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SOME BEHAVIOR PATTERNS OF
PLATYRRHINE MONKEYS
I. THE NIGHT MONKEY
(AOTUS TRIVIRGATUS)

By

M. MOYNIHAN

Director, Canal Zone Biological Area
Smithsonian Institution



(PUBLICATION 4533)

CITY OF WASHINGTON
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SOME BEHAVIOR PATTERNS OF
PLATYRRHINE MONKEYS
I. THE NIGHT MONKEY
(*Aotus trivirgatus*)

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THIS is the first in a series of papers on some behavior patterns of New World monkeys. The main emphasis of these papers will be comparative. Special attention will be paid to social signal patterns (including hostile and sexual signals) and other patterns that differ significantly in the various species. It is hoped that analyses of these patterns may throw some light on the evolution of the group as a whole.

INTRODUCTION

The Night Monkey (also called "Owl Monkey" or "Douroucouli") is a rather small monkey of distinctive appearance.

Although individuals vary considerably in proportions, all adults have relatively small heads and more or less elongated bodies. Their limbs are of moderate length, the hind limbs being somewhat longer than the front. Their tails are long and heavily furred, and not at all prehensile. The back, most of the head, and the outer surfaces of the limbs may be gray, brown, or even reddish brown, while most of the underside of the body and the inner surfaces of the limbs are usually clear buff or caramel colored. The upper part of the tail generally is the same color as the back, and the terminal half or two-thirds is blackish. The face and forehead are marked with conspicuous black and white stripes and patches (see the accompanying figures for an indication of the color pattern of Panamanian Night Monkeys). The distinctive appearance of the face is enhanced by the very large eyes. In bright light, the pupils are greatly contracted and the orange or hazel irides are conspicuous. In very dim light, the pupils expand enormously and the eyes appear to be completely black.

Young Night Monkeys look more like marmosets in some ways. They have relatively larger heads and shorter bodies and tails than

adults; and their eyes are relatively *smaller*, in proportion to the rest of the head (see figure 22).

This account is based primarily upon studies of captive animals, checked (whenever possible) by observations of wild animals living under natural conditions.

Fifteen Night Monkeys were kept in cages at the Smithsonian Institution laboratory on Barro Colorado Island between August 1958 and July 1963, for periods ranging from several months to more than 3 years. Some individuals were kept in small cages, 8' x 4' x 4', inside a house; but the majority were in larger cages outdoors in the forest. The outside cages varied in size from 6' x 6' x 8' to 30' x 12' x 8'. Generally each cage contained a single individual, a mated pair, or a family group; sometimes, however, larger groups (up to five individuals) were kept together in a large cage for a few days. All the Night Monkeys kept in captivity on Barro Colorado Island were wild-caught animals from mainland areas in Panama (probably, in most cases, from regions east of the Canal Zone) or were the offspring of such animals.

Some other captive Night Monkeys were observed briefly in the National Zoological Park, in Washington, D.C., in October 1959 and July 1960, and in Iquitos, Peru, in December 1958.

All observations of wild Night Monkeys were made on Barro Colorado Island, in both apparently mature and old second-growth forest (see Bennett, 1963).

The captive animals on Barro Colorado Island were sometimes observed from blinds; but such concealment usually was not necessary. Blinds were not used for observations of other captive individuals or the wild animals in the forest. Some of the captive individuals on Barro Colorado Island were accustomed to continuous but dim artificial light at night. This did not appear to affect their behavior after the first few nights. All other individuals were observed without using artificial light whenever possible. Sometimes moonlight was sufficient to reveal at least the most conspicuous and vigorous movements. Even in nearly complete darkness, it was sometimes possible to follow the behavior of the animals by the sounds of their movements and vocalizations. When artificial light was necessary, flashlights were used (either intermittently or continuously). This certainly affected the behavior of the animals, but did not always alarm them greatly or cause them to escape immediately.

According to Hershkovitz (1949), there is only one species of Night Monkey: *Aotus trivirgatus*; and the Panamanian population

belongs to the subspecies *griseimembra*. The exact provenance of the animals in the National Zoological Park in Washington, D.C., was unknown. The animals observed in Iquitos supposedly were caught in nearby areas and, therefore, were presumably representatives of the nominate subspecies (Hershkovitz, *op. cit.*) or the possibly distinct subspecies *vociferans* (Cabrera, 1957).

All references to the behavior of other platyrrhine monkeys in the following pages are based upon personal observation, unless specifically stated otherwise.

GENERAL HABITUS, LOCOMOTION, AND FEEDING

Some characteristic activities of Night Monkeys in the wild have been described in a number of earlier publications. The best general survey is by Cabrera and Yepes (1940), who summarize the reports of many early naturalists and travelers in South America; and the best account of Night Monkeys in Panama is by Enders (1935). It may be useful to recapitulate some of this information, and add a few details about locomotory and feeding habits, before discussing other aspects of behavior.

Night Monkeys differ from all other "true" monkeys in being almost completely nocturnal. Both captive and wild individuals are most active immediately after nightfall and just before dawn.

Wild Night Monkeys sometimes start to become active in the evening before it is completely dark, and may continue to move about for some minutes after it has started to become light in the morning. Captive individuals easily learn to move about in the daytime, and their adjustment to continuous artificial light at night is usually rapid. They appear to see quite well in all but the brightest light. This is not surprising, as there is some evidence (see, for instance, Hill, 1957, and Rohen, 1962) that the nocturnal habits of Night Monkeys are specialized rather than primitive among Platyrrhini. (The terms "primitive" and "specialized" are used, throughout this paper, as defined by Simpson, 1961.)

Wild Night Monkeys apparently are purely arboreal. On Barro Colorado Island, they usually move and feed in trees at heights ranging from 20 to at least 100 feet above the ground, and apparently never come lower than 10 feet above the ground. During the daytime, they sleep in holes in trees.

The fur of Night Monkeys is very thick and soft. This softness may be an adaptation to nocturnal and arboreal habits, possibly helping to reduce or muffle the sound of movements. It is probably

not coincidental that such unrelated animals as Kinkajous (*Potos*), Olingos (*Bassaricyon*), and Woolly Opossums (*Caluromys*), which are also nocturnal and arboreal, have fur of similar texture.



FIG. 1.—Two typical semierect preleaping postures.

Night Monkeys are extremely active and agile. (Hill, 1956, says that they are fairly slow moving; but this is certainly not true of individuals in the wild or of healthy captive individuals in adequate cages.) Like monkeys of the genera *Callicebus*, *Pithecia*, and *Cacajao*, they are expert and powerful leapers. Rapid movements through the

trees are usually accomplished by great bounds. When leaping, most of the propulsive power appears to come from the hind limbs, the forelimbs being used chiefly to absorb the shock of landing. The long and rather heavy tail seemingly is used as a counterweight, never as a prop or support. (This is another resemblance to *Callicebus* and *Pithecia*.) Night Monkeys run along branches less frequently than monkeys of the genera *Cebus* and *Saimiri* or tamarins such as *Saguinus geoffroyi*. (The generic names used in this paper follow Hershkovitz, 1958.)

As noted by Hill (1957), Night Monkeys are among the most nearly completely quadrupedal monkeys. Not only do they usually use both fore and hind limbs in locomotion, but they generally grasp a supporting branch with one or both hands even when sitting quietly. Just before leaping, however, they may take their hands off the supporting branch and sit or stand in a semierect posture, balancing on the hind limbs alone (see figure 1). The hind limbs generally are flexed in this posture, the back may be nearly straight or curved to an appreciable extent, and the front limbs may hang downward or the hands may be slightly raised (presumably in preparation for grasping a branch after the leap). An individual may remain poised in this way for several seconds or more.

Night Monkeys seem to eat a great variety of fruits and insects under natural conditions, and learn to eat artificial foods without difficulty in captivity. Their method of approaching and "handling" nonmoving food in captivity is interesting. They generally begin by sniffing at the food. (For other indications that they may have a good sense of smell, see below.) After sniffing for several seconds, an animal usually will seize the food with its teeth, and then sit up. Only then, in most cases, will it raise one or both hands to hold and possibly manipulate the food as it begins to chew.

The various ways in which different species of platyrrhine monkeys use their hands and fingers have not been well described. Some incorrect statements and misinterpretations are current in some of the published literature. Sanderson (1957), for instance, states that Night Monkeys have opposable thumbs and use their hands in much the same way as human beings. In a later passage, he also implies that they usually oppose the first two fingers of the hand against the last three (in much the same way as monkeys of the genera *Pithecia* and *Alouatta*). Both statements are somewhat misleading.

Night Monkeys often spread their fingers more or less radially when grasping an object. At such times, all the fingers tend to diverge

from one another to approximately the same extent. At other times, all five fingers of the hand may be kept pressed closely together. When some appreciable opposition does occur, it is perhaps most common for the thumb to be opposed to the other four fingers as a group; but this is by no means always the case. I have, in fact, seen Night Monkeys arrange their fingers in every possible way when grasping objects of different sizes and shapes. The first two fingers may be partly opposed to the last three; or the first three fingers may be partly opposed to the last two; or the first four fingers may be opposed to the fifth.

It is quite probable that this type of hand and use of fingers is primitive among Platyrrhini. (The actual structure of the Night Monkey hand is described in detail by Biegert, 1961.)

The most important general feature of the social behavior of Night Monkeys is their slight degree of gregariousness. On Barro Colorado they are seldom found in groups larger than a single pair or a single family of two parents with one young.

ORDINARY GROOMING AND CLEANING ACTIVITIES

New World monkeys perform two types of grooming: Self-grooming and mutual or social grooming, *i.e.*, the grooming of one animal by another. The former type may be called "autogrooming" and the latter "Allogrooming." (These terms have been suggested by the terms "autopreening" and "allopreening" applied to birds by Cullen, 1963.)

Most monkeys devote considerable time and effort to autogrooming; but different species tend to do this in slightly different ways.

The autogrooming of Night Monkeys consists almost entirely of scratching with the hands and/or the feet. Only very rarely does a Night Monkey use its teeth during autogrooming to "nibble" at its own fur or skin. The relative frequency of different types of autogrooming movements performed by some adult and subadult individuals in captivity on Barro Colorado Island is shown in the accompanying tabulation.

The actual frequency of autogrooming movements may vary widely, depending upon the situation. Most of this variation seems to be a function of the amount of dirt or ectoparasites in the fur, or of its disarrangement. In captivity, however, it is evident that most adult individuals tend to perform fewer autogrooming movements, on the average, than young individuals. This may be because adults tend to be less tame than young individuals in captivity. Night Monkeys seldom, or perhaps never, perform autogrooming movements when

they are either aggressive or alarmed. In this respect, they are quite different from many other New World monkeys, *e.g.*, species of the genera *Alouatta*, *Ateles*, and *Cebus*, which tend to perform particularly frequent and/or vigorous scratching in such circumstances.

It is my impression that young Night Monkeys also may tend to perform relatively more scratching movements with their feet, and

TABULATION OF ORDINARY GROOMING AND CLEANING REACTIONS

<i>Autogrooming performance</i>	<i>Number¹ of bouts</i>
Scratching the face with one hand.....	23
—the side of the head with the hand of the same side.....	1
—the chest with one hand.....	1
—the side of the body with the hand of the same side.....	24
—one hind leg with the hand of the same side.....	19
—one foot with the hand of the same side.....	5
—the genital region with one hand.....	4
—the tail with one hand.....	4
—one arm or hand with the other hand.....	16
—the tail with both hands.....	3
—the chin with one foot.....	2
—the face with one foot.....	11
—the side of the head with the foot of the same side.....	1
—the chest with one foot.....	1
—under one arm with the foot of the same side.....	1
—one arm with foot of the same side.....	7
—the side of the body with the foot of the same side.....	17
Nibbling the fur of the tail.....	1
 <i>Cleaning performance</i>	
Licking a hand.....	3
Rubbing the nose along the substrate.....	2

¹ This count is based upon observations of six individuals; two immatures and four adults. The longest period of observation of a single individual was 1 hour. The shortest period was 12 minutes.

relatively fewer scratching movements with their hands, than adults in similar situations. There may be two reasons for this: (1) Young individuals find it more difficult to balance with one hand off the ground and (2) they can reach most parts of their (relatively shorter) bodies with their feet more easily than can adults.

Unlike most other platyrrhines, Night Monkeys seldom perform allogrooming except in obviously sexual or partly sexual circumstances (see below). This presumably is correlated with their slight degree of gregariousness, but it is not due simply to lack of opportunity. Mated Night Monkeys rarely groom one another even when

they are close together if they are not also performing other sexual patterns.

A Night Monkey with dirt on its face sometimes removes the dirt by rubbing the face along a branch. These reactions are actually rare, but seem to be performed more frequently by Night Monkeys than by any other platyrrhines with which I am familiar except the tamarins of the genus *Saguinus*.

Night Monkeys clean their hands and fingers by licking.

The tabulation of autogrooming movements on page 7 also includes the cleaning movements performed by the same individuals during the same periods of observation.

HOSTILE BEHAVIOR

The term "hostile" may be applied to all behavior patterns resulting from a tendency to attack and/or a tendency to escape. In this sense, it is synonymous with the term "agonistic" as used in many other discussions of behavior (*e.g.* Scott, 1958).

The term "tendency" will be used in a broad sense throughout this paper, to designate any "readiness to show a particular type of behavior" (Marler, 1956).

In preliminary and essentially descriptive accounts of behavior based on observation rather than experiment, such as the present account of the Night Monkey, it is usually not necessary to distinguish between a great number of qualitatively different tendencies. Most social reactions can be characterized as the products of such broad tendencies as attack, escape, gregariousness, copulation, pairing, etc.¹

¹ The tendencies involved in the production of an otherwise ambiguous behavior pattern may be revealed by analysis of the other activities usually associated with the pattern. Conversely, the term "tendency" may provide a convenient and concise way of summarizing the circumstances in which a behavior pattern occurs. Thus, for instance, when a signal pattern such as a ritualized posture or a vocalization (see below) is said to be produced by the attack tendency, this means that an animal performing the pattern is likely to perform overt attack movements during or immediately after the pattern and/or give some outward indication that it "wants" to attack. When one signal pattern is said to be produced by a stronger attack tendency than another signal pattern, this means that the former is more likely to be accompanied or followed by overt indications of attack than the latter and/or is likely to be accompanied or followed by stronger indications of attack than the latter. (It should be stressed, in this connection, that when a particular behavior pattern is said to be produced by one or more particular tendencies it does not mean that other tendencies may not be activated in an animal performing the pattern at any particular time.)

This type of terminology has been criticized on various grounds. Among the most recent critics is Andrew (1963). The term "tendency" as used here is certainly a great oversimplification, but its convenience in actual practice may outweigh its disadvantages in theory. Most ethologists have been driven to use the same or a similar term, or the same concept in more or less disguised form, when describing a variety of different types of social behavior.

Andrew (*op. cit.*) suggests that all or most signal patterns of primates may be caused by "stimulus contrast." This is undoubtedly true—if "stimulus contrast" is defined broadly enough. But platyrrhine signal patterns are certainly not produced by a single range of qualitatively similar stimulus contrasts of differing strengths. Certain stimuli usually ("normally") provoke only sexual patterns, others generally provoke only hostile patterns, still others usually provoke only parental responses, etc. Thus the causation of platyrrhine signal patterns can be described in terms of stimulus contrasts only if distinctions are made between qualitatively different types of stimulus contrasts, *e.g.*, between hostile stimulus contrasts and sexual stimulus contrasts. It may be doubted if such a system is any more convenient or useful than the employment of terms such as tendency. It is certainly more difficult to use in descriptive passages. (And, in fact, Andrew himself does not use it consistently throughout his own description of primate signal patterns.)

All the vocal patterns cited in the following pages will be given names, such as "Moan," "Grunt," "Gulp," etc. These names are used purely for convenience. They are not meant to describe the acoustical properties of the sounds in detail; this will be done in the accompanying drawings of sound spectrograms. They are meant only to suggest that the sounds are somewhat similar (to human ears) to the common human and other everyday sounds called by the same names.

The term "sound" itself will be used in its ordinary, everyday sense throughout the paper.

All the hostile behavior patterns mentioned are those of adults, both males and females, unless specifically stated otherwise.

OVERT ATTACK BEHAVIOR

Night Monkeys are among the most aggressive New World primates. Adult individuals of the same sex usually fight savagely when put together in a cage. Adults of opposite sex, mates or potential mates, may not engage in violent fights, but they do direct a consider-

able variety of hostile patterns toward one another in at least some circumstances (see below).

This aggressiveness must be one of the factors keeping pairs and family groups apart in the wild. Captive adults of more gregarious species of the genera *Saimiri*, *Cebus*, *Ateles*, and *Alouatta* usually do not fight with one another as frequently or as vigorously as do Night Monkeys kept in similar conditions.

It is perhaps surprising, therefore, that overt fights between pairs and family groups of Night Monkeys seem to be relatively rare in the wild, at least on Barro Colorado Island. This seems to be due to the fact that different pairs or family groups simply do not come into contact with one another often. Each pair or family group seems to have its own territory or home range, in which it remains all or most of the time. (These territories or home ranges may be largely "traditional." Their boundaries may be established, originally, by means of disputes. Once established, the boundaries may be respected simply because the animals remember the results of the original encounters. If so, the territories of Night Monkeys on Barro Colorado Island are maintained in the same way as those of many birds occurring in the same area—see Moynihan, 1962a.)

(I have seen relatively large groups of wild Night Monkeys [including four or five individuals] only in the immediate vicinity of major food sources, *i.e.*, trees in fruit. In such cases, one pair or family group may have been so strongly attracted to the food that it crossed over the boundary of its territory or home range. Some of the individuals in these groups showed obvious hostility toward one another; and the groups always broke up within a few minutes.)

An aggressive Night Monkey may perform a variety of displays (see below) immediately before and/or after attacking; but the overt attack behavior itself is usually relatively simple.

An attacking individual usually begins by advancing, walking, slowly and cautiously toward its opponent. Then, when it has come close enough, it suddenly leaps forward and tries to bite the opponent and/or hit the opponent with its hands. This hitting is reminiscent of the jabbing of a human boxer. Usually two or three jabs are delivered with great rapidity one right after the other.

It is my impression that Night Monkeys strike with their hands during fights relatively more frequently than all or most other platyrrhines. This may be correlated with the fact that they do not have very long canine teeth.

A Night Monkey that has been attacked usually retreats as soon as possible; but its attacker seldom follows immediately. Even when

very aggressive, the attacker generally pauses a few seconds, before starting another slow and cautious advance, preparatory to another attack leap.

The Night Monkeys kept in captivity on Barro Colorado Island generally were quite silent while attacking; but once I heard an individual "spit," like a cat, at the very instant of jabbing an opponent. Hill (1960) mentions similar sounds in similar circumstances. So perhaps spitting sounds are a normal part of the attack behavior of Night Monkeys, at least in some populations of the species.

Sometimes two individuals will try to attack one another simultaneously. This may lead to a brief but extremely violent wrestling match, while each animal tries to bite and/or strike the other.

All these patterns, with the possible exception of "spitting," would appear to be expressions of the attack tendency alone. At least, they do not include any components that are unmistakable indications of any other tendency.

Other attack reactions may be less direct. It is not uncommon to see an aggressive animal leap over, or just to one side, of its opponent, instead of directly toward it. An aggressive animal leaping in this way is less likely to bite or strike its opponent than is an animal that has leapt more directly. In such cases, it would appear that the attack has been "deflected," probably by some counteracting tendency.

The tendency most likely to counteract attack during most hostile encounters is undoubtedly escape. There is considerable evidence that an escape tendency generally is activated to some extent, however slight, in all or most situations in which attack is activated. Even the most aggressive animals sometimes interrupt their attack behavior, by retreating briefly and/or performing displays which probably include an escape component.

Mated pairs of captive animals kept in adjacent cages may become engaged in vigorous disputes with one another. In such cases, it is obvious that usually males try to attack males while females try to attack females. Males also tend to attack more frequently, on the average, than do females.

Captive Night Monkeys seldom "redirect" (see Bastock, Morris, and Moynihan, 1953) attack upon individuals other than the ones provoking the attack. They certainly perform redirection attacks much less frequently than do individuals of many other species of Platyrrhini in similar circumstances. This seems to be due partly to the fact that direct expression of their aggressiveness is seldom or never impeded by any positively "friendly" gregarious tendency. Even

more important, mated Night Monkeys apparently never redirect attacks upon their mates or young.

This partial inhibition seems to be one of the more distinctive features of the behavior of Night Monkeys. It must be advantageous, and it may also be directly correlated with the social structure of the species. Although there is no proof, it seems likely that the pair-bonds of Night Monkeys are comparatively strong and stable. (At least, it is not uncommon to find two Night Monkeys in the same area of the forest, behaving in more or less the same way, for months at a time. It is difficult to believe that the individuals involved are not the same throughout the whole period.) Pair-bonds seem to be weaker and/or less continuous in some other New World primates, such as *Alouatta palliata* and *Cebus capucinus*, and the males of such species do perform redirection attacks upon females and young with considerable frequency (at least in captivity). There may have been strong selection pressure against such behavior in Night Monkeys simply because it is particularly important for them to avoid doing anything that might interfere with the maintenance of their pair-bonds.

The only redirection attacks observed during the present study were performed by one captive individual on Barro Colorado Island, when it was placed in a cage between two other cages that also contain Night Monkeys. When this individual became engaged in a dispute with one of its neighbors (fighting through the intervening wire mesh), it would occasionally interrupt the fight to make a rapid and absolutely unprovoked attack upon its neighbor on the opposite side.

I have never seen Night Monkeys jump up and down in rage, or shake branches of trees, or break off and drop branches, like so many other species of both New World and Old World monkeys (see, for instance, Carpenter, 1934 and 1935, Ullrich, 1961, and Hinde and Rowell, 1962). They may lack such patterns because they are rather small and light in weight.

Many other species of monkeys perform "play wrestling," all or most of which seems to be a type of partly inhibited attack. This also seems to be almost or completely lacking in Night Monkeys, presumably as another consequence of their slight degree of gregariousness. Even when several young Night Monkeys are kept together in the same cage, they do not perform any wrestling which appears to be anything but ordinary, uninhibited attack.

OVERT ALARM OR ESCAPE BEHAVIOR

The simplest alarm reaction of Night Monkeys is a brief "freeze." In the most common form of freeze, an animal remains motionless

in whatever posture it was in when it first perceived a disturbing stimulus. Such freezes tend to be performed as reactions to distant stimuli or familiar near stimuli. They are not usually associated very closely with vigorous movements or displays in such circumstances.

Sometimes an animal will close its eyes, briefly, immediately before, during, or immediately after pausing in a simple freeze.

The most conspicuous escape behavior of Night Monkeys in the wild or in large cages is simply rapid, running or leaping, retreat. This tends to be performed as a reaction to some strong, near and/or unfamiliar stimulus, such as actual attack or other overt aggressive behavior by another individual of the same species or the sudden approach of a "potential predator" such as a strange human being. Active retreats frequently are preceded and/or followed by elaborate displays.

In similar social circumstances, a Night Monkey in a *small* cage may either run or leap around its cage very rapidly or, alternatively, perform a pattern which is reminiscent of the simple freeze described above but somewhat more complex. In this pattern, the animal sits motionless with its head lowered (such lowering is not characteristic of ordinary freezes). The head is sometimes lowered almost to the level of the hands or the branch on which the animal is sitting. The animal may look straight down, or keep its head turned sideways in order to fixate the disturbing stimulus. At the same time, the limbs may be drawn in under the body and strongly flexed. This is obviously a preparation for (or an "intention movement" of) leaping. As a result of the lowering of the head, the back is more or less curved (but not raised). Some typical variations of this "head-down posture" are shown in figure 2.

It is possible that Night Monkeys also assume head-down postures in the wild under completely natural conditions. I never actually saw such reactions in the forest on Barro Colorado Island (they would be extremely difficult to distinguish in trees at night); but some of the animals kept in large cages, which approximated natural conditions, did assume head-down postures from time to time.

The captive individuals in large cages did not, however, assume head-down postures as frequently as individuals of many other species of platyrrhine monkeys in similar situations. And their head-down patterns were not as exaggerated in form as the homologous patterns of some related species.

All these overt escape or alarm patterns are usually silent. The fact that Night Monkeys customarily are silent during rapid retreats from potential predators is another distinctive feature of the species,

as all or most other platyrrhines utter special "Warning Notes" in such circumstances. It is probable, however, that the Night Monkey does have one pattern in its vocal repertory which is at least partly homologous with the Warning Notes of some other species, although uttered in a slightly different range of circumstances and subserving a different function (see discussion on page 43).

All the alarm and escape reactions of Night Monkeys would appear to be expressions of the escape tendency alone, in much the same way that the aggressive reactions described above seem to be expressions of the attack tendency alone. The circumstances in which the various patterns occur would suggest that simple freezes are produced by weaker motivation than either active retreat or head-down postures. The strength of the escape tendency may be approximately the same in the latter two patterns, the head-down posture being assumed only by individuals unable or unwilling to retreat, possibly for any one of several different reasons.

The head-down postures are the most interesting of these patterns from a functional point of view. Both head-downs and ordinary freezes seem to be primarily attempts to hide, and to hide the whole animal, *i.e.*, to prevent a potential opponent or predator from noticing any or all parts of the motionless animal. Some of the head-down patterns may also be advantageous in a slightly different way. When an animal in a head-down posture looks straight downward, its black and white facial pattern and its eyes usually are partly or wholly concealed. These facial features seem to be the characters that release attack most frequently, or toward which attacks are usually directed. Thus an individual in a head-down posture of this type may not be attacked by an opponent or (possibly) a predator, even though the rest of its head and body are perfectly visible, and have in fact been noticed. In such cases, the head-down may function as "appeasement," reducing the attack tendency of an opponent without increasing its escape tendency (see Moynihan, 1955). The closing of the eyes during some ordinary freezes may subserve a similar function, although presumably less effectively.

DISPLAY BEHAVIOR

The most common hostile behavior patterns of Night Monkeys are "displays."

