zoological Park the following specimens were available for study during the fall and winter of 1964-65: a group consisting of a mated pair of *A. belzebuth* with their single offspring and three adult female *A. geoffroyi* and a group of four adult *A. fusciceps robustus*. The *A. fusciceps* group consisted of one male and three females. One female had an infant born during the study and a second female had a juvenile with her during part of the study.

DESCRIPTION OF THE BEHAVIORAL ELEMENTS AND THEIR FUNCTIONAL CONTEXTS

In this section the units of behavior displayed by *Ateles geoffroyi* will be defined and interpreted. The behavior patterns are similar for all four species observed and no attempt will be made to enumerate species differences systematically. The field observations pertinent to the functional interpretation of the behavioral units will be introduced at this time.

MAINTENANCE BEHAVIOR

LOCOMOTION

Ateles employs four primary modes of locomotion: the quadrupedal crossed extension pattern, the bipedal run or walk, leaping, and brachiation. Descriptions of locomotion are complicated by the fact that the prehensile tail, as well as the limbs, is involved in arboreal activity. Free-living spider monkeys seldom descend to the ground, but in captivity terrestrial locomotion is common (table 10).

During terrestrial activities the animals employ a typical crossed extension pattern of quadrupedal locomotion with the fore and hind limbs of the opposite sides of the body in synchrony. They may, however, gallop with the fore and hind limbs alternately striking the ground. The bipedal mode of locomotion is adopted for short periods and the arms are often held up at head level to maintain balance. During both bipedal and quadrupedal locomotion the tail may be held in an S shape or wrapped around the animal's body.

During arboreal locomotion the tail is constantly employed to grasp branches and provide support whether the animal is moving quadrupedally or bipedally and even when brachiating (figs. 1 and 2). When the animal is moving bipedally in the trees it is surrounded with branches so that the hands and tail are continually providing support. The animal thus is able to distribute its weight over several small branches and twigs and effectively support itself at the extremities of tree crowns. Brachiation and leaping are employed during rapid, arboreal progress. Leaping may involve a vertical descent to a lower level in the foliage, and leaps of 15 to 25 feet are not at all uncommon. When climbing vertically the animals employ either a crossed extension synchrony of limb movements or a series of hops. The hop involves an alternate extension of the body while supporting with the hind feet, followed by a grasp with the forefeet, and pullup while releasing the hind feet.

In addition to the common methods of locomotion, the animal may slide along a tree branch on its stomach, chest, and forearms while propelling itself with the limbs. In captivity an animal may adopt a scooting method of locomotion where it propels itself with the arms while sliding on its rump or thighs. This latter behavior pattern is common in infants and juveniles (table 10).

MANIPULATION OF THE ENVIRONMENT

The hands, feet, teeth, lips, and tail are all employed in feeding and in testing objects. The genus *Ateles* is characterized by the

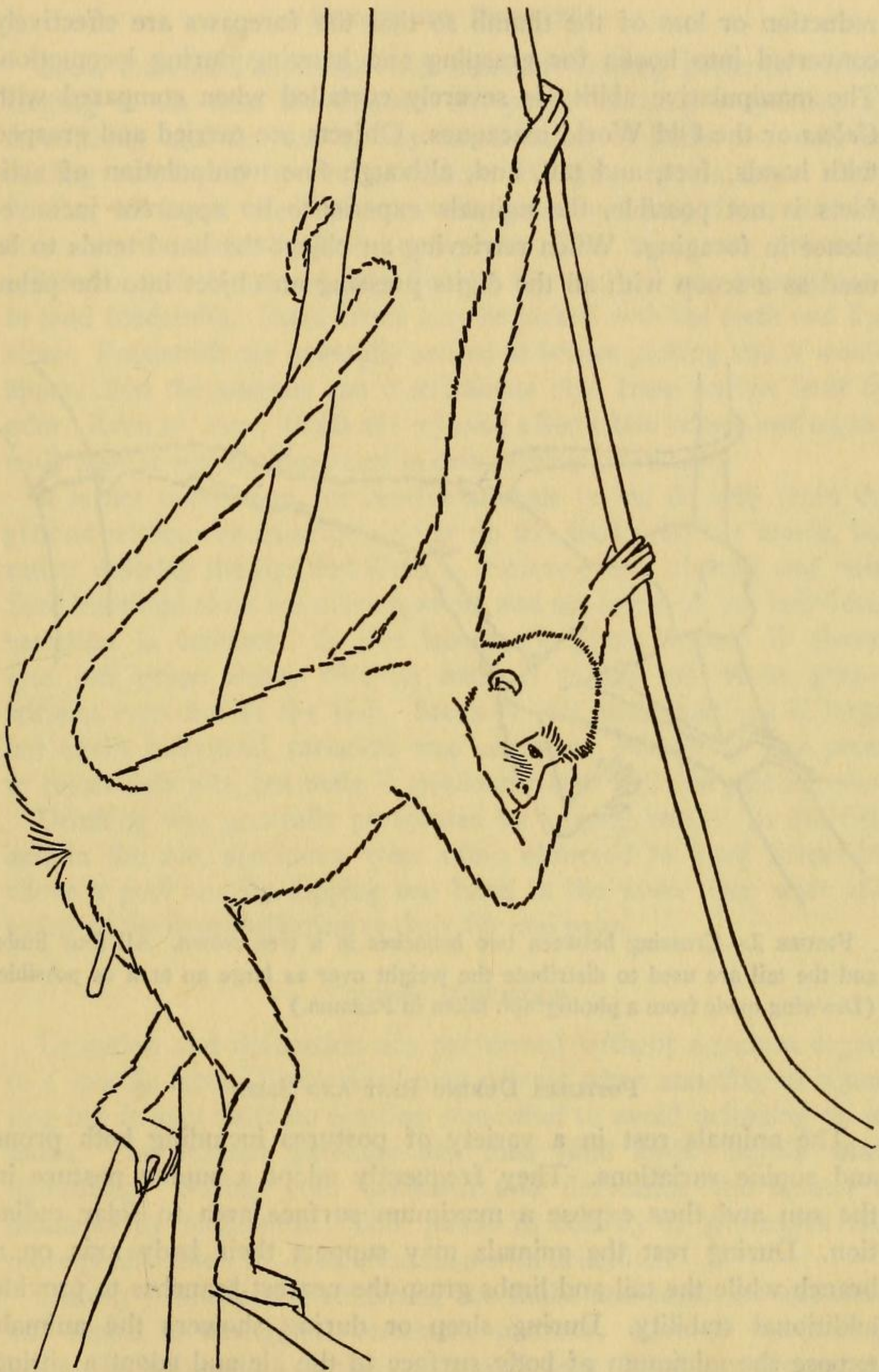


FIGURE 1.—Hanging by the forelimbs and the tail. Note the clitoris of this female *A. geoffroyi*. This is the most obvious visual character for differentiating the sexes. (Drawing made from a photograph taken in Panama.)

reduction or loss of the thumb so that the forepaws are effectively converted into hooks for grasping and hanging during locomotion. The manipulative ability is severely curtailed when compared with *Cebus* or the Old World macaques. Objects are carried and grasped with hands, feet, and tail, and, although fine manipulation of artifacts is not possible, the animals experience no apparent inconvenience in foraging. When retrieving an object the hand tends to be used as a scoop with all the digits pressing an object into the palm.

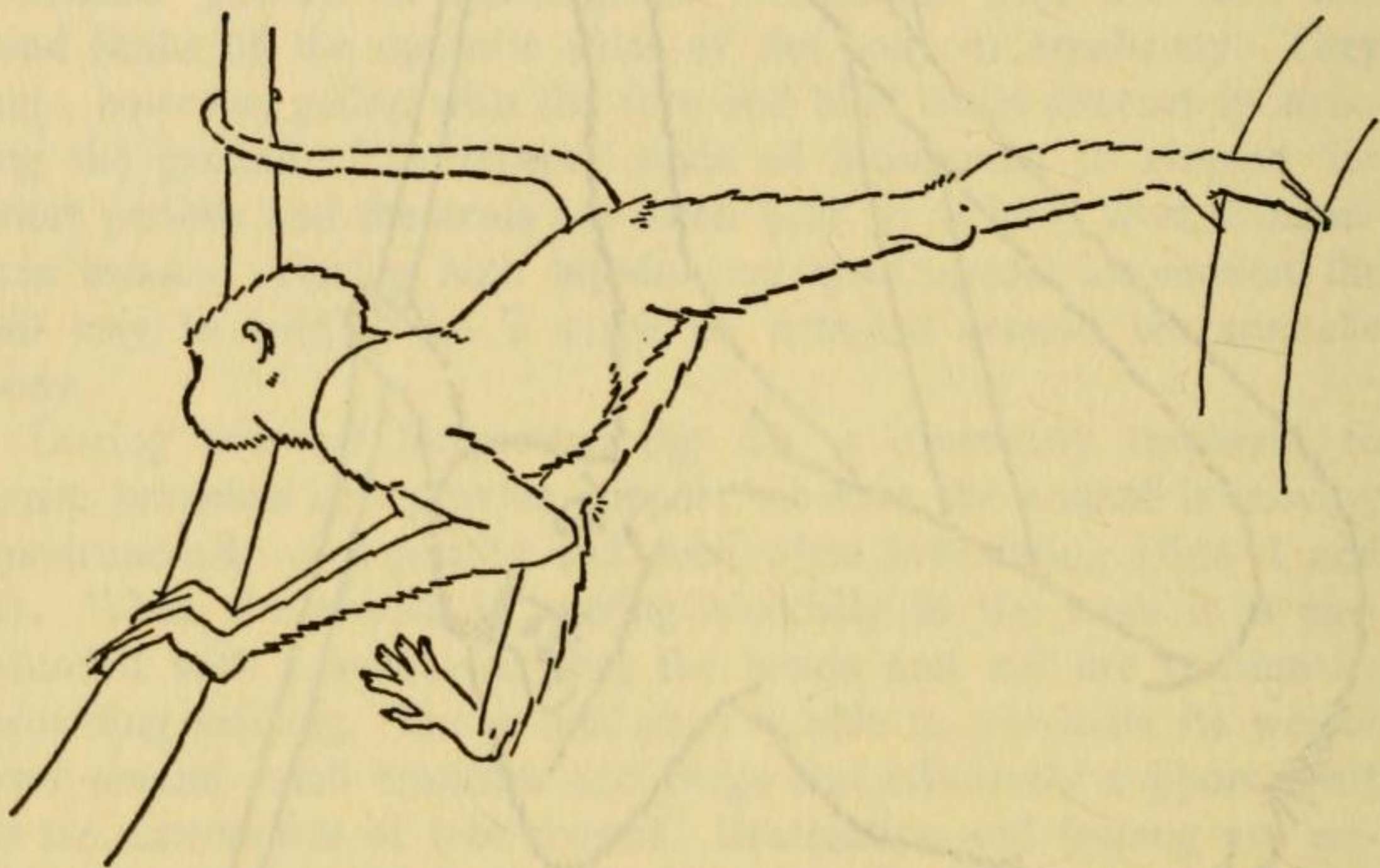


FIGURE 2.—Crossing between two branches in a tree crown. All four limbs and the tail are used to distribute the weight over as large an area as possible. (Drawing made from a photograph taken in Panama.)

POSTURES DURING REST AND SLEEP

The animals rest in a variety of postures including both prone and supine variations. They frequently adopt a supine posture in the sun and thus expose a maximum surface area to solar radiation. During rest the animals may support their body axis on a branch while the tail and limbs grasp the nearest branches to provide additional stability. During sleep or during showers the animals expose the minimum of body surface to the air and adopt a sitting position with their arms wrapped around their legs while their heads are lowered onto their chests. Two or three animals often sleep together, embracing each other while doing so.

FEEDING AND DRINKING

Great individual variation was noted in feeding patterns. While feeding in the field the animals are prone to hang suspended by three limbs and the tail or any combination of limbs and tail, including suspension by the tail alone. Hanging upside down while feeding on fruits effectively prevents juice and pulp from running down on the animal's limbs and chest. The hands are primarily utilized to pick fruits and nuts, but the feet and tail may be employed to hold foodstuffs. Small fruits may be picked with the teeth and lips alone. Foodstuffs are generally sniffed at before picking and it would appear that the animals can discriminate ripe from unripe fruit by odor. Even so, many fruits are rejected after a bite or two and apparently taste is equally important in determining palatability.

It is not uncommon for captive animals to eat directly from the ground without necessarily picking up the food with the hands, but rather utilizing the lips and teeth to retrieve pieces of fruit and nuts. Seed hulls and rinds are often spat out and not ingested, but individual variation is common. In the laboratory group female D always spat out grape skins, whereas male B would eat whole grapes without rejection of the skin. Seeds or pits were spat out if large, but again individual variation was common. Female D was prone to reject date pits, but male B swallowed over half the pits ingested.

Drinking was generally performed by lapping water. In the field and in the zoo, specimens were often observed to hang suspended above a pool and by dipping one hand in the water they were able to lap up the drops adhering to their fur and palm.

COMFORT MOVEMENTS

Urination and defecation are performed without apparent regard to a specific locus. The animal may urinate when standing or squatting but it may shift its position somewhat to avoid urinating on its limbs. The animals generally flex their hind limbs slightly when defecating. During both urination and defecation the animal is momentarily motionless. This pause in activity is prolonged and more predictable with defecation than with urination.

During yawning and stretching the limbs and torso are extended and flexed in the typical vertebrate patterns. Care of the coat is primarily a function of the hands and feet. Most carnivores, rodents, and ungulates employ the tongue, teeth, and lips in this care of the body surface, but *Ateles* relies less on the mouth as a cleaning organ and more on the hands. The fingers may be licked after

feeding and the fur also may be licked, but the most common comfort movement is scratching. Scratching may involve either the hands or the feet, and generally the whole hand or foot is rubbed over the surface to be "scratched." Discrete finger movements may be employed in scratching, but it is far more common for the lower surface of the fingers or toes, as well as the palm or sole, to be employed. A self-grooming pattern involving the mouth and hands does occur, but it is infrequently shown. This grooming pattern involves parting the fur with the fingertips and licking the exposed skin, or removing foreign particles with the lips, tongue, or teeth. If an animal has been bitten it treats the wounded area with similar movements—parting the fur and licking the bite. The animals may rub their bodies against branches or, in the case of captive animals, against artifacts such as wire or wooden posts. The mouth may be rubbed on leaves after feeding, and the chest may be rubbed on branches. A frequent movement distinct from scratching includes stroking downward with a forepaw from the pectoral gland (pp. 18, 26) to the abdomen. This has been termed the *pectoral stroke*.

Ateles also engages in sunning, which has been described on page 6. Sunning generally occurs in the early hours of the morning after feeding or in late afternoon. If the animals become wet during a rainstorm they generally sun themselves whenever the first opportunity presents itself. The pectoral stroke is often associated with sunning, and one is led to hypothesize that the secretions from the pectoral gland may be deliberately spread on the fur during exposure to the sun. If these secretions are reingested when the fur is licked, it is possible that the pectoral gland secretions are involved in the synthesis of some essential dietary supplement. Further research is necessary to clarify this point.

Self-manipulation of the external genitalia is not common either in females or males. The pendulous clitoris of the female is often examined but little attention beyond tugging or licking is shown to the external genitalia. During an erection the males may touch their penises or lick them from time to time but no induced ejaculations were observed.

Young animals frequently exhibit finger-sucking.

Several patterns are included in this subsection which remain ambiguous as to their function. These include urinating on the fingers and spitting on the fur. Occasionally female C was observed to place her hand in the stream of urine which she was releasing. The urine-soaked fingers were licked slightly and no further at-

tention to the hand was noted. Spitting on the fur involved a repeated expulsion of saliva by C onto the hair of her abdomen or thighs. This saliva was then spread with tongue or fingers. Urinating on the hands was noted with captive *Cebus* (Fiedler, 1957). Ulrich (1954) noted excessive salivation in *Lagothrix* accompanied by smearing the saliva on the cage walls and then rubbing the breast in the deposited saliva.

PATTERNS OF SOCIAL BEHAVIOR

EXPRESSIVE MOVEMENTS

1. Head shake.—While looking directly at the partner the head is moved back and forth in the horizontal plane. This pattern was seen in the field and captive settings. It accompanies an initial contact or a renewed contact where the animal is ambivalent in its approach. It may also occur when a contact situation is about to break up as a result of mixed agonistic tendencies on the part of the other animal. Head shaking could be elicited from our captive specimens when human observers imitated the movement.

2. Turn away.—This movement may involve the head only or head and body. It was frequently shown by an animal apparently indifferent to the approach of another.

3. Grooming solicitation.—The whole body is turned exposing the back and the animal sidles toward the partner. Such a movement is to be distinguished from the simple turning away.

4. Look at.—Obvious meaning. Again the head alone or the whole body may be involved.

5. Grimace.—A facial expression involving partial opening and retracting of the corners of the mouth combined with raising the upper lip, thus exposing the teeth. This expressive movement was seen in the field, zoo, and laboratory. It may be accompanied by a rush, moving away, or a slap; however, the expression itself is often sufficient to induce moving away in an approaching animal. The signal value for the grimace appears to alter with experience. In the encounter series the effect of the grimace in inducing moving away varied for each encountering pair of animals considered (table 1). In the A-C encounter series, the male's grimace had little initial effect in inducing moving away by the approaching female. However, the male did not reinforce the grimace with slaps or chases. After a month, including 10 encounters, a recheck on the signal value of the grimace indicated the male was reinforcing about 40 percent of his grimaces with slaps or chases and achieving a high response

from female C. In the C-B encounter series, the male virtually ignored the grimace of the female in the initial two encounters; however, the female was reinforcing about 50 percent of the grimaces. A subsequent sample indicated a higher response rate by the male and about the same reinforcement level for the female. In the D-B series, the female D often reinforced with bites and slaps, achieving a high level of moving-away responses from the male. In a later sampling, the female's grimace rate had fallen considerably as a result of the stable relationship achieved (fig. 3).

TABLE 1.—*Changing signal value of the grimace.*

Subjects	Initial two encounters			Average of three encounters 20 to 40 days following		
	n	Prop. ma	Prop. reinf.	n	Prop. ma	Prop. reinf.
A to C	9	.22	.00	15	.66	.40
C to B	10	.00	.50	19	.68	.53
D to B	20	.80	.30	6	1.00	.33

Legend: n—total number of grimaces. Prop. ma—proportion of grimaces that induced moving away. Prop. reinf.—proportion of grimaces reinforced by a slap, rush, or bite.

6. Pursed lips.—A facial expression involving an extension of the lips. The teeth are rendered virtually invisible. This expression is assumed during contact-promoting behavior (pl. 1a).

7. Open mouth.—An ambiguously defined expression involving four subtypes. The mouth may be partially or widely opened. In either case canines may be exposed or unexposed. A partially opened mouth with canine exposure differs from the grimace only in that the corners of the mouth are not retracted.

8. Pilo-erection.—Varying degrees of hair erection were noted when the animals were highly aroused. This pattern was not quantified.

9. Shaking the branches (or bars).—A movement performed by jumping up and down alternately flexing and extending all four limbs while gripping a fixed object with the tail.

10. Chin-up.—The face is thrust forward by tilting the neck, presenting a "chin-up" posture.

11. Eye closure.—Eye closure ranged from wide-open eyes with pronounced scalp retraction to eyes almost completely closed. Generalized correlations among selected expressive movements are included in table 2.

VOCALIZATIONS

Unless specified, the following definitions apply to sounds produced by adults. When physical measurements are given the species from which the recordings were made will be designated. Although the vocal patterns appear similar for all species it is not intended that a set of measurements from one species be generalized to all species.

1. Tee tee.—A sound of approximately one-half second duration with the greatest energy concentrated between 2,200 and 4,500 cps (*A. geoffroyi*). Although it may be repeated two to three times, the sound is not repetitive in character. Each individual call consists of three to four pulses, each rising and falling within about .20 seconds over a range of about 2,300 cps. This call is given at the approach of a troop member or familiar attendant and appears to function as a greeting call. The call has been noted for *fusciceps*, *geoffroyi*, and *belzebuth*. (pl. 1b).

TABLE 2.—Correlations among selected expressive movements.

1. Open mouth	
a. Canines exposed	Generally correlated with a direct stare
b. Canines unexposed	Correlated with head shake and varying degrees of eye closure
2. Pursed lips	Variable associations including slitted eyes and head shake but most frequently the brows are raised with concomitant scalp retraction
3. Grimace	Associated with a direct stare
4. Lips almost closed	Associated with partial eyelid closure and the production of high-pitched sounds
5. Head shake	Most frequently associated with pursed lips or open mouth with no canine exposure
6. Chin-up	Can be associated with almost any facial expression and appears to be a concomitant of tensing the throat for high-pitched sounds; it is most frequently associated with slitting of the eyes and the whinny or chirp series

2. Whinny.—A sound of 1.5 to 2.5 seconds in duration. It has a vibrato form with the greatest energy concentrated from 1,000 to 4,600 cps (*A. geoffroyi* and *A. belzebuth*). At any given emission the sound is relatively pure in tone. It is strongly correlated with feeding when the animals are dispersed. It would appear to function in maintaining spatial awareness or assembly, but it does not promote

physical contact (see pl. 3a). The lips are virtually closed during this vocalization. This sound has been noted for all species studied.

