

M. MOYNIHAN

*Some Behavior
Patterns of
Platyrrhine Monkeys
II. *Saguinus geoffroyi*
and Some Other Tamarins*

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ABSTRACT

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The Rufous-naped Tamarin, *Saguinus Geoffroyi*, is a rather small species of Panama and northern Colombia. It is diurnal, slightly gregarious, omnivorous (with a preference for insects), quadrupedal, and most characteristic of dense scrub and low forest in areas of medium humidity. It interacts with some other species in peculiar ways which may involve social mimicry. It has a few tactile and olfactory signals, a moderate number of vocalizations, and many kinds of visual signals, mostly displays. The communication systems of other members of the genus seem to be similar. They all include points of resemblance to both the Night Monkey, *Aotus*, and the marmosets, *Callithrix* and *Cebuella*. Some of the resemblances are difficult to interpret. The phylogenetic relationships among the three types, and between them and *Callicebus*, remain thoroughly obscure. There must have been considerable parallel or convergent evolution of either behavioral or morphological characters during the history of the group.

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M. Moynihan

Some Behavior Patterns of Platyrrhine Monkeys II. *Saguinus geoffroyi* and Some Other Tamarins

INTRODUCTION

The group of New World primates (or Platyrrhini) which is most frequently recognized as a distinct assemblage includes the genera *Callimico*, *Leontideus*, *Saguinus*, *Callithrix*, and *Cebuella*. (The genera accepted here, and their scientific names, follow Hershkovitz, 1958.)

Sometimes all the members of this group are called "marmosets." It is more convenient, however, to restrict this name to species of *Callithrix* and *Cebuella* and to refer to all the others as "tamarins."

Saguinus is the largest and most varied genus of tamarins. It also is the most widely distributed, ranging through a large part of warm tropical South America and a small part of Central America.

The only Central American form should be called *geoffroyi*, according to Hershkovitz (1949). It may be provisionally recognized as a distinct species. (Hershkovitz, 1966, relegates it to the status of a subspecies of *S. oedipus*. He does not, however, cite his evidence in favor of this arrangement. The two forms certainly are closely related, but they differ in some characters which may be of considerable biological significance. See also below.)

Saguinus geoffroyi does not have any generally recognized English vernacular name which is both

suitable and exclusive; i.e., which has not also been applied to other species. I would suggest, therefore, that it be called "the Rufous-naped Tamarin." This emphasizes the most conspicuous of its distinctive morphological features.

The social behavior of the Rufous-naped Tamarin is the principal subject of the following account. A few other forms of *Saguinus* will be discussed very briefly, and some behavior patterns of the genus will be compared with those of other New World primates, especially other types of tamarins, marmosets, the Night Monkey (*Aotus trivirgatus*), and titi monkeys (*Callicebus moloch* and *C. torquatus*). All references to the last two genera are based upon Moynihan (1964 and 1966). All references to other Platyrrhini are based upon personal observation (summarized in Moynihan, 1967) unless specifically stated otherwise.

SAGUINUS GEOFFROYI

This is a rather small monkey (medium sized for a tamarin). Individuals of both sexes have the same color pattern, which is quite complex (see the accompanying illustrations). The face is largely bare (more so in adults than in young) and dark gray in color, but there are stripes of white hair on the cheeks and the sides of the nose or snout. There also is a triangular patch or "blaze" of white on the forehead and front of the crown, and the sides of the bare face are framed by another pair of whitish stripes (passing behind the

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FIGURE 1.—A typical leaping posture of an adult Rufous-naped Tamarin, with Tail-ruffling.

naked black ears). The rear part of the head and the nape are chestnut or rufous red. The upper part of the body is largely brindled black and grayish-yellow (the precise arrangement of black and yellow differs considerably in different individuals). The underparts and most of the arms and legs are white, sometimes tinged with yellowish-orange on the breast and belly (see also page 21). The proximal part of the tail is deep rufous, and the distal part is black (with a white tip in all or most infants and young juveniles).

As a whole, this pattern is conspicuous in some circumstances and "disruptive" in others.

The species ranges from the Chocó region of northern Colombia to at least central Panama.

In Panama, it seems to be most characteristic of regions of moderate humidity. The Pacific side of the isthmus is generally less humid than the Atlantic side. Rufous-naped Tamarins are abundant in some parts of the Pacific coastal region, and also occur in some central areas approximately equidistant from both coasts. To my knowledge, however, they are completely absent from the whole of the Atlantic coast of the isthmus, except for one small, highly modified or "unnatural" area (see below).

They also are most common in forest and scrub which are dense but not very tall. They do not seem to flourish in either high rain forest or mature humid seasonal ("monsoon") forest with little understory vegetation.

This may be illustrated by the history of the species on Barro Colorado Island. The island is located in Gatun Lake, in the center of the Canal Zone in central Panama, and has a rather humid climate. Nevertheless, tamarins were abundant there in the 1920s and early 1930s (Chapman, 1929, and Enders, 1935), when much of the island was covered with obviously young second-growth forest. Since then, the forest has been allowed to grow up, and large parts of it seem to be approaching maturity, becoming typical monsoon forest (Bennett, 1963). During the same period, with the gradual change in the vegetation, the tamarins have become increasingly rare.