The term "display" may be used to include all "ritualized" patterns, *i.e.*, all vocal patterns and all movements and postures that seem to have become specialized in form and/or frequency to serve signal

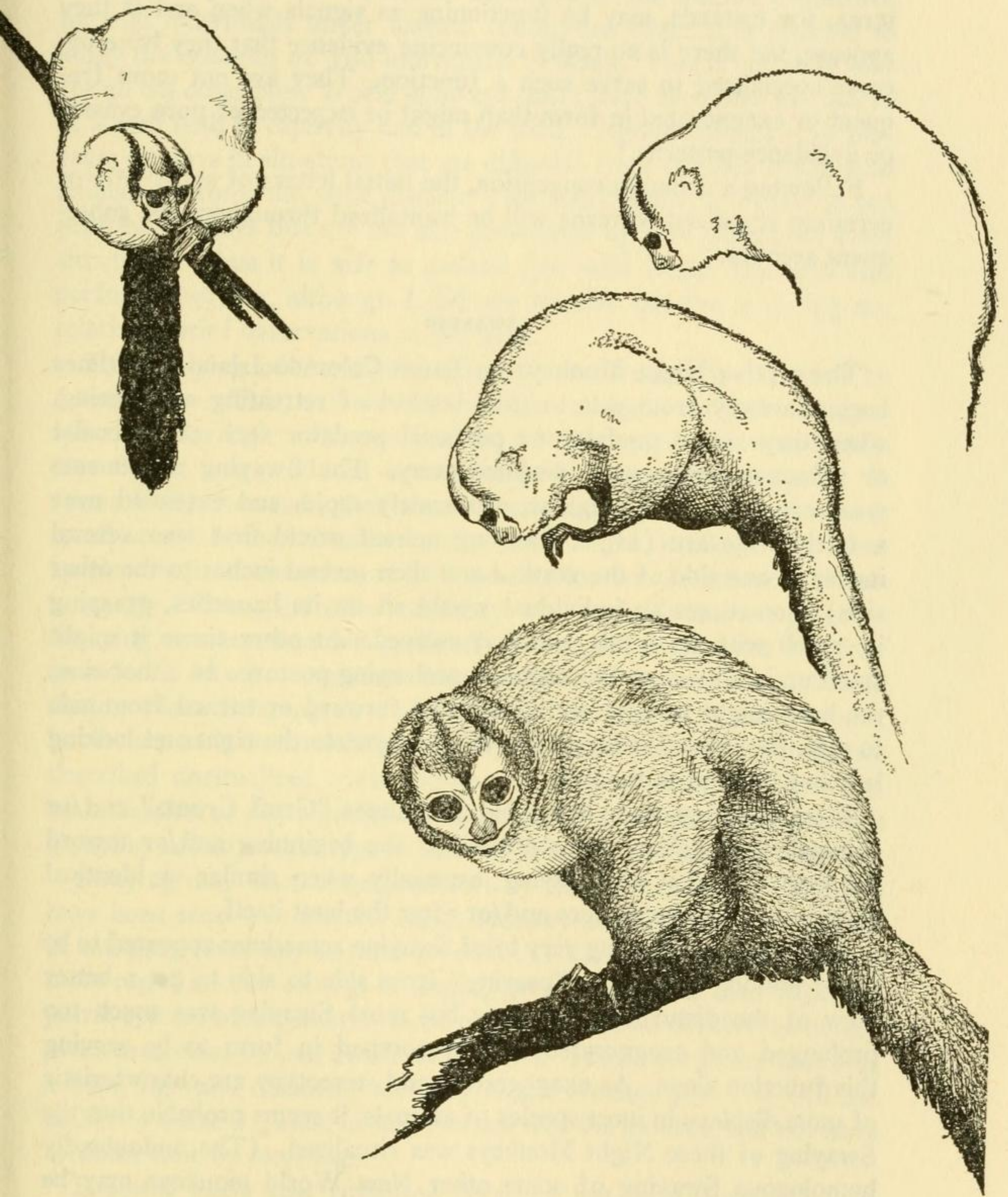


FIG. 2.—Four head-down postures.

functions. (This does not mean that all patterns that may function as signals are necessarily displays. The head-down and eye-closing patterns, for instance, may be functioning as signals when and if they appease, but there is no really convincing evidence that they have become specialized to serve such a function. They are not more frequent or exaggerated in form than might be expected of pure evasive or avoidance patterns.)

Following a common convention, the initial letters of apparently or certainly ritualized patterns will be capitalized throughout the subsequent account.

SWAYING

The captive Night Monkeys on Barro Colorado Island sometimes began to sway from side to side, instead of retreating or freezing, when they saw a predator or potential predator such as an ocelot or a human being some distance away. The Swaying movements were usually smooth, regular, moderately rapid, and extended over a fairly wide arc (*i.e.*, a Swaying animal would first lean several inches to one side of the vertical and then several inches to the other side). Sometimes an individual would sit on its haunches, grasping its perch with its hands, while it swayed. At other times it might stand up in a more or less extreme preleaping posture. In either case, the head might be kept facing straight forward or turned from side to side, the animal looking right as it swayed to the right and looking left as it swayed to the left.

Most Swaying was silent; but sometimes "Gruff Grunts" and/or "Gulps" (see below) were uttered at the beginning and/or toward the end of a bout of Swaying, especially when similar or identical sounds were uttered before and/or after the bout itself.

An animal performing very brief Swaying sometimes appeared to be doing nothing more than "peering" from side to side to get a better view of the disturbing stimulus; but most Swaying was much too prolonged and exaggerated and stereotyped in form to be serving this function alone. As exaggeration and stereotypy are characteristic of most displays in most species of animals, it seems probable that the Swaying of these Night Monkeys was ritualized. (The undoubtedly homologous Swaying of some other New World monkeys may be even more exaggerated in form and is undoubtedly ritualized.)

Unfortunately, the function(s) and, to a lesser extent, the causation of the Swaying of Night Monkeys remain partly obscure, primarily because the behavior was never observed in the wild.

One comment may be inserted here. Experience has demonstrated that ritualized patterns performed by captive individuals are always found to be part of the "natural" repertory of the species, performed by wild individuals under natural conditions, when it is possible to study the behavior of wild individuals in detail. This is certainly true for all the other New World monkeys that I have been able to observe at length both in captivity and in the wild. Captive animals may perform displays in situations that are different from those in which wild animals perform the same displays (see also below), but they do not perform displays that are not also performed by wild animals in some situations. Thus it is safe to assume that wild Night Monkeys also perform Swaying, although I did not actually observe it during my relatively brief observations in the wild.

The Swaying of the captive animals was frequently followed by overt escape. This, and the fact that it was apparently always provoked by the sight of a predator or potential predator, would indicate that it was produced by activation of the escape tendency. It seems likely, however, that some other tendency was also involved, as all or most other ritualized patterns of Night Monkeys and other species are produced when at least two tendencies are activated simultaneously. If so, the other tendency was probably attack, as some Swaying was accompanied by Gruff Grunts, and these notes certainly include an attack component (see below). If attack was activated during silent Swaying, it was obviously much weaker than escape, but it may have been relatively slightly stronger than in the previously described unritualized overt escape and alarm patterns. There was no indication of any significantly close or regular association between Swaying and any other type of social ("friendly" or sexual) behavior.

Swaying may discourage predators by letting them know that they have been seen. An alerted Night Monkey should have no difficulty in escaping from any natural predator. Night Monkeys are lighter, more rapid, and/or capable of leaping greater distances than any sympatric species of carnivore. Most of the individual carnivores in any given area must be well aware of this fact. Thus a carnivore that sees a Swaying (and obviously alerted) Night Monkey probably will not bother to chase it. This, in turn, means that the monkey will not have to waste time by escaping.

It seems likely that ritualized Swaying has been derived, in the course of evolution, from unritualized "peering." Some of the sideways components of Swaying may also have been derived from intention movements of turning away (from an alarming stimulus).

SILENT ARCH POSTURES

All the captive animals on Barro Colorado Island assumed distinctive "Arch Postures" quite frequently.

In these postures, the back was raised, usually to a considerable extent, and strongly arched or curved. The raising movement itself was always rapid, but the posture generally was maintained for an appreciable length of time (up to a minute in some cases). Sometimes an individual stood up on its hind limbs as it assumed an Arch Posture. In this case, the front limbs were allowed to hang downward, usually with the elbows more or less akimbo. Generally the hands were held with the backs facing inward and the palms outward and the hind limbs were straight or only slightly bent at the knees. A typical Arch Posture of this type is shown in figure 3c (such postures were quite similar to some semierect preleaping postures in many respects, but could always be distinguished by the more extreme curvature of the back). In other Arch Postures, the performing individual did not stand up, but remained clasping the perch with both hands and feet. In such cases, all four limbs were usually nearly straight. Typical Arch Postures of this type are shown in figures 3a and 3b. (It will be noticed that the relative positions of the head and back are nearly the same in both Arch Postures of this type and some head-down postures; but the effect is achieved by different methods in the two patterns, lowering the head in one case and raising the back in the other, and the general impression or "gestalt" of the two patterns is quite different.)

Irrespective of these minor variations in physical form, the Arch patterns of the captive animals could be divided into two main categories—one silent; the other accompanied by Resonant Grunts (see below).

Silent Arch Postures were assumed during all sorts of purely and partly hostile intraspecific encounters; but they were most common, and most long-sustained on the average, during the longest and most violent disputes between previously unacquainted individuals of the same sex and between "territorial" rivals in adjoining cages. They were often preceded and followed by a great variety of purely or partly hostile vocal patterns, produced by both attack and escape tendencies (see below), and/or by ambivalent unritualized hostile movements. When they were closely associated with an unambiguous unritualized hostile reaction, however, it was always overt attack, *not* escape. Individuals assumed silent Arch Postures with appreciable frequency both before and after delivering overt attacks.

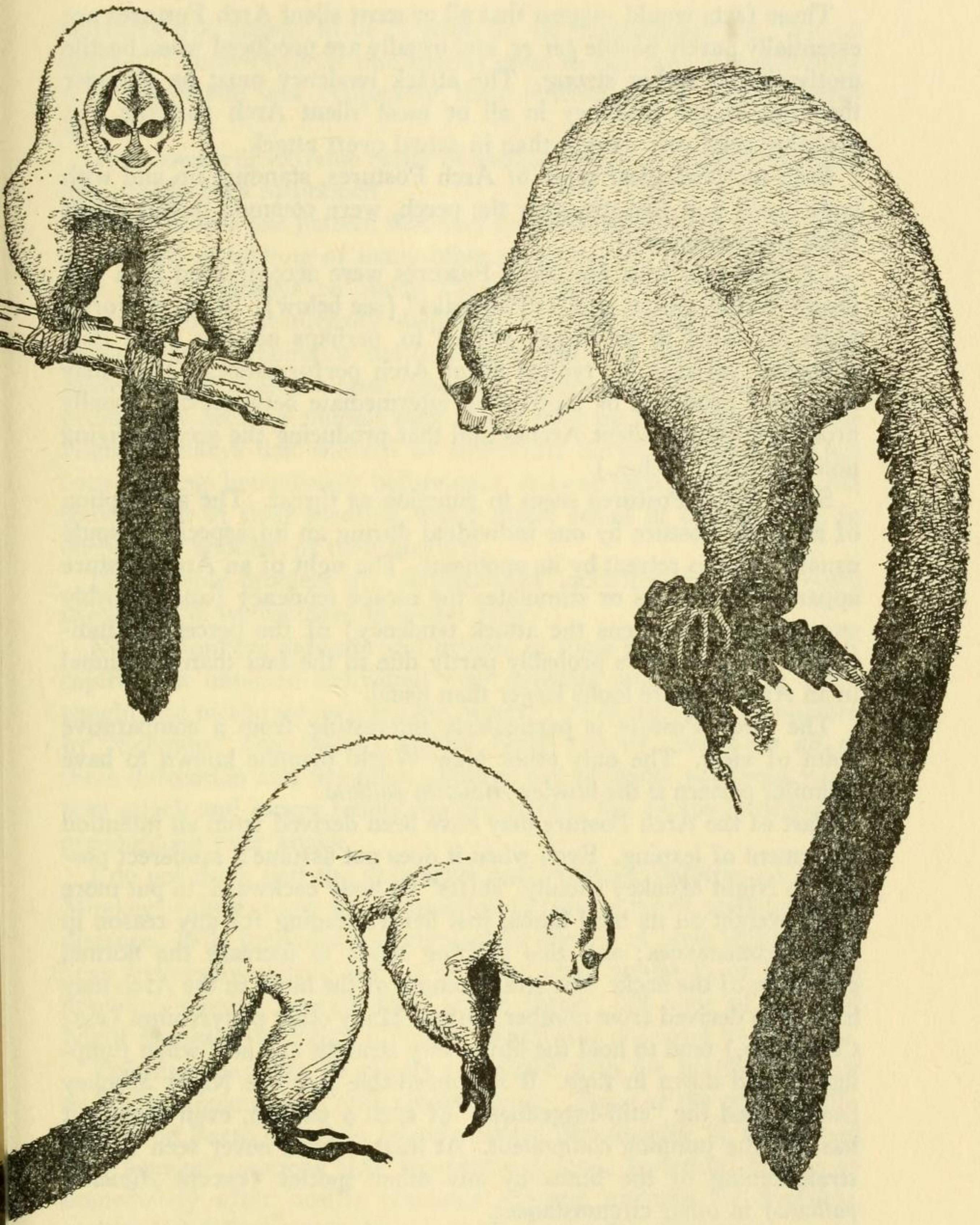


FIG. 3.—Arch Postures.

Upper left and right, two typical Arch Postures with hands grasping the perch. Bottom, an Arch Posture with hands raised off the perch.

These facts would suggest that all or most silent Arch Postures are essentially purely hostile *per se*, and usually are produced when hostile motivation is rather strong. The attack tendency must be stronger than the escape tendency in all or most silent Arch patterns, but probably relatively weaker than in actual overt attack.

Both morphological types of Arch Postures, standing up and with both hands and feet grasping the perch, were common during silent Arch performances.

(A relatively very few Arch Postures were accompanied by a few Gruff Grunts, Gulps, and/or "Squeaks" [see below]. These performances appeared to be closely related to, perhaps nothing more than abnormal variants of, typical silent Arch performances. They may have been produced by motivation intermediate between that usually producing typical silent Arches and that producing the accompanying notes without Arches.)

Silent Arch Postures seem to function as threat. The assumption of an Arch Posture by one individual during an intraspecific dispute usually induces retreat by its opponent. The sight of an Arch Posture apparently activates or stimulates the escape tendency (and probably suppresses or weakens the attack tendency) of the perceiving individual. This effect is probably partly due to the fact that an animal in an Arch Posture looks larger than usual.

The Arch Posture is particularly interesting from a comparative point of view. The only other New World primate known to have a similar pattern is the howler *Alouatta palliata*.

Part of the Arch Posture may have been derived from an intention movement of leaping. Even when it does not assume a semierect posture, a Night Monkey usually "shifts" its body backward, to put more of its weight on its hind limbs, just before leaping for any reason in any circumstances; and this shifting tends to increase the normal curvature of the back. The straightening of the limbs in the Arch may have been derived from another source. Many other platyrrhines (*e.g.*, *Cebus* spp.) tend to hold the limbs very straight and stiff when jumping up and down in rage. It is conceivable that the Night Monkey has retained the "stiff-leggedness" of such a pattern, even though it has lost the jumping component. At least, I have never seen similar straightening of the limbs by any other species (except *Alouatta palliata*) in other circumstances.

OTHER VISUAL PATTERNS

An important negative feature of the hostile repertory of Night Monkeys is the comparative rarity of "displacement" activities, *i.e.*,

activities that appear to be "irrelevant" or "extraneous" or "out of context." Individuals of this species seem to perform such activities relatively much less frequently than individuals of many related species.

The absence or extreme rarity of autogrooming in hostile situations has already been mentioned.

There is only one pattern that may be partly equivalent to the "displacement" scratching of many other platyrrhines. Some of the captive Night Monkeys on Barro Colorado Island sneezed repeatedly during some high-intensity disputes. In other situations, sneezing seems to be a cleaning or comfort movement of a peculiar type used to clear or clean out the nose. Sneezing is very common after feeding, presumably because animals tend to get food up their noses. As the Night Monkeys that sneezed so frequently during disputes had not been feeding immediately beforehand, it is at least conceivable that some or all of their sneezing was a direct result or consequence, in one way or another, of their hostility.

(The whole problem of "displacement" activities by New World primates will be discussed in a later paper.)

Night Monkeys defecate and urinate in some hostile situations. A captive but untamed individual may defecate and/or urinate when caught and picked up by a human being. This is usually accompanied by "Screams" (see below) and/or Gruff Grunts. Some or all of these defecation and urination patterns are probably produced when both attack and escape tendencies are strong, but escape is definitely predominant over attack.

I do not think that the defecation and urination patterns of Night Monkeys subserve any signal function or help to repel predators at a distance. Wild individuals of many other species of New World monkeys frequently urinate and/or defecate upon predators or potential predators passing beneath them in the forest; but none of the wild Night Monkeys on Barro Colorado Island was observed to do so.

Vomiting may also be closely associated with the hostile behavior of Night Monkeys in certain circumstances. Some of the captive individuals on Barro Colorado Island vomited occasionally, or performed the "heaving" motions that frequently precede vomiting, during or immediately after hostile reactions (escape movements, Swaying, and/or Gruff Grunts) to the approach of a human observer.

Night Monkeys have fewer signal patterns designed to be perceived by the eye than many other New World primates; and most of the signal patterns of this type that they do have are comparatively crude or "gross," produced by simple movements of the whole body and/or

head. They lack the variety of facial expressions (*e.g.*, frowns, baring of teeth, pursing of lips) which are important signal patterns in such platyrrhines as *Cebus* and *Ateles* species. They also lack the special elongated tufts and ruffs of hair on the head and around the face which are typical of many marmosets and tamarins, and which can be erected or depressed to convey signal information. The absence of such characters may be correlated with nocturnality. Adult Night Monkeys frequently become separated (by distances of at least several yards) from their mates and subadult young while feeding and moving in the forest at night. In such circumstances, they probably cannot rely upon perceiving visual signals, especially small and complex signals, from their companions as frequently or as easily as can adults of other platyrrhine species which are diurnal or crepuscular (see also discussion on page 45).

Andrew (*op cit.*) says that Night Monkeys open the mouth in threat. I never saw this except when sounds were uttered at the same time.

The complex black-and-white head pattern of Night Monkeys (more complex than the corresponding patterns of any other New World primate) may provide a partial substitute for a variety of facial expressions, whenever Night Monkeys are close enough together to perceive the pattern clearly. Because the black and white stripes and patches are convergent and divergent, and some of them are curved, a slight alteration of the position of the head relative to an observer will tend to alter the whole appearance or "gestalt" of the pattern (see the accompanying sketches). This must help to emphasize the signal effect of head movements.

GRUFF GRUNTS

Most of the vocal patterns of adult Panamanian Night Monkeys can be divided into eight main categories: Gruff Grunts, Resonant Grunts, Screams, Low Trills, Moans, Gulps, Sneeze-grunts, and Hoots. All except the last seem to be purely or partly hostile.

Gruff Grunts are among the most common of the vocal patterns. I heard them uttered by both wild and captive individuals on Barro Colorado Island and by all the other captive individuals studied. The typical Gruff Grunts of almost all individuals were similar or identical in sound (to the human ear), low-pitched, moderately long, and moderately loud. Figure 4 is a sketch of a sound spectrogram of a single note of this type.

(All the sound spectrograms illustrated in this paper are derived

from recordings of captive individuals on Barro Colorado Island. The recordings were made by an Ampex 601, using an Electrovoice 666 Variable D Cardioid microphone.)

Gruff Grunts usually are uttered singly or in short series of two to five notes. Each note of a short series seems to be essentially the same as a single note, and the successive notes may be uttered at slightly irregular intervals. Series are frequently repeated, but successive series generally are separated by relatively long pauses (much longer than the longest intervals between notes of a single series).

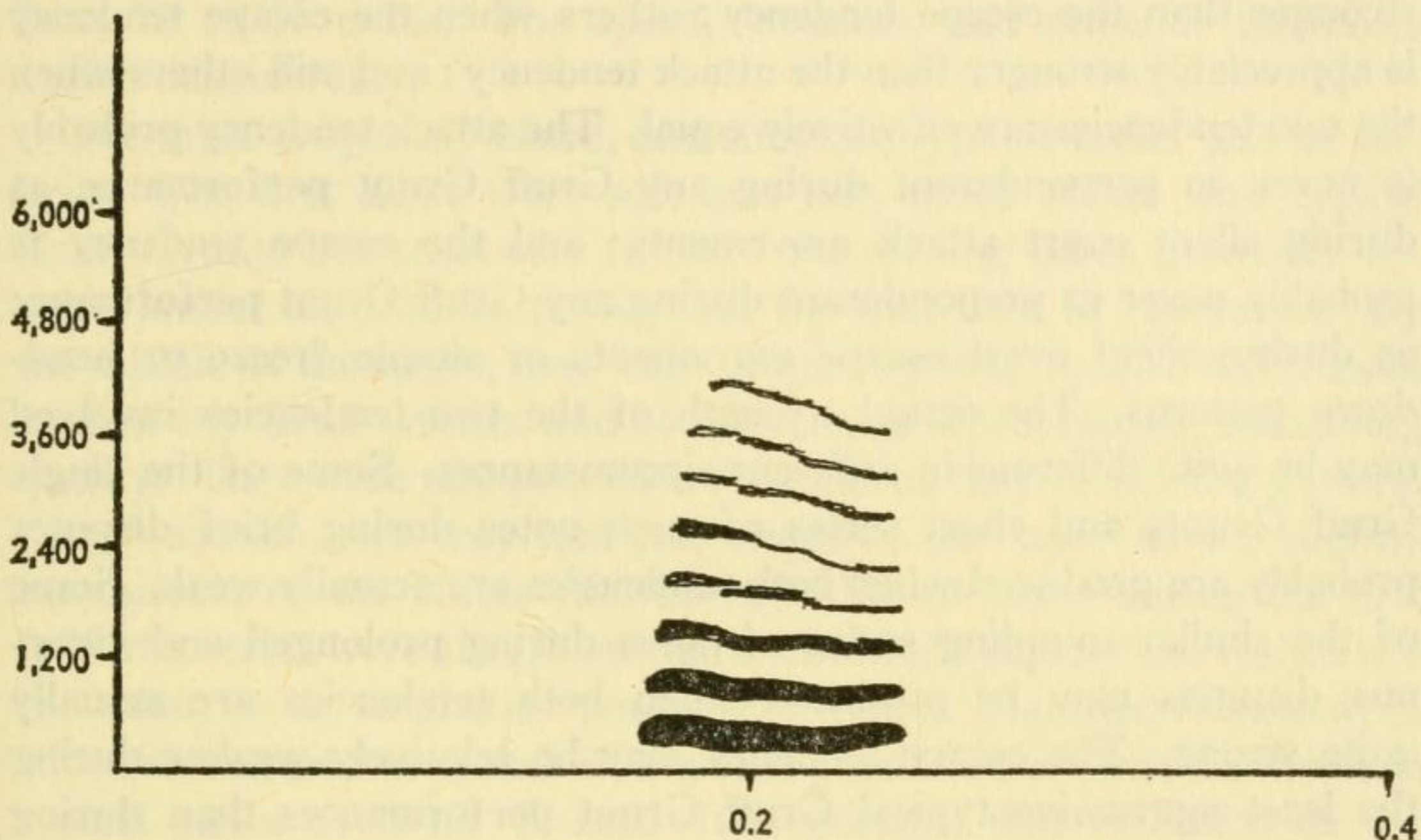


FIG. 4.—A typical Gruff Grunt, uttered by an adult.

Based upon a sound spectrogram made by a Kay Electric Co. "Vibralyzer."

In this and all the following sketches of vocal patterns, the figures along the vertical axis indicate cycles per second and the figures on the horizontal axis indicate elapsed time in seconds.

All Gruff Grunts seem to be uttered with the mouth almost or completely closed; but they are usually, or perhaps always, accompanied by conspicuous inflation of the throat region, the throat swelling up just as a note begins, and then subsiding immediately as soon as the note ends (even when the note is part of a series).

Both single Gruff Grunts and short series of such notes are uttered frequently during all sorts of hostile encounters, apart from partly sexual situations, during both brief and prolonged intraspecific disputes in the wild as well as in captivity, and as reactions to the appearance of a predator or potential predator. During intraspecific disputes, they are uttered by aggressive individuals before and after

attacking, by obviously frightened or defensive individuals before and after performing overt escape movements, and by individuals that perform both overt attack and escape movements as well as other displays. They are also uttered during some encounters between mates or potential mates (see below), but they are relatively (if not always actually) uncommon in such circumstances. These facts would suggest that all or most Gruff Grunts are produced by simultaneous activation of the attack and escape tendencies, and these tendencies alone. The range of motivation is probably quite broad. Some Gruff Grunts seem to be produced when the attack tendency is appreciably stronger than the escape tendency; others when the escape tendency is appreciably stronger than the attack tendency; and still others when the two tendencies are effectively equal. The attack tendency probably is never as preponderant during any Gruff Grunt performance as during silent overt attack movements; and the escape tendency is probably never as preponderant during any Gruff Grunt performance as during silent overt escape movements or simple freeze or head-down patterns. The actual strength of the two tendencies involved may be quite different in different circumstances. Some of the single Gruff Grunts and short series of such notes during brief disputes probably are produced when both tendencies are actually weak. Some of the similar-sounding series of notes during prolonged and vigorous disputes may be produced when both tendencies are actually quite strong. The escape tendency may be relatively weaker during the least aggressive typical Gruff Grunt performances than during silent Swaying; or, if the relative strength of the two hostile tendencies is the same in the two types of performance, their actual strength may be greater during the Gruff Grunts than during silent Swaying. Similarly, the most aggressive Gruff Grunt performances may be less aggressive than typical silent Arch Postures or, perhaps less probably, produced when the total actual strength of the hostile motivation (the attack and escape tendencies together) is less than in the silent Arches.

Gruff Grunts certainly function as threat during intraspecific disputes. They probably do not have a regular signal function when provoked by the appearance of a potential predator.

Some of the captive individuals on Barro Colorado Island were heard to utter single but frequently repeated soft notes which sounded as if they might be nothing more than weak or muffled versions of typical Gruff Grunt notes. Some of these were so soft that they were little more than audible expirations of breath. They were uttered by untamed individuals watching me approach, and were followed (when I came closer) by moderately vigorous escape movements, sometimes

with Gulps and/or Sneeze-grunts. They may have been produced by weaker hostile motivation than typical Gruff Grunt performances and have contained a relatively stronger escape component. (The difference in causation between these soft Grunts without Swaying and silent Swaying with typical Gruff Grunts was not clear.)

RESONANT GRUNTS

Resonant Grunt performances are much more complex in form than typical Gruff Grunt performances, and seem to be much rarer.

All the Resonant Grunts heard were uttered in long series of at least 10 to 15 notes. The speed, loudness, and pitch of the notes varied considerably.