3. Chirp series.

a. Slow whinny.—A series of sounds with each element lasting .15 seconds in duration and separated from the next element by an equal quiet interval. The chirps are uttered in a series about 2 to 3 seconds in total duration. The greatest energy lies between 1,700 to 3,300 cps (*A. fusciceps*). The sound is harmonic in structure and repetitive, but the energy is more broadly distributed than is the case with the true whinny. It has been noted in all species and appears to accompany contact-seeking behavior. Generally the chin is up and the lips are virtually closed during this vocalization (pl. 2a).

b. Yip yip.—A variant of the preceding vocalization, which appears under similar circumstances. The lips are pursed and evidently modify the tonal quality of the sound. It was repeatedly noted with *A. fusciceps*.

4. Twitter.—Similar to the preceding but higher in pitch and softer. It is harmonic with the greatest energy at 3,500 and 5,500 cps (*A. fusciceps*). The sounds are less than .1 second in duration and are delivered in a burst of evenly spaced sounds. Each burst lasts about 1 to 2 seconds. Each discrete sound rises and falls over a range of about 500 cps. This vocalization has been noted in adult females and juveniles in a contact-seeking circumstance. It has been heard in *A. geoffroyi* and *A. fusciceps*. (pl. 2b.)

5. Grunt-Trill.—A relatively pure sound with harmonics, consisting of a sustained series of individual pulses. It generally ascends the scale with energy concentrated at 2,000-3,500 cps (*A. fusciceps*) or 1,900-3,650 cps (*A. belzebuth*). The sound may be delivered rapidly with fusion of the individual pulses (pl. 3b) or delivered more slowly with a full recognition of the individual elements. Often the call terminates with a nonharmonic grunt termed the *caw*. The *caw* is discussed separately at the end of this section. Much energy may be contained in the upper harmonics of 8-9,000 cps in the call of *A. fusciceps*. It is generally given when one animal is isolated from another or it may be given when seeking contact.

6. Squeak.—A simple note often repeated and having an average duration of .35 seconds with the energy of the signal concentrated at 3,600 to 4,100 cps (*A. belzebuth*). This sound was given by the captive female C when she was seeking contact with a male but at the same time approaching slowly as a result of a previous rebuttal. It was also given by the female during the initial phases of primary

sexual behavior. The sound was heard in juvenile and adult *A. geoffroyi* in different contexts (see end of this section and pl. 4a).

7. Chitter.—A complex, pulsed sound with several defined harmonics. The sound may be given once or repeated two or three times. Duration ranges from 1.0 to 2.0+ seconds. The energy is concentrated in two major distributions: 1,000 to 1,500 cps and 7,400-7,900 cps.

All species exhibited the sound, and recordings were analyzed for *A. paniscus* and *A. fusciceps*. The sound was always associated with extreme autonomic arousal (e.g., piloerection and labored breathing). The animal would frequently leap at the cage and shake the bars. One could discern definite elements of threat in the behavior (pl. 4b).

8. Ook ook.—A short, grunting sound repeated rapidly. Harmonic structure is blurred; the maximum energy in the signal, however, is concentrated from 1,000 to 1,400 cps. The individual utterances average .28 seconds in duration. This sound is 100 percent correlated with grappling, both in the field and laboratory (pl. 5a). It is recorded for *A. belzebuth* and *fusciceps*, but noted as well for *geoffroyi*. The ook ook varies slightly in its tonal quality depending on the facial expression accompanying the sound production. With the lips pursed the sound is hollow, but, if the mouth is open with the canines exposed while vocalizing, the tone is flat and harsh. This latter expression may be shown before a transition to growling and the accompanying vocalization has been termed the ak ak variant (see p. 16).

Low ook ook.—This differs from the preceding in its low intensity (see p. 19).

9. Bark.—A short but intense sound often repetitive and noted in all species. The duration averages .38 seconds. Although the sound is harmonically structured, the harmonics are blurred. The energy distribution ranges from 500 to 3,400 cps (*A. belzebuth*). This sound is commonly displayed in situations where novel animate stimuli are encountered. In the field it is a common initial response to the presence of human observers (Carpenter, 1935; Wagner, 1956) (pl. 5b).

10. Growl.—A sound of about .5 seconds duration with a blurred harmonic structure. The maximum energy distribution ranges from 700 to 2,600 cps (*A. belzebuth*). The sound was noted in all species and is associated with aggressive arousal (table 3, pl. 6a).

11. Roar.—A sound similar to the growl but longer in duration,

generally exceeding one second. It also is associated with aggressive arousal.

12. Cough.—This vocalization is quite discrete in its onset and termination and has virtually no harmonic structure. The energy tends to be concentrated from 700 to 2,000 cps. It is associated with a strong tendency to rush or slap (pl. 6b).

13. Scream.—A harsh shriek, often repeated. This is given by an injured animal as a result of fighting. It was not recorded but was noted for *A. geoffroyi*.

14. Hiss.—An unvoiced expiration during aggressive interaction.

15. Champing.—Sound produced by striking the teeth together and associated with aggressive arousal.

TABLE 3.—*Vocalization patterns and their associated circumstances.*

Vocalization	Circumstances and Supposed Function
1. Tee tee	Given by a group member at the approach of second member who has been absent for some time; the sound appears to function as a greeting call
2. Whinny	Given by group members at the onset of feeding; the sound appears to function as a feeding call and although it promotes assembly it does not promote physical contact
3. Chirps	Given during contact promoting behavior—often shown between juveniles
4. Twitter	Circumstances and function similar to above
5. Grunt-trill and caw	A sound produced by an isolated animal; function unknown
6. Squeak	Given by an approaching animal, often after it has been repulsed; it appears to function as an appeasement and contact promoting signal
7. Chitter	Correlated with a strong autonomic arousal, generally induced by an alien stimulus
8. Ook ook	Completely correlated with grappling; a low intensity variation accompanies primary sexual behavior
9. Bark	Response to an alien stimulus serves to alert group and focus attention on the responding animal
10. a. Growl b. Roar c. Cough d. Hiss	Agonistic sounds which accompany threat or attack behavior
11. Scream	Response of injured or frightened animal

Additional sounds occasionally heard but not recorded or adequately defined include the following: *oo oo*—a low sound uttered by young and adults; *caw*—heard several times in the field from *A. geoffroyi* and given by an animal isolated from the main group, may grade into the grunt-trill; *low squeaks*—heard between two animals during mutual aid at a crossing point (see pp. 53-54); *rapid squeak series*—approximating a chitter and heard when an infant *geoffroyi* slipped and fell to a lower branch while climbing.

It should be stressed that many of these sounds are heard in conjunction with a second or third sound type. As we have mentioned, the grunt-trill and caw are often associated. In a similar fashion the animals can move from a chirp series to a twitter and from a twitter to a chitter apparently depending on the, as yet undefined, interaction of external stimuli and the motivational state of the animal. Ook ook may grade into a growl or roar but these sound types are generally distinct. The tee tee, whinny, bark, cough, scream, and squeak are least frequently associated with other call types.

The infantile and juvenile sounds are necessary to complete a description of the origin and functional change in the elaboration of the vocal repertoire of *Ateles*. Although our present ontogenetic data are incomplete it would appear that the infant II and juvenile I age classes produce the twitter, squeak, chirp, and chitter sound types. The whinny, bark, cough, growl, and roar appear later on in development. This is not to imply that the infant is incapable of producing all major sound types. In the normal course of development the young animal clings to the mother and is often not presented with a stimulus situation which would elicit the strongly agonistic calls. Thus the brief comments concerning infant and young juvenile calls merely reflect the relative frequency with which the call types were noted.

Table 4 compares the best defined sounds with respect to four characteristics: duration, repetition rate, predominant frequency, and tonal purity. As can be seen, the sounds can be grouped into three classes: sounds with high frequencies and a rather discrete tone; sounds with low frequencies and a blurred harmonic structure or broad spectrum energy distribution; and a class of intermediate sound types. Class A sounds are associated with contact maintenance or contact promotion, whereas Class C sounds are agonistic in part. The series twitter, squeak, tee tee, grunt-trill, and whinny make a related group of sounds that differ chiefly in their duration as do the agonistic series cough, growl, and roar. The Class B sounds of

ook ook, bark, and chitter form in some respects an intermediate group with respect to the four polar attributes of duration, repetition rate, pitch, and tonal clarity. These latter three sounds form a series from short to long and repetitive to nonrepetitive. Bark and ook ook are related to the agonistic sounds with respect to pitch and tonal clarity, whereas chitter is related to the agonistic sounds with its nonrepetitive character. Because of its inherent difficulty in measurement the parameter of sound intensity has been left out of consideration.

TABLE 4.—*Classification of the physical characteristics of Ateles vocalizations.*

Sound Type	Characteristics							
	Duration		Repetitive	Non-repetitive	Dominant Frequency		Clear Tone	Blurred Harmonics
	Long	Short			High	Low		
A.1. Twitter		xxx	xx		xx		xx	
2. Squeak		x	xx		xx		xx	
3. Tee tee		xx		x	xx		xx	
4. Chirp		x	x		x		x	
5. Grunt-trill	x		xx		xx		xx	
6. Whinny	xx		xx		xx		xx	

B.7. Ook ook		xxx	xxx			x		x
8. Bark		xx	xxx			x		x
9. Chitter	xx			x	x		x	

C.10. Cough		xxx		xxx		xx		xxx
11. Growl		x		xx		xxx		xxx
12. Roar	xx			xxx		xxx		xxx

Table 3, insofar as possible, summarizes the correlations between circumstances of occurrence and vocalization pattern, while table 5 includes the correlations between facial expression and vocalization. The configuration of the mouth influences the tonal quality of certain vocalizations. For example, the ook ook has a deep resonant quality when the lips are pursed, but if the animal shifts to an open mouth the sound becomes flat and harsh. This can then grade into a roar if the sound is prolonged rather than pulsed. As mentioned previously the yip yip sound appears to be a variant of the slow whinny with the former sound involving pursed lips and the latter sound accompanying a virtually closed mouth expression.

PATTERNS OF INTERACTION

1. Unspecified patterns.

a. Approach.—One animal moves toward another by any of the described modes of locomotion. Generally the approaching animal looks directly at the other. No special facial expression or sound necessarily accompanies an approach.

b. Move away.—The animal moves away by any of the major types of locomotion. There is no particular associated facial expression or vocalization.

2. Contact and contact-promoting patterns.

a. Extend.—The act of extending an arm, leg, or the body in order to touch another animal.

b. Touch.—Contacting a second animal by touching lightly with the foot, hand, or mouth.

c. Embrace.—This behavior pattern may be mutual or performed by one member of an interacting pair. It involves placing the arms around the body of the second animal.

TABLE 5.—Major correlations of expressions with vocalizations.

Sound Type	Expression					
	Open mouth		Pursed lips	Lips closed or slightly parted	Chin-up	Head shake
	Canines exposed	Canines unexposed				
1. Tee tee				xxx	x	
2. Whinny				xxx	xx	
3. Chirp series			xxx	xxx	xx	
4. Trill			xx	x	xx	
5. Twitter			xx	xx	xx	
6. Chitter		xx	xxx		xx	
7. Squeak				xx		
8a. Ook ook	x	xxx	xxx			xx
b. Ak ak (variant)	xxx					
9. Bark	xx	xxx				
10. Growl-Roar	x	xxx	x			
11. Cough		x	(head jerked up and down)			
12. Hiss	x	x				
13. Scream	xx					
14. No sound	xxxx					

xxxx = very strongly associated (12-15 associations)

xxx = strongly associated (7-11 associations)

xx = often associated (3-6 associations)

x = occasionally associated (1-2 associations)

From a total of 117 recordings

d. Pectoral sniff.—A complex act which occurs only during an embrace. It involves lowering the head and placing the nose or mouth close to the pectoral gland or axilla of the partner.

e. Anal-genital investigation.—A pattern whereby the nose and mouth are brought near to the anal-genital area of the partner.

f. Grooming.—This act may involve soliciting (see p. 9). The groomer parts the hair of the groomed individual with its forepaws and (employing the tongue, lips, and teeth) licks and nibbles at the skin and fur.

g. Grappling.—A complex pattern accompanied by the ook ook vocalization. Grappling involves elements of the embrace: pushing away, pulling toward, mock biting, and slapping. Ook ook sounds may grade into roars and the bout may end in a chase. Certain elements of sexual behavior including mutual manipulation of the genitalia with the mouth, hands, or feet also occur. In the field, ook ook sounds were common in the early evening just after sunset. These sounds often graded into roars and clearly suggested that male-female grappling was in progress. Since grappling may be a prelude to sexual behavior (see p. 19) we assume that much of the sexual behavior of *Ateles* takes place at dusk in the sleeping trees.

h. Face to face.—During an embrace or when sitting or hanging together, the animals will often bring their faces together.

3. Agonistic and Avoidance Patterns.

a. Chase-flight.—This behavior may involve all mixtures of quadrupedal, bipedal, and brachiating locomotion.

b. Slap (tag).—A directed movement of one limb, resulting in a blow to the partner's body, often including a grimace expression.

c. Bite.—A swift slash with the canines or a hard incisor nip.

d. Kicking.—A directed blow with one or both hindfeet, often while hanging suspended by the arms or tail.

e. Rushing.—A swift movement toward the partner, involving any of the various modes of locomotion. A rush may conclude with a chase but if the partner faces the oncoming animal certain attitudes of threat may occur.

f. Threat.—A nonspecific term which includes roaring, hissing, champing or coughs while facing the partner. Branches or cage artifacts may be shaken and slaps may be directed at the partner.

4. Sexual patterns.—Complete sexual behavior has not been described for *Ateles* and it is seldom observed in the field or captive situation. There is reason to believe that primary sexual behavior takes place at night as we have outlined in the previous section.

The paucity of data prompts us to include here a partial description of the sexual behavior of *Ateles belzebuth*:

March 17, 1964; 1435-1550; Animals A and C.

Following a grappling bout the female approached uttering the repeated squeak; her lips were pursed from time to time. The male was sitting on the swing, producing a very low intensity ook ook sound. The female hung above the male and then sat in his lap; they embraced face to face and sat together vocalizing for slightly over one minute. They then separated for twelve to fifteen minutes. The male then initiated a low ook ook series and was observed to have an erection. He approached the female who was braced standing upright in a corner of the cage. The male braced himself in front of her and exhibited a pelvic thrust, whereupon he turned and brachiated away to sit on the swing. The female followed, giving the squeak vocalizations and sat in his lap; she then moved away, followed by the male. They hung facing one another for perhaps ten seconds when the male turned and returned to the trapeze followed by the squeaking female. This move-follow sequence occurred four times within a minute after which the male suddenly remained hanging and manipulated his genitals. The female hung opposite, facing him while the male exhibited a pelvic thrust. She moved away and he remained hanging. She approached again and manipulated his genitals. The male moved away and the female followed. Again they faced one another still producing their respective sounds. The male exhibited a pelvic thrust, then the male moved to the swing and sat. The female followed and hung over him. The male manipulated her clitoris, and then hanging up behind her he grasped her legs with his feet and thrust. The female moved slightly, froze, and then moved away to hang suspended and facing the male.

Total time elapsed—23 minutes.

Although intromission was not actually seen, several definite elements of sexual behavior can be described: (1) contact behavior including the embrace, (2) genital manipulation, (3) erection, (4) pelvic thrusts by the male, (5) sitting in the lap, by the female, (6) mounting by the male. It is noteworthy that the low ook ook and squeak vocalizations were associated with this interaction. Previous observations of A and C had shown all these elements except (4) and (6). The female played an active role in approaching the male and sitting in his lap. The male also approached the female and attempted mounting and thrusting. In any case, no clearcut dominance was exhibited by the male over the female.

Elements 3, 4, 5, and 6 of sexual behavior were not seen in the field; however, all other elements of social interaction described in this section were observed in the free-living group studied in Panama.

THE ORGANIZATION OF THE BEHAVIOR PATTERNS

THE ENCOUNTER*

The two-animal encounter initially followed a typical course of action. After a 2-week separation the animals exhibited a variable contact latency ranging from 20 minutes to less than 1 minute. Contact was established after a series of approach, touch, and withdrawal maneuvers. After the initial touch phase, an embrace with a pectoral sniff generally occurred. Contact was furthered by anal-genital investigation and embracing. Depending on the animals involved, the course of the encounter could then lead to mutual indifference, avoidance, and mild agonistic interaction, or grappling which often led to elements of sexual behavior.

Animals B and C were judged to be younger than A and D. Female D was quite old and in general avoided strong interaction and grappling. Male A was also prone to avoid the playful attentions of female C, but he could dominate her when aroused. Male B and female C were active and playful, but male B could be aroused to dominate female C. Table 6 summarizes the total interactions of the four animals in terms of chasing, biting, and the ratio of moving away to approaches. Whenever molested or teased the older female D responded by chasing or biting. This happened rarely and the younger animals (B and C) soon learned to leave her unmolested. Male A never formed a stable relationship with her, but she was not completely dominated by him. Male A could displace female C, but B and C were very evenly matched. The older female tended to move away submissively when approached by B and C, but this in no way reflected her inability to defend herself—it rather indicated her tendency to avoid the advances of the younger animals. By the same token male A tended to move away from female C as often as he approached her but this again did not reflect dominance but rather a tendency to avoid the younger animal's attempts to initiate play. Clearcut dominance, then, did not often manifest itself. Differences in behavior were more strongly correlated with the age of the animals rather than their respective sexes.

* The following discussion refers to the two-animal encounters run in the laboratory at Vancouver (see pp. 2-3).

THE EFFECT OF SUCCESSIVE ENCOUNTERS

THE B-D SERIES

Successive encounters between the male *paniscus* and female *geoffroyi* were characterized by a sharp decline in the intensity of interaction. Early attempts by B to engage in grappling were met by chases and bites from female D. Encounters in later months proved to be very stable with only nasogenital investigation by the male remaining as a contact-promoting behavior. The animals would sit side by side or ignore each other except for occasional periods when D groomed B or solicited grooming from B (fig. 3).

TABLE 6.—Relations among the laboratory *Ateles*.

		Chase				Bite				Ma/App			
Recipient →		A	B	C	D	A	B	C	D	A	B	C	D
Effector	A	-	-	4	0	-	-	4	0	-	-	1.0	.72
	B	-	-	4	0	-	-	0	0	-	-	.69	.92
	C	0	6	-	0	0	1	-	0	.69	1.9	-	.50
	D	7	2	1	-	1	6	1	-	.92	4.0	2.8	-

THE B-C SERIES

The male *paniscus* established no contact relationship with the female *belzebuth* until early December. Their interaction from September to late November consisted of a continual interplay of approach, tag, and move away. This interaction was quite stereotyped and involved a sustained dispute over the possession of the swing. In general the male was more approach-prone. As soon as he would leave the swing the female would take possession of it, only to be eventually displaced by the male. In late November male B became ill with an intestinal ailment. During the phases of recuperation female C was allowed to encounter with him. At this time his overall activity was depressed and a stable contact relationship was established. During subsequent tests in January a grapple form of interaction was present (fig. 4).

THE A-C SERIES

This was the only series of male-female encounters where the animals were of the same species. Aside from the male's tendency to avoid the sustained play engagements of the female, the animals

indulged in contact-promoting, grappling, and sexual patterns of behavior.

THE A-D SERIES

The male *belzebuth* was never able to establish a stable relationship with the female *geoffroyi*. Grappling was virtually absent while grimacing; biting and slapping were of common occurrence. The male never ceased to approach the female except after being bitten.