The one area on the Atlantic coast where tamarins are definitely known to occur is the Atlantic side of the Canal Zone and adjacent parts of the Republic of Panama, where all or most of the original forest has been destroyed by human activities and replaced by second growth. In all probability, the tamarins have invaded this area only recently.

It is conceivable that some aspects of the ecology of the species are different in Colombia. Much of the Chocó region is very humid indeed. Unfortunately, however, it is not known if the tamarins occur throughout the region as a whole or only in particular, restricted, and possibly drier, areas within it.

During the course of the present study, I observed a substantial number (at least 125) wild Rufous-naped Tamarins living in more or less natural conditions.¹

Most of my observations were made in three different areas of the isthmus of Panama: (1) Ancon Hill, an "enclave" between the towns of Balboa and Ancon, on the Pacific coast, east of the canal; (2) near several roads (currently called K-6 and K-9), and in the adjacent Rodman Naval Station, on the Pacific coast, west of the canal; and (3) in the Canal Zone Forest Reserve, in the center of the isthmus approximately 10 miles north of Balboa. Most of Ancon Hill is covered by dense vegetation which could be described either as tall scrub or low forest. Some of this may be mature. It may be prevented from growing higher by edaphic factors (the rocky soil and steep slopes of the hill). The area on the west side of the canal includes

¹ Obviously, no conditions in Panama or adjacent regions at the present time are really completely natural. Man's influence has been exerted everywhere, in some form or another, for thousands of years. But the term "natural conditions" is useful, and will be used in this paper, as a general label for environments and situations in which man and his artifacts are not overwhelmingly evident at all times.

a variety of different types of young second-growth forest and scrub. Most of the Reserve is composed of somewhat older second-growth forest.

Briefer observations of a few wild individuals were made on Barro Colorado Island, on the Atlantic side of the Canal Zone, and in the lower hill forest of Cerro Campana approximately 30 miles west of the Canal Zone.

I also studied some 35 individuals kept in captivity. These animals were housed in a variety of cages and pens of different sizes and shapes on Barro Colorado Island. (The pens were outside in the forest. They were made of wire netting, and roofed with the same material. The animals in the pens were given food, but left exposed to the external climate. They did very well in these circumstances, and some of them bred. This would suggest that the recent decrease of the wild tamarin population on the island may have been due to increasing scarcity of suitable food in the maturing forest.)

Both wild and captive individuals were observed intermittently, at very irregular intervals, between August 1958 and August 1967.

Habitus

Rufous-naped Tamarins are essentially arboreal insofar as they almost always prefer to remain in trees or large bushes. They do come down to the ground occasionally, but apparently only in special circumstances; e.g., in order to get certain special foods, such as the fruits of *Cardulovica palmata* (C. M. Hladik, personal communication) or when they cannot pass from one bush or tree to another by any other means. In forest, they move through a wide range of heights above ground. In areas such as the Forest Reserve, they are most frequently seen between 10 and 40 feet above ground. They may go much higher in certain other environments. They usually move and feed near the edges of forest and scrub; and they seem to like the vicinity of the upper edges, the top of the forest, at least as well as areas near the lateral borders. Thus, the relatively few individuals inhabiting very tall forests, such as the remnant on Barro Colorado, frequently range as high as 60-75 feet above ground.

It should be stressed that this preference for the vicinity of edge is not quite the same thing as a preference for edge itself. Rufous-naped Tamarins ob-

viously try to remain several inches, or even feet, *inside* the outermost or uppermost limits of the edge. This habit may be protective, an adaptation to reduce vulnerability to aerial predators. (I have never seen tamarins actually preyed upon. And the only reliable record of apparent predation is an observation by N. G. Smith, personal communication, who saw a Tayra, *Eira barbara*, carrying a dead tamarin in its mouth. M. H. Robinson, personal communication, has observed extreme alarm reactions to snakes by captive tamarins. But it is obvious that these monkeys are at least as frightened of most birds of prey. In my experience, they keep a weather eye out for possible aerial predators much more consistently than for any other kind of danger. And their reactions to the actual appearance of a hawk usually are quite unmistakable. See page 10.)

Under natural conditions, they move along a great variety of tree trunks and branches of very diverse sizes. They also show a strong preference for dense "tangles" of vines or lianas. They usually avoid palms and other large monocotyledons such as *Heliconia* and related genera (except when they are searching for a few special foods and/or the leaves of a monocotyledon provide the only convenient "bridge" between other trees or bushes which are particularly favored).

They are almost completely quadrupedal. They only stand up on their legs (hind limbs) very occasionally, during certain disputes (see page 39) or to get a better view of some distant animal or object. They usually run on the ground and on branches in much the same way as squirrels. But they tend to leap from branch to branch somewhat more frequently than do the squirrels which occur in the same habitats, and their leaps seem to be somewhat longer on the average (see also Figure 1). Their tails are not really or fully prehensile. In locomotion, they are used only as balancing "counterweights" or signaling organs (see page 45 et seq.). When an individual sits or stands, however, it may "drape" its tail over an adjacent branch; and this may enhance the stability of its position or posture.