The most frequently heard, and simplest, type of series was as follows. The first notes were soft and low, much softer than typical Gruff Grunts but otherwise similar. Succeeding notes gradually became louder and louder throughout the first half of the series. By the middle of the series, they were often very loud indeed, much more so than any Gruff Grunts, and had developed a penetrating, resonating quality. They were still gruntlike (insofar as they retained a guttural "rrrr" sound), but they had also acquired an "ooo" sound slightly reminiscent of the Hoots (see below). All the notes during the first half of a series were always uttered exceedingly rapidly one right after the other, in an emphatic "pumping" rhythm. The intervals between successive notes were much shorter than the intervals between notes in typical series of Gruff Grunts. It is possible that the pitch of the successive notes gradually became higher during the first half of some of these Resonant Grunt series, but this change (if it actually occurred) was always slight. Once the climax of a series was reached, the next few notes remained essentially similar, loud, resonating, and rapid. Then, during the final quarter (approximately) of the series, the rhythm usually slowed down a little and, at least in some cases, the notes became successively lower and/or softer.

Series of this type were heard only among the captive individuals on Barro Colorado Island. One male uttered 30 to 40 series during a violent dispute with neighbors in adjoining cages immediately after being reintroduced into a cage with which he was thoroughly familiar after an absence of several weeks. One female uttered one series toward the end of a long and violent dispute with a male to whom she had just been introduced. Another female, alone in her cage, uttered several series after being disturbed by a human being, just *after* the human being had left and disappeared from her sight. These three individuals uttered their series of Resonant Grunts at night; and they

certainly were not aware that their performances were being observed by a human being (from a blind). A very tame hand-reared male kept in a cage in the animal house, with a female to whom he was well adjusted, frequently uttered similar series at night and (more frequently) in the morning well after dawn, usually just as or just after an animal-keeper passed by his cage and/or some howler monkeys (*Alouatta palliata*) in an adjacent cage uttered "barks" and/or "roars" (see below).

The simple series of all these individuals except the solitary female were composed of essentially monosyllabic notes. At least some of the notes of the solitary female were definitely bisyllabic. Unfortunately, it was not possible to record any of these performances. The series of monosyllabic notes might be transcribed by something like

"Roo roo roo roo . . ."
rr rr rr rr

while the series of bisyllabic notes were something like

"Rooa rooa rooa rooa. . . ."
rrr rrr rrr rrr

In all these performances, the individual uttering the Resonant Grunts assumed a moderate or extreme Arch Posture as soon as it began a series and went out of the posture as soon as the series was ended. Most of these postures were identical with typical silent Arches, with both hands and feet grasping the perch. The male engaged in disputes with his neighbors, however, tended to stand up on his hind limbs when he assumed an Arch. During some or all of these standing postures, his arms hung downward as usual but his elbows went in and out in rhythm with the accompanying notes. I think that the elbows always went in as a note was uttered and out between notes. Night Monkeys have a large ventral air-sac communicating with the larynx (Hill, 1960). It is possible that the inward movements of the elbows helped to expel air from the sac and that the outward movements helped to draw air into the sac. This may have facilitated sound production. (The other individuals were able to utter similar and probably equally loud notes without similar movements; but they did not utter as many series of notes in a short period of time.)

All these series of Resonant Grunts were immediately preceded by more or less prolonged periods of intense activity, the performing animal running and leaping madly about its cage and uttering many Gruff Grunts, Gulps, and Sneeze-grunts (and sometimes Moans and/or Low Trills).

The tame captive male occasionally uttered series of Resonant Grunts which continued to accelerate throughout. In some cases, these series ended in a "bubble" of very, very short rapid notes. In other cases, they accelerated to such an extent that the terminal notes "ran together," to form a continuous or semicontinuous and moderately loud "Roar." Both types of accelerated series were uttered in the same circumstances as the simpler series of the same male, in association with the same other patterns.

Dr. John H. Kaufmann (personal communication) heard one or more wild Night Monkeys on Barro Colorado Island utter Roars which may have been the culmination of similar accelerated series of Resonant Grunts. These patterns were uttered during a prolonged dispute between two pairs or family groups feeding, or attempting to feed, on a palm tree in fruit. Unfortunately, the postures and movements accompanying the notes were not observed. I heard two series of Resonant Grunt-like notes apparently uttered by wild Night Monkeys on Barro Colorado, again without being able to see the animals while the calls were uttered. The first series was composed of from 10 to 15 moderately loud and long bisyllabic grunts, all essentially similar and very low in pitch. The second series followed shortly after the first, and included many more notes. The notes were monosyllabic, and the series rose and fell in pitch at least twice. The general effect was almost singing. These series were probably uttered by one or both members of a mated pair, just before retiring to their sleeping hole at dawn. I could not determine what (if any) external stimuli provoked the performances.

With these few and enigmatic exceptions, Resonant Grunts were not heard to be uttered by wild Night Monkeys on Barro Colorado Island. It is possible that I missed many Resonant Grunt performances (see below), but I was out in the forest frequently enough to establish that such performances must at least be relatively very rare on Barro Colorado.

The association of Resonant Grunts with Arch Postures, their similarity in sound to undoubtedly hostile Gruff Grunts, and their occurrence during some disputes, would indicate that they are at least partly hostile. Although some Resonant Grunts show a slight resemblance to Hoots, and the latter are undoubtedly sexual (see below), none of the individuals observed to utter Resonant Grunts appeared to be sexually aroused at the time. They did not perform any overt pairing or copulatory reactions. This would suggest that all Resonant Grunts may be purely hostile. The rarity of Resonant Grunts, the complex forms of the series of such notes, and their close association

with periods of intense activity and obvious excitement would suggest that they are very high intensity patterns, produced when the total hostile motivation is very strong. They probably are higher intensity on the average than either typical Gruff Grunts or typical silent Arch performances. They certainly appear to be much more closely associated with, or confined to, periods of intense excitement than either of the latter patterns. Approximately half of the Resonant Grunt performances of the male engaged in disputes with his neighbors were followed immediately by his performing overt attack. The remainder were followed by a variety of ambivalent movements and/or other vocal patterns, all or most of which probably included an escape component, but never by actual, complete, overt escape. It may also be significant that the only captive individual that uttered Resonant Grunts while obviously aware of being watched was the very tame hand-reared male, the only individual that was not at all afraid of human beings. These facts would indicate that Resonant Grunts are at least as aggressive, on the average, as the most aggressive Gruff Grunts or (more probably) silent Arch patterns. (In other words, the preponderance of the attack tendency over the escape tendency may be as great in Resonant Grunt performances as in silent Arch postures, although the actual strength of both tendencies is greater in the former than in the latter.) The escape component may be almost as minimal in some Resonant Grunt performances as in some overt attack patterns, especially the "deflected" attacks.

The complete Resonant Grunt performances of the captive male engaged in disputes with his neighbors appeared to function as threat; but it was impossible to distinguish between the signal effects of the notes themselves and those of the accompanying Arch Postures.

The Resonant Grunt performances are reminiscent of the most spectacular vocalizations of some other platyrrhine monkeys. In particular, they sound much like some calls of titi monkeys, *Callicebus* spp., and the howler *Alouatta palliata*. The former have not been studied in sufficient detail to permit discussion of probable homologies and analogies; but the situation is clearer with respect to the latter. The Roar at the end of some series of Resonant Grunts seems to be strictly homologous with the loud and prolonged vocalization of *Alouatta* spp. which is responsible for the vernacular name of the genus. In the case of *A. palliata*, this is the pattern which Carpenter (1934) calls "type 1 vocalization" and describes as "a voluminous barking roar," and which Altmann (1959) calls the "roar or howl, type A1." It often sounds like nothing more than a much amplified and prolonged version of the Roar of the Night Monkey, and is frequently

preceded by barking or loud grunting noises which may be largely or completely homologous with typical Resonant Grunts. At low intensities of motivation, male *A. palliata* may utter series of similar or identical sounds (probably the notes that Altmann calls "male bark, type C1" and "incipient male bark, type C2") without ever breaking into an actual roar. Some of the lowest intensity and softest versions of such series, when heard at a distance, are remarkably difficult to distinguish from the simplest series of Resonant Grunts heard close up.

The resemblance between the two patterns is so great that the tame male Night Monkey had been uttering Resonant Grunts occasionally for several weeks before I realized that they were not being uttered by the howlers in the adjacent cage.

It has already been mentioned that the Resonant Grunt performances of this tame Night Monkey were sometimes uttered during or immediately after roars and barks by the adjoining howlers. Possibly they were directly released by the sound of the latter. If so, this would help to explain why this Night Monkey tended to utter Resonant Grunts in the morning rather than at night.

The apparent facilitation of Resonant Grunts by the roars and barks of howlers might be additional evidence that the patterns are related to one another.

(Although individuals of *A. palliata* may assume Arch Postures while uttering certain types of barks, they apparently do not usually assume such postures while uttering roars or the barks most closely associated with roars.)

The roars and barks of *A. palliata* are certainly hostile. Individuals of this species tend to associate in bands; each band seems to have its own home range or territory; and members of different bands usually utter roars and/or barks whenever they come close together (see Carpenter, 1934, and Collias and Southwick, 1952). If the Resonant Grunts of Night Monkeys are provoked by similar stimuli, the rarity of such notes in the forest on Barro Colorado Island may be partly due to the rarity of encounters between different pairs and family groups (see page 10). The roars of *A. palliata* apparently also function as long-range proclamations of territorial ownership (see Altmann, *op. cit.*), and are uttered quite regularly apart from close-range or face-to-face encounters with rivals or neighbors. It seems very unlikely that the Resonant Grunt performances of Panamanian Night Monkeys can serve a similar function with any appreciable frequency.

(It is possible, however, that some of the same or closely related patterns may do so in other populations of Night Monkeys. Hill,

1960, cites several descriptions and transcriptions of calls uttered by South American Night Monkeys which may be Roars or typical Resonant Grunts or similar notes. There are enough records of such calls to suggest that they may be common among South American populations. It is conceivable that the typical Resonant Grunts and/or the Roars are becoming "obsolescent," in process of disappearing, among Panamanian Night Monkeys.)

Some of the Resonant Grunt performances of Panamanian Night Monkeys may function as "triumph ceremonies" in certain circumstances. The performances by captive individuals *after* being disturbed or irritated, when the cause of the disturbance was leaving or had left, appeared to be "proclamations" of the fact that the performing individuals had defended their territories successfully.

(It is possible that Night Monkeys have some sort of "territorial motivation," a tendency which is satisfied by the possession of a territory, in addition to the ordinary attack tendency (see page 53). This might be involved in the causation of some Resonant Grunt performances. If so, it might help to explain why Resonant Grunt performances in which escape seems to be minimal do not always lead to immediate attack.)

Intermediates between typical Resonant Grunt and typical Gruff Grunt performances do occur, but apparently are always rare. I heard such intermediates only three times. All took the form of series of notes. Each note was similar to an ordinary Gruff Grunt in loudness and tone, but the successive notes of each series first rose and then fell in pitch in much the same way as in typical Resonant Grunt performances. One series of this type, including a great many notes, occurred in the same dispute in the forest on Barro Colorado Island in which typical Resonant Grunts also were heard. It was not possible to see the postures and movements accompanying this performance. A similar series was uttered by one member of a captive pair on Barro Colorado when disturbed by some stimulus (possibly an ocelot?) outside its cage. This was uttered from a crouch posture. Several shorter series were uttered by the mate of the captive male who uttered typical Resonant Grunts while engaged in disputes with his neighbors. She usually started a series just after the male had begun a series of Resonant Grunts, or just after he had finished—thus providing a peculiar "echo" to his performances. Her series were uttered from typical Arch Postures, with both hands and feet grasping a perch.

SCREAMS

The captive Night Monkeys on Barro Colorado Island and at Iquitos usually uttered loud Screams when caught and handled by a human being. (I presume that all Night Monkeys are capable of uttering similar or identical sounds; but none of the other individuals studied was caught and handled.) These Screams were always high pitched but wavering. Many of them were quite prolonged. Figures 5 and 6 are sketches of sound spectrograms of two typical Screams.

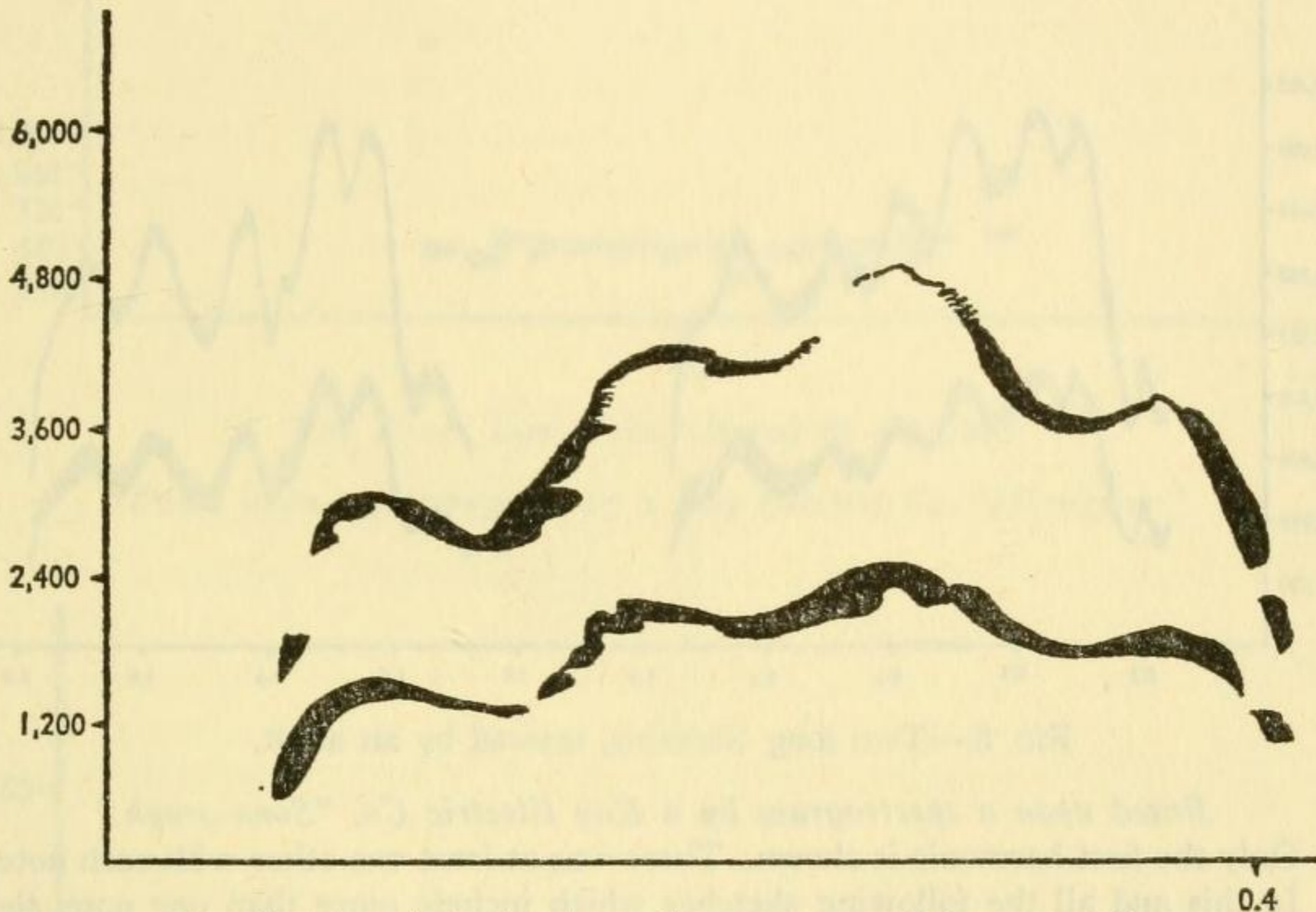


FIG. 5.—A relatively short Scream, uttered by an adult.

Based upon a spectrogram by a "Vibralyzer."

Only the first harmonic is shown. There certainly was at least one other present.

All the observed Night Monkey Screams were uttered with the mouth wide open, but they were not accompanied by any conspicuous inflation of the throat region.

All the captive animals struggled violently when first picked up. Most of the struggling movements were obviously attempts to escape; but many of the animals also tried to bite their captors whenever possible. The animals usually uttered many Screams during the initial struggles, when both their escape movements and attempts to bite were most vigorous. If the animals were held firmly for several minutes, however, they usually calmed down, gradually, and their struggles subsided. At this stage, they generally stopped Screaming and started to utter Gruff Grunts and/or Gulps.

These facts would indicate that the Screams were produced when hostile motivation as a whole was very strong, when the escape tendency was much stronger than the attack tendency (although probably less preponderant than in the silent overt escape and alarm patterns). The actual strength of the hostile motivation as a whole during Screams was almost certainly greater than in any Gruff Grunt pattern in which escape is predominant.

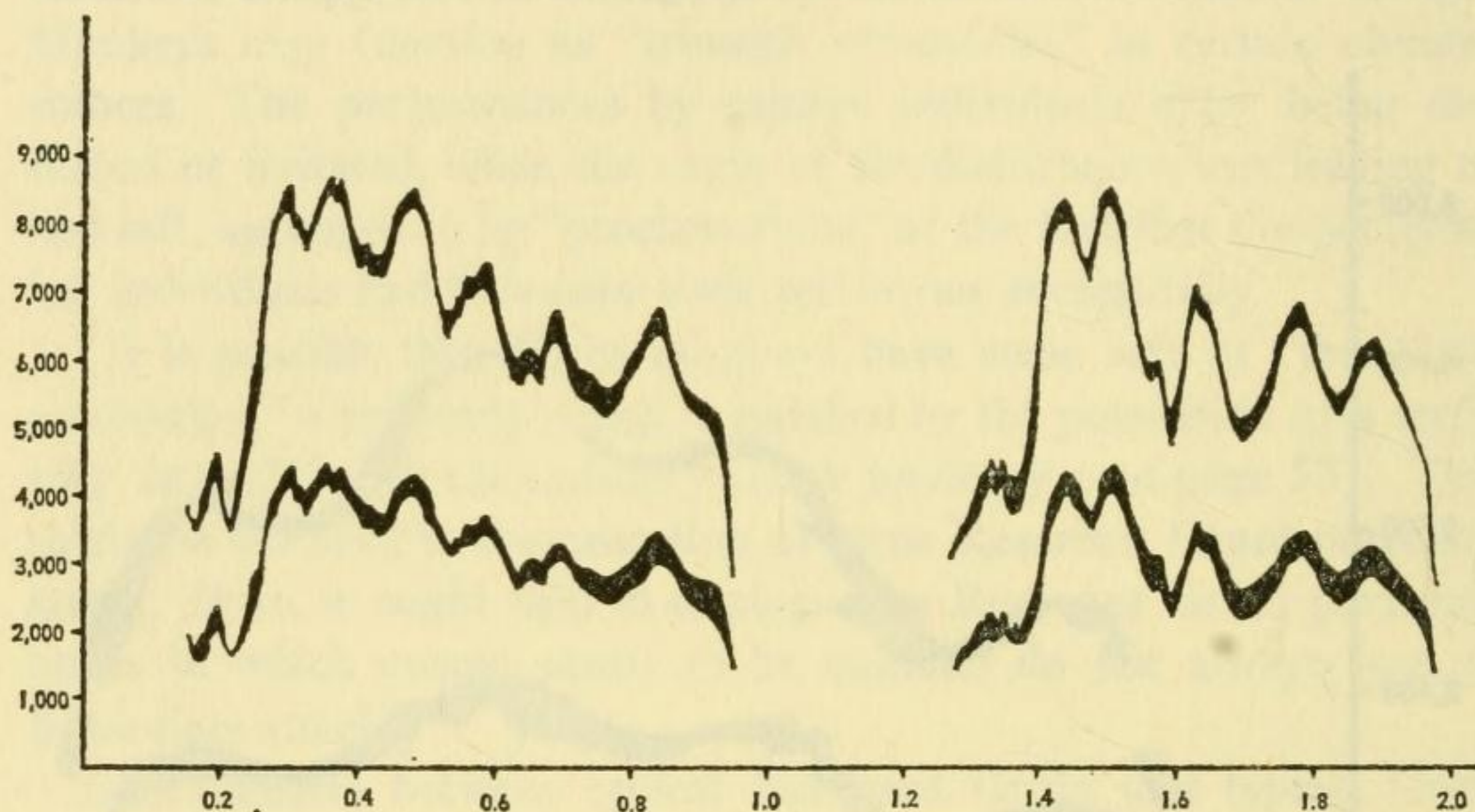


FIG. 6.—Two long Screams, uttered by an adult.

Based upon a spectrogram by a Kay Electric Co. "Sona-graph."

Only the first harmonic is shown. There was at least one other with each note. In this and all the following sketches which include more than one note, the interval(s) shown between notes are the actual interval(s).

Screams may be adapted to frighten or startle a predator, and thus give a screaming animal a better chance to escape.

LOW TRILLS

Night Monkeys utter a variety of sounds that can be described as Trills.

The most common sounds of this type uttered by captive adults on Barro Colorado Island were "Low Trills." A single Low Trill was a "bubbling" series of short low-pitched notes, uttered *very* rapidly one right after the other but still distinguishable by the human ear. All or most of the individual notes in a series were slightly plaintive in tone, and sounded somewhat like abbreviated versions of simple Moans (see page 36). The number of notes in a single series varied

from three to at least twelve. The successive notes tended to rise slightly in pitch. Sketches of sound spectrograms of three more or less typical Low Trills are shown in figures 7, 8, and 9.

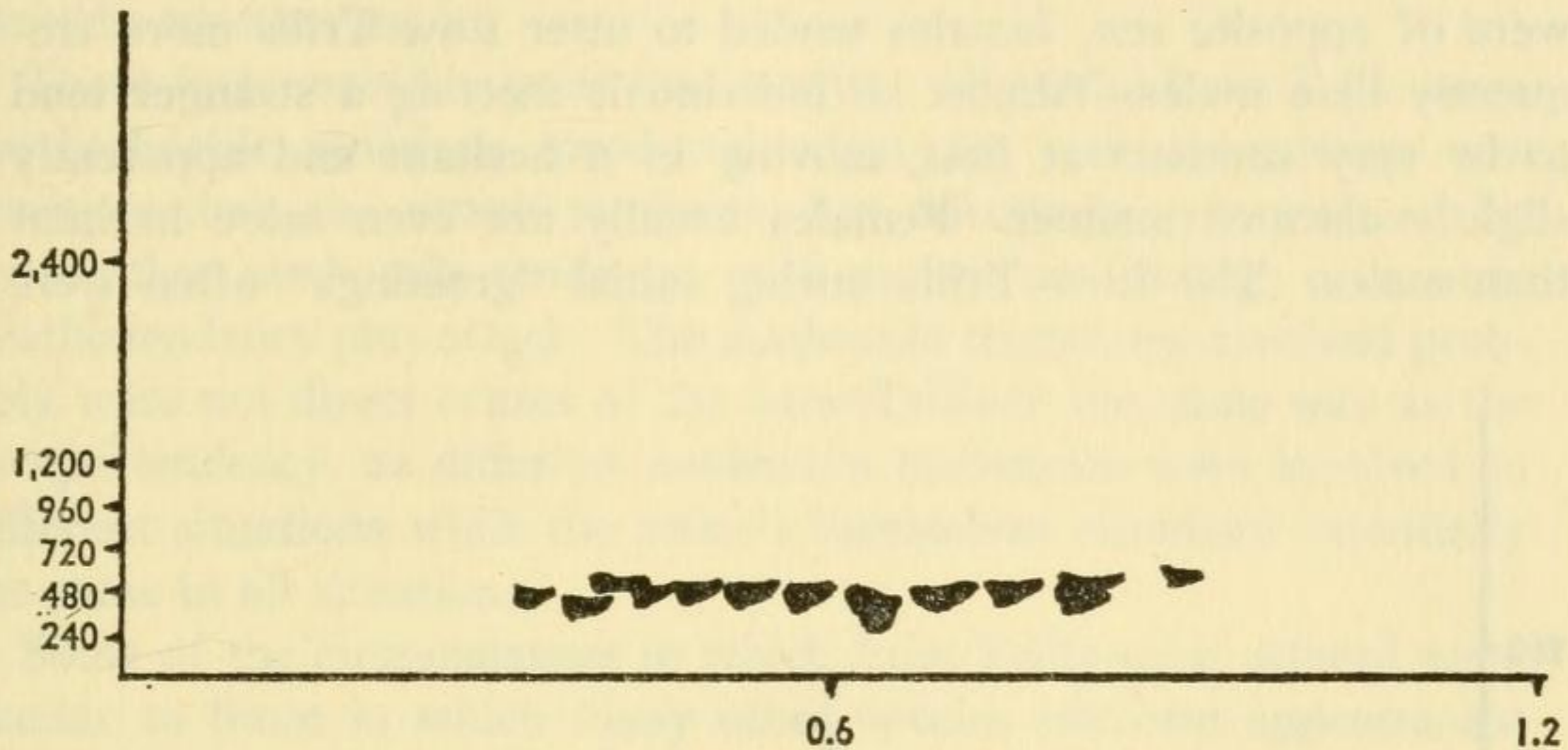


FIG. 7.—A Low Trill, uttered by an adult.

Based upon a spectrogram by a Kay Electric Co. "Missilyzer."