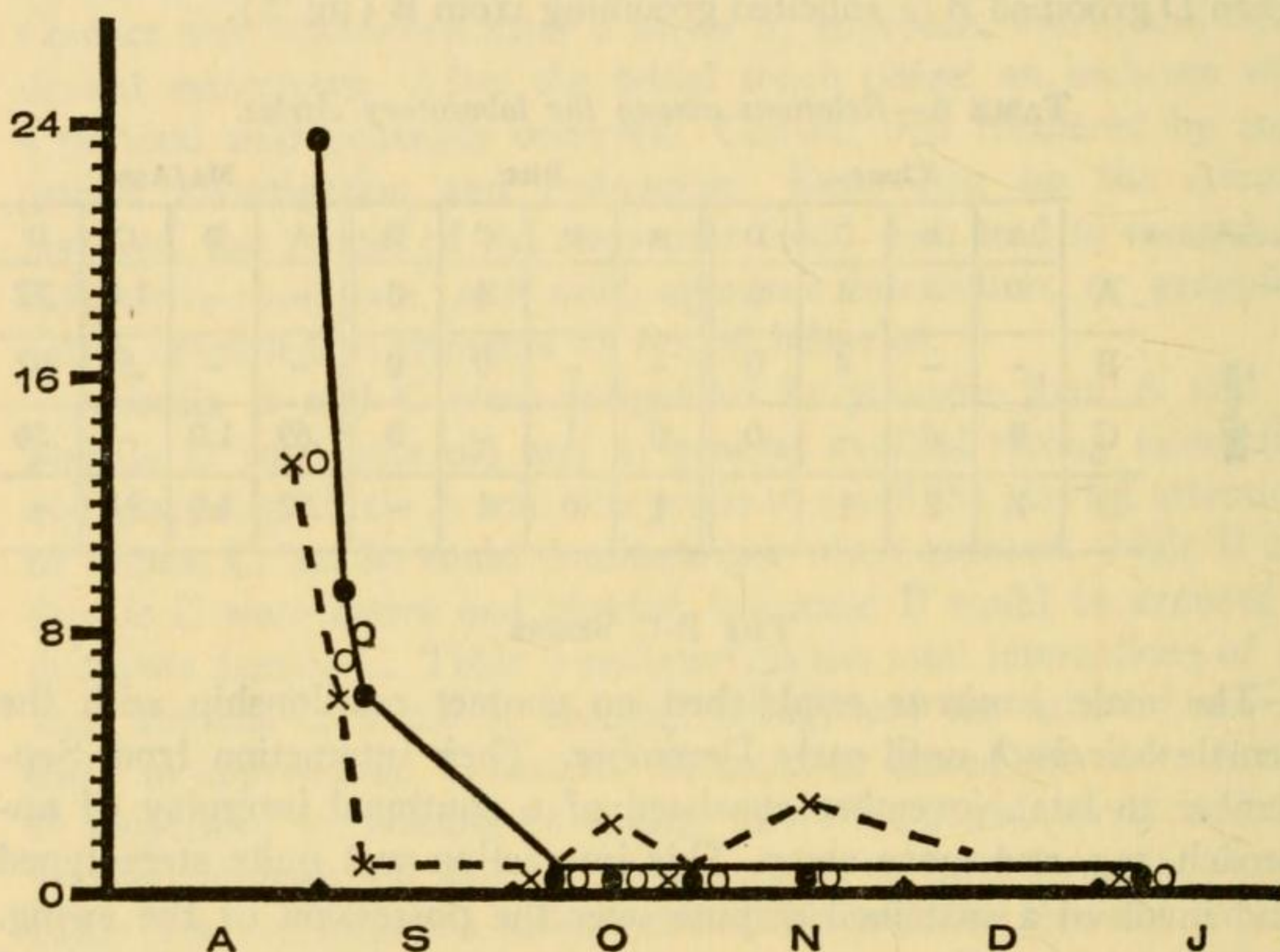


FIGURE 3.—Stability of the B-D relationship. Open circles refer to bouts of grappling; dots refer to tagging by B to D; crosses refer to grimaces by D to B. Acts were totaled for 20-minute encounters sampled over a 5-month period. Note the decline in all behaviors after the initial three encounters.

The female was generally willing to move off when approached, but she would not tolerate attempts at grappling or sexual contact.

In summary we can say little concerning the effect of species and age differences on the type of encounter displayed; however, it is surprising how consistent the encounter form was for any given matched pair of animals. Once initial contact had been made and the animals had learned the idiosyncrasies of their partner, the course of a given encounter was quite predictable.

DISCUSSION

A captive study utilizing an encounter technique has several limitations. Cage pathologies such as grappling with the self and stereotyped movements in a confined space must be evaluated and deleted from a normative description. As one can see in the description of the behavioral elements several behavior patterns simply do not appear in a confined situation. A captive encounter results in an

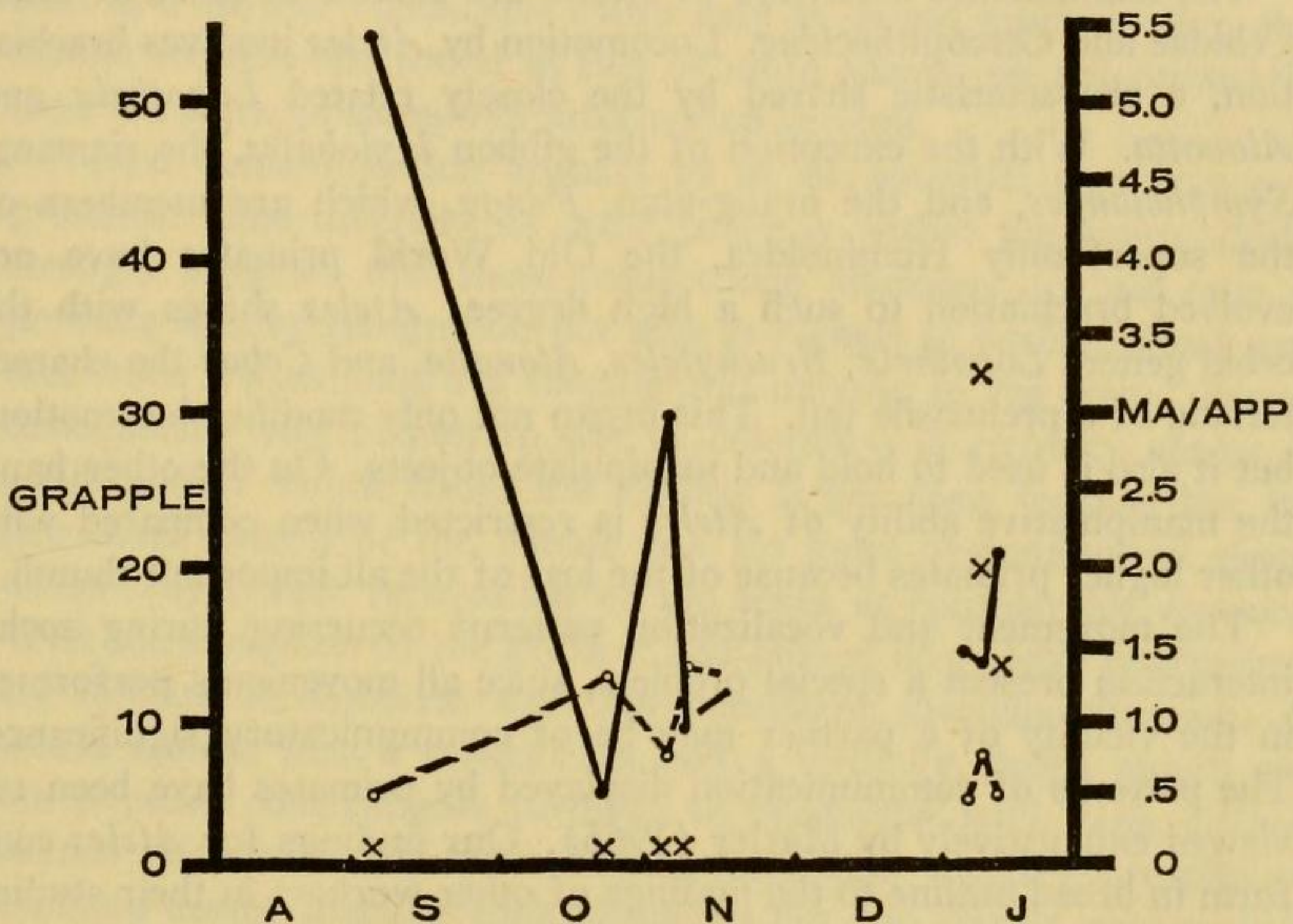


FIGURE 4.—Change in grappling intensity in B-C relationship. Crosses refer to bouts of grappling; dots refer to C and open circles to B with respect to their approach-move away ratios. B retained a low tendency to move away whereas C exhibited a higher but more erratic tendency to move away. Note the onset of grappling following B's illness.

intensification of behavior which may result in severe distortions with respect to frequency and intensity of display. It is noteworthy, however, that in utilizing the field as a control situation almost all captively determined elements were found to be represented in the field in situations comparable to the captive ones. It is our belief that much critical work can be accomplished with confined populations, but only if a field check is available to correct any interpretations of pathological behavior induced by confinement.

Species differences in the defined elements of behavior were not obvious. Our sample is too small to permit a detailed analysis, but

the major behavior patterns of *geoffroyi* appeared to be identical with *belzebuth*, *fusciceps*, and *paniscus*. Although variations in the patterns of vocalization were noted, these could well have been a result of individual variation. We have no doubt that species differences exist, but the differences are probably slight. It would seem that differences in coat color and odor would be most likely to insure correct sexual selection in cases of sympatry rather than differences in the overt behavioral elements.

The maintenance behaviors of *Ateles* are similar to those of other Cebidae and Cercopithecidae. Locomotion by *Ateles* involves brachiation, a characteristic shared by the closely related *Lagothrix* and *Alouatta*. With the exception of the gibbon *Hylobates*, the siamang, *Symphalanges*, and the orang-utan, *Pongo*, which are members of the superfamily Hominoidea, the Old World primates have not evolved brachiation to such a high degree. *Ateles* shares with the cebid genera *Lagothrix*, *Brachyteles*, *Alouatta*, and *Cebus* the characteristic of a prehensile tail. This organ not only modifies locomotion, but it also is used to hold and manipulate objects. On the other hand the manipulative ability of *Ateles* is restricted when compared with other higher primates because of the loss of the all important thumb.

The movement and vocalization patterns occurring during social interaction present a special problem, since all movements performed in the vicinity of a partner may be of communicatory significance. The patterns of communication displayed by primates have been reviewed exhaustively by Marler (1965). Our findings for *Ateles* conform in broad outline to the findings of other workers in their studies of cebids and cercopithecids. We have approached the problem of communication by describing the sounds, movements, and postures which have an inherent communicatory value; however, information content can be rigorously established only when an outside observer can consistently correlate a presumed signal from a sender with a predictable response by a receiver. We attempted to employ this rigid criterion to the grimace, and, as demonstrated in table 1, the signal value or information content seems to alter with the experience of the interacting animals. Many presumptive patterns of communication are correlated with a given set of circumstances and may be called "situation-specific," but their information content is not firmly established (tables 3 and 5).

Andrew (1963 a, b) has discussed the origin and evolution of expressions and vocalizations in primates. He asserts that an expression does not necessarily reflect a specific emotional state of the

sender. This would seem to be true for many expressions such as the grimace shown by *Ateles*, since it can occur when the animal is about to slap or when the animal is mildly disturbed and is tending to avoid contact. In either case the grimace often induces moving away or checks an approach. It is interesting to note that in *Macaca mulatta* the grimace is associated with avoidance and not with a potential attack. This has led Hinde and Rowell (1961) to describe this expression as a "fear" grimace in *M. mulatta*. These observations lead to a further conclusion which may be stated most simply: that similar expressions found in two or more species do not necessarily have the same presumptive information content.

Visual communication appears to be of potential significance in primates. The diversity of color patterns within the genus *Ateles* strongly suggests that these conspicuous markings act not only to promote species recognition but also as signals to permit visual contact when the animals are feeding and moving in the trees. Sexual dimorphism with respect to size or coloration is virtually absent in adult *Ateles*. Adult males are slightly larger than females but the pendulous clitoris of the female is a far more obvious visual signal which may permit recognition of the sexes at considerable distance. With the exception of the grimace and pursed lips, facial expressions are difficult to associate with any consistent stimulus situation. It would appear that a raised chin and a virtually closed mouth are the physical concomitants involved in producing loud, high pitched sounds with relatively pure harmonics. This facial expression is common during distance communication but also during nonagonistic contact. The pursed lips are associated with contact receptivity whereas the grimace is the antithesis of this expression, both in appearance and context. The open mouth without canine exposure does not appear to be an expression associated with an attack tendency, but the open mouth with canine exposure is associated with agonistic vocalizations and an attack or withdrawal tendency (table 5).

The facial expressions of *Ateles* are apparently not as rich as those shown by the genera *Cercocebus*, *Cercopithecus*, and *Macaca*. The eyelids are not contrastingly colored and the many expressions observable in certain species of Old World monkeys are lacking completely. However our descriptions of *Ateles* facial expressions fell within the general primate range as set forth by Van Hoof (1963).

Tactile communication appears to be facilitated by touch, embrace, grooming, anal-genital investigation and manipulation, and grappling. With the exception of the embrace and grappling activities, these are

all common mammalian patterns. Chemical communication is strongly implied during the anal-genital investigation and the pectoral sniff. The presence of a pectoral gland lying at the top of the sternum has been described by Wislocki and Schultz (1925). The ritualized embrace-pectoral sniff implies a role for this gland as a mediator of chemical information, although the axillary glands may be equally or more important.

Auditory communication by *Ateles* appears to be well established for some sounds, especially the whinny, ook ook, squeak, and the high-intensity agonistic sounds such as the roar and cough. Rowell and Hinde (1962) divide the calls of *Macaca mulatta* into "harsh" and "clear" calls. As in *Ateles* many of the harsh calls are agonistic in their character, a trait also noted by Tembrock for a variety of mammals (Tembrock, 1959). However there remains the problem of the harsh calls which are obviously not entirely agonistic in *Ateles* and *Macaca*. It would appear that these calls involve other important parameters such as repetition rate and intensity that may be important in delineating the overall tonal gestalt to the receiving monkey. The auditory repertoire of *Ateles* consists of 16 sounds, including the discernible intermediate calls. Of these, 10 are frequently heard. This is a slightly lower number than the possible 20-30 calls which Rowell and Hinde postulate for *Macaca*. Schaller (1963) described 22 sounds for the gorilla (*Gorilla gorilla beringei*); however, only 8 of these occurred with any appreciable frequency. Carpenter (1940, 1934) describes 9 calls for the gibbon, *Hylobates lar*, and 20 for the howler monkey, *Alouatta palliata*. It would appear then that *Ateles* lies within the range of known primate "vocabularies."

As was indicated in table 6, overt aggressive behavior is exhibited with a very low frequency of occurrence. This is in marked contrast to baboon and macaque studies. Primary sexual behavior is also seldom observed and probably takes place at night. There are no ritualized mounting patterns employed in social control which are characteristic of old world macaques and baboons. Penile erection displays as noted for the cebid genus *Saimiri* (Ploog and MacLean, 1963) are also absent, but the male *Ateles* will exhibit an erection during precopulatory interaction. The signal value of this pattern has not been evaluated.

In concluding this discussion, the behavior patterns of *Ateles* will be contrasted with three orders of mammals which exhibit a range of behavioral adaptations and are sufficiently unrelated to provide a broad basis for comparison. For example, when one compares the

maintenance behavior of *Ateles* with species of insectivores, carnivores, and rodents, several obvious differences are apparent. The movement patterns of *Ateles* have stereotyped elements but the elements are combined in a versatile manner. Stereotyped, complex sequences of cleaning movements found in rodents (Eisenberg, 1963; Bürger, 1959) are not present in *Ateles*. Rather, we find a stereotyped wiping and scratching movement utilized in a much less ritualized pattern. Locus specificity in urinating and defecation, so common in rodents, carnivores, and insectivores (Eisenberg, 1963, 1964), is lacking in *Ateles*. The stereotyped elements of behavior utilized by some rodents, carnivores, and insectivores in burrowing, nest building, and food caching are also completely lacking in *Ateles*. We find instead in *Ateles* and other cebid and cercopithecoid primates a lack of many stereotyped sequences of maintenance patterns and a versatility with respect to those maintenance behaviors which they possess (table 7). When we turn to the social behavior patterns of *Ateles*, certain obvious differences set this and other primates apart from most rodents, carnivores, and insectivores. During an initial encounter, the spider monkey promotes contact by first reaching out and touching the partner and then embracing with a pectoral sniff. The embrace brings the animals face to face and the pectoral sniff evidently functions in chemical communication. Small rodents, carnivores, and insectivores being quadrupedal will generally initiate contact by touching noses (Eisenberg, 1963, 1964). Nasoanal patterns of contact are common to the spider monkey as well as small rodents, carnivores, and insectivores. During a male-female encounter, rodents typically further contact by the process of social grooming (Eisenberg, 1963); however, *Ateles* is not prone to groom during an initial contact. Although grappling, with sexual overtones, serves as a form of social interaction, social grooming in *Ateles* appears to develop out of a longer period of association than is the case with many species of rodents. As with all social mammals, *Ateles* exhibits contact-promoting behaviors during an encounter even in the absence of primary sexual consummation.

Referring again to table 7 it can be seen that *Ateles* and other higher primates differ from many small insectivores and rodents by the persistence of groupings of adults of both sexes; however, primate groupings do not generally exhibit a persistence of parental care by the male except for the marmosets, the Titi monkey, *Callicebus*, and the night monkey, *Aotes* (Grüner and Krause, 1963; Mason [pers. comm.]; Moynihan, 1964). Some male parental care

TABLE 7.—Behavioral comparisons among selected mammals.

Behavior Patterns	<i>Sorex vagrans</i>	<i>Perognathus parvus</i>	<i>Tamiasciurus* hudsonicus</i>	<i>Ateles* Geoffroyi</i>	<i>Canis lupus</i>
1. Nest building	nest and tunnels	nest and tunnels	leaf nest and tree cavities	none	earth burrow
2. Cleaning movements	simplified	elaborate stereotyped	elaborate stereotyped	labile elaborate	elaborate
3. Caching food	some	elaborate	elaborate	none	some
4. Defense of an area by group or individual	nest defense	nest and burrow defense	nest and surrounding area	reduced tendency	social unit closed to outsiders
5. Social group composed of adults of both sexes which moves as a unit	none	none	none	present	present
6. Contact promoting behavior outside of the primary sexual behavior	none	none	none	elaborate	elaborate
7. Pair bonding	none	none	none	none	present
8. Provisioning of female and young by male	none	none	none	none	present

* Diurnal and arboreal

is shown by *Macaca fuscata* and *M. sylvana*, but this is in no way comparable to the previously mentioned neotropical genera. On the other hand, some rodents live in closed social groups or colonies and a few insectivores show persistent social groupings based on a family group structure (Eisenberg, 1965). Within the carnivora certain species such as the wolf, *Canis lupus*, form social groupings of adults of both sexes, and male parental care is exhibited by means of food provisioning. This latter trait is unknown among the infra-human primates (table 7).

In conclusion then, it is not the case that a sharp dividing line separates primates from other mammals with respect to their social behavior. The primates exhibit, as a taxonomic order, all variations of sociality and, further, no linear evolution of sociality is distinguishable in any given family (Eisenberg, 1965). What appears to set many higher primates aside into a special category of sociality are the facts that adult males and females may move together as a unit and many higher primates have a rich repertoire of sounds and facial expressions with a presumptive communication function. However, the communicatory value of these sounds and expressions remains to be thoroughly investigated, and social groups of mixed sexes, although typical of higher primates, are not the prerogatives of primates alone within the class mammalia.

SOCIAL STRUCTURE IN A CAPTIVE COLONY

INTRODUCTION AND DEFINITIONS

A colony of *Ateles geoffroyi geoffroyi* was studied in detail from July 1963 until March of 1964 at the municipal zoological park in Vancouver, British Columbia. The number of animals in the colony fluctuated from 14 to 16 in the course of the study. After some practice each animal in the colony could be identified by means of individual markings and expressions. A list of the animals, including pertinent age and sex class data is included in table 8. Three of the animals suffered from a malformation of the hind legs, probably as a result of a vitamin deficiency during critical growth phases. These animals, A, H, and J, are therefore not included in the locomotion analyses. There were 10 adult females; 4 of these (E, F, L, N) had an associated infant or juvenile. Two of the remaining 6 females (B and C) were judged to be old and perhaps postreproductive. The other 4 females (J, D, A, and I) were mature but not carrying infants; D, however, was judged to be less than 3 years of age. Two additional

females were immature. M was an Infant-2* to Juvenile-1 in the course of the study. Female O was born during the study and passed from Infant-1 to Infant-2 before her death on February 29, 1964. There were 4 males of which only one, G, was an adult. Throughout most of the study K was a Juvenile-1, whereas H and X were designated Juvenile-2s. Male X died from a fall before the formal analysis was initiated.

TABLE 8.—List of members of the zoo colony.

Code letter	Sex	Age class	Remarks
A	female	adult	cripple, not <i>geoffroyi</i> , probably <i>vellerosus</i>
B	female	adult	no attached young
C	female	adult	no attached young
D	female	young adult	no attached young
E	female	adult	mother of H
F	female	adult	mother of K
G	male	adult	
H	male	juvenile-2	cripple
I	female	adult	no attached young
J	female	young adult	no attached young; cripple
K	male	juvenile-1-2	
L	female	adult	mother of M
M	female	infant-2 to juvenile-1	
N ₁	female	adult	mother of O; designated N ₂ after O's death
O	female	infant	born Nov. 1, died Feb. 29
X	male	juvenile-2	died Aug. 1963, before the formal study

Data were obtained by speaking into a tape recorder while observing the animals. The behavioral elements were coded and later transcribed onto sheets of paper employing a 10-second interval criterion for quantification (see Methods on page 3). In addition, actual durations of some acts were computed directly from the tapes. Two types of data were obtained: 1. Each animal was observed as an individual for 30 minutes during four separate periods of the day: morning, noon, afternoon, and during the late afternoon feeding period. This gave us 120 minutes of observations for each animal sampled during four distinguishable periods of the day. (2) Grouping data were recorded by sampling throughout the day and described the size and

* Age classes as described by Carpenter, 1935.

individual composition of every discernible group. The recorded behavioral elements were defined in the same manner as those listed under the Behavior Patterns of *Ateles*. In addition, the following definitions were employed:

Grouped (Social)—the animal was moving interactively with other animals or resting in contact with, or resting while interacting with, other animals.

Alone—moving or resting free of contact with other animals and without mutual interaction with other animals.

Resting—maintaining a single locus for at least 2 seconds with no more than 2 seconds interruption at any one time. Changes of body position at a given locus could occur.

Moving—locomotion which changed the locus of the body by more than one body length or width, lasted more than 2 seconds, and was not interrupted for longer than 2 seconds.