The diet of the species is being studied by C. M. Hladik at the present time. All I can say, here, is that it seems to be broad and varied. Captive individuals show a definite preference for insects, which they hunt, catch, and eat very efficiently. Some of their searching and catching methods are described by M. H. Robin-

son (in press). They also catch and devour small lizards of the genera *Anolis* and *Mabuya* (Robinson, personal communication), and will eat freshly killed bats and small birds. Wild individuals obviously search for and try to catch insects, but apparently they are frequently unsuccessful. During my own observations, most of the foods seen to be taken were vegetable, including a wide assortment of fruits and buds. Insects probably are less abundant, or less immediately available, than fruits and buds in many of the environments inhabited by the species, at least at certain times of the day or periods of the year. Nevertheless, it is quite possible, even probable, that an appreciable amount of animal food is absolutely essential to the tamarins. If so, this may help to explain some aspects of their choice of habitats, periods of activity, and social behavior (see pages 7 and 8).

They seem to be completely diurnal. Captive individuals always spend the night in boxes or holes in tree trunks, whenever these are available. It seems very probable that wild individuals also sleep in holes in trees at night. I have never seen them actually enter or leave such holes; but many individuals were seen to move toward tall trees which were known to have suitable holes in the late afternoon or evening, and then reappear in the same places in the morning.

Their activity rhythm during the day is highly distinctive. Unlike the other diurnal monkeys with which I am familiar, and most other diurnal mammals and birds in the same habitats, these tamarins do *not* become active at, or very shortly after, dawn. In the wild, they are never seen moving around until at least a quarter of an hour after it has become fully light. In most cases, they apparently do not get up until approximately three quarters of an hour, or more, after full light. (This habit may be advantageous for several reasons—see also below. But it is so remarkable that one wonders if the animals do not become torpid or semitorpid at night.) After arising, they remain quite active throughout most of the rest of the day. They may rest briefly in the middle of the morning. But, (again) unlike most other diurnal tropical mammals and birds, they usually show little or no tendency to slow down or take a "siesta" at noon or during the first part of the afternoon, when the heat is greatest. It is only approximately an hour or half hour before sunset that they gradually stop feeding and drift off in the general direction of their sleeping trees.

Social Organization and Territories

My observations of the social organization of Rufous-naped Tamarins in the wild were restricted in several ways. No attempt was made to follow individuals or groups continuously for long periods of time, simply because much of the vegetation in most of the areas inhabited by the species is too dense to permit quiet movement by a human observer. Instead, I repeatedly returned to particular places, more or less open paths and clearings (cleared long before this study began), and observed the animals whenever they appeared and as long as they remained in view. In some areas, where there was a fairly extensive network of paths and clearings, it was possible to obtain a rather detailed impression of many of the social activities of the animals throughout the day.

None of the individuals observed in the wild was collected, as it was considered undesirable to alarm other animals in the neighborhood. Nor were any wild individuals marked artificially. Thus, it often was impossible to identify adults personally, especially when all the members of a group were not visible simultaneously, or even to be sure of the sexes of particular animals. (There is little or no sexual dimorphism in size; and the sex organs are not distinguishable at a distance.) But infants and juveniles usually could be identified by their relative sizes, and some adults could be recognized by certain distinctive morphological characters (e.g., variant color patterns) and/or some consistent peculiarity behavior.

Rufous-naped Tamarins tend to be more gregarious than Night Monkeys, insofar as they may form "bands" which include more than a single adult pair with their young of the year. Some of these bands also are larger than the family groups which seem to be the typical "basic" social units of most *Callicebus moloch* observed in the wild (Mason, 1966).

Nevertheless, there is considerable variation in the actual size of *geoffroyi* groups. At one extreme, it is not uncommon to see apparently single individuals. At the other extreme, I have seen groups which included six or more individuals.

This may be illustrated by the figures in Table 1. They show the sizes of 28 social units (groups and apparently single individuals) observed under particularly favorable conditions in all the environments in which the species was studied.

TABLE 1.—*Social Units of Saguinus geoffroyi in the Wild*

<i>Number of Individuals per Unit</i>	<i>Number of Units Seen</i>
1	5
2	6
3	5
4	5
5	2
6	4
9	1

The total number of units counted was 28. The total number of individuals counted was 95. The average number of individuals per unit was 3.39.

All the single individuals seen were apparently adult. All the groups of two also were composed of adults, presumably mates in all or most cases. Some groups of three included one individual which was obviously young. And all the larger groups included one or more young.

Most Rufous-naped Tamarin social units seem to be quite stable. Groups of the same size, sometimes including identifiable individuals, can be seen in the same areas day after day for months on end. Naturally, some individuals disappear from time to time, and appreciable numbers of young are born each breeding season. But most of these changes are "accommodated" with minimal disturbance of the pre-existing social structure. I saw only one case of a "permanent" merger between two groups which had appeared to be distinct earlier, and no cases of permanent splitting of a large group.

Infants usually are carried by a parent, and young juveniles either are carried by or remain close to a parent (see also page 61). Adults and older juvenile members of a band sometimes stray 500 feet or more from (well out of sight of) the nearest other member of the band—or get left far behind when the rest of the group moves on—but this is not particularly common. Usually the adults and older juveniles are only 3–30 yards apart. And even the individuals which become most widely separated usually rejoin their companions, or are rejoined, within minutes rather than hours.

In view of the occasional variations which do occur, it may be useful to explain how the figures in Table 1 were derived. All the social units recorded in this table were observed for at least one-half hour. Most were observed repeatedly for at least several hours on different days. In a few cases, what was largely the

same unit was recorded twice. This occurred when there was a definite change in the composition of a group, an apparently permanent subtraction or addition of one or more individuals. In these cases, the unit was counted and recorded once before the change and once afterward. But none of these counts was made during the time of year when most of the young are born, when fluctuations in numbers are most frequent (see page 13).