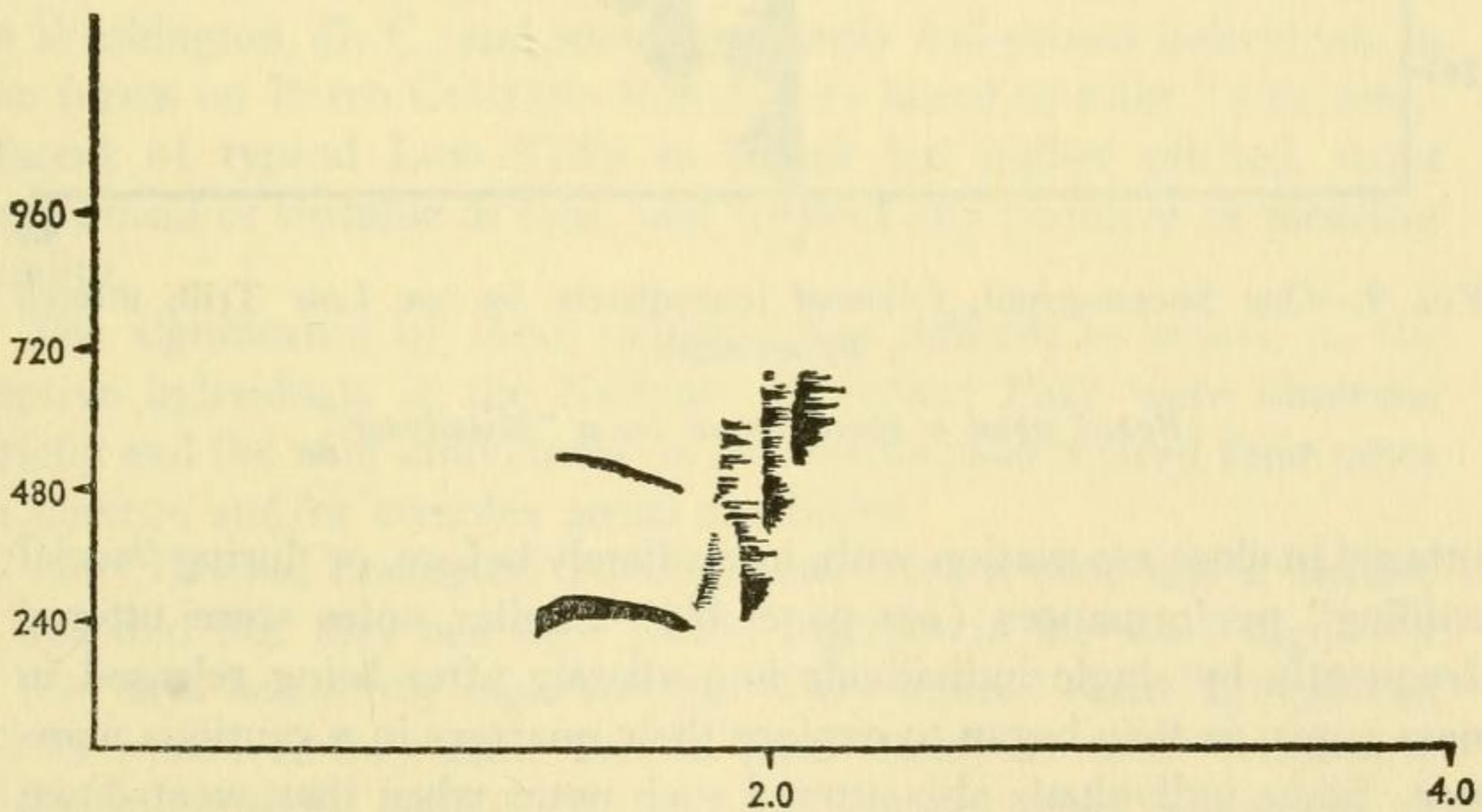


FIG. 8.—One Moan, followed immediately by one Low Trill, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

All Low Trills were uttered with the mouth closed or nearly closed. They were not accompanied by any conspicuous inflation of the throat region.

They were uttered in several different situations. They were com-

mon during the initial reactions between strangers, previously unacquainted individuals meeting one another for the first time. In such circumstances, they could be uttered by any one or all of the individuals involved. When the previously unacquainted individuals were of opposite sex, females tended to utter Low Trills more frequently than males. Almost all individuals meeting a stranger tend to be very cautious at first, moving in a hesitant and apparently slightly alarmed manner. Females usually are even more hesitant than males. The Low Trills during initial "greetings" often were

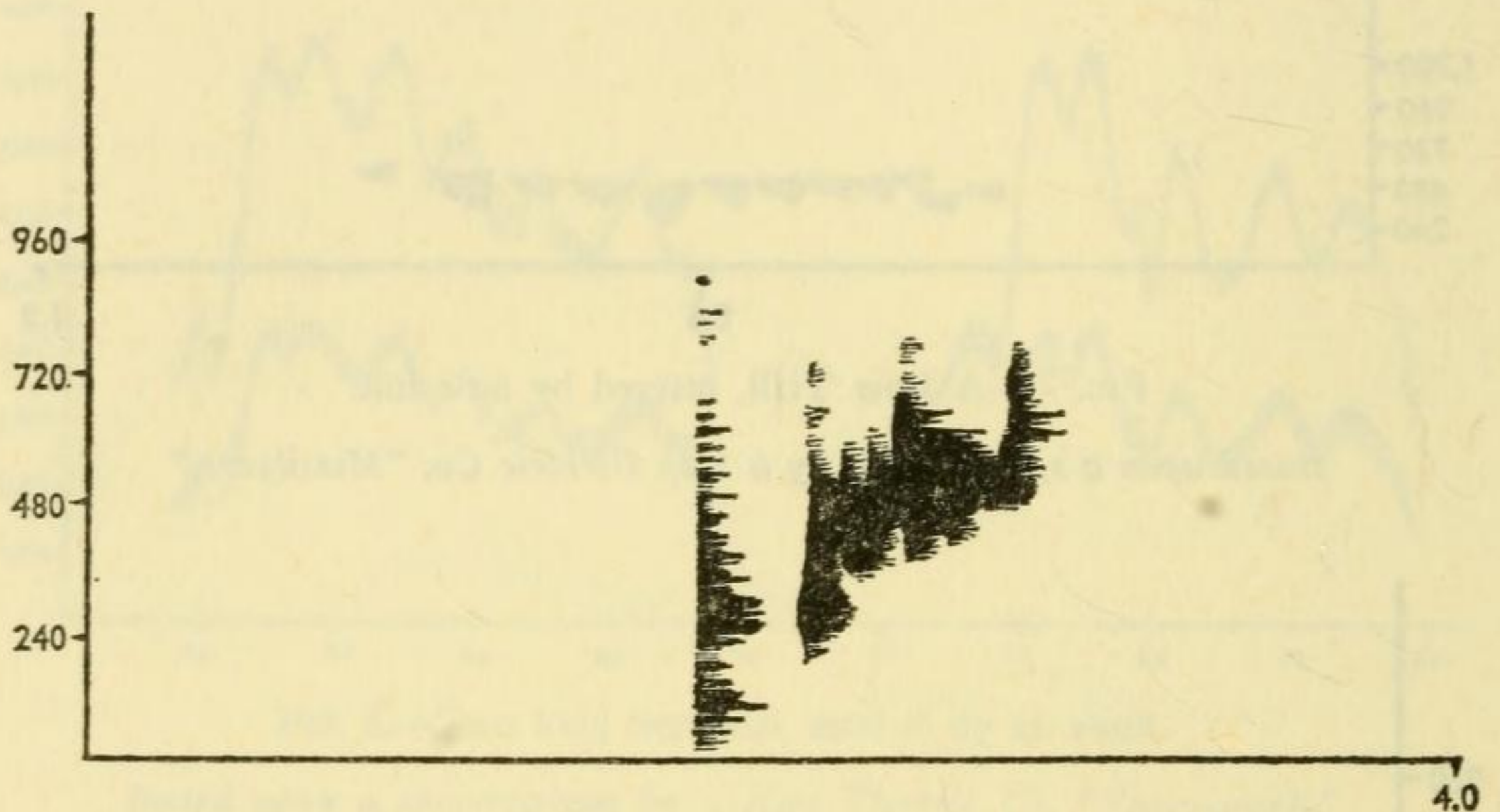


FIG. 9.—One Sneeze-grunt, followed immediately by one Low Trill, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

uttered in close association with, immediately before, or during "social sniffing" performances (see page 47). Similar notes were uttered frequently by single individuals immediately after being released in new cages, as they began to explore their quarters in a cautious manner. Some individuals also uttered such notes when they went down to get food from dishes on the ground, even when they were in familiar quarters and/or there were no other Night Monkeys nearby. Captive Night Monkeys tend to be slightly "nervous" whenever they have to come down to the ground, presumably because they would never do so under natural conditions. Although many Low Trills during "greetings" were eventually followed by overt, unritualized, hostile, and/or sexual behavior (depending upon the age, sex, and condition of the individuals involved), they were not usually uttered during or after

either actual fighting or copulatory reactions. The only prolonged and vigorous dispute during which I heard such notes uttered was an encounter between a male and a female that had fought with one another previously, been separated for several days, and then were brought together again.

These facts would suggest that many or all of the Low Trills were partly hostile reactions, produced when the escape tendency was stronger than the attack tendency, but effectively counteracted by some other nonhostile tendency, such as sex or feeding, or a non-hostile tendency plus attack. The nonhostile tendencies involved probably were not direct causes of the Low Trills in the same way as the escape tendency, as different nonhostile tendencies were involved in different situations while the sounds themselves remained essentially the same in all situations.

Some of the circumstances in which Low Trills were uttered were similar to those in which many other species perform appeasement displays. The Low Trills may have had a similar function; but I could not distinguish their exact signal effects from those of associated patterns such as social sniffing.

Two full-grown Night Monkeys at the National Zoological Park in Washington, D. C., and some apparently full-grown individuals in the forest on Barro Colorado Island were heard to utter Trills reminiscent of typical Low Trills in sound but higher pitched, more mechanical or metallic in tone, and without any plaintive or moaning quality.

The significance of these patterns was difficult to assess, as the captive individuals in the National Zoological Park were observed briefly and the wild individuals on Barro Colorado uttered their notes in obscure and/or complex social situations.

The National Zoological Park animals were a male and a female. I was told that they had been placed together in the same cage only a few days before my observations. They uttered their high-pitched Trills whenever they came face to face. Many of their Trills were followed by social sniffing, without any (other) overt indications of hostility. I did not hear them utter anything more closely similar to the Low Trills of the captive adults on Barro Colorado. This might suggest that their high-pitched Trills were equivalent to the latter, produced by the same or very similar motivation and serving the same function(s).

Unlike the Zoo animals, the wild Night Monkeys that uttered high-pitched Trills were also heard to utter typical Low Trills during the same social encounters.

I think that the high-pitched Trills of all these animals were very similar to, or even identical with, the High Trills of young Night Monkeys in sound (see page 69).

It is possible, therefore, that the apparently full-grown individuals heard to utter such Trills were really immature, in spite of their size, or had reverted to juvenile or infantile behavior for some reason (see discussion, page 58). It is also conceivable that high-pitched Trills are the only pattern of this type in the population from which the National Zoological Park animals were obtained.

As indicated in the accompanying figures, the notes of Low Trills are usually or always slightly higher in pitch than simple Moans. This might be evidence that Low Trills have been derived, in ontogeny and/or phylogeny, from a combination of typical Moans and High Trills.

Some or all Low Trills seem to have a slightly "liquid" quality, somewhat reminiscent of Gulp notes. There may be some sort of special relationship between the two types of patterns, either direct or indirect via the Gruff Grunt patterns (see both the accompanying figures and the comments below). Gulps, Moans, and Low Trills are all similar in some aspects of motivation.

MOANS

Many of the wild Night Monkeys on Barro Colorado Island and almost all the captive individuals at the National Zoological Park and at Iquitos as well as on Barro Colorado were heard to utter brief, soft, plaintive-sounding Moans (see figures 8 and 10).

Like the Low Trills, the simple Moans were uttered with the mouth apparently closed and were not accompanied by conspicuous inflation of the throat.

All or almost all the animals uttered Moans more frequently than Trills on the average. They uttered Moans in all the situations in which Low Trills were characteristic, and in other circumstances as well. Moans were relatively rare during the initial "greetings" between strangers and during the exploration of strange surroundings; but they were uttered frequently by individuals in familiar social and physical environments. They were the most common notes uttered by particularly tame (hand-raised) captive animals on Barro Colorado Island when I came within a few feet of their cages. At such times, they were uttered by animals approaching me in an apparently friendly or "curious" manner, as well as by animals performing slight retreat movements or intention movements. They were also uttered by mated

animals in captivity on Barro Colorado Island, if the mates were well adjusted to one another, when one individual rejoined its mate after being separated from it for a few seconds or minutes (the individuals that uttered Moans in such circumstances were long past the stage of uttering Low Trills as "greetings"). Moans were not usually directed by one individual toward its mate in other circumstances, *i.e.*, after they had been together for more than a few seconds. (The only exceptions were a few Moans uttered during the first parts of

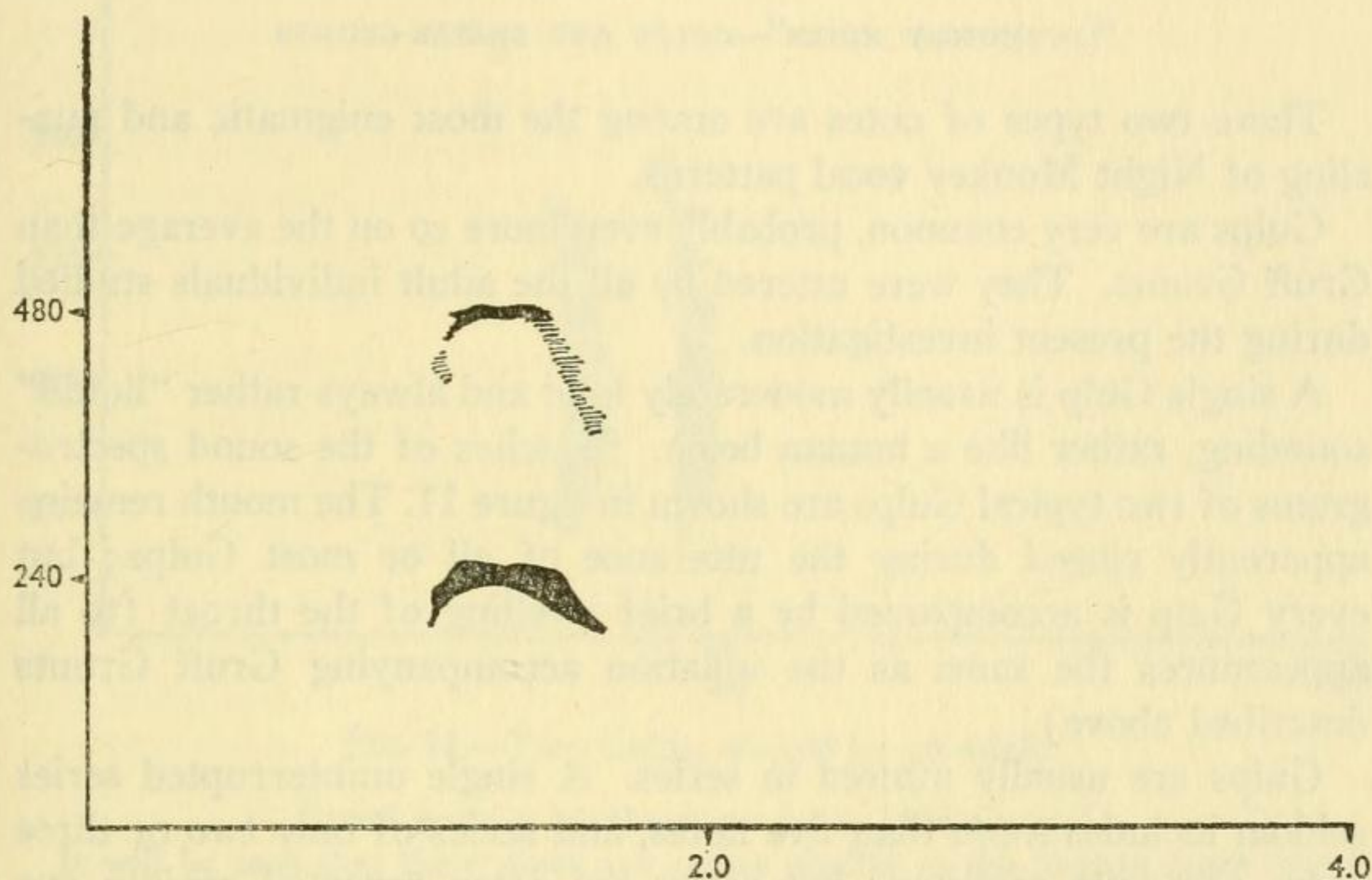


FIG. 10.—One Moan, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

long precopulatory sequences. The animals that uttered these notes did not utter more Moans immediately before or during the actual copulations.) Some captive individuals on Barro Colorado Island uttered Moans while they watched other individuals fight without becoming involved in the fights themselves. A few individuals at both Iquitos and Barro Colorado kept in cages with monkeys and marmosets of other species but with no other individuals of their own species uttered Moans regularly as they moved about their cages in an almost perfectly relaxed manner. The other vocal patterns with which Moans were associated most frequently were Low Trills, Gulps, and Sneezegrunts; *i.e.*, an individual that uttered Moans was quite likely to utter one or more of these other sounds immediately before and/or after the Moans. Both the Gulps and the Sneezegrunts seem to contain

an escape component, at least at times (see below). Moans also were associated with Gruff Grunts, but relatively rarely.

It is probable, therefore, that Moans are similar to Low Trills in being produced when both hostile and one or more types of nonhostile motivation are activated simultaneously; but the hostile component seems to be relatively (and probably actually) weaker in the Moans than in all or most Low Trills.

Moans may also function as appeasement.

"LOCOMOTORY NOTES"—GULPS AND SNEEZE-GRUNTS

These two types of notes are among the most enigmatic and puzzling of Night Monkey vocal patterns.

Gulps are very common, probably even more so on the average than Gruff Grunts. They were uttered by all the adult individuals studied during the present investigation.

A single Gulp is usually moderately loud and always rather "liquid" sounding, rather like a human belch. Sketches of the sound spectrograms of two typical Gulps are shown in figure 11. The mouth remains apparently closed during the utterance of all or most Gulps; but every Gulp is accompanied by a brief swelling of the throat (to all appearances the same as the inflation accompanying Gruff Grunts described above).

Gulps are usually uttered in series. A single uninterrupted series seldom includes more than five notes, and series of only two or three notes are quite common; but series are often repeated rapidly one right after the other, with only brief pauses between successive series.

An overwhelming majority of all the Gulps heard were uttered by individuals engaged in vigorous locomotory activities. They were uttered during most periods of really active running and leaping in almost all social circumstances.

One type of performance was particularly remarkable. As noted above, Night Monkeys generally are most active just after sunset and just before dawn. During the predawn periods, the captive animals kept in large cages on Barro Colorado Island usually ran and leapt around their cages rapidly and almost continuously for a half hour or more. Single individuals alone in their cages, mated individuals in cages with their mates, and individuals kept together in larger groups, all tended to behave in much the same way at such times. They seldom interrupted their running and leaping to feed or drink or groom themselves, and the individuals that had companions in their cages seldom performed unmistakable hostile or sexual patterns. They

all tended to utter many Gulps during such periods, but relatively few or no other notes (except Sneeze-grunts—see below). Most of the wild Night Monkeys on Barro Colorado Island also uttered many Gulps and relatively few obviously hostile or sexual calls just before dawn.

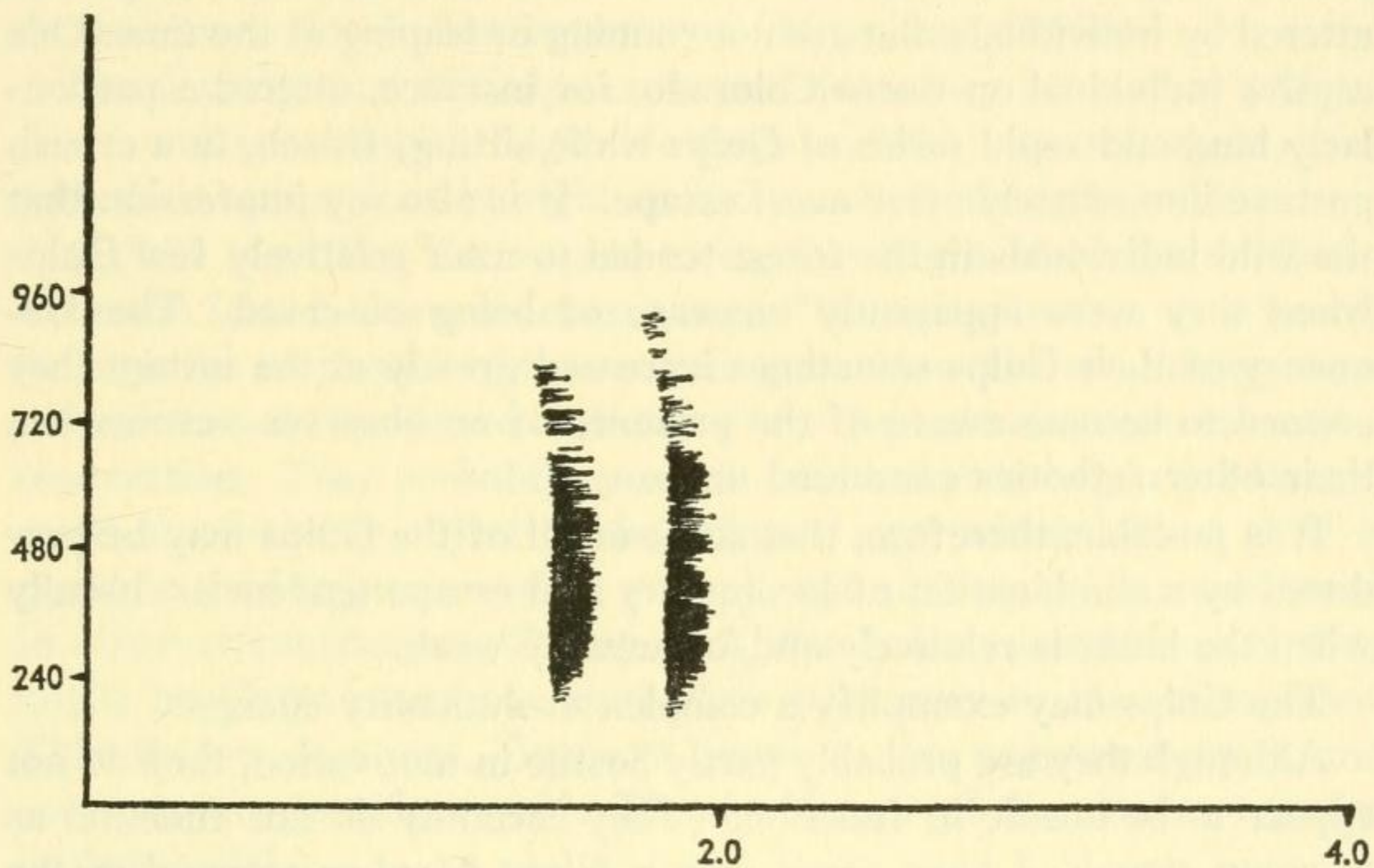


FIG. 11.—Two Gulps, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

It will be seen that these notes are rather similar to the Sneeze-grunt shown in figure 9. There are, however, a few definite differences. The Sneeze-grunt has a range of frequencies between 0 and approximately 650 cycles per second (c.p.s.), all starting at exactly the same time and having predominant amplitudes and longer signals around 100 c.p.s. and 260 c.p.s. The Gulps begin with high frequencies around 850 c.p.s., and drop rapidly in frequency to fairly equal amplitude signals between approximately 240 and 600 c.p.s.

The causation and function(s) of this intense (and often apparently "purposeless") activity were difficult to identify. It is possible that Night Monkeys, like some other mammals that normally range over large areas (*e.g.*, many canids—see Lorenz, 1952), have a strong "internal" tendency to perform locomotory movements, a tendency expressed by overt activity even when the other immediate needs of the animals (*e.g.*, food, water, and sex) can be fully satisfied without moving about very much.

If so, many or all Gulps may be expressions of the same "independent" locomotory tendency. They may be produced when the loco-

motory tendency is too strong to be completely expressed by running and leaping movements alone.

There are other indications, however, that some or all of the Gulps may be at least partly hostile. Although most overt escape and simple alarm patterns are silent (see page 13), Gulps are often uttered before and/or after such reactions. Very occasionally, Gulps are uttered by individuals that are not running or leaping at the time. One captive individual on Barro Colorado, for instance, uttered a particularly loud and rapid series of Gulps while sitting, frozen, in a crouch posture immediately after overt escape. It is also my impression that the wild individuals in the forest tended to utter relatively few Gulps when they were apparently unaware of being observed. The frequency of their Gulps sometimes increased greatly at the instant they seemed to become aware of the presence of an observer—even when their other activities continued unchanged.

It is possible, therefore, that some or all of the Gulps may be produced by a combination of locomotory and escape tendencies, usually when the latter is relatively and/or actually weak.

The Gulps may exemplify a complex evolutionary change.

Although they are probably partly hostile in motivation, they do not appear to be hostile in function. (They certainly do not function as warning signals. I have never seen a Night Monkey respond to the sounds of Gulps by performing overt escape.) They may well function as "contact notes." They may help to keep mated individuals and members of the same family group together under natural conditions. The utterance of Gulps by one individual should enable its companions to tell exactly where it is (especially as Gulps are very penetrating, even when not very loud).

No other species of platyrrhine monkey with which I am familiar utters similar notes with similar frequency in similar situations.² This would suggest that Gulps, as adult contact notes, are highly specialized. If so, they probably have been derived from some purely hostile Grunt pattern. (They are similar to Gruff Grunts in some aspects of

² Adult individuals of some other species, *e.g.*, some tamarins, may utter "lost" notes or calls when completely isolated; but such notes or calls are seldom or never uttered by individuals moving about near other individuals of the same species in the same way as the Gulps of Night Monkeys.

Adult howler monkeys of the species *Alouatta palliata* may utter some notes which help to maintain contact between the members of a band (Carpenter, 1934, and Collias and Southwick, *op. cit.*); but such notes seem to be uttered relatively much less frequently than the Gulps of Night Monkeys, and may be produced by rather different motivation.

form—see accompanying figures—and gruntlike patterns are widespread among many species of New World monkeys.)

It should be mentioned, in this connection, that the Gulps of Night Monkeys are uttered in almost exactly the same social circumstances as the contact notes of some species of Panamanian birds, and that the latter seem to have had a similar evolutionary history, also being derived from purely hostile patterns (Moynihan, 1963a).

The development of Gulps as contact notes may be another adaptation to nocturnal habits. Night Monkeys probably cannot keep in touch with their companions by sight as easily as can other platyrrhines.

(While recording the sounds of captive Night Monkeys on Barro Colorado Island, a few short and single “twanging” noises were heard, through the earphones of the recording machine. Unfortunately, these noises were always heard at times when the animals were not under observation. They probably were not mechanical in origin [at least, I could not find any object in the animals’ cage which looked as if it could be used to produce such noises]; but nothing similar was heard in other circumstances. To my ears, the noises sounded as if they might be Gulps uttered in *very* close proximity to the microphone. This theory does not, however, seem to be supported by sound spectrograms [see figure 12]. The significance of these noises remains problematical.)

One captive Night Monkey at Iquitos uttered series of gulping notes which had a distinctive hooting quality (rather as if “ooo” sounds were superimposed upon the ordinary Gulps of Barro Colorado animals). These notes were uttered while the animal was moving about its cage in a perfectly normal manner. They may have been a characteristic pattern of the local population of Night Monkeys, or an individual peculiarity, or (possibly) intermediates between typical Gulps and typical Hoots.

Both the wild and captive animals on Barro Colorado Island were heard to utter Sneeze-grunts.

A single Sneeze-grunt sounded like a single sneeze superimposed upon a single, loud, typical Gruff Grunt. The sound was always sharp and abrupt. Most Sneeze-grunts were also at least slightly nasal in tone (each note might be transcribed by something like “Aaanh”). Figure 9 includes a sketch of a sound spectrogram of a more or less typical Sneeze-grunt.

Sneeze-grunts were usually uttered singly. Sometimes two were uttered together in quick succession; but they never occurred in longer series like Gulps and Gruff Grunts.

They were uttered with the mouth closed or nearly closed, and

apparently were not accompanied by conspicuous inflation of the throat region.