Since only one adult male was present in the zoo colony (see pp. 29-30) most analyses of the behavior patterns refer to age classes. The term "young-free adult" refers to the adult male or a female without an attendant infant or juvenile. The terms "young-associated adult" or "mother" refer to a female with an attendant juvenile or infant (females E, F, L, N₁).

LOCOMOTION AND ACTIVITY ANALYSIS

The data in table 9 clearly indicate that regardless of age, sex, or time of day the captive animals spent about 87 percent of their time resting. The length of uninterrupted rest averaged 8.67 10-second intervals, whereas the average length of time spent in continuous movement was slightly less than 10 seconds. The percent of the total time spent in locomotion for each of the five locomotion forms is presented in table 10. Quadrupedal climbing and running or walking were about equal in frequency and accounted for about 73 percent of all locomotion. Brachiation and bipedal walking comprised roughly 20 percent of the locomotion time, but females with infants walked bipedally only half as much as did those adults without a clinging infant. Infants and juveniles climbed more and scooted significantly more than did the adults. The bipedal walk was virtually absent in the juvenile and infant monkeys.

SELF-CARE ANALYSIS

A full consideration of self care (grooming, scratching, and licking) is best deferred until the rank order is discussed. The

TABLE 9.—*Activity analysis.*

Category	Measure	Class	MNA	F
Resting	Prop	Y-fr	.884	.837
		M	.870	.830
		J & I	.910	.898
Moving	\bar{D}	Y-fr	10.40	5.28
		M	7.79	3.91
		J & I	10.59	10.03
	\bar{D}	Y-fr	1.00	.95
		M	.80	.76
		J & I	.74	.72

Probability of a difference between MNA and F or between animals in a class or between classes were greater than .10 and judged to be not significant.

Legend: Prop—proportion of 30 min. observation period. \bar{D} —mean number of 10 second intervals/30 minutes observation period. MNA—average for morning, noon, and afternoon periods. F—average for feeding periods. Y-fr—young-free adults. M—mothers. J & I—juveniles and infants.

amount of self grooming is, to an extent, inversely correlated with the amount of social grooming in which the animal engages. Higher ranking animals indulge in more social grooming and thus exhibit less self grooming. Table 11 presents the proportion of self-care behavior devoted to scratching and grooming. The average duration of a scratching bout is remarkably constant for all age and reproductive classes (4.0-5.6 sec.); however, the average duration for self grooming is quite variable (3.0-26.8 sec.). All animals spent less than 10 percent of their time engaging in self care. Scratching was the most frequent self-care pattern shown and accounted for roughly 70 percent of the total time spent in self care.

THE SOCIAL STRUCTURE

Given the definition of a social group in section A, exact records of the individuals composing a group were kept. It was therefore

TABLE 10.—*Locomotion analysis.**

Class	Quadrupedal		Jump	Scoot	Bipedal	Brachiate
	Plane surface	Climb				
Y-fr	.370	.357	.018	.026	.124	.106
M	.325	.407	.009	.067	.069	.124
J & I	.227	.369	.002	.299	.000	.102

* Figures represent the proportion of the total time spent moving.

possible to compare the proportional distribution of the observed group sizes with a proportional distribution derived from the supposition that grouping occurred with equal probabilities for joining or avoiding another individual or group of individuals (fig. 5). Before the death of infant O, the most frequently observed group size was four. After the death of O, the most frequently observed size shifted to three.

TABLE 11.—*Self-care analysis.**

Subjects	Scratching		Grooming		Pd T
	Pd	\bar{D}	Pd	\bar{D}	
Y-fr					
A	.70	4.0	.29	7.3	.090
B	.62	5.6	.38	13.8	.081
C	.79	5.3	.21	5.6	.051
D	.97	4.6	.03	3.0	.028
G	.87	5.0	.11	6.5	.040
I	.41	3.7	.59	26.8	.120
J.	.89	5.2	.11	6.1	.072
N ₂	.76	5.1	.23	16.7	.090
Mothers					
E	.98	5.1	.02	5.0	.057
F	.99	4.5	.01	1.0	.067
L	.94	4.7	.06	3.2	.037
Inf. & juv.					
H	1.00	5.6	—	—	.036
K	.88	4.8	.12	13.0	.048
M	1.00	9.2	—	—	.051

Legend: \bar{D} —average duration in seconds of the specified act. Pd T—proportion of time spent for all observation periods in self care. Pd—proportion of the total duration of all self care for all observation periods.

* Licking has been left out and accounts for the remaining proportion.

The calculated maximum frequency of group size based on chance alone for the same two periods ranged from eight to seven. Clearly then the grouping tendencies were not based on a model which assumes a constant probability for joining regardless of group size. Further, if the identity of the individuals comprising a group of a given size were held constant and the frequency of occurrence of each combination calculated, then 50 percent of all constant composition combinations sighted were within the size range of two to four individuals. There are two other significant departures from a chance process of aggregation: 1. If we calculate the probability

based on equal chance alone of observing only young-free adults or only young-associated adults in a group, we find that the observed combinations are not in accordance with an equal-chance model. There is a tendency for the young-free adults to form subgroups separate from the young-associated adults (table 12). 2. When large

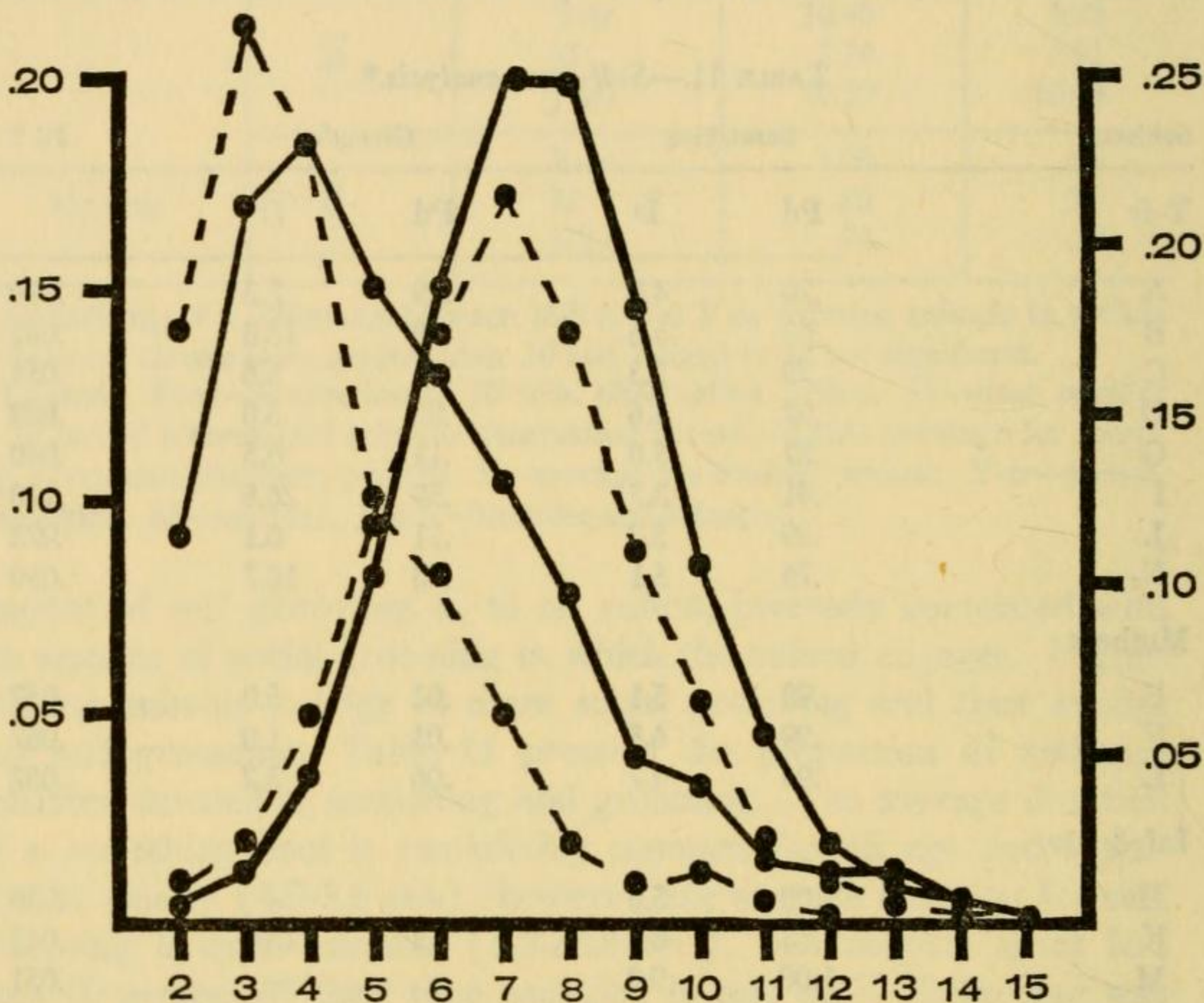


FIGURE 5.—Proportional distributions by sizes of possible and observed combinations for *Ateles* groups. Solid lines based on data before O's death; dotted lines represent theoretical and observed values after O's death. Theoretical values are based on a binomial expansion assuming an equal probability for joining or avoiding a group regardless of the group size. Graph was based on the following data: Before O's death, total observed combinations, 872; number of observation periods, 27. After O's death, total observed combinations, 415; number of observation periods, 15.

groups were formed in the cage, the females with young were present in these groups with a frequency exceeding that frequency calculated by assuming an equal chance process (table 13). Therefore we feel that group formation in this colony of *Ateles* was structured, and although the females with young tended to form a distinct subgroup, they also served as a focus to promote grouping whenever large numbers of animals began to join a resting group. The mothers

TABLE 12.—*Proportions of possible and observed combinations in each class of adults.*

Class	Possible		Observed	
	p	f	p	f
Young-free only	120	.004	56	.064
Mothers only	247	.008	57	.065
Mixed combinations	32385	.988	759	.871
Totals	32752		872	

Legend: p—proportion of total. f—frequency of occurrence.

may serve as a nucleus for grouping because they are less mobile; however, this assumption appears to be invalid because movement of females with young was equal to that of the young-free adults (table 9). We believe, therefore, that the mothers may promote grouping because they dispense a considerable amount of grooming to those animals which join their group, and equally important the mothers also receive grooming from many individuals (pp. 41-42).

Within the zoo colony certain grouping tendencies were observed more often than others. There were definite preferences and antagonisms which appeared to reflect a subtle series of dominance relationships. The animals were seldom overtly aggressive and fighting or chasing were infrequent. At the same time, one cannot say that the subjects were extremely demonstrative of interindividual dependency.

TABLE 13.—*Theoretical and observed probabilities of the presence of mothers in combinations of varying sizes.*

Group size	Number of mother-infant pairs							
	All 4 pairs		At least 3		At least 2		At least one pair	
	e	o	e	o	e	o	e	o
2	—	—	—	—	—	—	.038	.053
3	—	—	—	—	—	—	.114	.326
4	—	—	—	—	.004	.037	.224	.795
5	—	—	—	—	.022	.295	.360	.970
6	—	—	.001	.025	.064	.558	.506	.992
7	—	—	.006	.101	.143	.780	.652	1.000
8	.0001	.016	.022	.194	.263	.839	.781	1.000
9	.001	.050	.063	.350	.424	.875	.883	1.000
10	.007	.036	.145	.750	.608	1.000	.952	1.000
11	.026	.273	.219	.818	.798	1.000	.988	1.000
12	.077	.500	.508	1.000	.930	1.000	1.000	1.000
13	.200	.600	.771	1.000	1.000	1.000	1.000	1.000
14	.467	1.000	1.000	1.000	1.000	1.000	1.000	1.000
15	1.000	—	1.000	—	1.000	—	1.000	—

Social grooming was of minor importance in the life of an individual *Ateles* when compared with the social grooming activities of macaques and baboons.

In order to determine the differences in social responsiveness for each individual within the colony, the data were analyzed and all two-animal encounters were abstracted. Whenever two animals interacted outside a defined group their behaviors when approached were categorized either as "Avoid" or "Stay." From these data two calculations were made for each individual, giving numerical results which are termed the induction ratio and the response ratio. The

TABLE 14.—*Response and induction ratios for the adults.*

Response ratio			Induction ratio**		
Subject	Ratio	n	Subject	Ratio	n
*N ₁	.00	13	G	.43	43
*L	.08	66	*F	.26	42
G	.13	30	D	.25	64
*F	.16	36	C	.24	34
C	.18	28	*E	.23	62
I	.25	36	A	.21	43
N ₂	.31	19	B	.21	24
*E	.31	36	N ₂	.21	29
B	.33	57	I	.20	41
J	.36	45	J	.19	26
A	.39	23			

* Mothers. Note E's baby (H) is a juvenile-2 and the most nearly independent of the four.

** L and N₁ were omitted since number of encounters were too low for significant computation. Criterion for inclusion was at least 25 encounters.

response ratio represents the number of times the approached animal moved away, divided by the total number of times it was approached. The induction ratio represents the number of times the approaching animal caused a second animal to move away, divided by the total number of times the approaching animal initiated a contact. Thus a low response ratio indicates that the subject moved away seldom when approached, whereas a high induction ratio indicates that the subject often elicited avoidance when it approached another. Table 14 summarizes the ratio for each individual adult. The adult male, G, had the highest induction ratio. Almost one half of the subjects he approached moved away. The remaining adult females have remarkably uniform ratios and indicate no significant rank order. When one considers the response ratio, some differences occur. The

adult male G, the older female C, and the three young mothers are not prone to move away at the approach of another animal. Female I seems to fall intermediate between the preceding category and the second category of females with nearly grown (E) or no young (N_2 , B, J, A, and D). This latter series has a uniformly higher tendency to move away when approached. Using the response ratio as the sole criterion for determining a dominance order would be fallacious, since the induction ratio already suggests quite a differ-

TABLE 15.—*Summary of adult two-animal interactions for the Ateles colony.*

Responder	A	B	C	D	*E	*F	G	I	J	*L	*N ₁	N ₂	Σ_1
A	—	1,4	1,0	4,5	0,1	1,2	0,0	2,8	2,4	1,9	0,0	0,1	45
B	8,1	—	0,5	2,2	0,2	1,2	0,2	1,0	2,1	0,1	0,2	0,1	33
C	0,0	1,2	—	0,2	3,1	1,9	0,4	1,0	2,1	0,4	0,3	0,0	34
D	3,4	6,9	1,5	—	5,8	0,0	3,8	1,1	2,9	0,3	0,3	0,0	71
*E	2,4	2,6	1,2	9,6	—	0,1	1,4	1,4	1,3	0,7	0,2	4,7	68
*F	2,1	2,5	1,5	2,2	2,0	—	0,2	2,8	0,2	0,3	0,1	1,1	42
G	1,0	6,2	1,1	1,0	1,2	3,4	—	2,3	2,3	2,4	0,0	1,1	39
I	0,3	0,1	0,1	3,3	0,1	0,5	0,1	—	5,2	1,4	0,1	0,1	33
J	0,2	0,4	0,1	4,1	1,3	0,0	0,1	0,0	—	0,8	0,1	0,0	26
*L	0,0	1,1	0,0	2,0	1,1	1,1	0,2	0,1	2,3	—	2,0	0,0	17
*N ₁	1,0	0,0	0,2	0,0	0,2	0,2	0,0	0,0	0,0	1,12	—	0,0	20
N ₂	1,0	1,4	0,1	4,1	12,4	1,4	0,2	0,2	3,1	1,4	—	—	46
Σ_2	32	58	28	53	49	38	30	37	50	65	13	21	—

Legend: Numbers refer to: left entry—total move away and flee; right entry—total stay responses.

* Mother.

Σ_1 Sum of all approaches or chases involving the given animal.

Σ_2 Sum of all responses for the given animal.

ent interpretation from that of the response ratio. We believe that the simultaneous integration of several behavioral measurements is a necessary procedure and therefore postpone further discussion along these lines until page 41.

There were differences in the intensity and form of interaction when one inspects each possible class of two-animal encounters. Table 15 summarizes the data for all two-animal interactions where the interacting individuals were outside any defined group. Chase-flight patterns as well as moving-away patterns are included in this tabulation. The negative relationships included a persistent antagonism for: B to A; E to D; N_2 to E; G to B. These data only partially reflect direct unquantified observations of these relationships. Definite preferences

included the following: 1. "mother" associations E to L, N to L; 2. female associations A to I, A to L, C to F, D to J, E to B, F to I, J to L; 3. male-female associations D to G. Female E and D initiated the most approaches; conversely, females B, D, E, J, and L received the most approaches.

When one analyzes the data for pectoral sniff and social grooming, additional inferences can be made concerning the social structure. Table 16 summarizes the data for two types of pectoral sniff, mutual and individual. In the latter case the act was performed by the initiator. Male G and female F were involved in the greatest number of pectoral sniffs. Female A, who was an outcast in many respects, received the least number of sniffing interactions. It is worth noting

TABLE 16.—*Frequency of engagement in the pectoral sniff.*

Subject	Mutual sniff	Individual sniff		Total
		Initiator	Recipient	
A	1	0	0	1
B	4	3	1	8
C	5	1	1	7
D	4	0	2	6
*E	2	1	2	5
*F	9	2	3	14
G	7	2	3	12
I	6	2	0	8
J	2	1	1	4
*L	3	3	2	8
*N ₁	4	0	2	6
N ₂	1	2	0	3

* Mother.

that after N lost her baby she dropped to a small number of sniffing interactions. Of additional interest is the fact that female B sought out male G on three occasions to perform a pectoral sniff and yet throughout the course of the study male G tended to respond negatively toward her.

An examination of the grooming relationships yields more evidence for the existence of a social rank order. Figures 6 and 7 attempt to indicate several trends. Although not highly significant, figure 6 suggests that as an animal gives more grooming it is liable to receive more in return. Figure 7 indicates two possible trends: 1. within all observation periods as the total duration of social grooming decreases for an animal, the total duration of all self-grooming

increases. 2. in a similar manner, as the total duration of social grooming received decreases, the total duration of self-scratch periods increases. With this in mind an analysis was run on the relation among the duration of social grooming given, the duration of social grooming received, and the number of different individuals from which a subject received grooming. Table 17 summarizes the results.

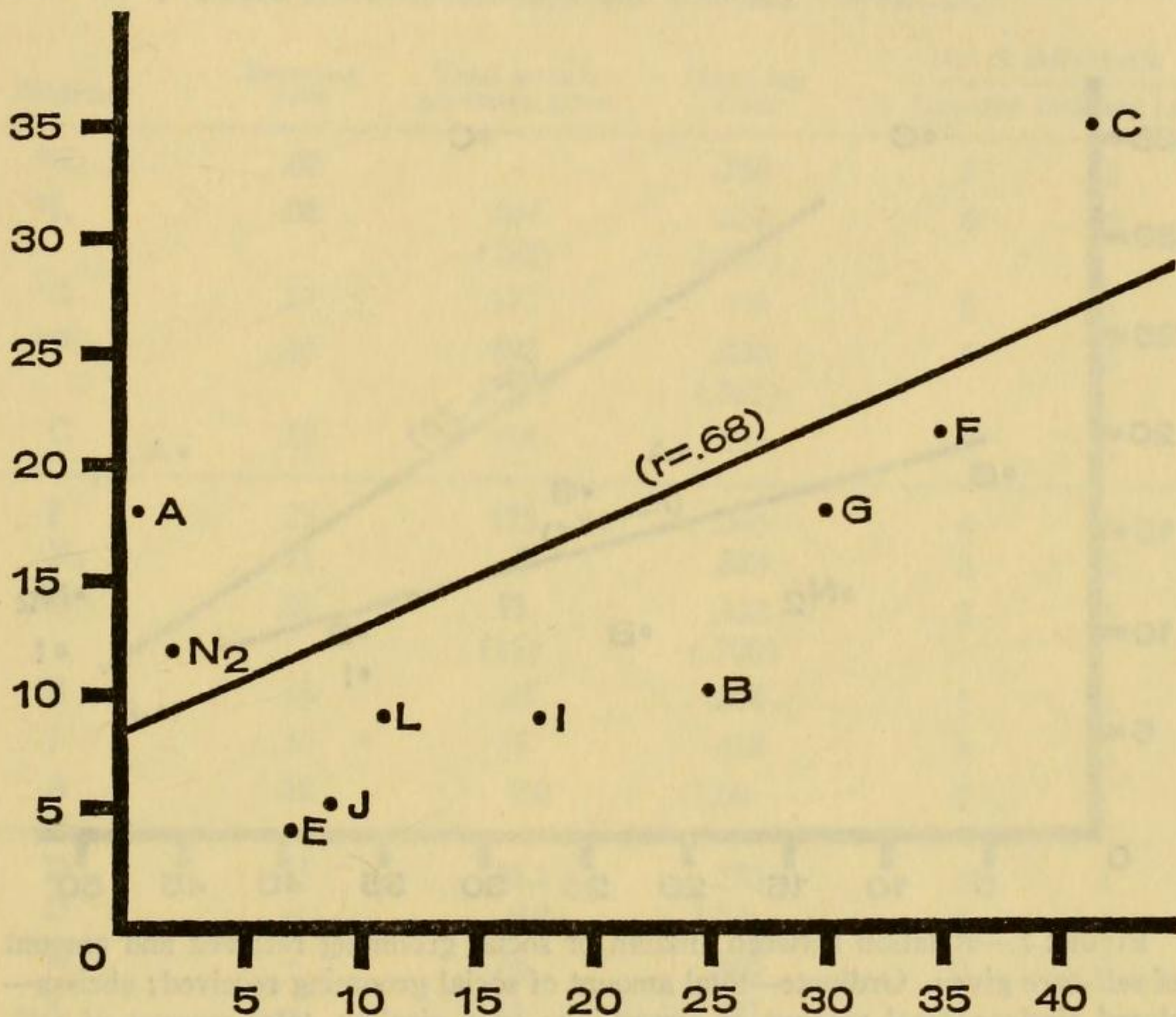


FIGURE 6.—Relation between amount of social grooming received and amount of social grooming given. Ordinate—total amount of social grooming received; abscissa—total amount of social grooming given. Units indicate number of 10-second intervals corrected to nearest five seconds. An r of .68 is significant at the .05 level of confidence.