It should also be noted that these counts probably do not convey a perfectly accurate picture of the "normal" population structure of the species under completely "normal" conditions. Possibly, I overlooked one or more individuals in some counts of the larger groups. More important, Rufous-naped Tamarins are hunted intensively in many areas, such as some of those west of the canal, and this certainly must affect the average size of groups.

Thus, it seems likely that the population of *geoffroyi* in central Panama has been affected in two different and partly contradictory ways by human settlement and activities. The cutting of mature forest, followed by shifting agricultural activities and the subsequent spread of second growth, probably has increased the area of habitats suitable for tamarins. But hunting probably has reduced the density of tamarin populations in all or most of the most favorable localities.

Chapman (op. cit.) states that *geoffroyi* individuals occur in groups as large as 12 or more. Various inhabitants of the Canal Zone have reported seeing equally large groups in recent years. I think, however, that many or all of these recent records must be gross over-estimates.

Apart from some parent-young relations, there usually are very few overt, conspicuous, indications of special personal connections among the members of a large band in the wild. Certainly, none of the groups observed was found to have a definite "leader," consistently controlling or initiating group movements. But the appearance of general social homogeneity probably is misleading. More precise and detailed studies probably would reveal that some individuals are dominant over others and/or usually are more friendly to some fellow members of the group than to others. There certainly were some dominant-subordinate relationships among the tamarins kept in captivity. Even more important, the captive individuals tended to form definite pair bonds. When several males and females were kept together, each individual tended to select an individual

of the opposite sex as its "mate." Mates tended to associate more closely with one another than with the other individuals in the same cage, to perform all or most of their copulatory behavior together, and to fight with one another less frequently than with other individuals (see also below). Some of the pair bonds between captives were not only strong but long sustained, enduring for at least four years (as long as my observations continued in any given case). Of course, it seems overwhelmingly probable that the groups of only two adults (alone or with young) observed in the wild also were pairs of mates. Perhaps the members of larger groups in the wild are equally likely to form semipermanent sexual attachments among themselves. If so, their pair bonds may not be conspicuous, to a human observer, simply because mates do not stick particularly close together during the daily search for food. (I might add that I never saw copulations in the wild; i.e., I did not see the reactions which should reveal the existence of pair bonds most clearly.)

Each band of tamarins (and probably each individual living by itself alone) has its own "home range." These ranges may also be considered territories. They are defended, although usually in a rather peculiar way (see page 23). As would be expected, in view of the usual structure of social units, they tend to be quite stable for long periods of time. They also are quite large on the average. They are very diverse in shape, presumably in correlation with variations in topography and vegetation; but many of them extend for more than a quarter of a mile along their longest dimension.

These ranges are comparable in size to those of families or bands of other species of Platyrrhini in central Panama, such as the Night Monkey, the capuchin, *Cebus capucinus* (J. R. Oppenheimer, personal communication), and the howler, *Alouatta palliata*—or *A. villosa*—(Carpenter, 1934). They are very much larger than the ranges of *Callicebus moloch* families in Colombia (Mason, op. cit.).

Rufous-naped Tamarins always or almost always move through a large part of their ranges every day. They may even cover the whole of their ranges several times during the course of a single day. In this extreme mobility and speed of progression, they resemble both *Cebus capucinus* and (probably) *Aotus*, but differ greatly from *Alouatta*. Bands of howlers usually move through only a small part of their ranges each day (Carpenter, op. cit.). *Callicebus moloch* groups also cover all or most of their ranges each day; but their

ranges are so small that their travels usually are comparatively slow, and their degree of mobility is much more like that of *Alouatta* than like that of *S. geoffroyi* or *C. capucinus*.

These differences probably are correlated with, causally related to, differences in feeding ecology. *Alouatta* seems to be as nearly completely vegetarian as any primate known, and *Callicebus moloch* is hardly less so (Mason, op. cit.). These species apparently can find sufficient vegetable food, at least on any given day, in comparatively small areas. But the other species may have to move over large areas repeatedly and rapidly in order to obtain the insects and other animal foods that probably are essential to them.

There is very little overlapping of ranges among Rufous-naped Tamarins. Only very rarely will individuals trespass a few feet or yards into the normal ranges of others. And most trespassing seems to occur when the owners of the areas intruded upon are far way, at the opposite ends of their territories, at the time. In this respect also, the tamarins resemble the *Cebus capucinus*, *Callicebus moloch*, and (probably) *Aotus*; and differ from *Alouatta*. (Overlaps of ranges are relatively frequent among bands of howlers in Panama. This presumably is an inevitable consequence of the combination of large ranges with slow movements of individuals through the ranges.)

Tamarins whose ranges border on areas not occupied by other individuals of the same species (probably, in most cases, areas which are usually unfavorable at most times of the year) may make long "excursions" in exceptional circumstances. Thus, for instance, there usually are no tamarins in the gardens of the town of Balboa. But these gardens sometimes are invaded by tamarins who come to feed on mangoes when the fruit is ripe. The invaders obviously have descended from Ancon Hill. They probably are able to enter the gardens because there is no resident population of their own species to bar their way.

Such exceptional behavior indicates that Rufous-naped Tamarins are "opportunistic." Some individuals of the species probably are constantly "probing" new areas to determine if they are both available and suitable for occupancy.