They were almost always much less common than Gulps, but were uttered in the same types of situations, usually by individuals moving about very rapidly and energetically. They were frequently uttered in close temporal association with Gulps. In such cases, the most common arrangement was two or three Gulps, followed by a single Sneeze-

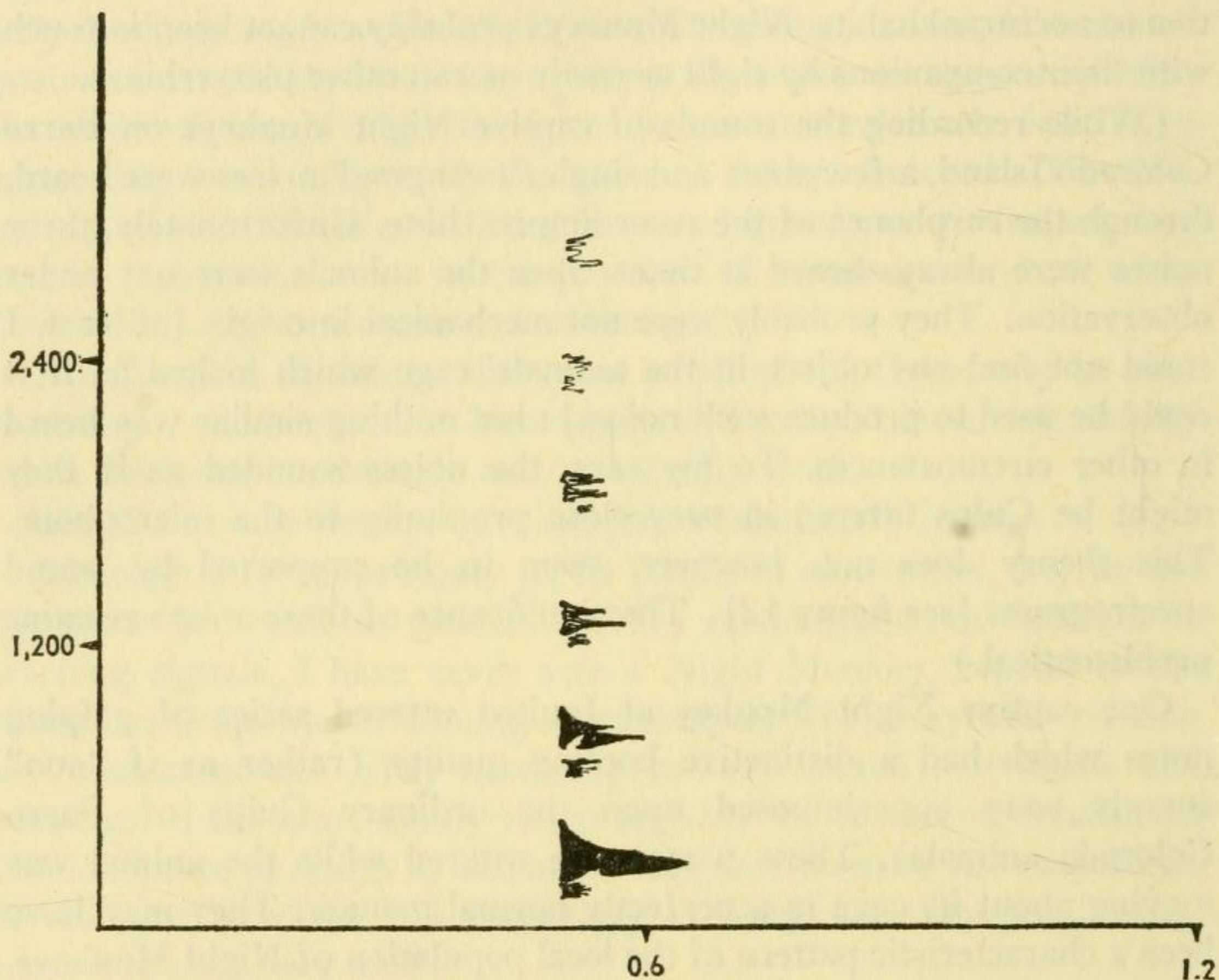


FIG. 12.—A single "twanging" noise heard while recording adults.

Based upon a spectrogram by a "Vibralyzer."

grunt, followed by two or three more Gulps, followed by another Sneeze-grunt, etc.

Sneeze-grunts also were uttered quite frequently in close association with Moans and Trill patterns. In such cases, the notes were usually arranged in "doublets" of one note of each type: A single Moan followed immediately by a single Sneeze-grunt, or a single Sneeze-grunt followed immediately by a single Low or High Trill, or (most frequently) a single Sneeze-grunt followed immediately by a single Moan. These arrangements were stereotyped enough to suggest that they may have become partly ritualized *per se*.

It seems probable that the Sneeze-grunts were produced by some combination of locomotory and escape tendencies similar to that producing Gulps. It was noticeable, however, that Sneeze-grunts were most likely to be uttered just before or just as an individual made a long leap, while Gulps were relatively more frequently associated with shorter leaps and running movements. Similarly, when wild Night Monkeys were encountered in the forest, they sometimes uttered Gulps when approached in the dark, switched to Sneeze-grunts when a light was put on them, and then retreated in overt escape. Such facts would suggest that the Sneeze-grunts may have been produced when the escape tendency was stronger than in all or most Gulps.

The Sneeze-grunt is the only Night Monkey pattern similar to the ordinary Warning Notes of many other New World monkeys in form. It resembles the latter in being loud, sharp, and usually single. It may well be phylogenetically related to the Warning Notes of other species, and may have functioned in the same way in the ancestors of the Night Monkey, alerting other individuals of the same species to possible danger in the environment and inducing them to escape. It does not, however, seem to function in this way at the present time. Its signal effect is obscure at present; but it may be another contact note like the Gulps.

DISCUSSION

The preceding list includes almost all the typical vocal patterns of adult Night Monkeys.³ It may be useful, therefore, to add some general comments about their vocal repertory as a whole.

Adult Night Monkeys do utter vocalizations which are more or less obviously intermediate between otherwise distinct types of notes. Some of these intermediates have been mentioned above; others include intermediates between Moans and Gruff Grunts, between Gruff Grunts and Gulps, and between Sneeze-grunts and Gruff Grunts.

Although some of these intermediate vocalizations are uttered with appreciable actual frequency, they seem to be comparatively rare, and are uttered relatively less frequently than intermediate notes in the repertories of adults of some related species, *e.g.*, species of *Saimiri*,

³ Some brief experiments with an ultrasound detector would indicate that neither the adults nor an infant kept in captivity on Barro Colorado uttered any calls or notes completely inaudible to the human ear. In this respect, Night Monkeys seem to differ from at least one other species of New World primate, the Pygmy Marmoset (*Cebuella pygmaea*).

Cebus, and *Ateles*. In these latter species, all or most of the major adult vocal patterns seem to intergrade with one another through nearly continuous series of common intermediate notes.

Such differences in organization of the vocal repertory presumably are correlated with different ways of functioning.

When an adult of a *Cebus* species is motivated by three or four different tendencies (*e.g.*, attack, escape, sex, and gregariousness), it may be able to express *all* the tendencies simultaneously by uttering a single ambivalent vocal pattern, more or less perfectly intermediate between the patterns which would be produced by each one of the tendencies (or pair of tendencies) if activated alone. A signal of this type must contain a relatively large amount of information. This in itself must be advantageous. But such signals may have disadvantages as well. It may be difficult for the receiver of a signal of this type to perceive or "decipher" all the information contained in the signal. Complex signals are probably more easy to misunderstand than simple signals containing less information. In these adult monkey repertories, it is also probable that the frequency of intermediate notes reduces the contrast between different signals. These features may induce momentary confusion in the individual(s) toward which the signals are directed. Even when confusion is avoided, they must tend to reduce the speed of the response to the signals. This is probably very disadvantageous. There is evidence that selection always or nearly always tends to favor increased rapidity of social responses (Moynihan, 1963b).

An adult Night Monkey motivated by a complex combination of tendencies usually does not utter intermediate notes, but rather a series of different types of notes, each one of which expresses only one or two of the tendencies. Thus, for instance, a wild adult surprised by a disturbing stimulus may utter a rapid "jumble" of Gruff Grunts, Moans, Gulps, Low Trills, and Sneeze-grunts, *not* a single vocal pattern expressing the complete combination of attack, escape, locomotory, and (possibly) other tendencies by which it is motivated. This sort of message may be able to convey as much information as a single note expressing all the tendencies simultaneously, if the arrangement of the different notes is not random and if the receiver's reaction to the first note does not interfere with its reactions to the later notes; but it is certainly produced with greater physical effort and, more important, more slowly. The principal advantage of this sort of message presumably is that each one of its constituent notes, being an expression of only one or two tendencies, is a comparatively simple signal and, therefore, difficult to misunderstand.

The principal differences between these two types of platyrrhine vocal repertoires may be summarized as follows. In one type, the information is coded very rapidly in an economical form but may be difficult to read, or difficult to read rapidly. In the other type, the information is coded less rapidly and efficiently but can be read more easily and/or more rapidly.

The relative importance of the advantages and disadvantages inherent in each type of repertoire may be different depending on the circumstances and environments. The type of repertoire possessed by adult Night Monkeys may be another (partly indirect) adaptation to nocturnality.

Adults of *Saimiri*, *Cebus*, and *Ateles* can avoid some of the disadvantages inherent in their type of vocal repertoire by combining the information received from auditory signals with information derived by another method of perception. They are all thoroughly diurnal, and must usually be able to see other animals and objects in their environment quite clearly at considerable distances. As noted above, both *Cebus* and *Ateles* species have a wide variety of facial expressions which function as signals. They also have many other display postures and movements involving other parts of the body; and so does *Saimiri*. Any adult individual of these species hearing calls or notes from another individual of the same species usually will perceive visual signals and/or receive visual clues from the physical environment at the same time. These visual aids should enable the individual to grasp the significance of any vocal pattern, even when the latter is difficult to decipher or ambiguous in itself.

As adult Night Monkeys usually receive less visual information (because they are nocturnal and frequently become separated from one another and have fewer visual displays), they are more dependent upon auditory signals and more likely to misinterpret any possibly ambiguous vocal patterns. It must be absolutely essential for them to have a system of vocal patterns which are easily and immediately comprehensible, whatever the inevitable disadvantages of such a system.

It is probably significant, in this connection, that infant and juvenile Night Monkeys utter relatively more intermediate notes than do adults (see below). The vocal signals of infants to their parents may be supplemented by tactile stimuli, as the infants are always carried by their parents. Even when no longer carried, juveniles may be able to provide important supplemental visual information because they tend to remain very close to their parents.

To my knowledge, the only Old World monkey in which this aspect

of behavior has been studied is the Rhesus, *Macaca mulatta*. According to Rowell and Hinde (1962), the vocal patterns of this species also intergrade through frequent intermediates. Rhesus Monkeys are diurnal, and have many visual displays, including many different facial expressions (Hinde and Rowell, 1962).

These facts would suggest that there may be a general rule among monkeys that species or classes of individuals largely dependent upon auditory signals for the regulation of their social behavior tend to have discrete, sharply delimited vocal patterns, while species or classes of individuals less dependent upon auditory signals tend to have intergrading vocal patterns.

The major vocal patterns of adult Night Monkeys not only are discrete but also sound quite different from one another to human ears. This is true of patterns that look somewhat similar in sound spectrograms, *e.g.*, Gulps and Sneeze-grunts, as well as of patterns that look very different. There is every reason to suppose that the contrasts between different types of patterns are equally obvious to the Night Monkeys themselves. It is quite evident from their behavior that the hearing of Night Monkeys is at least as good as that of human beings.

Contrasts in sound may facilitate rapidity of comprehension when messages are composed of many notes of different types.

The probable importance of this feature is emphasized by the fact that all the associations between different types of notes that are particularly common and/or seem to be ritualized *per se* are associations between notes that contrast with one another in a particularly striking manner. In some cases, *e.g.*, Gulps and Sneeze-grunts, the associated notes seem to serve similar functions. In other cases, *e.g.* Sneeze-grunts and Moans, they seem to serve quite different functions. Associations between notes that are somewhat less conspicuously contrasting in sound, *e.g.*, Moans and Low Trills, seem to be less frequent and/or less close.

It is conceivable that information conveyed by contrasting stimuli may tend to produce stronger reactions (*i.e.*, may appear to be more "emphatic" to the receiver) than the same information conveyed by stimuli with less contrast; but this would be very difficult to prove.

In spite of the obvious differences between the hostile vocal patterns of adult Night Monkeys, there are some morphological resemblances between many or most of them. This is certainly true of Gruff Grunts, Resonant Grunts, and Sneeze-grunts. A few similarities between Gulps and both Gruff Grunts and Sneeze-grunts have already been mentioned. It may be convenient to refer to all these patterns, together,

as the "Grunt Complex." The low-pitched Moans and Low Trills may be related. It is possible that all the patterns of this complex have been derived, in whole or in part, from a single pattern or a single group of completely intergrading patterns (perhaps comparable to the "basic agonistic sound" of the Rhesus Monkey described by Rowell, 1962) in the course of evolution.

The hostile vocalizations of adult Night Monkeys seem to be produced when motivational conflict is stronger, *i.e.*, when incompatible tendencies are more nearly equal in strength, than when many or most of the nonvocal hostile displays are produced. A similar arrangement occurs in some species of birds (see, for instance, Moynihan, 1962b). It may be characteristic of most higher vertebrates.

Some other aspects of the vocal behavior of Night Monkeys will be discussed below, in connection with the Hoot and Squeak patterns.

SOCIAL SNIFFING

This is the most common of the "greeting" patterns. In captivity (at least), it is almost always performed whenever any two previously unacquainted individuals meet one another for the first time, and it also occurs in certain other social circumstances.

It may be initiated by either one of the individuals involved, or by both simultaneously. A sniffing animal simply approaches another, stretches its neck forward a little, and smells the other, usually for at least several seconds. When sniffing is initiated by one individual, the individual being smelled remains motionless at first, but usually responds by sniffing in return if the first individual continues long enough. Sometimes two individuals will sniff one another alternately. More often their sniffing overlaps in time, even when they do not begin simultaneously.

Most sniffing—both mutual sniffing and sniffing by only one individual—begins "nose to nose." An individual usually starts by bringing its face as close as possible to the face of its "partner" in the performance. It also may sniff into the armpit or under the arm and/or at the perineal region of its partner. This is relatively (if not actually) rare as an initial reaction, but it is very common immediately after nose-to-nose sniffing. Occasionally, two individuals will sniff at one another's perineal regions simultaneously. This is done less frequently by Night Monkeys than by some tamarins (for which it is the usual form of social sniffing).

It seems likely that this behavior is guided by, or orientated toward, special scent glands. The skin glands of Night Monkeys have been

described by Hill, Appleyard, and Auber (1959) and Hanson and Montagna (1962). Apocrine glands are largest in the face and genital areas. Lateral to the alae of the nose they are intermingled with large sebaceous glands. There are also larger and more specialized glandular organs in the sternal region and at the base of the tail. It is possible that individuals which appear to be sniffing in the armpits of their "partners" are really trying to get at their sternal organs.

When complete strangers are introduced to one another, they may repeat social sniffing whenever they come close to one another during the first few hours (or nights) after the introduction. This behavior may disappear, gradually, as the animals become familiar with one another. Only in the case of males and females that become mated to one another does social sniffing remain frequent in certain situations. Mates often perform social sniffing immediately before copulation and related patterns (see below).

Social sniffing was performed by all the captive animals observed, at Washington and Iquitos as well as on Barro Colorado Island. It seemed to be performed with approximately equal frequency by all individuals in similar circumstances in captivity.

Very tame, hand-reared individuals in captivity on Barro Colorado Island sniffed at human beings occasionally, especially if they were familiar with the person involved but had not been visited by him or her for some time.

Although social sniffing may be followed by high-intensity hostile behavior as well as (or instead of) copulatory reactions and may be accompanied by a variety of vocalizations, such as Trills and Squeaks, it is probably purely investigatory in itself. The first part (at least) of social sniffing seems to be essentially the same as the sniffing of food described above.

SEXUAL BEHAVIOR AND ASSOCIATED OR RELATED PATTERNS

The term "sexual behavior" will be used in a broad and general sense throughout the following pages to include all behavior patterns characteristically directed by adult individuals of one sex toward adults of the other sex, or performed by adults of one sex in the presence of the other.

The causal factors responsible for the performance of sexual activities by Night Monkeys are particularly difficult to identify, even tentatively, for several reasons.

In many species of higher vertebrates, all or most sexual activities

seem to be produced by two main types of motivation: A pairing tendency, which is satisfied by the presence of a mate, and a copulatory tendency, which is satisfied by the performance of a successful copulation (or ejaculation in the case of male). Night Monkeys may have the same two tendencies; but this could not be confirmed, during the present study, because of the practical difficulty of observing the usual long-term sequence of sexual reactions under natural conditions.

In many other species of New World monkeys, it is possible to distinguish between the sexual tendencies and a gregarious tendency, which is satisfied by association with other adult individuals of the same species irrespective of sex. This cannot be done in the case of the Night Monkey, simply because adults of this species do not usually associate with any other adults of the same species except their own mates. It is conceivable, however, that the complex of factors producing the sexual behavior of Night Monkeys includes components homologous with the gregarious tendencies as well as the strictly sexual tendencies of related species.

HOOOTS

Both wild and captive adult Night Monkeys on Barro Colorado Island uttered Hoots. So did a subadult individual, who seemed to be behaving in an essentially adult manner, at Iquitos. Among the captive individuals on Barro Colorado Island, Hoots were uttered by both males and females. The individual Hoots of all these animals sounded similar or even identical (apart from some variation in loudness) to my ears.

They were low-pitched, moderately prolonged, and at least moderately loud. Each individual Hoot sounded to me like a single note. I seem to have been misled, however. A sketch of what sounded to me like three Hoots is shown in figure 13. It will be seen from this that each one of the apparently unitary Hoots was actually compound, composed of one or two relatively long sounds, followed by two to five short sounds, with only very brief intervals between them.

In spite of this discrepancy, it will be convenient to refer to each hooting pattern that sounded to me like a single note as a "Hoot" or "a note." The briefer sounds making up a Hoot, in this sense, will be referred to as "components of a Hoot." Using these terms, it can be said that the intervals between the components of a Hoot were always *much* shorter than the intervals between successive Hoots or between a Hoot and any other type of call or note.

(The Hoots sketched in figure 13 were uttered by an adult female. Unfortunately, these were the only Hoots uttered by an adult of

which it was possible to make spectrograms. They seem to have been somewhat different from the Hoots of a young male sketched in figure 20. I think that the differences between the Hoots of these two individuals were due to the difference in their age, not their sex.)

The adult Night Monkeys on Barro Colorado Island uttered Hoots singly and in short series of two, three, and four notes. Two was the most common number. The Iquitos animal apparently always uttered Hoots in series of three or four.

The postures and movements accompanying Hoots were observed only in captive individuals. The Barro Colorado adults uttered their Hoots while sitting in a perfectly normal unritualized posture, hind

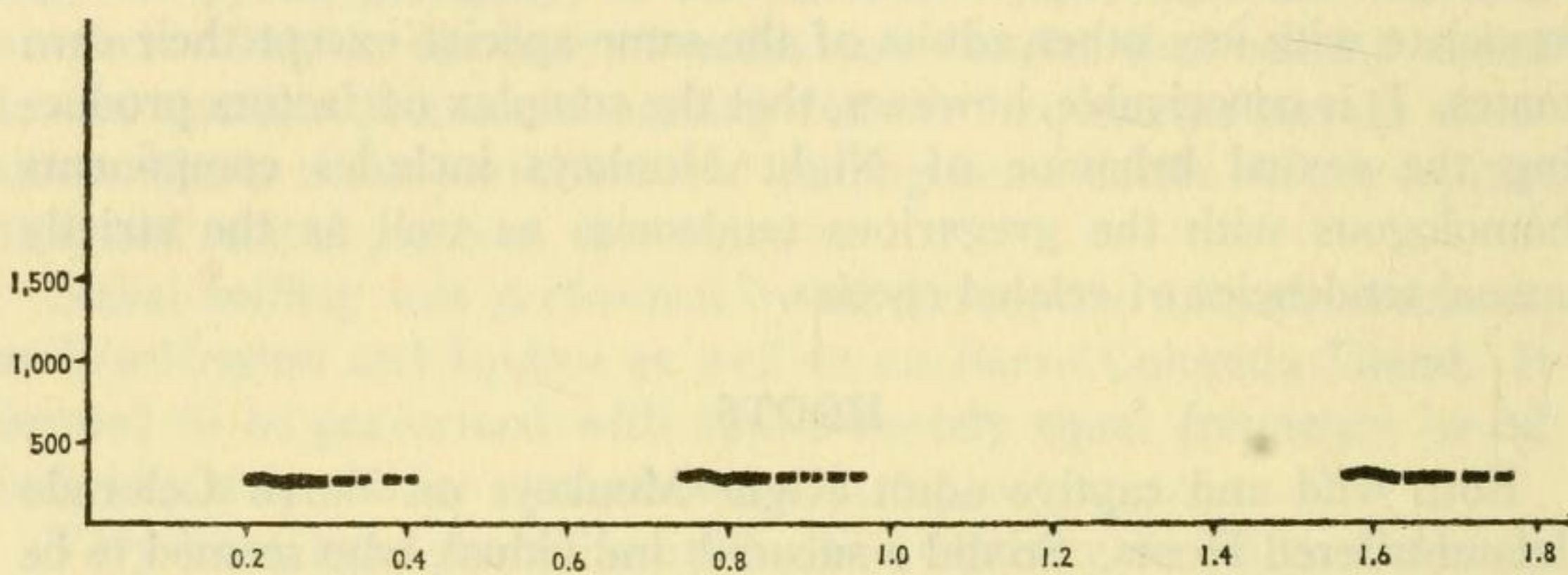


FIG. 13.—Three Hoots, uttered by an adult female.

Based upon a spectrogram by a "Sona-graph."

The harmonics accompanying these notes are not shown.

limbs flexed, back slightly curved (as in all sitting postures), and hands firmly grasping the perch. They usually looked more or less straight forward throughout their performances. The mouth was opened slightly as each Hoot was uttered, and apparently closed between the successive notes of a series. The throat and upper breast were inflated with each note, and subsided between notes. The Iquitos animal sat in a similar posture but looked almost straight downward throughout its performances. This may have been a low intensity indication of a head-down pattern (the animal had not been in its cage very long, and it may have been somewhat shy). A single adult female on Barro Colorado looked downward briefly (and perhaps lowered her whole head) as she uttered Hoots in otherwise typical series, but she always looked up (and perhaps raised her head) between each note of a series.

These captive individuals were always (with one exception—see page 51) alone in their cages, or at least the only individuals of their

own species in their cages, at the times that they uttered Hoots. Any adult that had been Hooting regularly every night always (again with the same single exception) stopped Hooting as soon as another Night Monkey was put in the same cage. The Hoots stopped irrespective of whether the animals fought with one another and/or performed copulatory reactions or did neither. (I might add that Hoots were not uttered during disputes between individuals in different cages, even "long-range" hostile reactions between individuals in cages quite far apart from one another.)

As far as I could tell, all the wild individuals heard to utter Hoots were also alone at the time.

These facts would suggest that the Hoots of adult individuals are produced when a gregarious and/or a pairing tendency is thwarted by the absence of a suitable companion.

Although I was never able to observe responses to Hoots in the forest on Barro Colorado Island, it seems likely that their primary function, when uttered by unmated adults under natural conditions, is to attract potential mates. If so, they are essentially similar to certain types of bird vocalizations which have been called "song." (Another resemblance to most "song" is that an individual uttering Hoots, *i.e.*, "wanting" a companion, apparently always remains stationary, instead of going in active search of a companion. It has already been mentioned that the captive individuals sat during their Hoots. Wild individuals frequently moved from tree to tree between series of Hoots, but they were never heard to move during the utterance itself.)

The single case of Hooting by an adult in the same cage with another individual of the same species, cited above, occurred immediately after a male and a female had been brought together again after a long separation. They were probably mated before, but may have become incompatible during the period of separation. The female uttered many Hoots during the first few nights after the animals were brought together again; but all her Hoots were unusually soft and probably low intensity.

The Hoots of Night Monkeys sound very much like some notes of owls. There is, in fact, one species of owl on Barro Colorado Island which utters hooting notes that are almost identical (to human ears) with those of Night Monkeys (except for the fact that they are always or almost always uttered singly). It is possible that notes of this type have acoustic properties which are particularly advantageous in tropical forests at night.

It seems probable that the pitch, at least, of almost all the char-

acteristic vocal patterns of adult Night Monkeys is a specialized adaptation to such conditions. Apart from the Screams (and the Squeaks, if they are a "normal" pattern of adults—see page 58), all the adult calls and notes are comparatively low in pitch. The vocal repertory of adult Night Monkeys is lower, on the average, than the adult repertory of any other New World primate with which I am familiar, except the howlers of the genus *Alouatta*. It is certainly much lower than the repertory of any other New World monkey of comparable size. All other factors being equal, a low-pitched sound will carry farther than a high-pitched sound of equal energy value at the starting point. In all circumstances, the energy of high-pitched sounds will be used up more rapidly than that of low-pitched sounds. Another property of low-pitched sounds may be particularly significant in a forested environment. The relatively long sound waves of low-frequency noises will be less affected, *i.e.*, deflected or scattered, by obstructions such as twigs and branches than the shorter waves of high-pitched sounds. Low-pitched sounds may be particularly useful to adult Night Monkeys because they are largely dependent upon auditory signals for long-distance communication.

It must be significant, in this connection, that the high-pitched Screams seem to be the only purely hostile vocalizations of adults that are always short-range signals. Similarly, the only Squeaks that may be a regular part of adult behavior are uttered only when two individuals are in actual physical contact with, or in very close proximity to, one another (see below).

RUBBING

The only individuals observed to perform this pattern were the captive adults on Barro Colorado Island.

In the most complete and vigorous Rubbing performances, an individual would flex its hind legs, press its perineal region against a branch, and then rub the whole region against the branch with rapid side-to-side movements. Generally there were two or three movements in each direction. The tail was usually lifted at the same time, and frequently twitched from side to side. The gland at the base of the tail may have brushed against the branch during these movements, but I was never able to make sure of this.

Low-intensity Rubbing consisted of nothing more than one or two sideways "swipes" at a branch, sometimes very poorly orientated.

All Rubbing was usually silent.

Some individuals had favorite Rubbing sites—particular spots

where they performed Rubbing much more frequently than elsewhere. All or most of these sites were places where there was a slightly projecting irregularity on the surface of a branch, or even the stump of a projecting twig.