In this table the animals are listed provisionally according to the rank order determined by the response ratio in table 14. The juveniles and infants are included in an arbitrary order after the adults. It can be seen that in terms of the total time spent in giving grooming to another, the top ranking mothers (L, M) and adults C and G dispensed the most grooming. When a grooming ratio is calculated by dividing the time spent receiving grooming by the sum of the total times grooming was given and received, the mothers and top

ranking adults (C and G) have low ratios. The mothers L and F have ratios less than .50 when their infant grooming is excluded, which indicates that they give more grooming than they actually receive. Animals receiving a great amount of grooming included the infants and the low ranking females A, B, and N₂. The ratios of J and D are out of line with their response rank and this may be a result of their relative youth. A further discussion of this point will

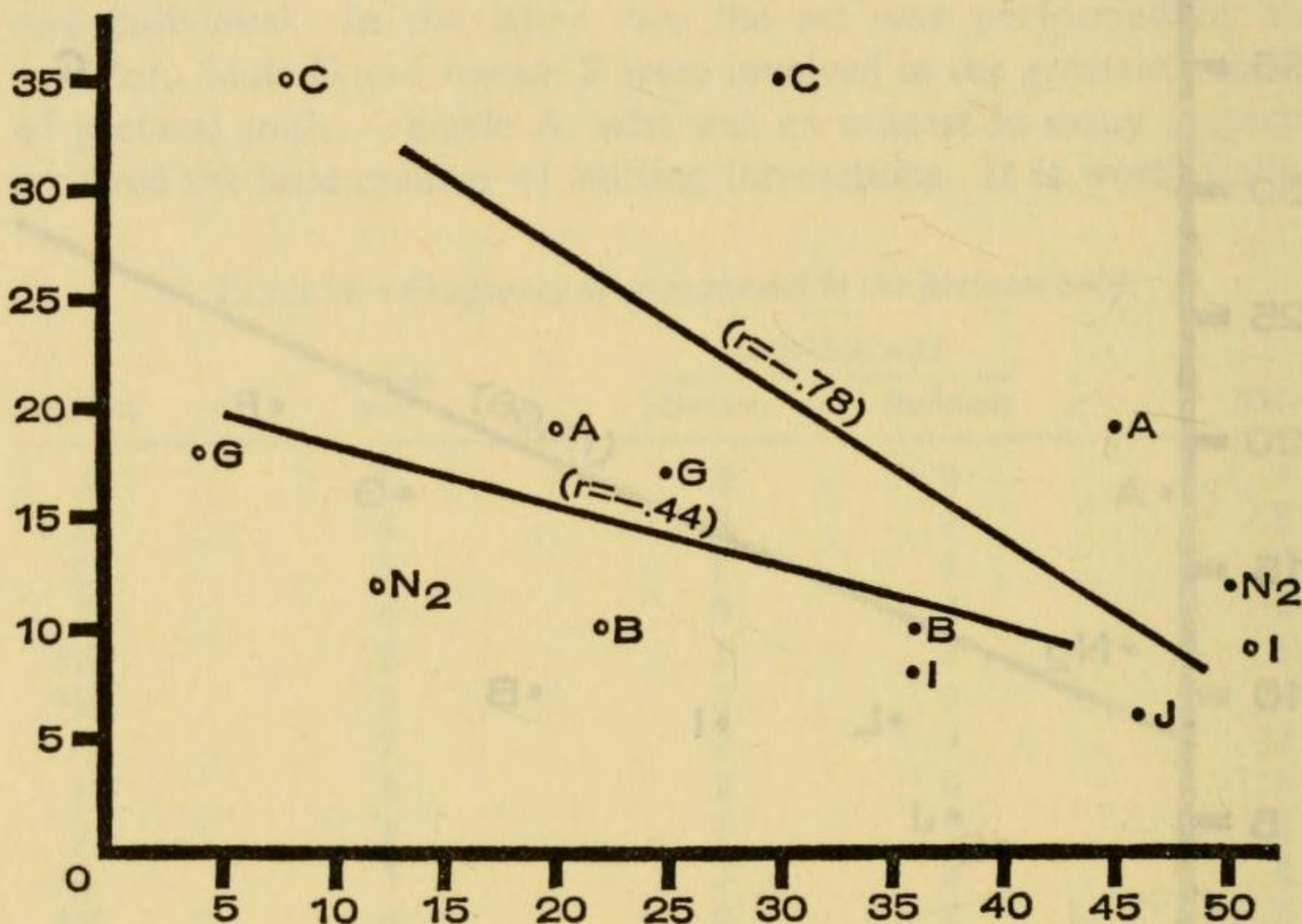


FIGURE 7.—Relation between amount of social grooming received and amount of self-care given. Ordinate—total amount of social grooming received; abscissa—closed circles: total amount of scratching; open circles: total amount of self-grooming. Units as in figure 4. An r of $-.44$ is not significant but an r of $-.78$ is significant at the .01 level.

follow. It is also interesting to note that female E with her almost-grown juvenile does not rank with the mothers L and F. It would be interesting to know if a female's status changes with the change in her reproductive state, but the data on N, before O's death, are insufficient for a comparison with the subsequent rank of N. Such data as are available indicate that N had a high grooming ratio even when she was carrying O.

The last column in table 17 indicates how many different individuals were groomed by, and how many individuals gave grooming to, a given subject. The low ranking females and infants gave grooming

to few animals. The high ranking adults (C and G) groomed many individuals but received from only a few. The mothers L and F gave to many and received from many. The data describing interindividual relationships are summarized in figure 8. This is a sociogram modeled after those of Kummer (1957). In this diagram, male G and female

TABLE 17.—*Response ratio and grooming correlations.*

Subjects	Response ratio	Total seconds grooming given	Grooming ratio	No. of individuals	
				Groomed	Groomed by
*N ₁	.00	—	.758	3	3
*L	.08	304 (192)	.232 (.324)	6	5
G	.13	175	.498	8	3
*F	.16	693 (335)	.230 (.361)	9	6
C	.18	416	.455	8	2

I	.25	175	.346	4	3
N ₂	.31	15	.888	3	3
*E	.31	71 (15)	.333 (.706)	2	3
B	.33	25	.800	1	4
J	.36	85	.418	4	4
A	.39	0.0	1.00	0	7

D	.45	35.1	.373	3	4
O	—	0.0	1.00	0	3
M	—	76	.666	3	2
K	—	11	.971	2	3
H	—	0.0	1.00	0	5

Legend: () includes corrections for mothers where infant-mother grooming has been subtracted.

* Mother.

C have been placed in the top category and the mothers in the second category. This change in rank order is consistent with our interpretation that the response ratio does not completely reflect the "relative rank order" but rather that the rank, based on the high number of animals groomed, coupled with a low number of animals received from, does reflect a consistent order. When the animals are arranged in order, based on a consideration of the response ratio and the number of animals from which grooming was received, there is a general

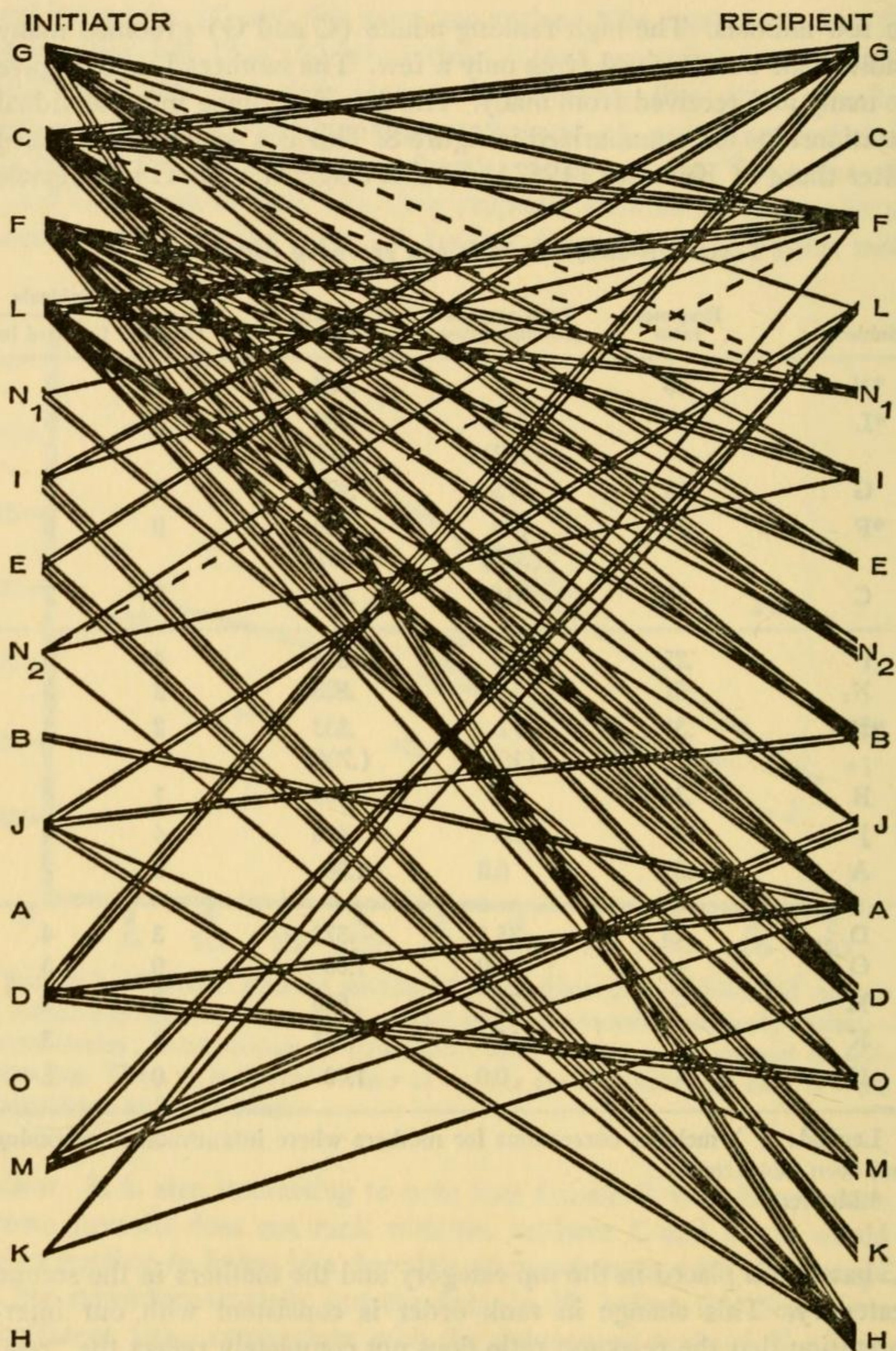


FIGURE 8.—Grooming relationships in an *Ateles* colony. Letters refer to the individual specimens. The left column indicates the groomer; the right column designates the recipient. The lines indicate cumulative durations of grooming. Dotted lines refer to less than 5 seconds. One solid line indicates more than 5 seconds but less than 10. Two lines indicate on the average 10 to 45 seconds, and three lines indicate 50 to 400 seconds. These solid lines correspond roughly to a frequency of 1, 2 to 6, and 7 to 20 times.

trend indicating that higher ranking animals groom lower ranking animals more frequently than the reverse situation.

The facts that the mothers consistently give more grooming than they receive and are less easily displaced contribute to their rather high position in the determined rank order. Mothers may be, on the other hand, somewhat outside the typical adult rank order in a manner similar to mother langurs, *Presbytis entellus*, discussed by Jay (1963). This sociogram shows a clear trend in that higher ranking tend to groom lower ranking animals with the greatest frequency.

TABLE 18.—*Noninclusion in large groups.*

Subjects	Frequency for the group sizes					Total
	10	11	12	13	14	
G	9	3	2	3	0	17
C	14	1	0	0	0	15

*L	5	2	0	0	0	7
*F	9	3	0	0	0	12
I	11	6	2	0	0	19
*E	12	1	0	0	0	13
*N ₁	5	2	1	1	0	9
B	11	4	5	4	1	25
J	13	4	2	0	0	19
A	20	7	4	2	0	33
D	13	5	2	0	0	20

O	5	2	1	1	0	9
M	3	2	0	0	0	5
K	8	3	0	0	0	11
H	13	3	2	1	0	19

Observations based on: 27 occasions; 52 combinations; 56 sightings.

* Mother.

G and C formed a grooming relationship, and the only consistent transgression of rank occurred when infants or juveniles groomed high ranking individuals. Since female D consistently displayed this juvenile tendency, we conclude that this reflects an incomplete socialization by a young animal as was found by Kummer for his young juveniles in a *Papio hamadryas* colony (Kummer, 1957).

An analysis was undertaken in order to determine the degree of absence from large groups. We reasoned that as a group becomes very large there would be a pronounced tendency to join the group and exclusions would be equally improbable for all animals in the colony. An inspection of table 18 indicates that such was not the

case. The mothers were almost always in the larger groups as were their infants. The young-free adults and juveniles were less prone to be found in large groups. The most frequent absences from large groups included the juvenile male H, the low ranking females A and B, and the adult male G. In view of G's otherwise high status we are led to conclude that perhaps adult males are less bound to core groups (pp. 53-55).

A final analysis was undertaken to determine the effect of feeding on the tendency to group. It was found that at feeding time the young-free animals were less grouped during the 30-minute observation period, but the tendency to be alone fell off at the end of 20 minutes (tables 19 and 20). A similar trend existed for the mothers but it was not significant.

TABLE 19.—*Sociality at feeding time.*

Category	Class	MNA	F
Proportion of 30 minute period(s) social	Young-free Adults	.581	.230*
Average duration of 30 minute period(s) social	do.	18.99	3.50*

Legend: MNA—Morning, noon, afternoon. F—Feeding.

* Significant at the .01 level.

TABLE 20.—*Average number of seconds alone throughout the feeding period.*

Class	Quarters			
	First	Second	Third	Fourth
Young-free adults	294	339	340	198
Mothers	103.3	85	168.9	38.3

SUMMARY OF THE DIFFERENT ROLES AND RELATIONSHIPS WITHIN THE ZOO COLONY

THE MATERNAL-YOUNG RELATIONSHIP

Mother and infants show a close bond. The infant clings to the female's ventrum for about the first 4 to 5 months of its life. Gradually the infant begins to ride on the female's back and is carried for another 1 or 2 months. During this stage of life the infant (*geoffroyi*) has a dark, dusky pelage which changes to the adult bicolor pattern toward the end of its first year. Following Carpenter's (1935) terminology we have designated young animals as a Juvenile-1 when they are in the transition phase of coat color and Juvenile-2 at the

stage of adult pelage. Male H was a Juvenile-2 during most of the study and figure 9 indicates the percentage of time he spent with his mother, female E. His average of approximately 20 percent is in marked contrast to Juvenile-1 K and Infant-2 M, who were bound to their mothers 85 percent of the time.

The infants nurse from the mother and are groomed in turn by the mother and other associated females. An Infant-1 may be carried by other females but this was observed only once. Juveniles and Infant-2s groom themselves, their mothers, and associated animals.

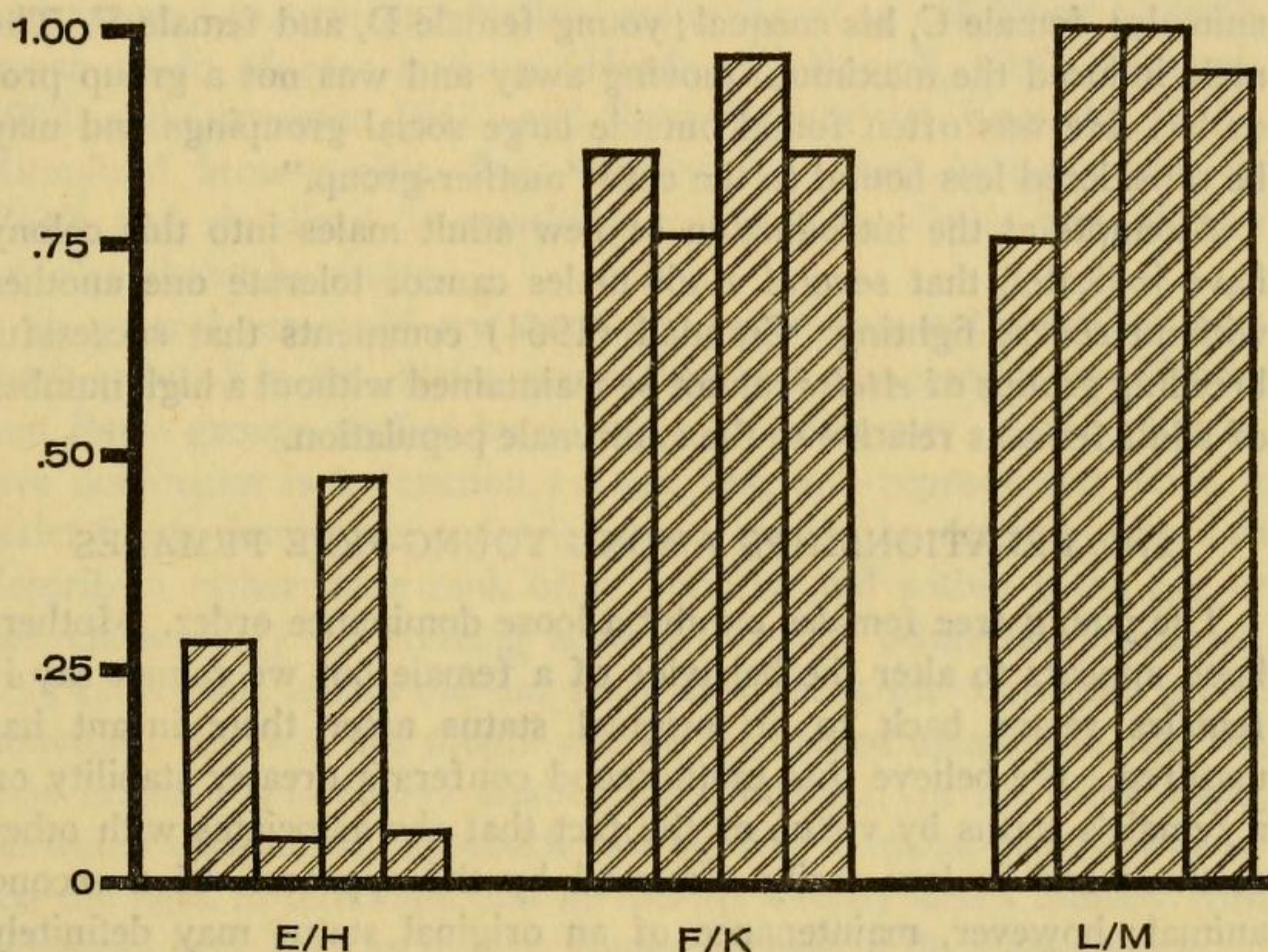


FIGURE 9.—Percent of total observation period in which the infants were associated with their mother. The four separate divisions for each of the three mother-infant pairs refer to the morning, noon, afternoon, and feeding periods of observation.

THE ROLE OF FEMALES WITH YOUNG

Mothers are characterized by moving away less when approached. This does not seem to be correlated with a high dominance status since they induce little moving away. Mothers with young infants spend more time grooming other animals than they do grooming themselves. This probably results from an overall increase in their grooming tendency as a result of the stimuli from the infant. Mothers dispense

grooming to and receive grooming from several other adults. The mothers with infants are prone to form a separate subgroup but this subgroup evidently promotes grouping by other animals. In short, within the zoo colony the mothers act as group promoters.

THE SOCIAL ROLE OF THE ADULT MALE

Male G appeared to enjoy a status only approximated by female C. As discussed previously, G and C shared several social traits which led us to consider them the top animals in social rank. The male groomed many individuals but received grooming from just three animals: female C, his coequal; young female D, and female F. The male induced the maximum moving away and was not a group promoter. He was often found outside large social groupings and may be considered less bound to the core "mother-group."

Attempts at the introduction of new adult males into this colony have indicated that several adult males cannot tolerate one another without severe fighting. Crandall (1964) comments that successful breeding groups of *Ateles* cannot be maintained without a high number of adult females relative to the adult male population.

THE RELATIONSHIPS AMONG YOUNG-FREE FEMALES

The young-free females exhibit a loose dominance order. Motherhood appears to alter the behavior of a female but we cannot say if females revert back to an original status after their infant has matured. We believe that motherhood confers a greater stability on a female's status by virtue of the fact that she associates with other mothers and is less easily displaced by the approach of a second animal; however, maintenance of an original status may definitely occur as was suggested by the data from N before and after her infant's death (table 17).