Relations with Other Species

Many other species of vertebrates feed on the same fruits and buds as *S. geoffroyi* and search for and

catch insects in the same places. Some of the same species, and many others, also compete with *geoffroyi* for other features of the environments; e.g., branches to move along, holes to sleep or nest in, shelters from heavy rain, and lookout posts.² As would be expected, therefore, the social, ecological, geographical, and temporal relations and interactions among the tamarins and some of the other species are complex and/or highly specialized.

The other primates which occur in Panama are *Alouatta palliata* (or *villosa*), *Ateles "geoffroyi" panamensis*, *Ateles "fusciceps" robustus*, *Cebus capucinus*, *Saimiri "oerstedii"*, and *Aotus trivirgatus*.³

Alouatta, *Ateles*, and *Cebus* are (or were at one time) widespread in Panama. They also are diurnal. But they are all much larger than *S. geoffroyi*, and largely or completely inhabitants of tall forest. *C. capucinus*, the smallest and least vegetarian of these large forms, is the only one which might compete with the tamarins to any appreciable extent. But I have never seen any overt behavioral interactions between the two species, or even observed them in the same area at the same time. And *S. geoffroyi* is so rare in the areas where *capucinus* is common that one cannot be sure that the usual lack of contact between them is not purely accidental.

² The terms "compete" and "competition" are used in a very broad or probabilistic sense in this paper. Two animals will be said to compete with one another when one occupies or uses a resource which otherwise would be available to the other. It is assumed that the second animal would be in a position to utilize the resource if it were not already preempted by the first. This assumption seems very highly probable in all the examples cited, but I have no conclusive evidence to prove it in any given case. It also is assumed, and seems to be equally probable, that the resource being used or occupied is actually or potentially in short supply and/or that some examples of the resource are more "favorable" or "advantageous" than others. (This latter statement may be clarified by an example. There obviously are many lookout posts in any given patch of forest, but some are much better placed; e.g., give better views of possible sources of food and/or danger, than are others. An individual occupying a better placed post presumably has a significant advantage over an individual occupying a less well placed post.)

³ As noted in Moynihan (1967), all the forms of *Ateles s.s.* may be conspecific. Certainly, *A. "geoffroyi" panamensis* and *A. "fusciceps" robustus* hybridize in Panama (or did hybridize until a very few years ago, before their populations were greatly reduced by hunting). It also is possible that *Saimiri "oerstedii"* is only a well-marked subspecies of *S. sciureus*.

(C. M. Hladik [personal communication] saw individuals of the two species close together once. The tamarins were uttering Loud Sharp Notes—see below—and performing other alarm reactions. These behavior patterns appeared to be directed toward the *capucinus*.)

Possible relations between Rufous-naped Tamarins and Squirrel Monkeys of the genus *Saimiri* are even more problematical. It is not definitely known that they ever come into actual contact with one another. Squirrel Monkeys have been observed and collected in many areas of the province of Chiriquí, the westernmost of the Pacific coastal provinces of Panama, approximately 250–300 miles west of the Canal Zone (see, for instance, Goldman, 1920). They certainly are still abundant in some parts of the province (personal observation). To my knowledge, there are no published records of the species east of Chiriquí in the isthmian region. As noted above, Rufous-naped Tamarins certainly occur in the eastern half of the Pacific side of Panama, from the Colombian border to Cerro Campana, approximately 30 miles west of the Canal Zone. They are abundant in many areas at least as far west as the Zone. On Cerro Campana, they have been seen only around 1000–1500 feet elevation. These facts are well established. They do not, in themselves, indicate sympatry between the two species. But there are other data which tend to confuse the issue. There is one recent and reliable sight record of a small band of Squirrel Monkeys at 3000 feet elevation on Cerro Campana (F. A. McKittrick and N. G. Smith, personal communication). There is a nineteenth-century record of a Rufous-naped Tamarin from Chiriquí (Alston, 1879). This was questioned by Goldman (op. cit.), who noted that there had been no further records of the species from this province up to his own time. But Carpenter (1935) says that the species occurs in the Coto region of Chiriquí, although “very scarce” there. He does not, however, expressly state that he saw any individuals himself. Two brief visits by members of the staff of the Smithsonian Tropical Research Institute to the Burrica Peninsula, the countryside around Puerto Armuelles, and coastal areas south of David, all in Chiriquí, in February and July of 1967, failed to reveal any tamarins. Many other visits by some of the same and other scientists to Pacific side areas between Cerro Campana and Chiriquí have not produced any records of either species.

Thus, even if the two species are not completely

allopatric, they are nowhere both abundant in the same area. It seems very likely, in fact, that they definitely tend to exclude one another. They are at least potentially strong competitors. Squirrel Monkeys are comparatively small, only slightly larger than *S. geoffroyi*, and apparently completely diurnal. In Panama, they also are primarily animals of second growth and forest edge. They certainly feed on vegetable matter, and search for insects, in much the same way as tamarins. The only obvious ecological difference between the two species in Panama is that all or most of the areas inhabited by Squirrel Monkeys are usually more humid than most of the areas inhabited by tamarins. It probably would not be too much of an oversimplification to say that Squirrel Monkeys fill the “Rufous-naped Tamarin niche” in wet forest edge and second growth in Panama, while Rufous-naped Tamarins fill the “Squirrel Monkey niche” in most slightly drier areas of superficially similar vegetation. Either species would be expected to extend its range if the other became extinct.