As an intraspecific reaction, Rubbing was performed almost exclusively during encounters between males and females, usually encounters in which either one or both individuals also performed overt (and often high-intensity) hostile and copulatory patterns. Low-intensity Rubbing might be performed by either one or both individuals during such encounters; but complete and vigorous Rubbing generally was performed only by females. Most male Night Monkeys tend to be slightly dominant over females. It may be significant, therefore, that the only male observed to perform high-intensity Rubbing during an intraspecific encounter was obviously subordinate to the female with which he was associated at the time. He would seem to have been playing a feminine role. Although usually subordinate, the females that performed high-intensity Rubbing were not very frightened. They usually did their Rubbing as they approached males, to initiate either overt hostility or precopulatory behavior (or both).

Some very tame individuals performed low-intensity Rubbing movements when approached by human beings. A moderately tame individual (almost certainly a male), in a cage with its mate and young, repeatedly performed vigorous and complete Rubbing after being approached by a human being, as the latter walked away.

These facts would suggest that Rubbing is usually produced by some combination of hostile and sexual tendencies. (Some other "friendly" social tendency may take the place of sex in some circumstances.) Possibly some territorial motivation is also involved. (It is not yet clear how the motivation of Rubbing differs from that of Moans or Low Trills. There is not enough evidence to permit a choice among the several possibilities that come to mind.)

Rubbing is probably related, phylogenetically, to the "territory marking" patterns of many other mammals (which are very similar in form). Night Monkeys may spread some odoriferous substance on the branches that they rub against. But I have never seen a Night Monkey smell or sniff at the Rubbing site of another individual in an unusually attentive manner.

The Rubbing by the individual with its mate and young appeared to be a "triumph ceremony," proclaiming the successful defense of its territory, in much the same way as some Resonant Grunt performances.

Hill (1960) says that captive Night Monkeys may moisten the palms of their hands and the soles of their feet with urine, and he compares this habit to the similar pattern of nocturnal Lorisoidea which has been interpreted as a method of marking territory. I never saw anything like this in any of the Night Monkeys that I studied. It may be confined to other populations of the species and/or a result of special conditions in captivity.

I might add, in this connection, that I have never seen such behavior performed by Tufted Capuchins (*Cebus apella*) kept in captivity on Barro Colorado or in the Zoo at Lima, Peru, although Nolte (1958) reports it as common among some individuals of the same species kept in captivity in Rio de Janeiro. This sort of behavior may be extremely variable among Platyrrhini.

COPULATIONS, ALLOGROOMING, AND ASSOCIATED PATTERNS

Like many other New World primates, Night Monkeys seem to perform overt copulatory reactions rather infrequently under natural conditions. I never saw copulations by the wild individuals on Barro Colorado Island. Copulations are also at least relatively rare among captive individuals. The only captives observed to perform copulatory reactions or closely related patterns were the ones on Barro Colorado Island. Even here, the copulatory reactions of mated individuals kept together continuously were not only rather infrequent but also rapid, brief, and inconspicuous. The only really elaborate and conspicuous sequences of copulatory patterns were performed by males and females coming together for the first time or rejoining one another after being separated and kept in isolation for several weeks or months.

The most simple forms of apparently successful copulations are simple indeed. In such cases, the male and female tend to approach one another silently. The male usually sniffs at the female's genital or perineal region, either immediately or after sniffing at her face. The female may sniff at his perineal region while he sniffs at hers. He then mounts her from the rear, clasps her around the upper part of her body with his arms, and maneuvers his body into a position from which he can insert his penis into her vagina under her tail (she may lift her tail, or shift it sideways, as he does so, but this movement is always very slight). After insertion, the male usually makes three or four pelvic thrusts. Ejaculation apparently occurs only during the last thrust, which sometimes is sustained relatively long. The whole lower part of the male's body may quiver visibly during this last thrust. The male then dismounts. Sometimes his dismounting seems to be accelerated by the female turning her head to look at him.

Apart from this, the female seems to remain essentially passive throughout the whole performance. Both individuals generally are silent throughout. The whole performance seldom or never takes more than a couple of minutes. Sometimes it is much briefer. There is no regular postcopulatory display; although it is not uncommon to see a female sniff at the male's perineal region, briefly, immediately after he dismounts.

Simple and rapid copulations of this type seem to be performed only when both the male and female are highly motivated and thoroughly familiar with one another.

A pattern frequently associated with less simple copulation attempts is Allogrooming. One of the individuals grooms the other, or they groom one another mutually. When only one individual performs Allogrooming, it may be either the male or the female. It is usually the male when the Allogrooming occurs in very close association with apparently successful copulation attempts. The form of the Allogrooming movements seems to be the same in both sexes.

One individual wishing to groom another generally begins by sniffing. The "groomer" usually sniffs most attentively at the sides, armpits, or perineal region of the "groomee." The actual grooming follows immediately after the sniffing. It is accomplished by use of both hands and teeth. The use of the teeth seems to be most important in Allogrooming (unlike autogrooming). The grooming individual nibbles at the fur and/or skin of the individual being groomed, presumably separating matted hairs, removing dead hairs and patches of dead sloughed skin, and also any small arthropods that may be present (both ticks and chiggers are common, at times, on Barro Colorado). The hands are used both to "curry" or comb the fur of the individual being groomed and, even more frequently, to separate the fur so that the grooming individual can get at the base of the hairs and the skin with its teeth. During some Allogrooming, the groomer uses its hands to push or pull the groomee into a position or posture to facilitate the grooming.

The groomer may groom any and all parts of the groomee, in almost any sequence; but it usually devotes most of its attention to the sides, back, crown and back of the head. The two animals generally sit side by side during Allogrooming, facing in the same or opposite directions, and the groomer reaches the groomee from the side and/or the rear (see figure 14).

Allogrooming may lead to mounting. This "grooming mounting" may intergrade with the type of mounting that occurs during copulations, and intermediate performances are common, but in its typical

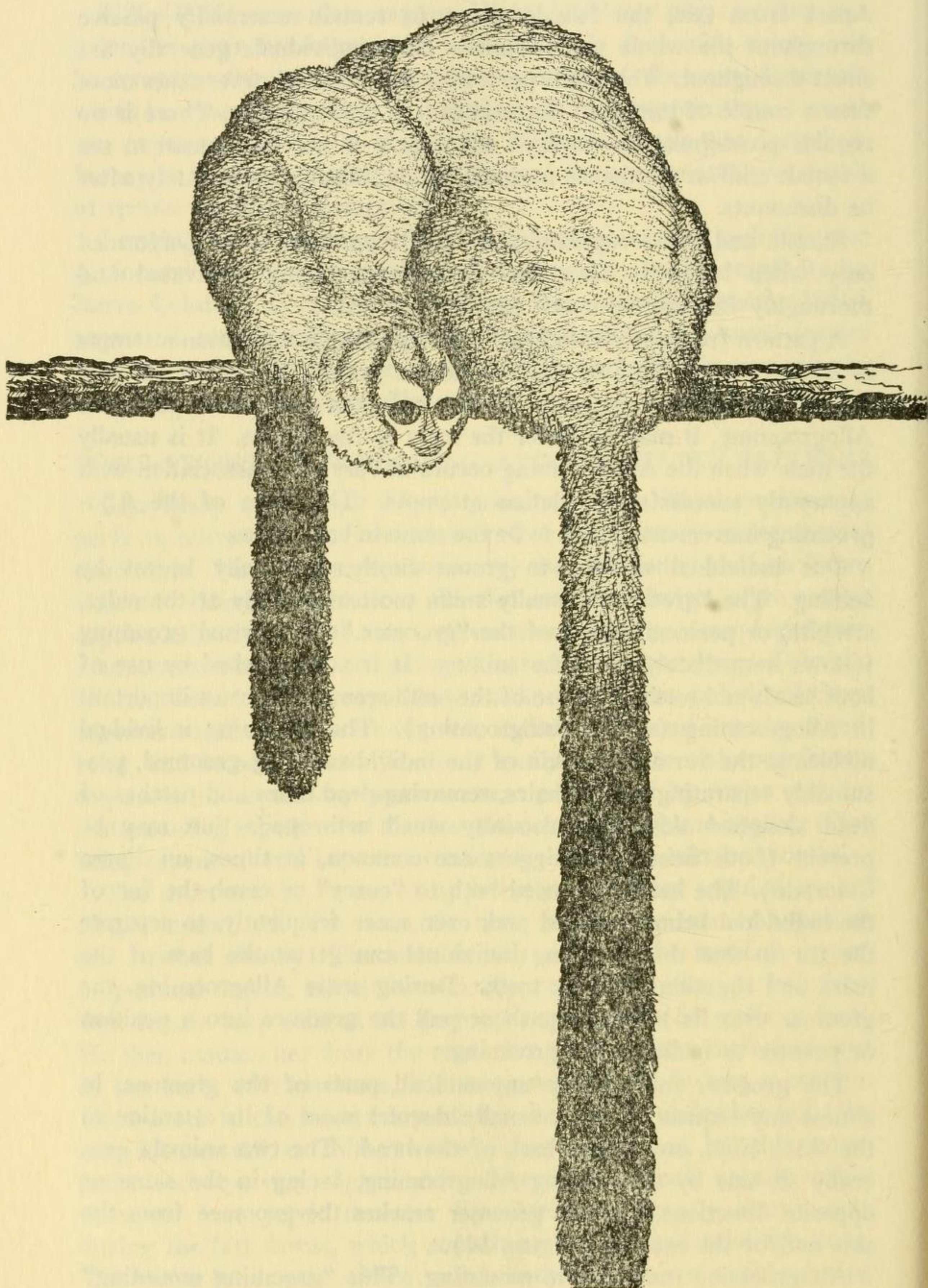


FIG. 14.—Positions and postures sometimes assumed by mated individuals during Allogrooming.

The individual on the right is grooming the individual on the left. The lowering of the front part of the body by the latter is probably a balancing reaction, *not* an indication of a head-down posture.

form it is quite distinct. It occurs when the groomer wants to groom areas on the far side of the groomee. In its attempt to get at these areas, the groomer may climb up on the back of the groomee. It usually climbs up from the side, not from the rear as in the case of a male mounting a female during a typical copulation attempt. A grooming individual also tends to keep its head pressed down into the fur of the groomee. (A male generally does not lower his head as much during copulation). The only individuals observed to perform grooming mountings were males; but this may have been largely due to the fact that most of the females observed were slightly subordinate to their males and somewhat reluctant to handle them roughly (there is no obvious reason why females should not be able to perform such mountings in suitable circumstances).

If the individual being groomed does not object to the process (and rough or awkward Allogrooming may provoke disputes—see below), it remains passive, sitting quietly. Only rarely does it shift position voluntarily to present particular areas that it wants to have groomed.

Night Monkeys do not seem to have any special “soliciting” posture to invite (initiate) either copulation or Allogrooming (unless sitting quietly by the side of another individual can be considered such).

Some Allogrooming performances are quite silent. Others are accompanied by Squeaks and/or a variety of wholly or partly hostile notes (see below). Hostile notes are relatively very rare except during the obviously “unsuccessful” performances which break up in open disputes.

Allogrooming may occur immediately before and/or after both successful and unsuccessful copulation attempts. It may also occur apart from overt copulation attempts, but only relatively rarely. Almost all the individuals observed to perform such grooming were known to be in reproductive “mood,” copulating with the individuals they groomed on succeeding and/or preceding nights, even if not always immediately before or after the actual grooming.

These facts would suggest that the copulatory tendency may be at least one of the causal factors producing Allogrooming in all circumstances.

The detailed relations or interactions between Allogrooming and overt copulatory movements are rather complex. In spite of their frequent association, and their apparent similarity in motivation, the two types of behavior seem to be mutually exclusive, to some extent, on a short-term basis. Allogrooming appears to serve as a partial “substitute” for copulation. It is very common to see a male groom

a female *briefly* before mounting and performing an apparently successful copulation; but he will almost certainly *not* copulate successfully, or at least will not copulate successfully immediately after the Allogrooming, if he grooms her vigorously for more than a few seconds.

This would suggest that the performance of prolonged Allogrooming tends to "consume" an appreciable amount of copulatory motivation, *i.e.*, raises the releasing threshold of overt copulatory behavior in at least many circumstances.

Allogrooming may have several functions. Its successful performance may help to reduce the actual or potential hostility between male and female. The close physical contact involved may also provide some direct sexual stimulation.

Either one or both of these effects may be very rapid. They may be more rapid but less long sustained and/or have less potential strength than the effect of raising the threshold for copulatory behavior. If there are such differences in speed, and possibly strength, between the contradictory effects of Allogrooming, this would explain why successful copulations frequently follow brief grooming and rarely follow prolonged grooming.

Repeated Allogrooming may also have the relatively very long-term effect of strengthening the pair bonds between mates.

If the Allogrooming of Night Monkeys does function in these different ways, it is basically similar to many "precopulatory" patterns of other species, *e.g.*, the Allogrooming of many other mammals and the Food-begging and Allopreening of many birds.

The penis of a male Night Monkey may be erected before he mounts during copulation, but it is not "shown off" to the female. This behavior pattern does not seem to be a ritualized display like the penile erection of Squirrel Monkeys, *Saimiri*, described by Ploog and MacLean (1963).

The only other patterns which must be considered in connection with the sexual behavior of Night Monkeys are Squeak notes. These seem to be typical of young animals and infants, but are uttered also by adults in certain circumstances.

Many of the Squeaks uttered by adults may be reversions to, or persistent remnants of, juvenile behavior; and may be produced by some or all of the same wide range of causes as the Squeaks of juveniles (see below). Squeaks are certainly uttered more frequently by adult individuals that have been raised in complete or partial isolation from other individuals of their own species than by adults raised in the wild under natural conditions; and the retention of juvenile

patterns by adults is the sort of phenomenon which might be expected to be produced by the abnormal circumstances of captivity. (If nothing else, young animals raised in captivity tend to regard the human beings that take care of them as their parents, and often retain this attitude after reaching maturity, long after they would have become independent of, or separated from, their parents in the wild.)

Other Squeaks uttered by adults may have a different significance. Many of the captive adults on Barro Colorado Island uttered frequent Squeaks during sexual reactions. This occurred often enough to suggest that Squeaks may be a normal part of the adult repertory, a normal accompaniment of sexual behavior even if not of any other adult activity.

Squeaks were uttered by both adult males and females. They were uttered most frequently by individuals approaching their mates, and just beginning to perform Allogrooming, but were relatively much less frequent during the later stages (when Allogrooming was in full swing and most vigorous). Squeaks also were relatively rare during copulations and overt disputes between mates.

As far as I could tell by ear, all the Squeaks uttered by adults were similar to, or identical with, the "pure" Squeaks of juveniles in form.

The function(s) of adult Squeaks in sexual situations were obscure. They did not seem to produce any overt, positive, response in the individuals toward which they were directed. They may, conceivably, have functioned as some sort of appeasement pattern. One might expect that any behavior pattern that is performed most frequently by infants and juveniles would tend to reduce hostility (especially aggressiveness) in any adult toward which it is directed, even when it is performed by another adult.

EXAMPLES

Some of the different sequences and combinations of Allogrooming, copulatory, hostile, and other patterns during different types of encounters between males and females may be illustrated by extracts from my notes made at the times of observation.

The first is an example of the behavior of experienced males and females.

February 4, 1962. Z male and X female. These two animals are mates. They were separated several days ago. The male has been kept in the cage in which the pair lived previously. The female has been kept in another cage (out of sight and hearing of the male) by herself.

7:40 p.m. Female put back in cage with male. Male is in sleeping box at the

time. Female rushes straight toward him. He comes out of box. The two animals sniff at one another's perineal regions. Then the male mounts the female, from the rear. No hesitation or awkwardness. Copulation. Apparently successful. Lasts at least 20 seconds. Then the male dismounts. No postcopulatory display. Male walks away, female follows. She utters two Low Trills as she does so.

7:44. The two animals sniff one another's perineal regions again. And again. Silent. No Allogrooming or attempts to mount. Then sit side by side. One or both utter(s) a few Squeaks. Then male does begin to groom female. From side. Then mounts her again, from rear. One or both animal(s) utter(s) Squeaks as he mounts. Copulation. Female resists, but not violently. She just turns around to look at male. He dismounts, walks away. Female immediately assumes Arch Posture—and utters a series of Gulps! Then relaxes. Follows male around cage, 7:50. Then both animals retire to sleeping box . . .

7:56. Male is grooming female in box. This is accompanied by lots of sneezing by one or both animals . . .

8:02. Both animals come out of box. Sit side by side, facing in opposite directions. Female utters a few Squeaks. Then male begins to groom her. His movements are gentle. He devotes most of his attention to her lower back and rear. Female continues to utter Squeaks. Goes quite limp while male grooms. Possibly half asleep? Then she suddenly utters loud Squeaks, moves away from male. Goes into box. Male follows, continues Allogrooming in box . . .

8:17. Female apparently startled or annoyed by something. Bounces out of box, crouches in far corner of cage. Utters long series of Gulps. Male comes out of box, runs toward female, utters one Sneeze-grunt as he does so. Female runs back to box. Performs one burst of Rubbing movements in midst of run. Back into box. Male follows, resumes Allogrooming again . . .

The following extract illustrates the behavior of an inexperienced male.

January 28, 1962. O male and C female. This male has been hand reared, in partial isolation, ever since the age of approximately 1½ months. Now full grown. Since being taken from his parents, he has had only brief contacts with other Night Monkeys. He is not familiar with C female.

7:00 p.m. Female let loose in male's cage. Male leaps away, freezes and crouches in far corner. Female explores cage, uttering Low Trills as she does so. Approaches male. The two animals sniff one another, nose to nose. Male utters Squeaks. Female moves away, resumes exploring with Low Trills. Approaches male again. He sniffs at her perineal region and utters more Squeaks. She moves away again. Explores with Low Trills. Approaches male again. He utters more Squeaks. She moves away again . . .

7:06. Female approaches male. He suddenly clasps her back, from the side, but does not mount. She breaks away and resumes exploring. Then approaches male again. A vicious fight breaks out. Male apparently the initiator, striking at the female with his hands. Lots of running, chasing, and striking during fight. Both animals quite silent throughout. Then they separate. Male retires to corner and assumes Arch Posture. Female walks around, not very rapidly, uttering many Gulps and a few Sneeze-grunts . . .

7:18. Male starts to approach female. She assumes an Arch Posture, starts to advance toward him. He retreats . . .

This sort of inconclusive behavior continues until 9:10, when I decide to stop observations. Then, happening to pass the cage at 9:50, I find the animals copulating! Resume observations.

Copulation apparently successful. Male dismounts. Then mounts again immediately. No preliminary display by either animal. Copulation again apparently successful. Pelvic thrusts at intervals of at least several seconds. Then male dismounts. No postcopulatory display. Male walks away a couple of feet.

Back to female almost immediately. Approaches her from side. Sniffs at her side and utters Squeaks. Climbs up onto her back, mounting from side. Once mounted, he seems to be trying to shift around into a copulatory position. Gets half way there, but female turns around to look at him, and he slides off. Then walks away again . . .

10:01. Male approaches female again. From side. Sniffs at her side and utters Squeaks. Half mounts, from the side. Then he begins to groom the female, while he remains sprawled sideways across her back. His grooming movements are extremely vigorous, even violent, and very awkward looking. Female just sits. Male eventually slides off. Remains sitting beside female, one hand resting on her back, and utters many Squeaks at irregular intervals. Female eventually walks away. Male follows . . .

10:10. Male grooms female steadily for several minutes. Reaching her from side. He repeatedly turns her half way over on her back, apparently trying to get at something under her arm on the far side. Both animals silent. Finally the female breaks away. Male follows her. Uttering Squeaks. Then mounts her from the rear. Tries to copulate. Copulation attempt probably unsuccessful. Only one or two pelvic thrusts. Both animals silent. Then male slips off . . .

10:19. Male approaches female again. Silently. Mounts her immediately, from rear. Copulation. Apparently successful. Long sustained, with many pelvic thrusts. Male finally dismounts. Sits beside female. She sniffs at his flank region. He immediately starts to groom her. Grooming lasts only a few seconds. Then male mounts again, from the rear. Copulation. Apparently successful. Many pelvic thrusts; the last one very long sustained and accompanied by quivering of the rear part of the body. Male slips off. Immediately starts to groom female again. This Allogrooming is much more prolonged and violent than the Allogrooming immediately before the last copulation.

10:22. Male stops Allogrooming momentarily. Then starts again. Grooming movements even more violent than before. Again and again he twists the female over on her back. No attempt to mount. Female silent; male utters occasional Squeaks. Then the male stops Allogrooming and walks away.

He goes back to the female almost immediately. Mounts her from the front, climbing over her head. Lies on her back, his head over her tail, his tail hanging in her face! He slips off after a few seconds, and the two animals separate . . .

This sort of behavior, including many copulation attempts (all apparently unsuccessful) and much violent Allogrooming by the male, continues spasmodically as long as I continue to watch the animals, until 11:00 p.m.

During this encounter, it was obvious that the male had a strong copulatory tendency, but he seemed to have difficulty in orientating

his copulatory movements, and he was certainly somewhat hostile to the female at first. (His awkwardness persisted for at least 5 nights. But shortly afterwards he was observed to perform sexual reactions quite smoothly.)

The last extract illustrates the behavior of pairs when the female is dominant over the male.

January 24, 1962. P female and Z male. These animals may have had some previous sexual experience; but they are not acquainted with one another. They have been kept isolated in separate cages for several days.

6:45 p.m. The male is let loose in the female's cage. The female rushes to him. They sniff one another, nose to nose. The female utters one Low Trill during sniffing. Then they separate. The male runs around the cage, possibly frightened. The female moves around more slowly. Neither animal is following the other. One or both always assume(s) an Arch Posture when they come close to one another.

6:50. The two animals settle down to a routine, which does not change very much for almost three hours.

The male retires to a corner of the cage, and sits quietly in a crouching freeze posture whenever he is left alone by the female. Sometimes his freeze includes a trace of a head-down component. After an hour or so, when the female starts to become less active (see below), he occasionally closes his eyes, briefly, while continuing to sit in the same posture most of the time.

The female approaches the male repeatedly. When she approaches him slowly, or at a normal running pace, she usually sniffs him. She usually begins by sniffing at his face, and then sniffs his side and/or his perineal region. When she sniffs at his side, she often appears to be trying to smell under his arm or in his armpit. Sometimes she seizes his hands, arms, or head, in order to pull him into the right position to facilitate sniffing the area she is interested in at the time. Sometimes she grooms the male immediately after sniffing. This occurs first during her third approach. It becomes increasingly frequent as the evening wears on.

Sometimes the male moves away after the female begins to sniff at him. Sometimes he just sits still. Most frequently, he sniffs in return. In most cases, he sniffs more briefly than she does. He often appears to be unwilling to sniff, but unable to resist the stimulus provided by the female. He usually sniffs her perineal region after sniffing her face (the animals are then nose to tail).

Most of this sniffing and Allogrooming is accompanied by Squeaks by the female. One or both animals also utter(s) a few Low Trills and many Moans. The Moans are uttered most frequently around 8:50-9:00 p.m., presumably when the animals are becoming accustomed to one another.

Sometimes the Allogrooming develops into a dispute. When the female grooms too energetically. The male strikes at her with his hands. Silently. When the male does this, the female always responds by "bombarding" him. She runs away from him, uttering many Gulps and a few Sneeze-grunts, turns, faces him, pauses a second, performs a few Rubbing movements, and then leaps at him. Usually she leaps just above him, landing on the side of the cage an inch or less above his head. Her tail usually slaps into his face as she lands. Occasionally she crashes into him full force with her whole body.

She usually performs several leaps one right after the other, before resuming slower approaches and Allogrooming . . .

The male does not respond to the female's leaps as strongly as might be expected. Usually he just sits quietly throughout. Occasionally (especially during the first hour) he assumes an extreme Arch Posture just as the female starts to leap. Once or twice he strikes at her, but he never chases her . . .

8:45. The male starts to relax a little. Occasionally starts to follow the female when she goes down to the floor of the cage to get food . . .

9:45. The two animals are sitting side by side. Then the female goes down to the floor, picks up a piece of fruit, climbs up to a branch, about three feet from the male, and starts to eat. The male walks toward her slowly. Sniffs at her perineal region. Then suddenly mounts her, from the rear. Slightly awkward. The female does not lift her tail, so the male has to shift his body in order to insert his penis from the side. Copulation. Apparently successful. Several pelvic thrusts at irregular intervals. The female leans downward and forward during the copulation, still clutching food in her hand. Then the male dismounts. Sits beside female, facing in the same direction. Then turns around, sniffs at her perineal region again, mounts her again, and copulates again. Again apparently successful. Then he dismounts and sits beside the female as before. She calmly finishes eating her food, turns around, and sniffs his perineal region. Then both animals sit quietly . . .

BEHAVIOR OF YOUNG ANIMALS

Three baby Night Monkeys were born, to different parents, in captivity on Barro Colorado Island. One of these was left with its parents, but died when approximately 2 months old. The second was taken from its parents at the age of 1½ months, and raised by hand. The third was born only 9 weeks before this paper was written, and was left with its parents. Several other infants were bought in the Panama market, and hand raised successfully in captivity. Many of the other individuals kept in captivity on Barro Colorado Island were secured when they were still subadult. A few subadult individuals were observed in the wild on Barro Colorado.

The infants born in captivity on Barro Colorado Island were not watched very much while they remained with their parents, as it was feared that prolonged observation might disturb the parents unduly and cause them to abandon or neglect the young. It was only possible to note a few aspects of the parent-infant relationship.

For the first few days after birth, the infant is always carried by the mother, clinging to her breast or belly. Later it usually rides on the back of a parent.

Male Night Monkeys seem to play an important role in raising their offspring. Before they were 3 weeks old, two of the infants born in captivity on Barro Colorado Island were being carried by

their fathers most of the time when they were not actually being suckled by their mothers. The third infant was certainly carried by its father much of the time, but I could not determine exactly how much, simply because the father and mother were very difficult to tell apart (without catching them in the hand). This was the infant that was observed most frequently. It was first seen being carried by the father at the age of 9 days. This was also the first time that it was seen riding on the back of a parent. (It seems probable that these two developments were causally related. But carrying on the back is not a purely masculine pattern. The same infant sometimes rode on its mother's back before and/or after being suckled.) I was informed by a keeper at the National Zoological Park that a baby Night Monkey born to a captive pair there, and raised by its parents, also usually was carried by the father.

This parental behavior is interesting from a comparative point of view. Infants and young apparently are always carried by their mothers, as long as they are carried at all, in such genera of New World primates as *Alouatta* and *Ateles* (Carpenter, 1934 and 1935). The only other platyrrhines in which the father is known to carry the young regularly are the marmosets and tamarins (Sanderson, *op. cit.*, and Hill, 1957).