THE SOCIAL STATUS OF THE JUVENILES AND YOUNG ANIMALS

The juvenile male H ranked very low in the social order and did not enjoy social mobility as did the postjuvenile female D. It is noteworthy that H was roughly groomed and played with by many of the older young-free females. H rarely approached the adult male G. Juvenile and postjuvenile male mortality is high in this colony and no young males have survived to adulthood. This is surely caused by a heightened social tension in the confined area of the zoo colony.

The young females as typified by D evidently enjoy an undefined social status until they reach puberty. The exact age of sexual maturity for females is not known, but the evidence suggests that $3\frac{1}{2}$ years is approximately correct.

DISCUSSION

A comparison of *Ateles* with *Papio* and *Macaca* is appropriate since the latter two closely related genera are distantly related to *Ateles* and have been well studied in both the field and under captive conditions. *Ateles geoffroyi* does not exhibit ritualized presenting, as an appeasement gesture, or ritualized mounting as an exhibition of dominance as do *Macaca mulatta* (Hinde and Rowell, 1962; Altmann, 1962; and Carpenter, 1942) and *Papio hamadryas* (Kummer, 1957). Ritualized brow-raising, floor-slapping, and neck-biting shown by *Papio* and ritualized lip-smacking exhibited by *Papio* and *Macaca* are also absent in *Ateles*.

In general one could say that overt aggression and sexuality were more reduced in the *Ateles* group than was the case in the *Macaca* and *Papio* groups studied by Altmann and Kummer. Although relative dominance is a function of age, sex, and reproductive state, a strict linear dominance order in *Ateles* cannot be defined. One can describe a rather loose rank order between and within given age or sex classes only by utilizing several different behavioral measures. The adult male *Ateles* did not serve as a focus for controlling group activities. He was not sought out by frightened animals as was the case in the *Papio* colony studied by Kummer. On the other hand, he would occasionally approach two fighting animals, generally causing the fight to terminate, but he did not overtly assert himself with ritualized neck bites as did the dominant male in the *Papio* study.

THE BEHAVIOR OF FREE-RANGING SPIDER MONKEYS

INTRODUCTION

Carpenter (1935) conducted a 7-week field study and survey of *Ateles geoffroyi panamensis* in Panama. Within one observation quadrant at least four distinct groups were noted with a total population of approximately 100 animals. One typical group contained 33 animals that utilized in common the same trails, feeding sites, and sleeping trees within a given area. Carpenter noted that a given group tends to subdivide into subgroups ranging in size from 3 to 17 animals. With respect to age and sex composition, the subgroups

could be divided into four types: all male, several mothers and their young, a single mother and her offspring, or a group of several females and their young, plus one or more males. Within the total population, adult females outnumbered the adult males. The evidence strongly suggested that adult males are in part intolerant to one another when they accompany sexually mature females.

Wagner (1956) reported on *Ateles geoffroyi vellerosus* in Chiapas, Mexico. He concluded that the social structure of spider monkeys varied, depending on the hunting pressure and food supply. His populations in undisturbed habitats tended to exhibit a family group structure with one adult male and one or two adult females with their juvenile and infant offspring comprising a cohesive social unit.

In order to confirm and clarify these observations on *Ateles*, two preliminary field studies were undertaken. In 1964 and 1965 the senior author spent a total of 8 weeks in Panama studying the behavior of an introduced group of *Ateles* on Barro Colorado Island. In addition, in 1965, 8 days were spent in the west coastal mangrove region of Chiapas in order to census a wild population of *A. geoffroyi* living in a habitat conducive to the formation of small groups.

PATTERNS OF BEHAVIOR IN AN ARTIFICIAL GROUP

INTRODUCTION AND METHODS

In 1960 and 1961 several attempts were made to introduce post-juvenile specimens of *Ateles geoffroyi panamensis* on Barro Colorado Island in the Canal Zone Biological Area. One group of four females and a male has established itself. And in the spring of 1966 each of three females bore one young. The group was initially provisioned but now derives almost all of its food independently, and although exceedingly tame, the animals move freely and are quite independent of man. This group was selected for a preliminary study because it permitted almost continual contact by a human observer. This is not, of course, a "natural" group, but it did serve as a partial control for our captive observations.

Intensive field observations were made during a 4-week period from May 17, to June 11, 1964, and in 1965 supplementary observations were made from July 19 to August 8. Handwritten notes of the behavior patterns were taken down and the feeding, sleeping, and resting areas as well as the paths of movement were indicated on sketch maps. In addition the following technique was adopted to permit a quantification of the gross activity patterns. Four categories of activity were defined: moving, resting, feeding, and playing. For

the purposes of this study, tagging, chasing, and grappling were lumped into the category play. This introduces a degree of imprecision, but these adult females did exhibit a certain amount of behavior generally found only in juveniles. To facilitate recording, the artificial category play was adopted.

Using a stop watch, the activity of the group was censused every minute, and the number of animals engaged in each activity was recorded in this fashion, including at least four periods of observation for each hour of the day beginning at 0600 and ending at 1900. The average number of monkeys in sight during a given minute equalled 3.0. On four mornings the animals were followed from their sleeping tree and on four evenings the animals were observed until they came to rest in a sleeping tree. Aside from distinguishing the male and one female, the other three animals were not individually distinguishable with any accuracy.

GENERAL ACTIVITY

As indicated on page 23, the most frequently observed behaviors in captivity were also observed in the field. The females engaged

TABLE 21.—*Activity analysis for free-living Ateles.*

Category	0600 through 1800 hours												
	6	7	8	9	10	11	12	13	14	15	16	17	18
Rest	.00	.43	.43	.34	.50	.61	.67	.58	.92	.37	.17	.11	.22
Move	.35	.16	.40	.29	.30	.30	.13	.30	.07	.23	.36	.13	.28
Feed	.65	.26	.15	.24	.04	.09	.00	.12	.00	.29	.34	.65	.61
Play	.00	.15	.02	.13	.06	.00	.20	.00	.01	.11	.13	.11	.00

in embrace and pectoral sniff, grappling, grooming, and chasing. Locomotion by climbing, bipedal walk, brachiation, and quadrupedal walk were all observed in approximately the same proportions as was the case in the captive colony. Vocalizations and their contexts have already been discussed on pp. 11-16. It is noteworthy that this tame group did not often exhibit the barking responses to human observers which is so characteristic of wild troops (Carpenter, 1935; Wagner, 1956). Only once did the group bark at an observer and this occurred early in the morning when their arousal was being observed.

The quantitative data on activity are presented in table 21. It is evident that the animals have two primary peaks of feeding activity: an early morning peak from 0630 to 0730, and a later afternoon peak from 1600 to 1830. Resting, consisting of sitting or hanging by the tail, reached peak values at 1200 and 1400 hrs. Movement, either

directed or shifting in the same tree, was distributed evenly except during 1400 hrs. Play behavior was common during and after feeding in the morning and in the afternoon. From dawn to dusk the animals spent their time in the following proportions: .25 moving, .40 resting, .26 feeding, and .09 playing. Compared with the zoo colony the free-living animals were at least twice as active.

RESPONSES TO THE ENVIRONMENT

Figure 10 indicates the major patterns of movement and the major areas of utilization within the group's home range during the 1964 study. At least three sleeping trees were used and the animals moved out from these trees and spent the rest of the day foraging and resting. Certain trees which were in fruit served as loci for sustained feeding behavior. A definite trail stereotypy was shown and the same branches were used over and over again as the animals passed to and fro. The animals frequently crossed the two streams in their home range. Definite crossover points were used and in one case a palm tree was used to swing on, over a small ravine. This palm had been used so often that it was permanently sprung out of line. The palm crossing discussed previously is one example of the utilization of the elasticity of branches in order to gain momentum when leaping. A frequently employed technique involved jumping up and down on a limb while hanging onto a second branch with the tail. After several jumps the tail hold was released and the leap combined with the rebound of the branch contrived to impart a great deal of force to the jumping animal.

The animals were strictly diurnal. Dawn occurred at about 0530 and sunset at 1830. Four arousal times ranged from 0550 to 0645 whereas settling generally occurred from 1820 to 1835. Rain had an overall effect of depressing activity. Late afternoon showers caused the animals to move from the crowns to the understory of the trees. During severe downpours the animals moved close to the trunks of trees and huddled in groups of two or three. They often responded to the sound of an approaching shower with roars and increased activity. If the animals became wet or moved during a light shower they wiped and scratched continually at their fur. Wiping movements ranged from 27 to 39 strokes per minute when an animal's fur became soaked.

The choice of food trees appeared to be largely a function of habit and a matter of which trees were fruiting. In addition to an unidentified fungus the animals fed most frequently on the pods of

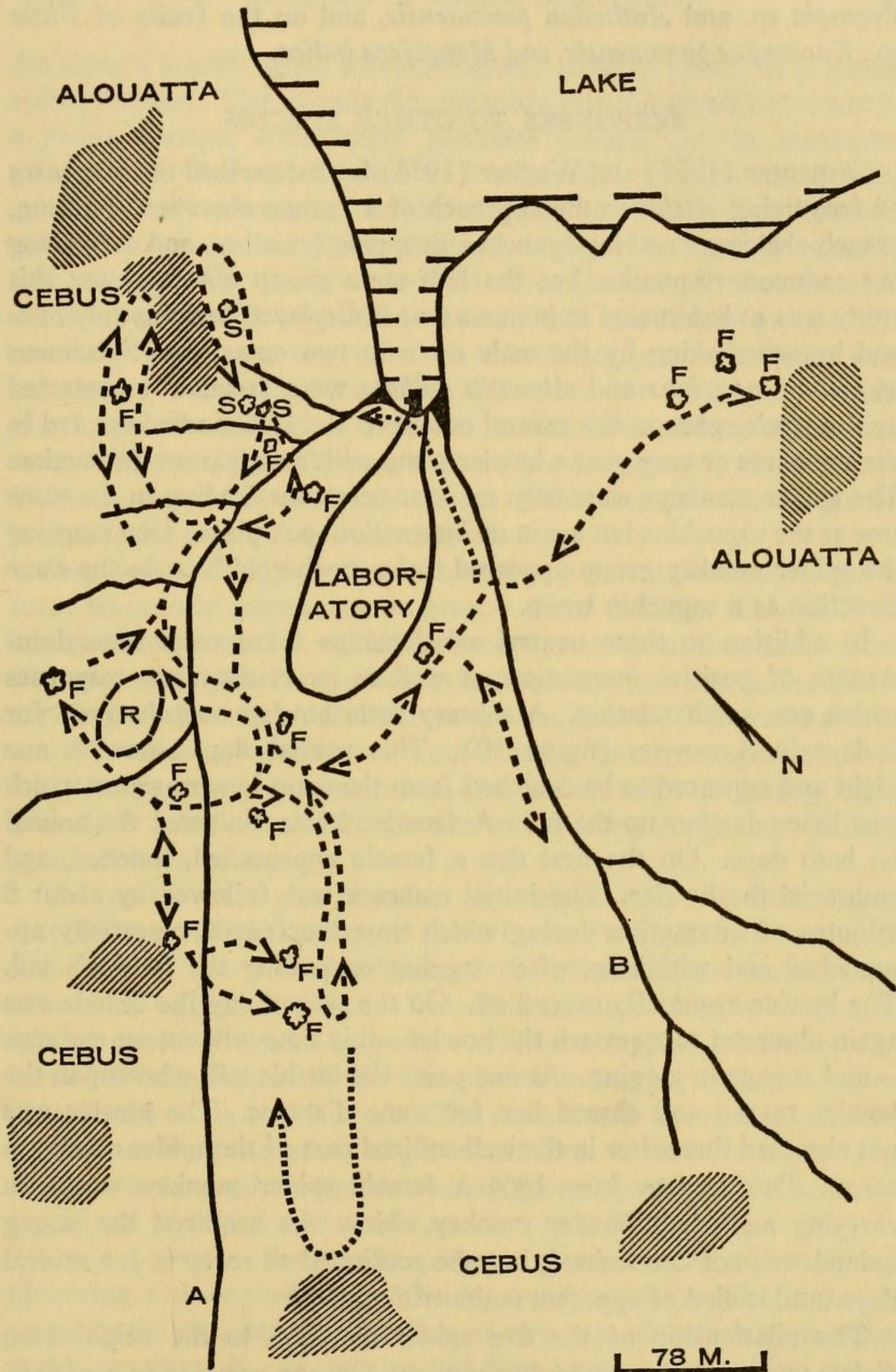


FIGURE 10.—Major routes for the free-ranging *Ateles* troop. This map indicates the major movement patterns of the *Ateles* troop. A and B refer to the two canyons flanking the laboratory clearing (lab). R indicates the primary midday resting area. Partial ranges of neighboring cebus and howler troops are indicated by crosshatching. Food trees are designated F and sleeping trees S.

Cecropia sp. and *Anthodon panamensis*, and on the fruits of *Ficus* sp., *Enocarpus panamensis*, and *Mangifera indica*.

RESPONSES TO OTHER SPECIES

Carpenter (1935) and Wagner (1956) have described the responses of free-living *Ateles* to the approach of a human observer. Barking, branch-shaking, breaking branches, dropping branches, and defecating are common responses, but the half-tame group observed for this study was so habituated to humans that it displayed barking only once and branch-shaking by the male on only two occasions. Specimens of *Cebus capucinus* and *Alouatta palliata* were frequently contacted by the *Ateles* group. On several occasions the spider monkeys fed in the same tree or very near a howler troop with no apparent interaction. The spider monkeys were seen on four occasions feeding in the same tree as the capuchins but again no interaction took place. One morning the spider monkey group appeared to be moving with or in the same direction as a capuchin troop.

In addition to these neutral relationships there were several instances of positive interaction as well as overt agonistic responses which are worth relating. A solitary male howler was observed for 2 days in A canyon (figure 10). This animal slept alone on one night and appeared to be detached from the main howler group which was living farther up the hill. A female *Ateles* contacted the animal on both days. On the first day a female approached, touched, and embraced the howler. The initial embrace was followed by about 8 minutes of interaction during which time the female repeatedly approached and withdrew, often tagging or pulling the howler's tail. The howler eventually moved off. On the second day the female was again observed to approach the howler—this time without an embrace—and engage in tagging. At one point she bit his tail, whereupon the howler roared and chased her for some distance. The howler was not observed thereafter in the well-utilized part of the spider monkey's range. During late June 1964 a female spider monkey was seen carrying an infant howler monkey. How she acquired the young animal was not determined, but she continued to carry it for several days until it died of apparent malnutrition.

The relationship of the five spider monkeys to the neighboring *Cebus* troops was exceedingly complex. On one occasion in a peripheral section of the home range the male *Ateles* was observed to leave the four females and actively follow a *Cebus* band moving to a new feeding area. On another occasion a *Cebus* troop was passing single

file along a branch which was serving as a sunning perch for a female spider monkey. The female did not move but continued to remain in a prone position while three juveniles paused and in succession groomed her for periods of 1 to 3 minutes. Although the females were generally tolerant of neighboring *Cebus* monkeys, on four recorded occasions the spider monkeys engaged in bouts of chasing and roaring with the *Cebus*. The most prolonged bout in 1964 occurred on June 1 when the male was with the female group. The area of conflict was one in which the *Cebus* had never been seen before and was generally used by the *Ateles* for feeding in the late afternoon. From 1706 to 1715 the *Ateles* interacted by chases and roars with the *Cebus*. The male was the most prone to chase and by 1720 the *Cebus* had departed. About 1735 three juvenile *Cebus* returned to the area and fed unmolested.

Carpenter (1934) mentions the tendency for *Ateles* and *Cebus* to form temporary mixed species groups when feeding. This habit of interspecific association should be investigated in much greater detail with natural populations before definite conclusions can be drawn. It may well be that troops of different species, such as *Cebus* and *Ateles*, can share areas of their home ranges and even move together; however, it appears from these data that the novelty of finding other animals in a heavily utilized portion of the home range can result in agonistic interactions.

The *Ateles* were also observed to interact with the semiarboreal coati (*Nasua narica*) and tayra (*Eira barbara*). A solitary male coati was "teased" for several minutes as he climbed—one female hung above him tagging at his tail. The male and four females responded to two courting tayras in quite a different fashion. Initially they barked for approximately 20 minutes while moving in the branches directly above the two animals. The male would descend to within a few feet causing the tayras to growl and hiss. Even after the barking response had ceased, the spider monkey group continued to observe the tayras and remained in the same tree for over 40 minutes.

On one occasion the female spider monkeys were in the same tree observing a three-toed sloth (*Bradypus tridactylus*). The sloth was moving and attracted the attention of two animals which approached and hung above it. At no time did they attempt to touch or slap at it and after several minutes they moved on.

SOCIAL RELATIONS

The four females were extremely cohesive in their movements. They slept together in the same tree, played in groups of two, three,

or four, and were slightly scattered only when resting or feeding. Even during these latter periods they were in vocal contact. When moving, the leading animal's movements were copied by the followers, especially at crossing points and often with respect to routes along specific tree branches. Assistance was rendered at crossings and two examples are noteworthy. In one instance a female had successfully bridged a gap between two branches and then turned to confront the following female. The follower made several attempts to reach across and then uttered several low squeals. The lead animal reached out, while holding the branch with her tail, and the animals grasped each other's arms. The follower then released her tail hold and swung across. Immediately after reestablishing footholds the animals embraced and mutually gave a pectoral sniff. In a second instance the lead animal reached across a gap and held onto the last branch with her tail. The follower then crawled across the bridge formed by the first animal's body.

Play was common in the female group and almost always involved grappling followed by growls and chases. At times all four animals could be engaged in a four-way grappling bout, hanging by their tails. This prolonged grappling behavior with its sexual overtones is here interpreted as abnormal. In the natural groups observed in Chiapas, play was confined solely to the juveniles (Carpenter, 1935). It can be assumed that these females without young were exhibiting abnormally prolonged juvenile behavior.

There was some indication of dominance within the female group, especially when settling for the night. Two of the animals generally slept huddled together while the third generally attempted to keep the fourth away as she settled next to the compatible pair. Usually the interaction was reconciled within 10 minutes with the fourth animal joining the huddled pair and the third animal resting about 3 feet away.

The male was typically more independent in his movements. In 1964 he was observed with the females on only 7 days out of the 26 days of observation. At other times he could be found feeding, moving, and resting alone. When he was alone the male was difficult to locate and was often not spotted for 3 days at a time. The dates of his extended association with the females include May 17, 18, 19, 26, 31, and June 1 and 4. Interactions between the male and the females included approaches, tagging, moving away (by females), grappling with *ook ook* and *roar* vocalizations by the male, chasing by the male, and grooming of the male by the females. On May 26 the

male followed the females throughout the afternoon and one female attached herself to him. They were seen moving independently from the three females until dusk. There is every reason to believe that they formed a pair relationship throughout the night.

The male would grimace, cough, and shake branches at a human observer. This behavior coupled with his occasional agonistic reactions to the *Cebus* and the deference that the females exhibited toward him sharply demarcated his behavior from the females.

BEHAVIOR AND GROUPING TENDENCIES IN A NATURAL POPULATION

From July 7 through July 14 a population of *Ateles geoffroyi vellerosus* was censused in southern Mexico, roughly 30 km west of Acapetahua, Chiapas. The study area included four "islands" of high ground within a strip of mangrove swamp approximately $\frac{1}{2}$ by 3 kilometers. One island comprises the field station of the Departamento Biologico, Tuxtla Gutierrez. During this period, nine groups were observed and counted. Of these nine groups four were censused completely with respect to age and sex classes. It is reasonably certain that these four counts were carried out twice each on the same two groups. These data are summarized in tables 22 and 23.

TABLE 22.—Group size in free-living ateles.

Location	Date	Time	Group size
Island I	7/11/65	0840	4
Island II	7/10/65	1100	3
Island III	7/ 7/65	1015	4
	7/ 7/65	1400	6
	7/ 9/65	1440	6
	7/ 9/65	1500	4
	7/10/65	1700	6
	7/14/65	0710	5
	7/14/65	0750	6

This mangrove swamp is not a typical *Ateles* habitat and must be considered as a special situation conducive to the extreme fractionation of *Ateles* groups. Primary feeding is confined to the restricted areas of high ground which support a variety of food plants. At this time of the year the animals were visiting the study areas primarily to acquire the late fruiting *Sideroxylon* sp. (Sapotaceae). Throughout the year at various seasons they are sustained by *Attalea gomphococca*,

Spondias lutea, *Chrysophyllum cainito*, *Heliostylus ojuche*, *Ficus* sp. and *Oreopanax oligocarpum*.* In addition, the monkeys utilized various cultivated plants which have been introduced by the human inhabitants of the islands.

Table 22 indicates the small size of the groups counted, which ranged from three to six with an average of 4.9 animals per group. In table 23 compositions of the two groups from Island III are presented. Troop A was encountered twice, whereas troop B was encountered four times. These troops were characterized by having only one fully adult male attached to them and conform to one type of social grouping observed in Chiapas by Wagner (1956). Furthermore these two groups utilized the same habitat but did so at different times. We have then a case of home range overlap but mutual avoidance.

TABLE 23.—Composition of troops A and B from Island III.