Aotus certainly is broadly sympatric with *S. geoffroyi*. It occurs throughout most of Panama, in both tall forest and at least some of the second-growth areas inhabited by tamarins. Like *Saimiri*, it is only slightly larger than *S. geoffroyi*. It eats some of the same types of fruits and buds, and possibly some of the same species of insects. It even sleeps in holes in trees. It is, however, completely “separated” from the tamarins in being completely nocturnal (and crepuscular) under natural conditions.

Probably equally or more important to the tamarins are many species of birds, especially flycatchers of the family Tyrannidae. These are all diurnal. Many of them are sympatric with tamarins in Panama, and have overlapping feeding habits. They also eat the same berries and fruits, and catch insects in many of the same places (although usually not with the same techniques).

Some of the sounds uttered by some of the flycatchers, e.g., *Myiozetetes* spp., *Tyrannulus elatus*, *Legatus leucophaeus*, *Elaenia flavogaster*, and *Megarynchus pitangua*, are similar to certain tamarin sounds, i.e., Trills and Long Whistles (see below), in form and pitch or tone, and possibly even motivation and function in some cases. (All names of birds cited throughout this paper follow Eisenmann, 1955.) As noted in Moynihan (1968a), it is possible, even probable, that some of these resemblances among fly-

catchers and tamarins are examples of "social mimicry." The tamarins may recognize areas that are favorable; i.e., in which food is abundant, simply because they hear many flycatcher sounds, similar to their own, coming from them.

It probably is significant, therefore, that the flycatchers also are partly separated from the tamarins by differences in timing.

Like most other diurnal birds (see above), the flycatchers are most active during the first hour or so after dawn, and tend to slow down during the middle of the day—in contrast to the tamarins which get up later in the morning, but remain active almost continuously afterwards. Both flycatchers and tamarins probably feed most frequently during their periods of greatest general activity. Thus, the tamarins probably do not compete with the flycatchers for food during most of the period when the birds are feeding most intensively, but they do feed frequently at the time when the birds are resting.

This distinction may be exaggerated by another factor. Data collected by C. M. Hladik (personal communication) suggest that tamarins may eat relatively more fruit in the morning (presumably they are most hungry then, and take everything that comes to hand) and relatively more insects in the afternoon (when they may be more discriminating). If the flycatchers take as many insects, per unit time period, in the morning as in the afternoon—as seems quite possible—this might tend to reduce interspecific competition for the most nourishing (protein) foods even further.

The flycatchers also vocalize most frequently early in the morning before the tamarins get up. This may facilitate intraspecific communication. Simply because some of the sounds of tamarins and flycatchers are so similar, they might tend to get their signals confused if they were all vocalizing with maximum frequency simultaneously. But this possible difficulty also is avoided or reduced by the different activity rhythms of the different species.

(These contrasts should not be interpreted as evidence against the existence of mimicry. Although flycatchers vocalize less frequently during the middle of the day than at dawn, they continue to be noisy enough at all times to permit the tamarins to notice them and to assess the suitability of different areas by the comparative frequency of flycatcher sounds coming from them.)

The fact that *S. Geoffroyi* is more or less effectively

separated from most of the principal competitors with which it is broadly (or frequently) sympatric, i.e., both *Aotus* and the flycatchers, in essentially the same way, i.e., by differential timing, would seem to indicate that this type of segregation is highly advantageous in the Panamanian environment.

It may, in fact, have one widespread general advantage in almost all areas, in relations among almost all species, plus a variety of other advantages in more limited sets of circumstances, in relations between particular individual species or small groups of species.

The general advantage probably is that it provides separation without fighting, and the consequent risk of physical injury, or the waste of time which might be entailed by the repeated performance of "repellent" interspecific displays (the only other "easy" ways of maintaining segregation among sympatric competing forms). This, in itself, must always be useful to some extent.

It may be the only advantage involved in the separation of Night Monkeys from Rufous-naped Tamarins. The segregation of these two species probably is maintained by adaptations which are "mutual," although not necessarily exactly equivalent. From the point of view of Rufous-naped Tamarins, it probably is advantageous to avoid encounters with Night Monkeys simply because such encounters might turn hostile and Night Monkeys are just large enough to be potentially dangerous opponents. *Aotus*, on the other hand, may have evolved (or retained) its nocturnal habits as an adaptation to reduce or control competition with a great many other species in addition to *S. Geoffroyi*. Its geographic range is very much larger than that of *Geoffroyi*, extending over more of Central America and most of tropical South America. Its nocturnal habits must limit the amount or severity of competition with many other species of Platyrrhini, including other tamarins, *Saimiri*, *Callicebus spp.*, *Pithecia spp.*, and *Cebus spp.*, some of which are larger and/or have more highly specialized and possibly more efficient methods of locomotion and feeding.

A comparable factor may be involved in the relations between *S. Geoffroyi* and the flycatchers. Rufous-naped Tamarins probably could not repel organisms as extremely mobile as birds without expending a great deal of energy over considerable periods of time.

Even more important, however, they cannot "afford" to repel flycatchers too effectively if they are to rely upon the birds as indicators of favorable areas.