There is at least one published record of a male Titi Monkey, *Calli-
cebus*, carrying young (L. E. Miller, quoted in Allen, 1916); but it is not known if the habit is regular in the species.

Hill's (1960) statement that Allen (in the same paper) cited evidence to show that male *Saimiri* frequently carry young is apparently erroneous.

The carrying of young by males may be primitive among Platyrrhine and/or an indication of close phylogenetic relationship between Night Monkeys and marmosets and tamarins. (Night Monkeys resemble marmosets and tamarins in a number of other characteristics.) In any case, such behavior must be adaptive. Its principal advantage may be the sharing of labor. When the male carries the young part of the time, neither parent will become as exhausted and "run-down" (and therefore susceptible to predators and disease) as the female would be likely to become if she did all the work herself. (Even if the male has the harder job because he carries the young most of the time, he can support the strain better than his mate simply because he does not have to produce milk. Males may get less tired also because they are usually, or perhaps always, slightly larger and more powerful than their mates.)

In all probability, the advantages of such behavior can be secured only when the sex ratio is effectively one to one and the pair-bonds between mates are close and long sustained. Species of *Alouatta* and *Ateles* probably cannot afford such behavior because they usually live in groups in which there are more females than males. There may occasionally be more infants than adult males in such groups. The looseness and brevity of pair-bonds among howlers must also tend to prevent the establishment of continuous bonds between males and infants. Infants must be fed by their mothers at more or less frequent intervals, and regular transfers from one parent to the other might be difficult to arrange when the parents do not stick together.

Thus, the type of parental behavior shown by Night Monkeys in captivity would seem to provide strong support for the hypothesis that males and females of this species usually form pair-bonds which are at least moderately long sustained under natural conditions (see page 12).

Like all baby monkeys, infant Night Monkeys have very strong clutching tendencies and try to keep in close physical contact with a parent at almost all times. The only exceptions occur when an infant moves from one parent to another before and after feeding (see next paragraph). When clutching a parent, an infant usually uses both hands and feet to hold on to the parent's fur, and may also keep its tail pressed against the parent's body. The infant born in captivity that was observed most frequently was very inactive, aside from feeding, during the first few days of its life. By the time it was 3 weeks old, however, it sometimes moved around most energetically on its parent's back.

My observations would suggest that an infant usually shifts from one parent to the other, at feeding time, under its own power. The parents do not lend a hand to lift or support the infant during the transfer unless it should start to fall.

The infants raised in captivity apart from their parents quickly learned to accept human beings as foster parents. They appeared to be almost perfectly satisfied to be carried by a human being, especially if they could ride on the head and clutch hair. Somewhat more slowly and reluctantly, they also learned to accept turkish towels as parent substitutes. An infant conditioned in this way usually spent all its time clutching its towel (unless it had to leave the towel to feed or drink).

Except when specifically stated otherwise, the behavior patterns of infants and juveniles described hereafter in this section were performed by young animals hand reared in captivity, after being sepa-

rated from their parents. All these individuals were at least $1\frac{1}{2}$ months old.

A perfectly content infant, with all its desires satisfied, is silent and motionless (and usually asleep). Sounds and movements are apparently always indications of dissatisfaction. When an infant is slightly dissatisfied, it may begin either movements or sounds first, or both together. (It is my impression that an infant is most likely to move without vocalizing when it "knows" in advance that it can remove its dissatisfaction by its own efforts.) The first movements may be nothing more than slight readjustments in the position of the limbs or other parts of the body. At higher intensities of dissatisfaction, the infant usually goes straight to whatever individual or object it expects will be able to satisfy its need (*e.g.*, a food dish when it is hungry) or, if this is not possible, makes vigorous searching movements.

The hand-reared infants apparently never moved about just for the sake of moving. They did not seem to have any trace of the independent locomotory tendency of adults. All their movements appeared to have an immediate "practical" end in view apart from the mere performance of the movements.

By far the most common vocal patterns of infant and young juvenile Night Monkeys are Squeaks and Squeaklike notes. A typical "pure" Squeak is brief, not very loud, and much higher in pitch than any of the Grunt Complex patterns. Sketches of sound spectrograms of pure Squeaks are shown in figures 15, 17, and 18. Each pattern of this type sounds like a single note to human ears. The sound spectrograms, however, indicate that at least many of the pure Squeaks are actually partly or wholly compound, composed of two or three sounds separated by *very* short intervals or two or three partly distinct "syllables." It will be convenient to refer to such patterns in terms similar to those applied to the equally compound Hoots described above. A pattern that sounded to me like a single note will be called "a Squeak" or "a note." The various sounds which spectrograms may show to be included in a single Squeak, in this sense, will be called "components of a Squeak."

All the accompanying sketches of vocal patterns by an immature individual are based upon recordings of a single male who was exactly 45 days old at the time of recording.

The pitch of a single Squeak seldom or never remains level throughout. In most cases, the pitch first rises and then falls. When a Squeak is composed of two more or less distinct components, the rise usually extends throughout the first component and the fall throughout

the second component. The rate of rise or fall may vary within the same component. When a Squeak is composed of three more or less distinct components, the first usually rises, the second usually rises or remains approximately level, and the third usually falls. More rarely, the pitch may rise or fall more or less steadily throughout a whole Squeak, or may first fall and then rise.

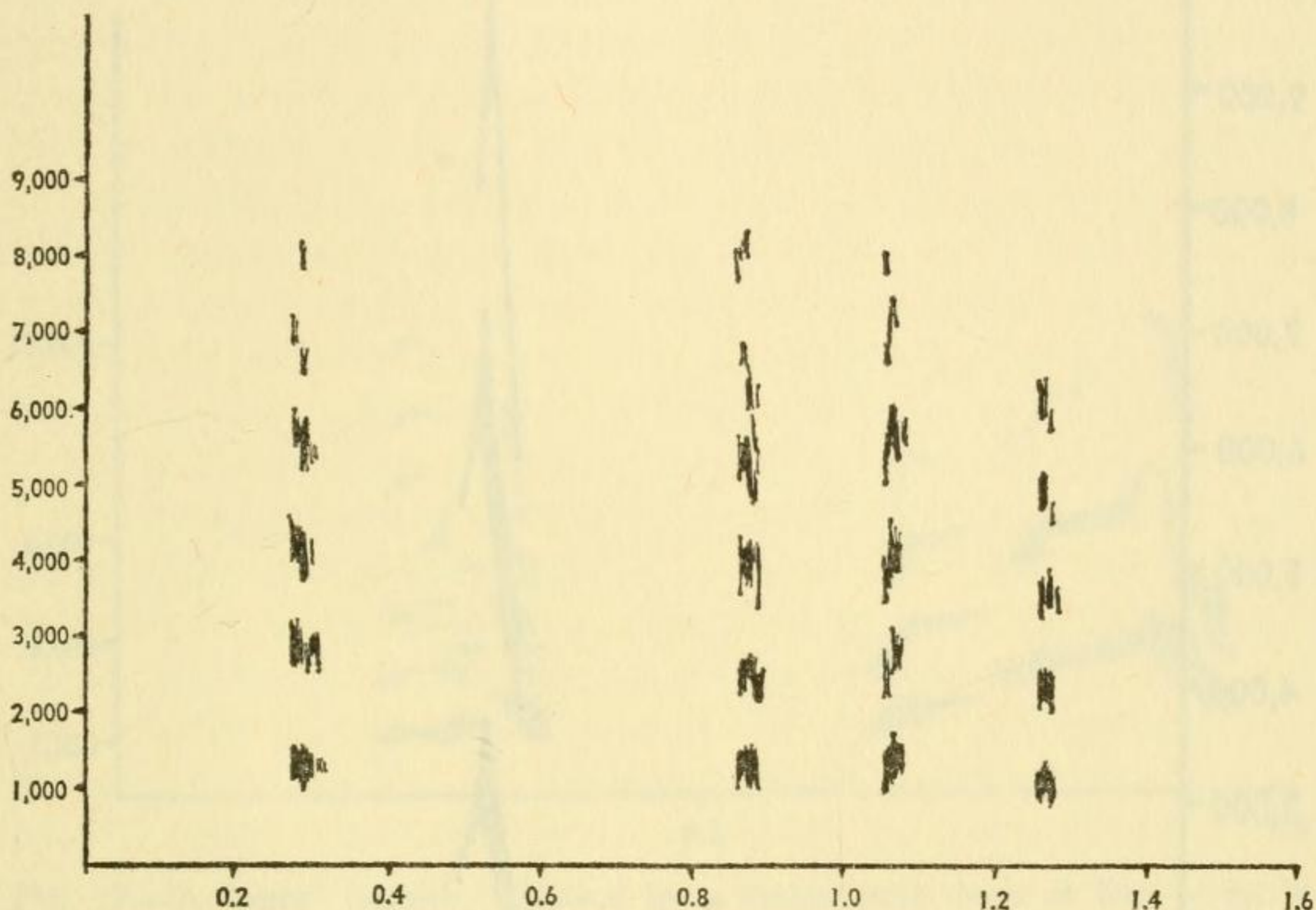


FIG. 15.—Four typical "pure" Squeaks, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

Some Squeaks are much louder than usual without being prolonged. Patterns of this type tend to extend over a particularly wide range of pitch (see figure 16).

In some Squeaks with both rising and falling pitch the rising part is loudest; in others the falling part is loudest.

The Squeaks of infants and young juveniles intergrade with both Screams and High Trills.

The "pure" Screams of infants and young juveniles sound similar to adult Screams, but are slightly softer and perhaps slightly plaintive in tone. The most extreme Screams of the young animals that I studied sounded as if they were approximately as long as the adult Screams shown in figure 5, and only slightly higher in pitch on the average. It is possible that infants and juveniles never utter Screams of as long duration as the adult patterns shown in figure 6; but I

never subjected any young individual to the stresses which would be expected to produce the highest intensity type of Screaming.

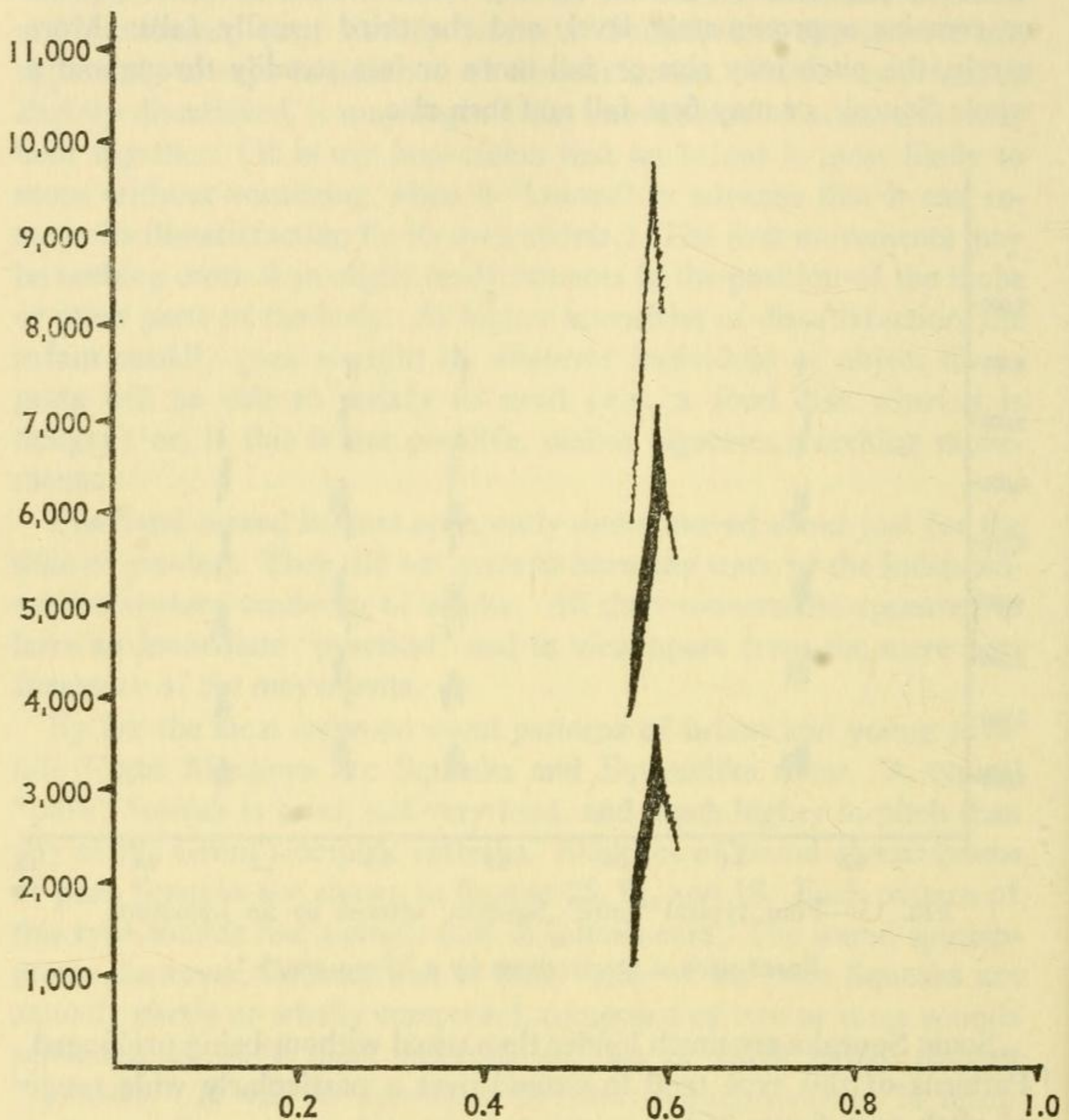


FIG. 16.—A single very loud Squeak, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

There were at least three more harmonics with this note that are not shown in the drawing.

Patterns intermediate between pure Squeaks and pure Screams are variable, but always more or less intermediate in length and sometimes slightly higher in pitch, on the average, than the lowest Squeaks. They also tend to fluctuate, rise and fall slightly in pitch, in much the same way as pure Screams, but the number of fluctuations is less than in the latter. Sometimes an intermediate pattern retains a trace

of the slight (inaudible to human ears) division into separate components which is characteristic of many Squeaks. Figure 17 includes a pattern of this type. The intergradation between pure Squeaks and pure Screams seems to be complete, insofar as infants and young juveniles utter every possible type of morphologically intermediate pattern.



FIG. 17.—A “pure” Squeak, followed by a longer note more or less perfectly intermediate between a Squeak and a short Scream. Uttered by an immature.

Based upon a spectrogram by a “Vibralyzer.”

Compare with the Scream shown in figure 5 and the Trills shown in figure 19.

“Pure” High Trills are conspicuously compound. To human ears, each High Trill sounds as if it were composed of three or four Squeaks uttered in rapid succession. Most sound spectrograms convey the same impression. A sketch of a more or less typical pure High Trill is shown in figure 18. The successive notes in a single High Trill are seldom exactly the same pitch. In most cases, the first one or two notes are largely or completely rising and the last one or two notes are largely or completely falling.

A remarkable feature of the vocal repertory of young Night Monkeys is that the arrangement of components within a single Squeak, *i.e.*, the sequence of changes in pitch and the relative distance between high points and low points is sometimes similar to the arrangement of successive Squeaks within a single High Trill. Thus, the

form of a pure High Trill may be essentially similar to that of a pure Squeak, only on a much longer time scale. The sequence of rises and falls in pitch within a single short Scream may be equally similar to the arrangement of the corresponding features within both a single Squeak and a single High Trill.

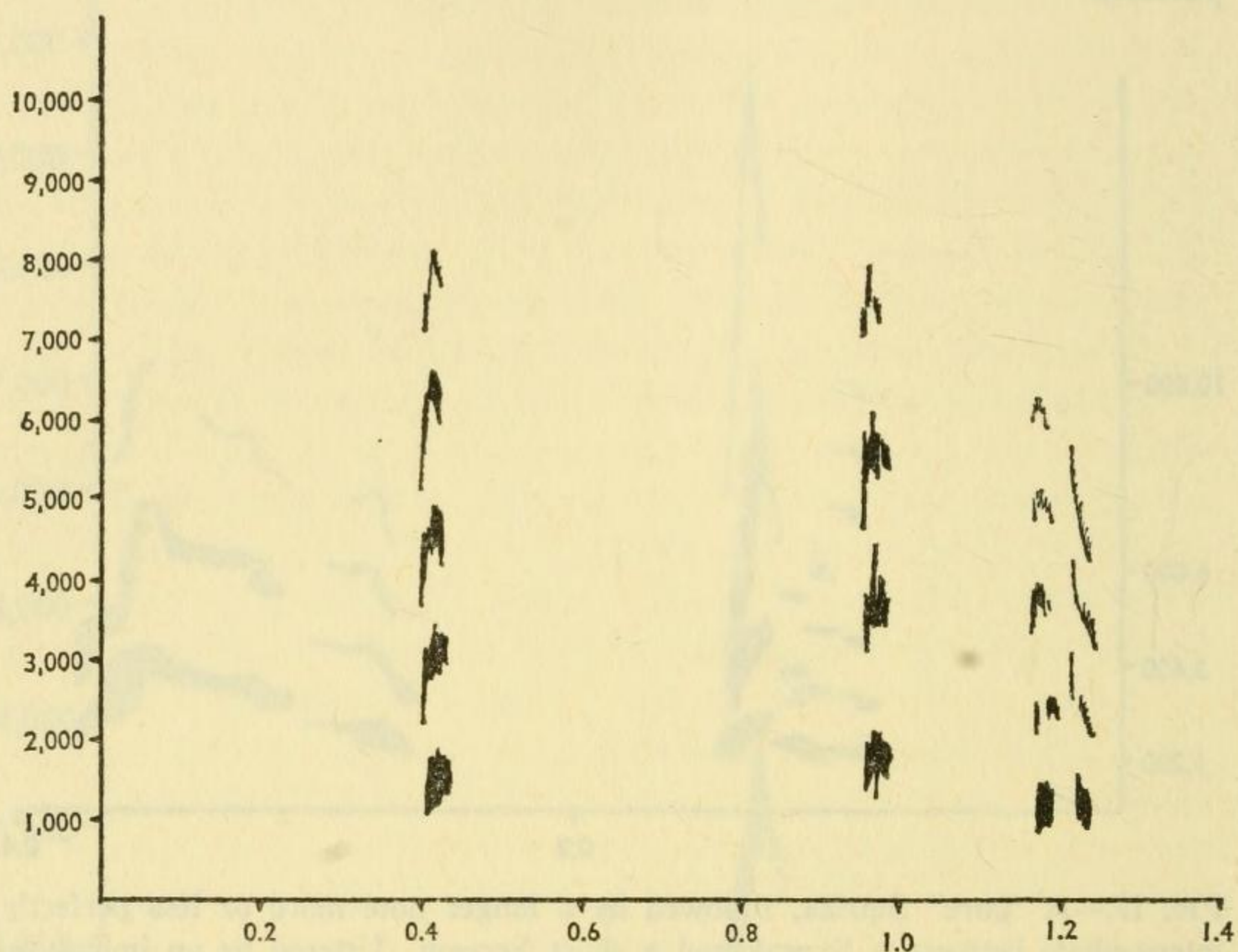


FIG. 18.—A series of four notes uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

This series sounded, to me, like one "pure" Squeak followed immediately by a short High Trill. As a whole, it is comparable to the series shown in figure 15, which sounded as if it were composed of four separate Squeaks.

Therefore, although most High Trills appear to be, or sound as if they were, accelerated series of several Squeaks, the same morphological effect might be produced by slowing down a single Squeak in such a way that the individual components within it become more distinct and widely separated from one another. Similarly, the effect of a short Scream could be produced either by slowing down and lengthening a single Squeak, while maintaining or strengthening the connections between its components, or by letting a series of several Squeaks "run together." In other words, many or most High Trills could be interpreted as discontinuous series of either Squeaks or components of Squeaks, while many or most short Screams could be

interpreted as continuous series of either Squeaks or components of Squeaks. (These relationships are difficult to describe or explain verbally, but I think that they will become clear if the accompanying drawings of sound spectrograms are studied in detail.)

In view of these facts, it is not surprising that the patterns intermediate between pure Squeaks and pure High Trills appear to be somewhat heterogeneous. Some intermediates are moderately rapid series of a few obviously distinct notes, apparently series of Squeaks which are not accelerated as much as the components of pure High Trills. Others are brief patterns which sound rather like single Squeaks with faint "rattling undertones." These may be Squeaks in which the internal components have become more distinct from one another than in typical pure Squeaks. The two intermediate types intergrade with one another. It is my impression, in fact, that the intergradation between pure Squeaks and pure High Trills is as complete as the intergradation between Squeaks and Screams.

Infant and juvenile Night Monkeys also utter many patterns that seem to be intermediate between Screams and High Trills. These are all more or less prolonged, discontinuous, and wavering. Figure 19 is a sketch of two patterns of this type (somewhat nearer to pure High Trills than to pure Screams). At least equally common are patterns that appear to be intermediate between High Trills, Screams, and Squeaks. These are similar to the intermediates between High Trills and Screams but shorter.

It is evident, therefore, that the patterns which have been called pure Squeaks, pure Screams, and pure High Trills in the preceding discussion are merely the extreme points of a continuum. This whole group of patterns may be called the "Squeak Complex."

It seems probable that all the vocal patterns of both adult and young Night Monkeys can be included in either this complex or the Grunt Complex.

The mouth is opened to a moderate extent during all or most notes of the Squeak Complex (see figure 22).

Infants raised apart from their natural parents utter Squeaks and intermediate notes closely similar to pure Squeaks very frequently whenever they are not clutching a foster parent or parent substitute (if they are not "distracted" by food or drink). A tame infant which has been silent while being carried by a human being will always begin to utter Squeaks (with or without other notes—see below) as soon as it is lifted away. It may also start to move in an obvious attempt to follow and rejoin the human being. Its Squeaks may become louder and more rapid if the human being then disappears from sight.

These facts would suggest that many or most of the Squeaks uttered by infants are produced when their tendency to keep in physical contact with a parent is thwarted.

This may not, however, be true of all their Squeaks. Infants clutching a foster parent or parent substitute may also utter Squeaks just before shifting the position of their limbs of their own accord, *i.e.*, before they can have lost contact. Once, an infant which had

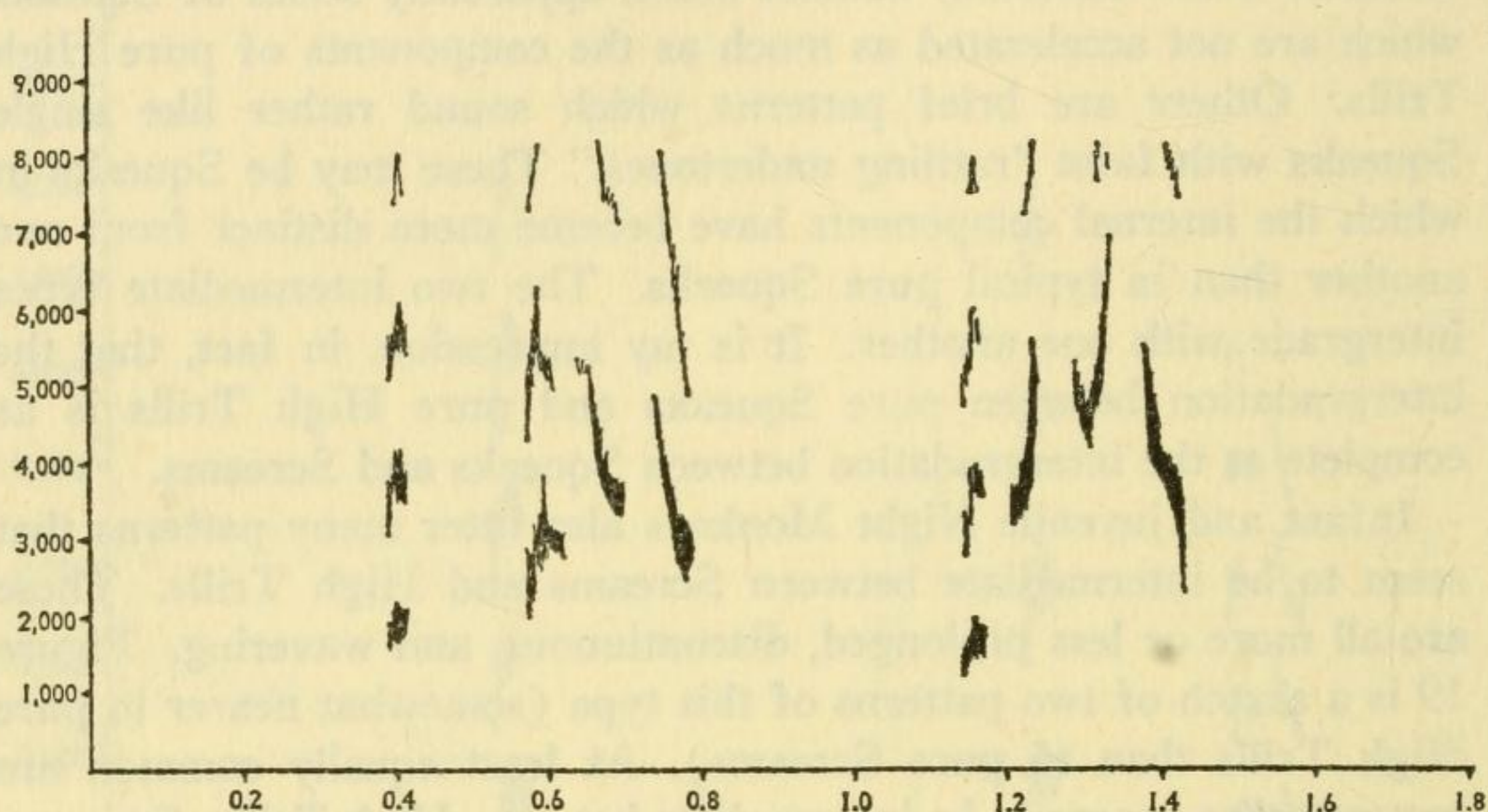


FIG. 19.—Two loud trilling patterns, intermediate between “pure” High Trills and Screams, but most similar to the former. Uttered by an immature.

Based upon a spectrogram by a “Sona-graph.”

Each trilling pattern is a series of four notes or groups of components. Each of these series seems to be similar to the series shown in figures 15 and 18, and to the components of the single Squeak and the intermediate between a Squeak and a Scream shown in figure 17.

Additional harmonics, up to at least 18,000 c.p.s., accompanied these trilling patterns, but are not shown in the drawing.

been quite silent while riding on my head suddenly began to utter Squeaks when rain began to fall, in spite of the fact that it continued to clutch me tightly.

Such incidents would suggest that infants may utter Squeaks whenever they become “uncomfortable” or feel “frustrated” in any one of several different ways. If so, their Squeaks can be considered a generalized distress reaction, strictly comparable to the “distress calls” of many young birds.