Troop	Adults		Juveniles		Infants		Σ
	Male	Female	Male	Female	I	II	
A	1	2	1	1	—	1	6
B	1	1	1	1	—	—	4

Observations of these two groups indicated that the males could initiate movements of the whole troop thus assuming a temporary leadership function. On the other hand the female with the Infant-II was observed on two occasions to move away separately, and on three occasions an adult male moved off without any immediate following response on the part of the associated female and juveniles. The female and associated juveniles or infant presented a much more cohesive social subunit.

DISCUSSION

Wagner (1956) reports that *Ateles geoffroyi* in Chiapas is typically found in family bands consisting of an adult male, several females, and their young. The males typically approach human intruders and bark, break branches, and drop branches on intruders. Females with young may participate in this threatening behavior, but generally retire to the rear. When spider monkeys are hunted such overt hostile behavior is often reduced or absent and concealing behavior is adopted. Wagner further comments that in the coastal lowlands of Mexico

* List provided by José H. Vasquez.

larger troops of 100 or more animals may be formed from the discrete family bands. He attributes these larger groups to the artificial conditions of hunting pressures. Dr. M. Alvarez del Toro (pers. comm.) described a typical *Ateles* group from the montane forests of Chiapas as consisting of four adult males, eight females and associated juveniles and infants, giving a total of some 20 animals. In addition, he reports the presence of solitary males in a given population. It should be remembered that there is no way to be certain that the presumptive isolated males are truly unattached or whether they are actually attached to a group of females but temporarily moving alone.

Carpenter (1935) found that *Ateles geoffroyi* in Panama lives in clans or troops that utilize a common home range and sleeping trees. Each troop is typically composed of subgroups. Fighting among males has been observed, and the evidence strongly suggests that adult males may join cohesive female groups and defend them against the close approach of other males. Males may also associate compatibly but it appears that when a male associates with a group of females he may be prone to react antagonistically to the approach of other males. It is entirely possible that young males need to escape the mother group and to form a separate subgroup with both other older and younger males. In captivity, the young males are perhaps severely stressed as they mature in a confined social group.

Undoubtedly the social structure of *Ateles* groups varies with the habitat. In an environment such as the mangrove swamp, cohesive groups may be small and approximate a family group structure. In other habitats with a more uniform distribution of food trees the troops may be large and more plastic in their structure.

Certainly the most cohesive social units within an *Ateles* troop are the groups of females with young. Peripheral groups of males may be loosely associated with a given female group but one or two males may by dominance attach themselves exclusively to an adult female group.

GENERAL DISCUSSION AND CONCLUSIONS

Most species of the Cebidae, Cercopithecidae, and Pongidae are group-living, gregarious mammals. The night monkey, *Aotus*, and the lar gibbon, *Hylobates lar*, are exceptional because they appear to live in family groups (Moynihan, 1964; Carpenter, 1940). The orangutan, *Pongo pygmaeus*, appears to be semisolitary, but an adequate appraisal is difficult because of the reduced populations of this species (Schaller, 1961). The gregarious primates have several common social trends:

a tendency for females with young to form a "core group" which is very cohesive; a dominance order for adult males and adult females which is often enforced through nonviolent, subtle communication mechanisms; contact-promoting behaviors involving vocalizations and mutual grooming, and a history of socialization which occurs as an infant matures in a rather stable social matrix. In addition, organized primate groups tend to utilize a given home range with some areas being almost exclusive to a given group and other areas overlapping with the home ranges of neighboring groups. Maintenance of an exclusive area may be accomplished by hostile display and aggressive behavior in *Macaca mulatta*, ritualized vocalizations in *Alouatta palliata* and *Hylobates lar*, or undefined but subtle mechanisms of interaction as in *Papio ursinus* and *Presbytis entellus* (Southwick, 1962). The evidence indicates that *Ateles geoffroyi* is characterized by the above trends, but it differs significantly when further comparisons are made with other primates.

The ground-dwelling macaques and baboons typified by *Macaca mulatta* (Carpenter, 1942; Altmann, 1962) and *Papio ursinus* (Hall, 1962a, b; Washburn and Devore, 1962; Bolwig, 1958) differ from *Ateles* in certain important respects. These ground-dwelling primates are sexually dimorphic and exhibit a strict dominance hierarchy, the male hierarchy being separate from that of the females. One or more dominant males serve as a focus for the group's movements and this male group is centrally located in a moving troop in association with the core mother subgroup. The young males are chiefly in the lead and on the periphery. The males are much larger than the females and actively defend the troop. Macaques and baboons are overt in their sexual behavior and ritualized mounting serves as a means of asserting dominance.

The terrestrial pongids exhibit still different syndromes of social behavior. *G. gorilla beringei* forms cohesive bands of mixed sexes. The dominant male definitely coordinates the movements of the group and plays a defensive role when the group is disturbed; however, overt aggressive and sexual behaviors are reduced when compared with macaques and baboons (Schaller, 1963). The chimpanzee, *Pan satyrus*, is characterized by an extremely loose social organization. Mother groups are common but shift in their composition. Overt male dominance is reduced and strict linear hierarchies are not determinable (Reynolds, 1963).

When we turn to arboreal species, the langur, *Presbytis entellus*, is characterized by troops of mixed sexes with a strict hierarchy

among the adult males, but a loose and amorphous rank order among the females. Tolerance among males is shown and the troop moves in a cohesive fashion. Males which leave a given troop are generally prevented from readily reentering and a number of males may be solitary or organized into loose associations outside an organized troop (Jay, 1963). The howler monkey, *Alouatta palliata*, is similarly organized into groups of mixed sexes. The howler group is very cohesive and the males are strongly dimorphic. In addition to their role in offensive and defensive display toward enemies, the adult males engage in vocal chorusing behavior which appears to aid in spacing out neighboring troops. Overt aggressive and sexual behavior appear to be reduced when compared with macaques and baboons.

Ateles is not a strongly dimorphic genus. The males are only slightly larger (Hill, 1962) and only the pendulous clitoris of the female renders her conspicuously different from the male. Although males appear to take the initiative in expressing hostile behavior to intruders, the males do not serve as a focus for troop movement and there is good reason to believe that adult males are relatively intolerant of each other when they are associated with an adult female group. Furthermore, the dominance relations among group members are not strongly expressed and a classical, linear hierarchy appears to be absent. Cohesion among troop members is not pronounced, with the possible exception of the core mother group and their associated young. *Ateles* is not overtly sexual and ritualized mounting as a form of dominance is lacking.

The phenomenon of a complex social life is not unique to the primates. Groups of mixed sexes may be found in some species of ungulates, carnivores, and cetaceans (Eisenberg, 1965). It may be argued that male ungulates are seasonal in their association with females and that during the breeding season male ungulates form harems and are intolerant of other adult males, but harem formation is not solely confined to nonprimate gregarious mammals and appears to be the rule for *Papio hamadryas* (Kummer and Kurt, 1962). Furthermore, the harem mating system is not the rule for all ungulates. Mating orders may be established through a dominance hierarchy, and several males may well associate with more cohesive female groups in such species as *Bos taurus* (Schloeth, 1961) and *Bison bison* (McHugh, 1958). The persistence throughout the year of groupings of mixed sexes in primate societies is somewhat unique, but the wolf forms cohesive social units throughout the year (Murie, 1944) as does the horse (Antonius, 1938; Zeeb, 1961). We wish to emphasize

that although complex sociality is a characteristic phenomenon in the order Primates, this trait is not expressed in a uniform fashion. While similar in many ways to other primates, *Ateles* appears to differ in the structure of its social organization so that in some ways it exhibits a structural complexity intermediate between the loose social organizations of some primates, many nonprimate mammals, and the cohesive, organized societies so typical of the macaques, baboons, and gorillas.

SUMMARY

The behavior of *Ateles geoffroyi* was studied in a laboratory, zoological garden, and field setting. In addition captive studies were conducted with *A. belzebuth*, *A. paniscus*, and *A. fusciceps*. Expressions, postures, and vocalizations were described in detail. Insofar as possible the functional role of these communication patterns was determined. Lip-smacking, tongue protrusion, and ritualized presenting so common in macaque and baboon expressive repertoires, are lacking or nonritualized in *Ateles*.

The following conclusions were drawn concerning the social structure of *Ateles geoffroyi*:

1. The social groupings are loosely organized; however, females with infants and juveniles may form a cohesive group.
2. Overt sexual behavior and aggressive behaviors are reduced when compared with macaques and baboons.
3. A loose dominance order is present within a group, but it is subtle and not as strictly delineated as is the case with groups of macaques and baboons.
4. Grooming relationships in a captive group reflect a rank order within a social group since high ranking animals groom more individuals but receive grooming from only a few animals.
5. Females with young are in some respects outside the normal dominance relationships.
6. In contrast to macaque and baboon groups, the adult males do not serve as a focus for social activity.
7. Tolerance and a reduced aggressive tendency permit the formation of large, loosely organized troops; however, the troops vary in numerical composition. The cohesive units are the small subgroups of females, infants, and juveniles that compose a troop dwelling in a given home range.
8. Adult males may dominate and attach themselves semi-exclusively to adult female subgroups.

9. All-male subgroups are common in a loosely organized troop.

The Cebidae, Cercopithecidae, and Pongidae are generally extremely social mammals, although differences among the social organizations of different species indicate a spectrum of social types. No sharp break in the form of primate social organizations appears to set them apart from the social organizations of some ungulates, cetaceans, and carnivores.

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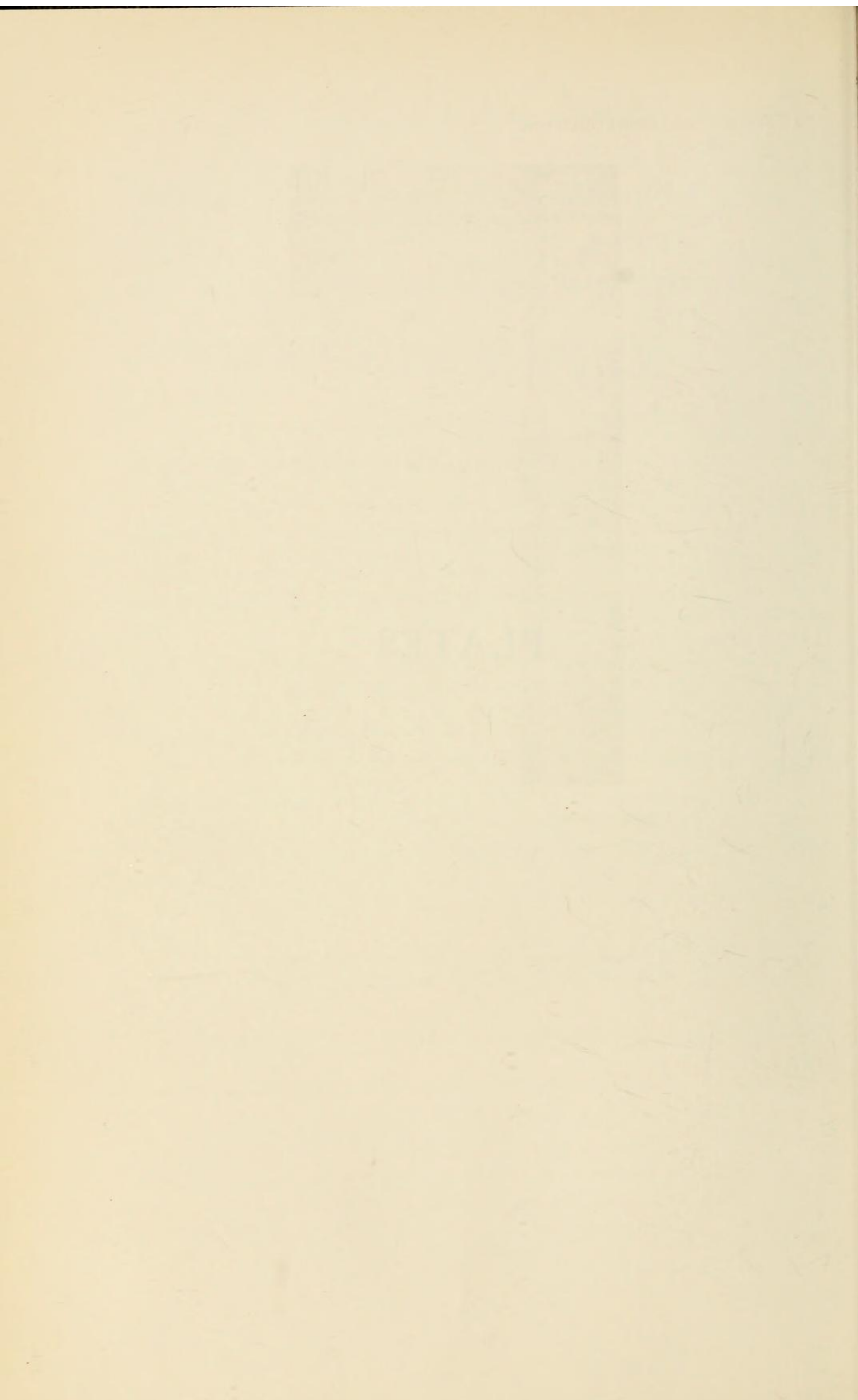
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PLATES



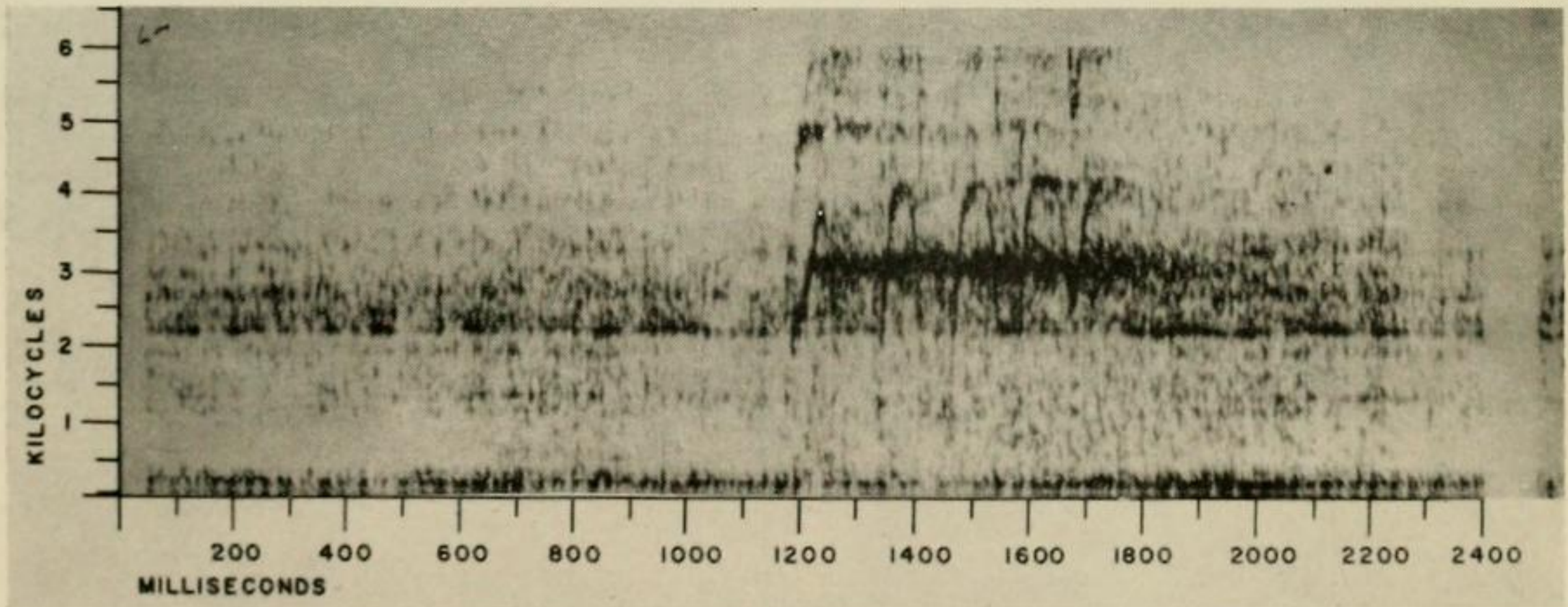


Plate 1

a. Pursed lips. This expression is the antithesis of the grimace and frequently accompanies the low ook ook and twitter vocalizations.

b. The tee tee sound. Neglect the constant background noise. The signal occupies the third quarter of the kymograph tracing (recorded from *A. geoffroyi*).

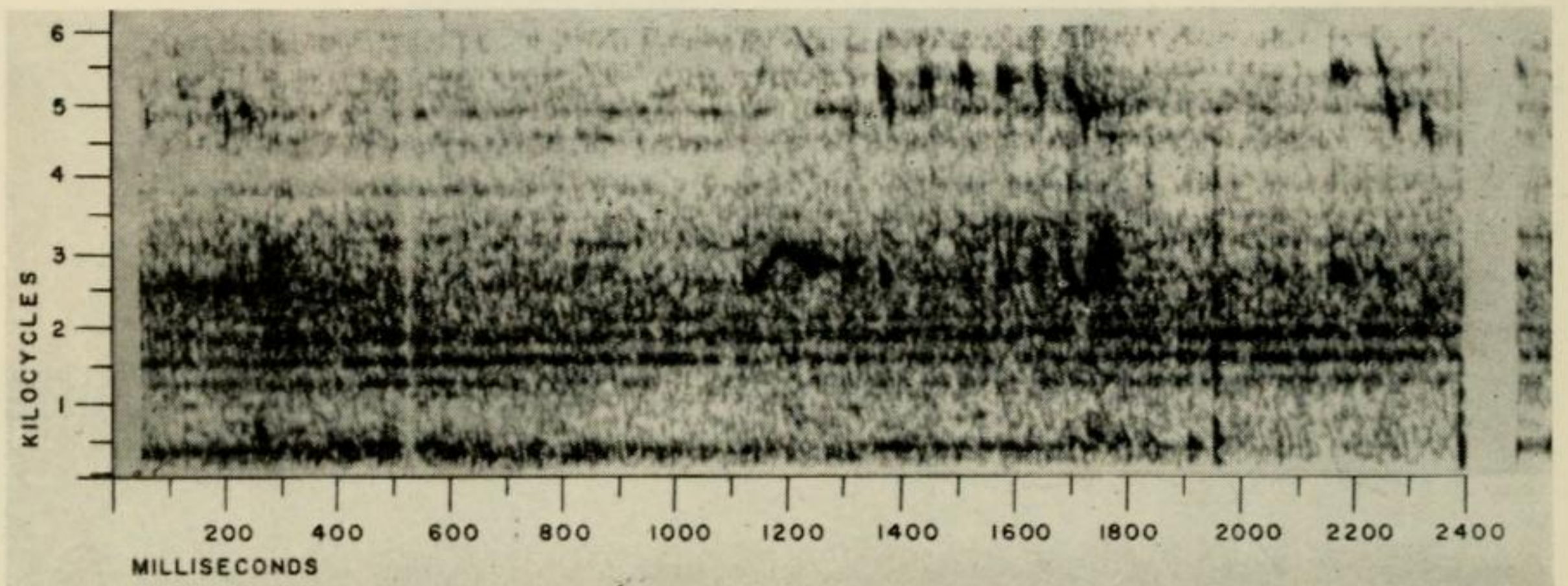
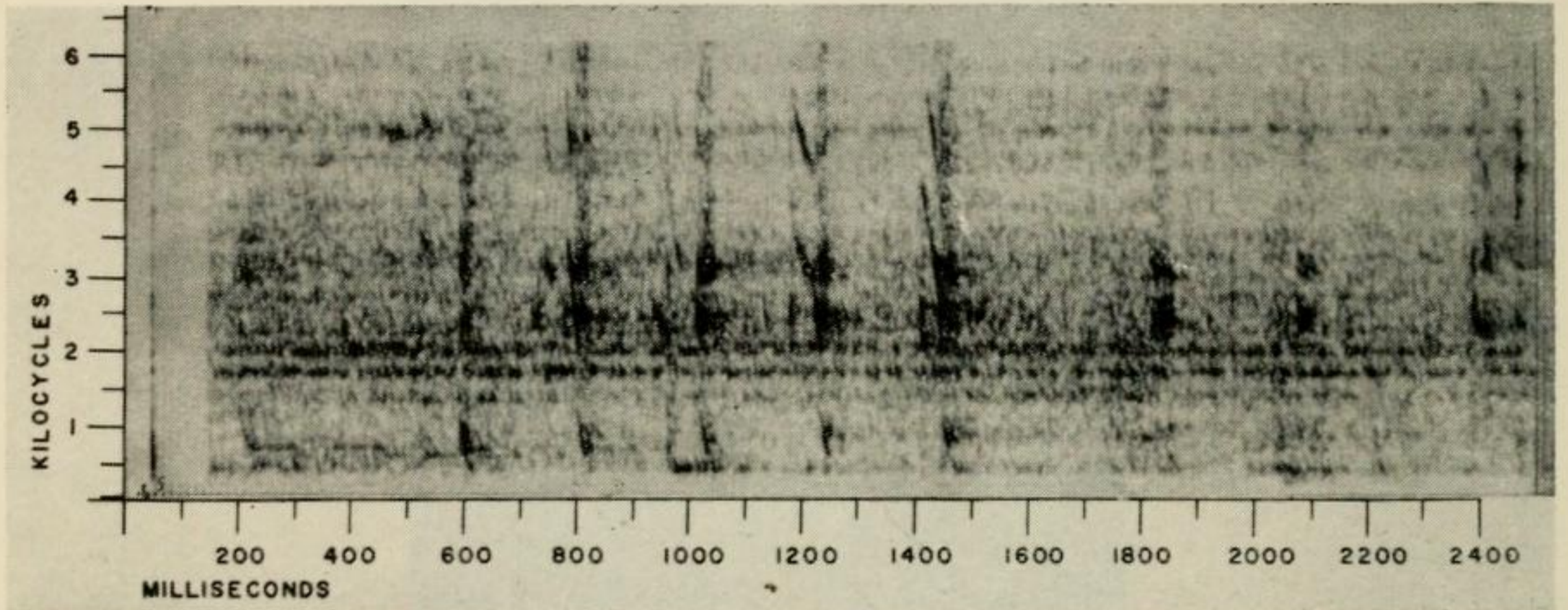


Plate 2

- a. A series of eight chirps recorded from *A. fusciceps*. Disregard the constant background noise in this and the following tracing.
- b. Portions of three twitter series. Note the double set of harmonics.