The peculiar activity rhythm of Rufous-naped Tamarins—so different from that of most other comparable species in the same environment—suggests that the special relationship between the tamarins and the flycatchers is essentially “one-sided.” The tamarins seem to have adjusted their activities to those of the birds; but there is no evidence that the birds have adjusted their activities to those of the tamarins.

Of course, this sort of relationship must have disadvantages as well as advantages. If the tamarins are “dependent” upon the flycatchers as suggested here, they are using what might be called “indirect” clues to locate necessary resources. There is reason to believe (Moynihan, 1968b) that species which use indirect clues comparatively frequently will tend to be more opportunistic (see also page 7), and consequently better able to colonize “new,” previously unfamiliar, areas and habitats than otherwise similar species which place greater reliance upon direct clues. This may help to explain why *Saguinus* is the only genus of tamarin or marmoset which has been able to invade Central America. But when the use of indirect clues is combined with segregation by differential timing, the situation may become very complicated indeed. Probably, the advantages of such segregation outweigh the disadvantages only in regions in which food is relatively abundant. The balance may well be different in regions in which food is scarcer, where it may be relatively more advantageous to spend more time looking for things to eat, irrespective of the dangers or difficulties of awkward interspecific encounters. If so, then the potential drawbacks of the differential timing method may help to explain why *Saguinus* is less widely distributed than some other genera of Platyrrhini such as *Cebus* and *Alouatta*.

Squirrels, as well as Squirrel Monkeys, may also compete with tamarins. There are several species of squirrels in Panama; but the only one I have observed at any length is *Sciurus granatensis*. Individuals of this species are abundant in some of the same areas as tamarins, move along many of the same “pathways” through trees and bushes, and sometimes eat the same fruits. It would appear, however, that there is some sort of avoidance reaction between the two species. This seems to be a matter of spacing rather than timing. The squirrels seem to be active throughout the day. But individuals of the two species are seen close together much less frequently than would be expected by chance alone in view of their abundance and habitat

preference. It has already been suggested (Moynihan, 1968a) that the similar coloration of the tail in the two species (largely rufous in *granatensis*, partly rufous in *geoffroyi*) may facilitate this avoidance. (In both species, the tail is conspicuous during locomotion. If nothing else, it must serve to emphasize the direction in which an individual is moving).

Only once did I see the two species within 50 feet of one another. This occurred when a group of tamarins approached a single squirrel. Apart from the approach itself, the tamarins appeared to ignore the squirrel, but the latter gave a long burst of loud vocalizations. These did not seem to be “friendly.” They probably were expressions of a strong escape tendency (alone or in combination with other types of motivation).

This would suggest that all or most of the usual avoidance between the two species is due to evasive action by the squirrels. Possibly the relationship between the two species is as one-sided as that between tamarins and flycatchers—with the tamarins playing the opposite “role.” There probably has not been strong selection pressure upon the tamarins to develop special timing mechanisms to regularize or minimize their contacts with squirrels because they would usually win, and win rapidly and decisively, any overtly hostile encounters between the two species. The squirrels are somewhat smaller and much less gregarious than the tamarins—and certainly no more agile. Thus it probably is the squirrels who have had to adapt to the tamarins rather than vice versa. (Why the squirrels have not adapted by developing a special timing mechanism of their own is another problem. And this can be solved only by further study of the squirrels. Possibly they cannot afford the periods of inactivity which such a mechanism might inevitably entail.)

As mentioned above, Rufous-naped Tamarins seem to be very much afraid of most birds of prey. They usually perform violent escape movements, with appropriate vocalizations (see pages 29 and 30), whenever a hawk flies by. In this respect, they differ very greatly from *Callicebus moloch*.

The probable importance and value of such reactions is revealed by the fact that the tamarins usually do not wait to make sure that an approaching bird of prey, or any other species of somewhat similar appearance, is really dangerous. Thus, for instance, they will burst into high intensity escape behavior when a Turkey Vulture (*Cathartes aura*) flies by, even though the

vulture is paying no attention to them and probably could do them little damage even if it wanted to.

To my knowledge, the only bird of prey which does not provoke such reactions is the Double-toothed Kite (*Harpagus bidentatus*). Single individuals and pairs of this rather small species frequently associate with bands of *Cebus capucinus* (probably feeding on reptiles disturbed by the monkeys, N. G. Smith, personal communication). They are much less regular attendants upon tamarins, but they will occasionally follow bands of the latter in areas in which *Cebus* is absent. The tamarins apparently always ignore the kites completely, even when they fly or land only a few feet away.

(Epple [1968] conducted some experiments with a few captive *S. geoffroyi* [which she calls *Oedipomidas spixi*]. She tested their reactions to "flying" objects. The objects presented included a stuffed buzzard—presumably *Buteo buteo*—a stuffed cuckoo, cardboard models of a buzzard and a falcon, a cardboard circle, a triangle, and a wooden staff. "When the objects suddenly appeared moving rapidly above the animals' heads, they reacted with warning calls." [Note: By "warning calls," Epple may mean something like the patterns which are termed "Loud Sharp Notes" in this paper. See also page 30.] "When the objects moved slowly, so that the animals could easily recognize them, only the buzzard elicited warning calls."

(Epple's discussion of the theoretical implications of marmoset and tamarin alarm behavior is not overwhelmingly clear in all respects. But she does say that "The warning and escape responses given to flying objects . . . may well be inborn." If so, and since Double-toothed Kites are quite *Buteo*-like in shape and coloration, it seems likely that the apparent indifference of the tamarins to the kites is acquired, the result of learning [presumably maintained by tradition].