Of all the other platyrrhines I know, only infant tamarins of the genus *Saguinus* utter distress notes as frequently as infant Night Monkeys in similar circumstances.

Under natural conditions, it seems likely that the parents of an

infant Night Monkey would respond to its Squeaks by trying to make it more comfortable, *e.g.*, by helping it to readjust its position or by feeding it.

Unfortunately, this could not be checked by observation of the infants raised by their own parents in captivity. The parents of both infants seemed to be attentive and conscientious, and the infants were silent most of the time, presumably because they were seldom sufficiently uncomfortable or thwarted in the right way to induce vocalizations. I did hear them utter a few Squeaks, quite like those of the hand-reared infants. They uttered these notes in a variety of circumstances, *e.g.*, while moving around on a parent's back, while trying to suckle, and (once) after falling off a parent's back. In most cases, the infants stopped vocalizing almost immediately, before the parents reacted. They apparently managed to achieve satisfaction by their own efforts. The infant that fell was retrieved by a parent, but I could not determine if this parental act was a response to the infant's Squeaks and/or to the scrambling movements that it made at the same time.

The fact that high-pitched notes will not carry as far as low-pitched notes has already been mentioned. It seems highly probable that the Squeaks of infants, like those of adults, are primarily short-range signals. Under natural conditions, they are probably almost always uttered by infants at least fairly close to their parents.

It is my impression that the Squeaks of both adults and young are slightly "ventriloquial." In the dark, I found it difficult to tell exactly where Squeaks were coming from. Their source was more difficult to locate than that of any other vocal pattern of the species (with the possible exception of some High Trills).

These features may be particularly advantageous because individuals uttering Squeaks may be so intent upon the activity in which they are engaged, or so distressed, that they may become less alert than usual to outside stimuli and fail to note the approach of a possible predator.

Infants may utter Squeaks (and/or closely related short intermediate notes) singly or in unaccelerated series (*i.e.*, series that are not at all Trill-like) of up to seven or eight notes. Longer series presumably are produced by greater distress than shorter series. Series are frequently repeated with only brief intervening pauses.

Infants also utter many series of notes which include both brief Squeaks or Squeaklike notes and longer Screams or Screamlke notes. The arrangement of notes in such series is quite variable. One common arrangement is three or four long notes followed immediately

by two or (less frequently) three short notes. Another common arrangement is four or five short notes followed immediately by a single long note. Other and more or less intermediate arrangements also occur, but seem to be somewhat less common.

Infants may "settle" on one particular type of mixed series, and repeat it without variation in form for appreciable periods of time, even when there is reason to believe that the strength of their motivation should be changing slightly. They sometimes seem to become "stuck in the same groove." This would suggest that the utterance of one type of series may facilitate repeat performances of the same series, but does not facilitate, and may even discourage, subsequent performances of different types of mixed series composed of the same notes in different sequence.

Some of the Screams and intermediates between Screams and Squeaks uttered by infants may contain a hostile component like the Screams of adults. The infant born and hand raised in captivity on Barro Colorado Island uttered many Screams and related intermediate notes during the first few days after being taken from its parents, a period during which it also performed an appreciable number of overtly and unmistakably hostile reactions. Infants also tend to utter Screams when handled somewhat roughly. But other Screams and intermediate notes are almost certainly not hostile. It was very common, for instance, to hear a captive infant which had accepted human beings as foster parents utter many notes of this type in immediate association with both Squeaks and Hoots (see page 75) when left alone. These notes were not accompanied by any trace of overtly hostile movements or Gruff Grunts, and both the Squeaks and the Hoots were certainly provoked by the thwarting of the infant's desire to be with its foster parents. It seems likely, therefore, that at least many of the patterns intermediate between Squeaks and Screams are similar to the former in being generalized distress reactions. This, and the complete intergradation between the two extreme types of patterns, would suggest that the Screams of infants are little or nothing more than the highest intensity form of their Squeaks. (It would not, in fact, be necessary to give the patterns different names if they were not so distinct, in both form and causation, when uttered by adults).

The captive infants uttered High Trills when approaching their food dishes and feeding, and also when I lifted them up and brought their faces close to mine. This would suggest that their High Trills were produced by the same motivation as some or all of the Trills of

adults and/or by the same factors as their own Squeaks plus an added component of alarm or escape.

Some of the brief Squeaks or Squeaklike patterns of infants have a slight "gulping" quality. They may be the source from which the Gulps of adults are derived in the course of ontogeny; but they certainly are not distinctive or well segregated when uttered by infants.

Infants utter Hoots occasionally. To human ears, these sound very much like slightly softer versions of the usual Hoots of adults; but sound spectrograms indicate that they are sometimes (at least) also higher pitched and more broken up (see figure 20). They are usually

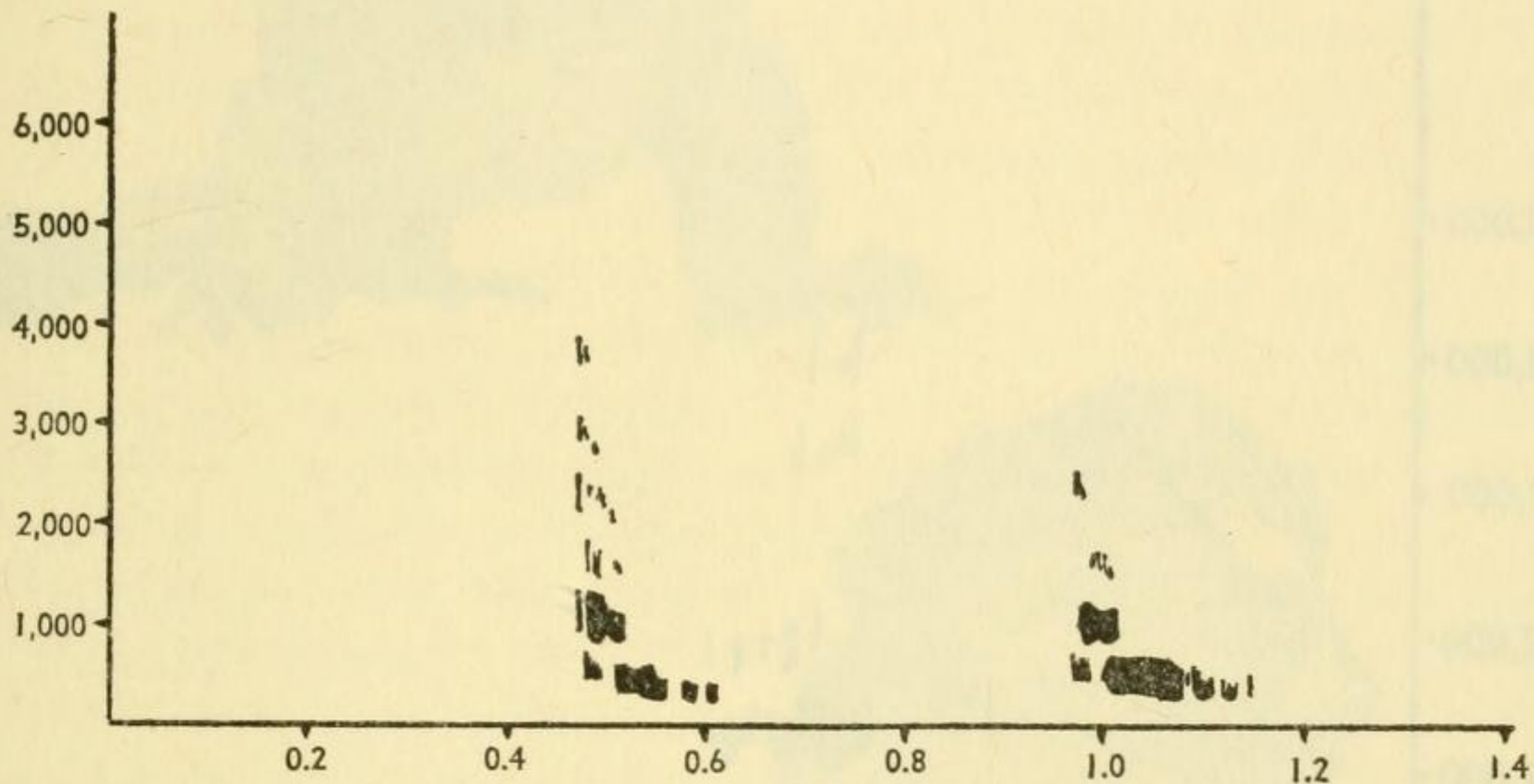


FIG. 20.—Two Hoots, uttered by an immature male.

Based upon a spectrogram by a "Sona-graph."

uttered in series of two or three notes, apparently always when an infant has become separated from its parents or parent substitute. Like adults, infants usually or always sit still while uttering Hoots. Their Hoots seem to be high-intensity patterns, produced when their desire to be with a parent is stronger, or more strongly thwarted, than when Squeaks or related intermediate notes are uttered. Thus, for instance, an infant suddenly separated from its foster parent or parent substitute may utter Hoots, intermediates between Squeaks and Screams, and more or less pure Squeaks at first, then stop uttering Hoots but continue the other notes, then stop the Screamlke notes but continue Squeaks, and finally fall silent, as it gradually becomes accustomed to being alone. Similarly, an infant accustomed to being carried almost steadily by a foster parent is apt to utter relatively more Hoots and fewer Squeaks than an infant used to being carried only occa-

sionally, when both are separated from their foster parents in similar circumstances and with the same degree of abruptness.

(It is interesting that the vocal patterns uttered by infants who want to attract or join their parents are similar to those of adults who want to attract or copulate with their mates. This might suggest that the sexual tendencies of adults develop from the infantile tendency to keep in contact with parents.)

The lowest intensity Hoots of infants (uttered toward the end of a period during which Hoots have become progressively less frequent)

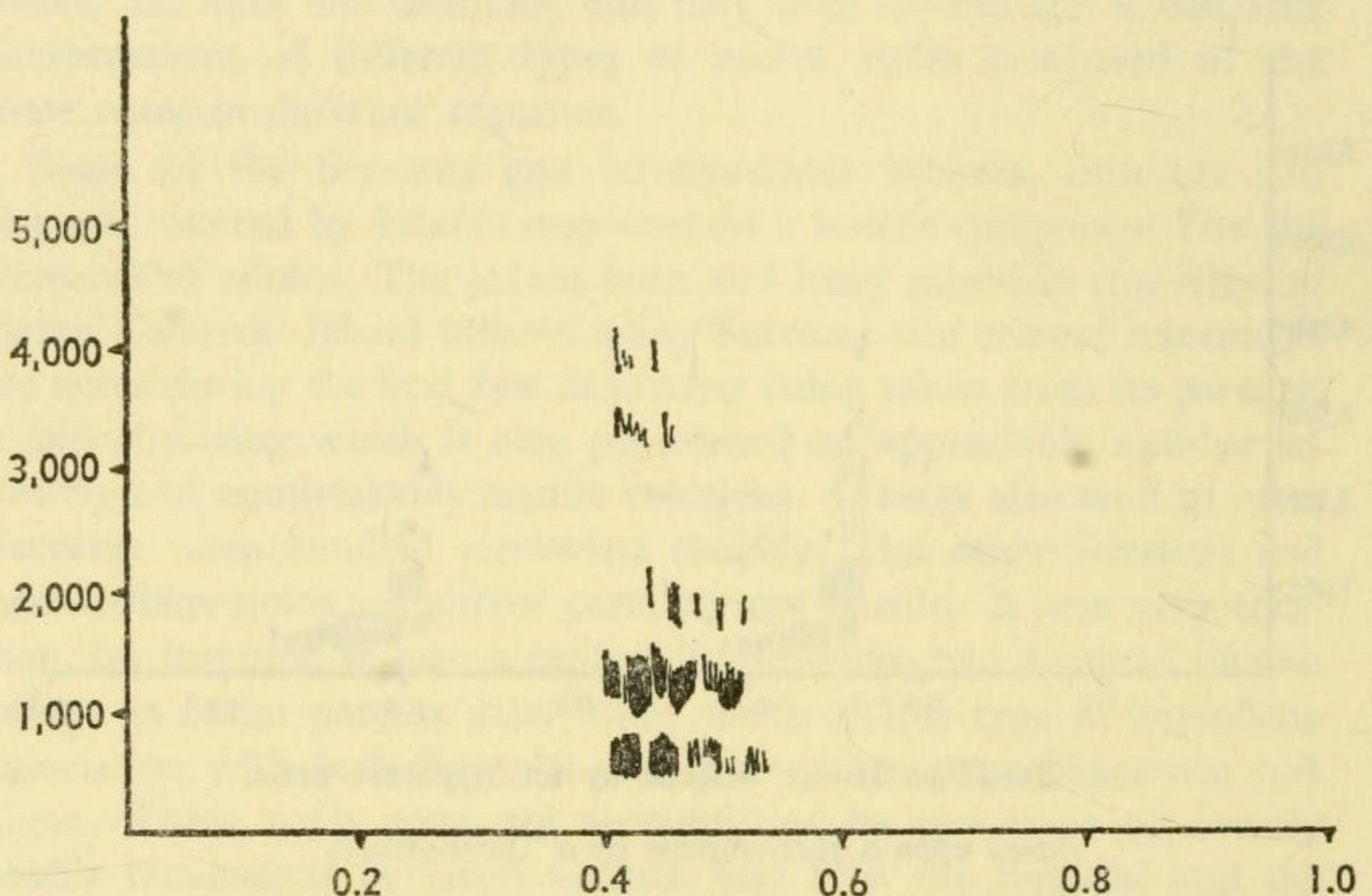


FIG. 21.—A single "Brrrrp" sound, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

This drawing does not show all the harmonics present.

are relatively very soft and somewhat reminiscent, to human ears, of the Moans of adults. The two types of patterns may be related ontogenetically.

The infant whose calls were recorded was heard to utter a few, rather low-pitched, rattling sounds (see figure 21). These sounds were relatively very rare, and were not heard to be uttered by other individuals. It seems probable that they were more or less "abnormal" variants of some more common pattern. They sounded, to me, as if they could be intermediate between High Trills and Gruff Grunts; but spectrograms suggest that they were related to Hoots. They may

have been incompletely formed Hoots, uttered without proper adjustment of the vocal apparatus.

That this sort of variation is possible is indicated by the behavior of howler monkeys. Male howlers usually utter lengthy roars at dawn.

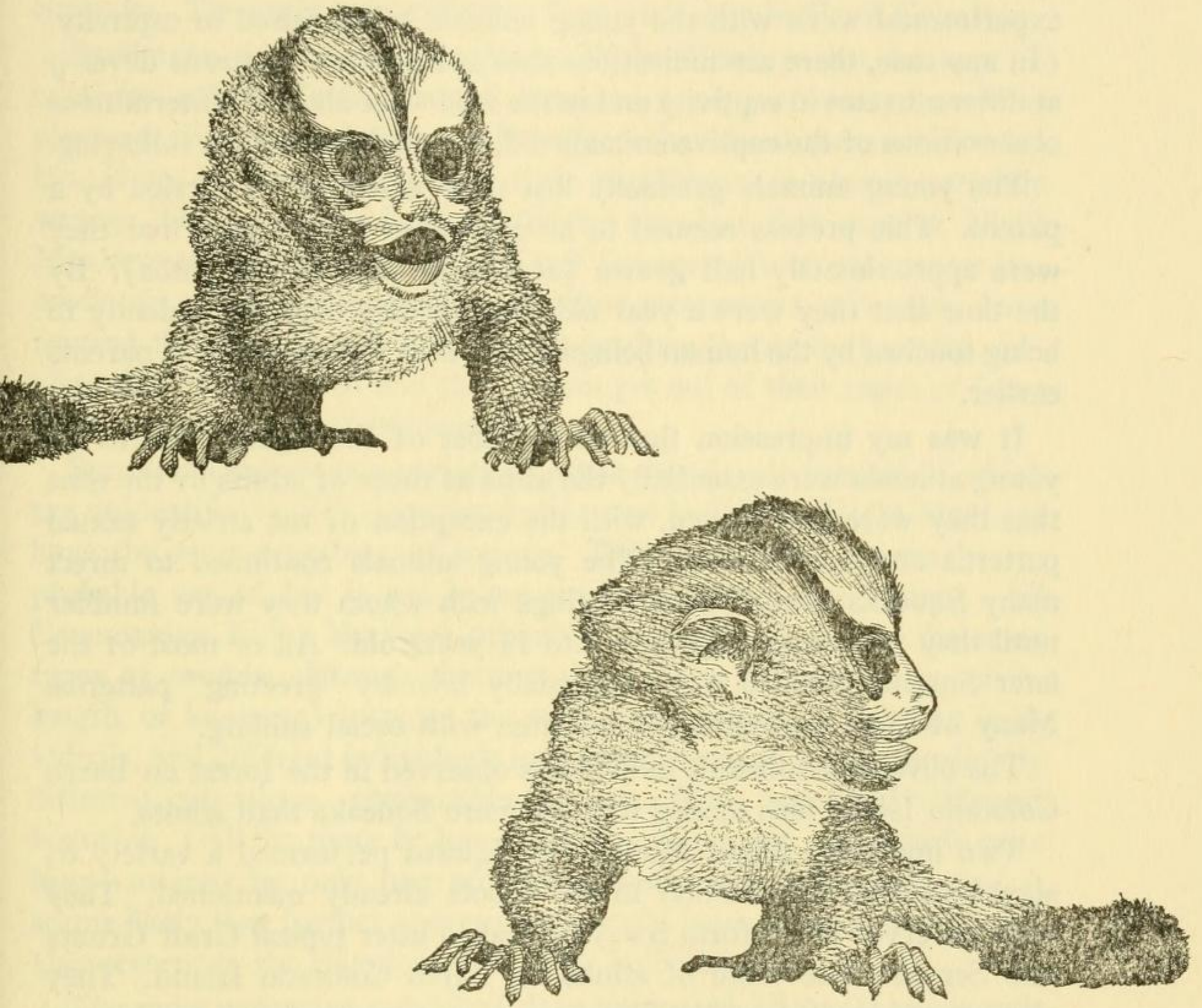


FIG. 22.—An infant uttering Squeaks.

This shows the characteristic shape of the mouth when opened most widely during vocalizations of the Squeak Complex.

When fully developed, each roar sounds absolutely continuous. But males of the species on Barro Colorado (*Alouatta palliata*) seem to take considerable time to “warm up,” and their first attempts to roar are apt to come out as wooden-sounding rattles (these may be the sounds that Altmann, *op. cit.*, describes as “pops”).

Infants utter Gruff Grunts which sound quite like the corresponding notes of adults and occur in similar hostile circumstances. They

also try to bite when handled, and perform other overt unritualized attack and escape patterns like those of adults as soon as they have developed adequate coordination of the limbs.

Changes in behavior between the infantile stage and maturity were not studied in detail, as it was not considered advisable to do much experimental work with the young animals being raised in captivity. (In any case, there are indications that at least some patterns develop at different rates in captivity and in the wild—see above.) Intermittent observations of the captive animals did, however, reveal the following.

The young animals gradually lost their desire to be carried by a parent. This process seemed to be completed by the time that they were approximately half grown (at the age of 6 or 7 months). By the time that they were a year old, they usually objected violently to being touched by the human beings whom they had regarded as parents earlier.

It was my impression that all or most of the signal patterns of young animals were essentially the same as those of adults by the time that they were half grown, with the exception of the strictly sexual patterns and the Squeaks. The young animals continued to direct many Squeaks toward human beings with whom they were familiar until they were approximately 1 to 1½ years old. All or most of the later Squeaks seemed to be essentially friendly "greeting" patterns. Many of them were closely associated with social sniffing.

The obviously subadult individuals observed in the forest on Barro Colorado Island also tended to utter more Squeaks than adults.

Two immature Night Monkeys at Iquitos performed a variety of signal patterns in addition to the Hoots already mentioned. They were observed to perform Swaying and to utter typical Gruff Grunts and Screams like those of adults on Barro Colorado Island. They also uttered many Squeaks like those of young animals of similar age (or stage of development) on Barro Colorado.

PREVIOUS DESCRIPTIONS OF NIGHT MONKEY BEHAVIOR PATTERNS

A number of signal patterns of Night Monkeys have been described, more or less briefly, in previous publications. Some of these descriptions have been cited above. It may be useful, however, to mention some others, try to identify and classify the described patterns according to the terminology used in this paper, and discuss some apparent discrepancies and problems.

Hill (1960) summarizes several accounts by earlier observers and quotes some of their transcriptions of vocal patterns. The notes variously transcribed as "oo-oo-oo," "bu-bu-bu," and "boom" may be the same as the notes I have called Hoots. The notes transcribed as "chip-chip-chip," "chui-chui," and "kweep-kweep" presumably are Squeaks. The notes transcribed as "urr-urr" may be Gruff Grunts.

Sanderson (*op. cit.*) says that a Night Monkey that he kept in captivity uttered "grrrrrrmph" notes as a sign of contentment or pleasure. His transcription would suggest that the notes were Grunts; but, if so, his interpretation of their significance is almost certainly wrong. He may have been misled by the fact that captive Night Monkeys sometimes utter many Gruff Grunts without extreme or immediately recognizable attack and escape movements, *after* they have learned that such movements do not produce the desired results, *i.e.*, after they have learned that they cannot get out of their cages or force their captors to retreat permanently.

Sanderson mentions a variety of other sounds, all or most of which are unidentifiable. He also says that no two individual Night Monkeys have the same repertory of sounds. This is not only extremely improbable *per se*, but is not borne out by my own observations. All Panamanian Night Monkeys probably utter almost exactly the same types of sounds, although there may be slight differences (in pitch, length, or loudness) between the equivalent sounds of different individuals, and different individuals may utter the same sounds in slightly different situations, presumably because they have had different histories. (All the more or less distinctive notes and calls which were heard uttered by only one individual were extremely rare; and it seems likely that further observations would have shown that they are also present in the repertories of other individuals.)

The most extensive published descriptions of Night Monkey calls are by Andrew (*op. cit.*). His account is based upon observations of two individuals in the laboratory. Unfortunately, he does not say where his animals came from or describe the conditions in which they were kept. As a result, it is difficult to interpret some of his findings.

All or most of the patterns that he calls "twitters" would seem to be varieties of what I have called Squeaks. So, in all probability, are the notes that he calls "guinea-pig squeaks." (It may be worth mentioning that none of the Squeaks or Squeaklike notes of the individuals kept on Barro Colorado appeared to have "traces of clicks" like those which Andrew describes as being superimposed upon twitters.) The patterns which Andrew calls "trills" may be "High Trills" according

to the terminology used here. (His account would suggest that the individuals that he studied were either young or adults which had retained juvenile characteristics.) The patterns which he calls "waver-ing squeaks," "sharp calls," and "booms" are not precisely identifiable, although the latter two (at least) would appear to belong to the Grunt Complex.

One further comment may be added. There may be some geographic variation in the form of some vocal patterns of Night Monkeys; but it seems unlikely that the differences between the patterns of different populations or subspecies are as great as might be inferred from some of the published accounts.

SUMMARY

This is the first in a series of papers on the social signals and some other behavior patterns of New World primates.

Night Monkeys are moderately small. Under natural conditions, they are purely arboreal and nocturnal. In Panama, at least, they are not very gregarious. They are seldom found in groups larger than a single family of two adults and one young, and even mated individuals may stray some distance apart from one another.

The hostile behavior of adult Night Monkeys includes unritualized attack and escape movements and a variety of ritualized displays. A few of these displays are special postures and movements, *i.e.*, visual signals, but the great majority are notes and calls, *i.e.*, auditory signals. The sexual behavior of adults includes olfactory and tactile signals in addition to unritualized patterns and a few auditory signals.

Some of the most distinctive features of this display behavior seem to be direct or indirect consequences of, or adaptations to, nocturnality.

Adult Night Monkeys have fewer visual displays than any other platyrrhines whose behavior has been studied. The few that they do have are relatively crude, produced by simple movements of the whole head and/or body. Some of their visual displays are less exaggerated in form than the homologous patterns of related species. They do not have any facial expressions, or erectile tufts or ruffs of hair around the face which could be used in signaling. It seems likely that they have lost, or failed to develop, an extensive and complex system of visual signals simply because they frequently cannot see one another clearly in the forest at night.

As partial compensation, they utter "contact notes" more frequently than other platyrrhines. These may help to maintain social cohesion between the adult members of a family group in the dark.

The whole vocal repertory of adult Night Monkeys is composed of discrete units, nine or ten distinctly different types of notes and calls. These patterns do not intergrade with one another to any appreciable extent. Intermediates between different types of notes and calls are comparatively (if not always actually) rare. Complex messages are given in the form of series of different notes or calls, each one of which contains part of the message, not in the form of a single intermediate or ambivalent note or call containing the whole message in itself. This type of vocal repertory is quite different from that of any other monkey whose behavior has been described. It is also quite different from the repertory of infant and young juvenile Night Monkeys. It may be an adaptation to ensure that vocal messages cannot be misinterpreted, even when they are not accompanied by any relevant nonvocal information. In many circumstances, adult Night Monkeys must have to react to, and rely upon, vocalizations alone.

There may be a general rule, among all monkeys, that species or classes of individuals that are largely dependent upon auditory signals for the regulation of their social behavior tend to have discrete, sharply delimited vocal patterns, while species or classes of individuals that are less dependent upon auditory signals tend to have intergrading vocal patterns.

Most vocal patterns of adult Night Monkeys are very low pitched. They are lower on the average than those of any related species of similar size. As low-pitched sounds should carry farther than high-pitched sounds, this may be another adaptation to ensure that vocal messages are as clear as possible. The only high-pitched vocal patterns of adult Night Monkeys are short-range signals.

Some peculiar negative features of the behavior of adult Night Monkeys may be correlated with their slight degree of gregariousness. Unlike adults of many related species, they seldom perform "Allogrooming" (the grooming of one individual by another) except in copulatory situations, or perform redirection attacks upon other individuals of their own species. They also seem to lack vocal patterns whose primary or only function is to warn other individuals of possible danger in the environment.

Other distinctive features of the species include: Care of the young by the male (this may be possible only because the sex ratio is one to one and pair-bonds are close and long sustained); comparatively frequent use of the hands during fighting (possibly because the canine teeth are small); the apparent absence of any tendency to

jump up and down and break off branches in rage (this may be correlated with the small size of the species); and the apparent absence of "displacement" scratching or grooming.

Most of the vocal patterns of infants are high pitched and completely intergrading. Infants may be able to afford such behavior because they are always in close contact with their parents. The effects of their vocalizations may be supplemented and reinforced by tactile and visual stimuli.

Some of the display patterns of Night Monkeys are particularly reminiscent of howler monkeys (*Alouatta*), titi monkeys (*Callicebus*), and/or tamarins (*Saguinus*).

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