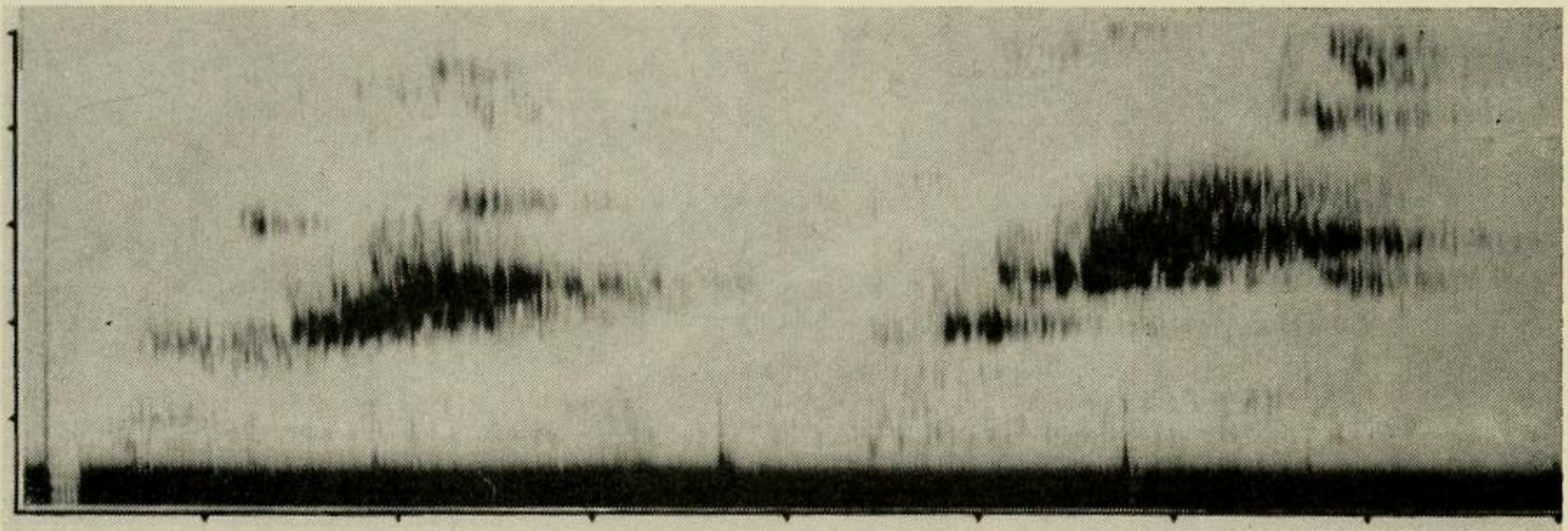
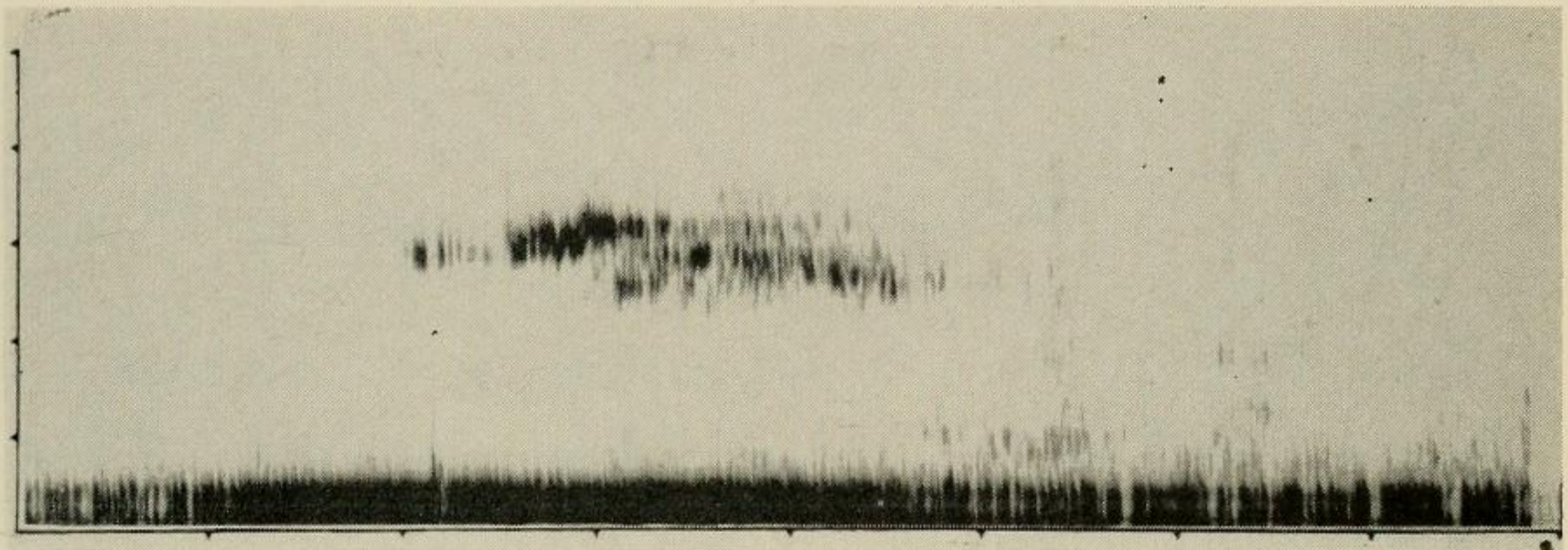


Plate 3

a. Whinny (*A. belzebuth*, male). (Note: unless specified, plates 3 through 6 display an ordinate of 1000 cps increments and an abscissa of .3 sec. increments).

b. Grunt Trill (*A. belzebuth*, male).

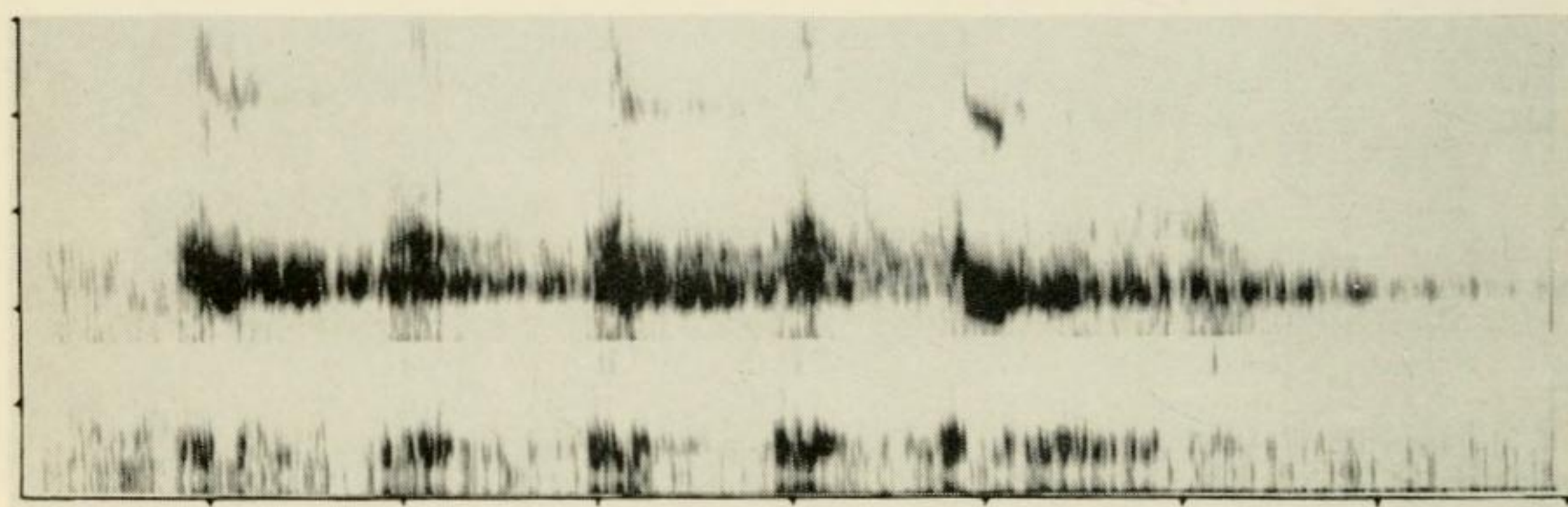
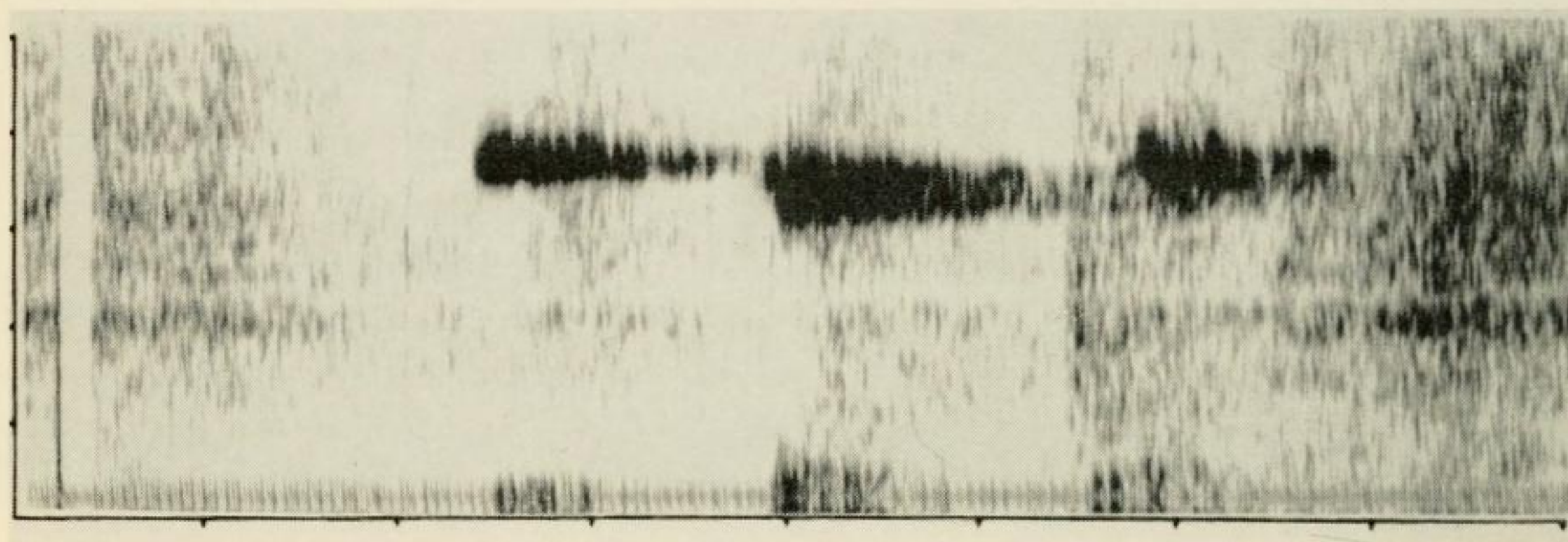


Plate 4

- a. Low squeak. Note the relatively narrow frequency range.
- b. Chitter; very high pitched, pulsed sound. Ordinate in 3000 cps increments; abscissa in .1 sec. increments. (*A. paniscus*, male).

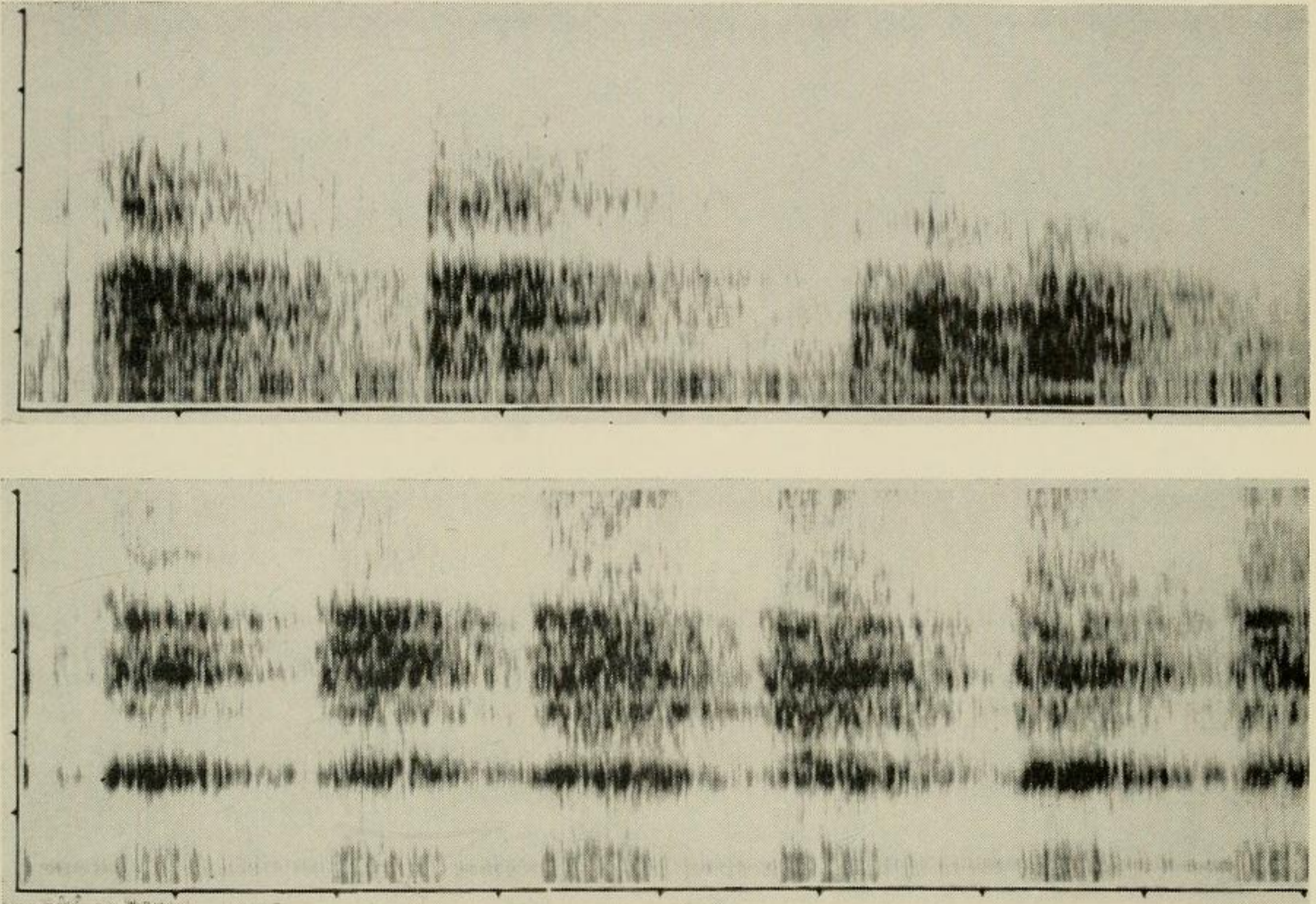


Plate 5

- a. Ook ook (*A. belzebuth*, male).
- b. Bark (*A. belzebuth*, male).

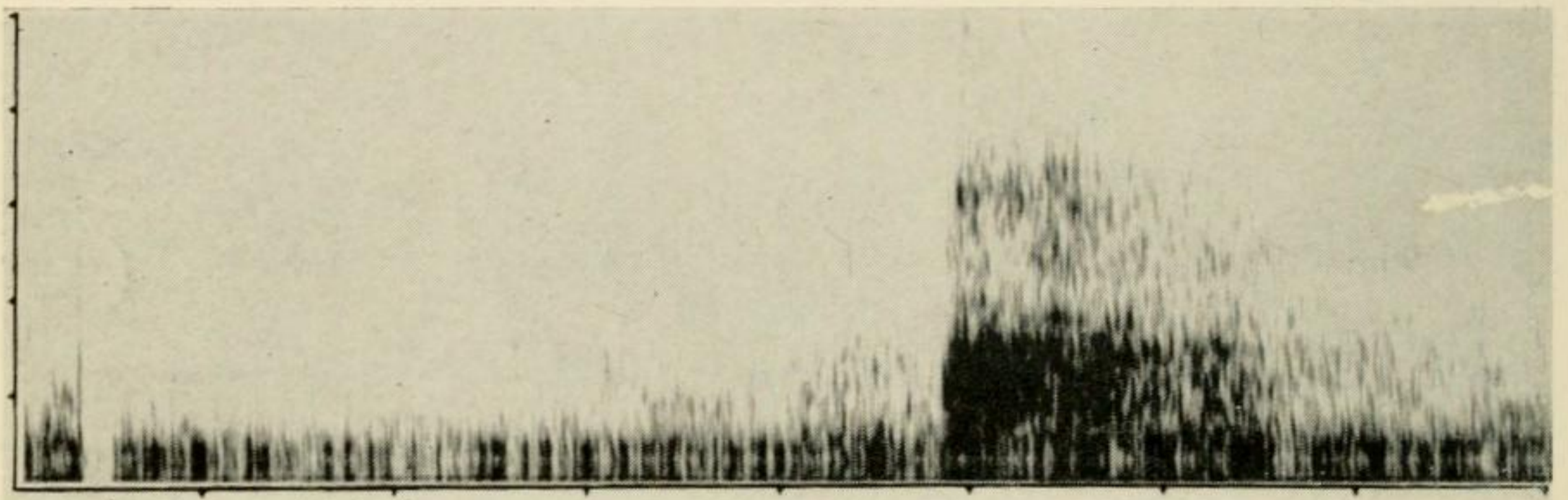
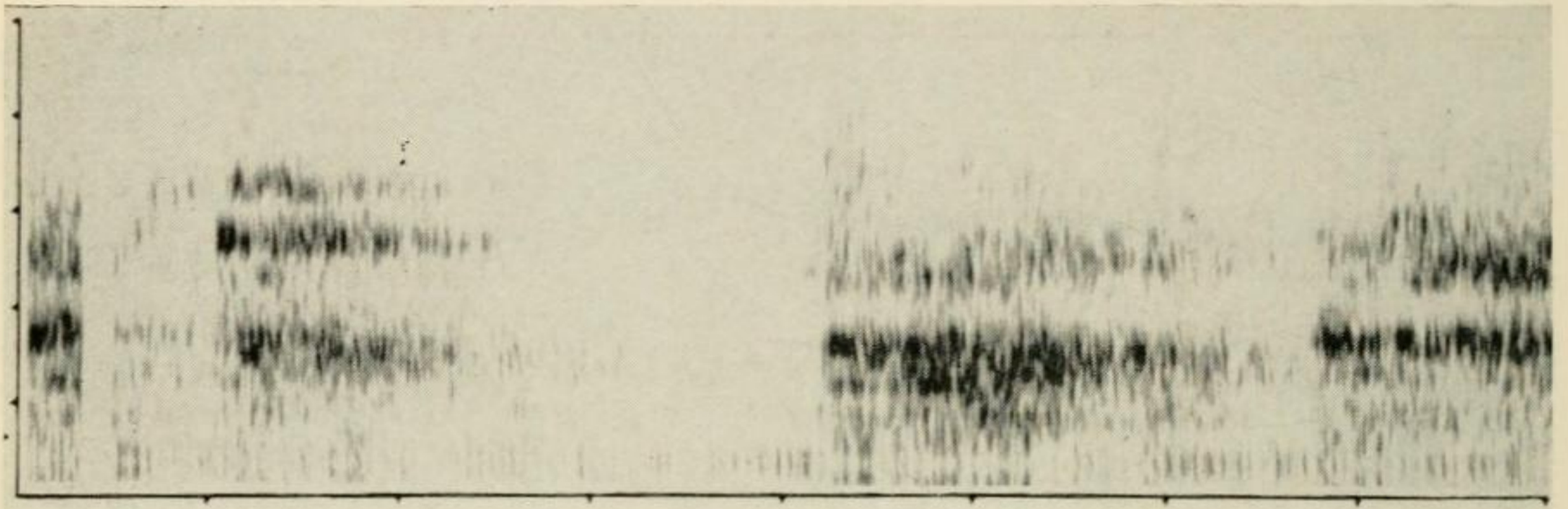


Plate 6

- a. Ook, followed by a growl (*A. belzebuth*, male).
- b. Cough (*A. belzebuth*, male).