(This indifference is all the more remarkable if wild tamarins ever feed on lizards in the same way as some captives [see page 4]. In this case, they would have come to tolerate a direct [and synchronized] competitor. But they probably have had little choice. They do not have the physical equipment to drive away even a small hawk. And they can hardly avoid a direct follower, especially something as swift and active as a bird, if the latter is going to search them out or wait for them to appear at any time of the day.)

It may be added that motion is not always necessary to provoke alarm among tamarins. I have seen wild individuals become greatly disturbed, obviously fright-

ened, upon catching sight of perched and immobile birds of prey such as *Buteo magnirostris*.

Signal and Other Social Behavior Patterns of Adults

The term "social" should be used in a very broad sense, to include all reactions, even hostile (agonistic) and sexual, among any two or more individuals. The terms "hostile" and "agonistic" may be applied to all behavior patterns produced by a tendency to attack and/or a tendency to escape. The term "sexual" may be applied to all patterns which are largely or completely restricted to encounters or other reactions between individuals of opposite sex. The term "signal" may be applied to any pattern which often and effectively conveys information from one individual to another, even if it has other functions as well. Any signal which seems to have become "ritualized," i.e., specialized in form or frequency or any other way, expressly as an adaptation to permit or facilitate communication among individuals may be considered a "display." All vocalizations are almost certainly displays in this sense. So are many distinctive postures and movements, and all patterns which produce or distribute pheromones.

The following account will be concerned with both the intraspecific social relations of Rufous-naped Tamarins and the various signal patterns, especially displays, which they may use in intraspecific and/or interspecific communication.

For practical reasons, it will be convenient to distinguish between "adult" and "infantile" patterns.

Some of the patterns classified as adult here also are performed by older infants and juvenile individuals as soon as they become partially independent; i.e., as soon as they are no longer carried by their parents all or almost all the time. Juveniles may not show very much in the way of high intensity sexual (at least copulatory) behavior, but they certainly can, and sometimes do, perform many of the same hostile patterns as completely mature individuals. They probably also show the whole of the adult range of friendly or gregarious responses.

At the same time, they continue to perform some typically infantile patterns; e.g., some vocalizations, with appreciable frequency (see pages 62 and 63). This is true of both wild and captive individuals, but not always to the same extent. Individuals which are hand-raised by humans in captivity tend to retain the

habit of uttering essentially infantile calls relatively frequently until much later stages of juvenile development than individuals which are raised by their own parents. This may be partly due to the fact that hand-raised young tend to adopt their human keepers as parent substitutes. The humans are never completely satisfactory in this role (again see page 63); but they always remain overwhelmingly larger than the young tamarins, and highly "impressive" or intimidating, while continuing to provide food and some other comforts and pleasures.

Thus the behavior of juveniles, as a whole, is strongly "bivalent," combining adult and infantile patterns, rather than intermediate.

Completely mature and "normal" adult individuals do not perform infantile patterns in most circumstances, but they may "revert" to an earlier phase in a few situations of apparently extreme "stress."

The behavior of adult individuals, including their reversions, will be described immediately below. The behavior of infants will be described on page 60 et seq.

"PURE" ATTACK, ESCAPE, AND FIGHTING

Overt and active attack, with or without subsequent fighting, can be induced very easily among Rufous-naped Tamarins in captivity. It is not rare among groups of three or four individuals kept in fairly small cages (8x8x8 feet), even when the individuals have been kept together for a long time and are thoroughly familiar with one another. It is a common, almost inevitable, reaction when any individual is introduced into any cage, even a very large one, already occupied by other individuals who are not acquainted with the introduced animal and who have been in the cage long enough to have adopted it as their own home range or territory.

Attack itself takes the form of a more or less rapid approach to an opponent. If the opponent retreats, the aggressor may follow. This may develop into a rapid chase. If the opponent does not retreat, or does not retreat fast enough, the aggressor may leap upon it.

Attack movements may be quite silent and unritualized in all respects. In this case, they may be considered "pure" attack, and probably are produced when attack motivation is relatively very much stronger than any counteracting tendency. But other attack movements, essentially similar in form, may be accompanied by or combined with Long Rasps, Broken Rasps,

and/or various Pilo-erection patterns⁴ (see below). As these latter patterns also occur in some other circumstances, it seems likely that they also express some other types of motivation. Thus, the attacks with which they are combined probably are more ambivalent than the silent unritualized attacks.

When an attacking individual leaps onto another, the two animals usually begin to wrestle. This is accompanied by biting, and sometimes kicking. It may be so violent that both individuals roll off the branch on which the fight began and fall down to the ground. In all cases observed, one individual managed to disengage itself after a few seconds or minutes, and then ran away. Such breaking away may or may not be followed by (further) chasing.

Some fighting is completely unritualized and silent, but most is accompanied by Long Rasps, Broken Rasps, and Pilo-erection.

Once, I saw a chase among captive animals which ended with the two individuals standing up on their legs, facing one another, and striking one another with their hands. But this case was thoroughly unusual.

The fact that Rufous-naped Tamarins use their teeth as offensive weapons much more frequently than their hands is a marked difference from Night Monkeys. It may be correlated with differences in the dentition of the two species. Tamarins have much sharper teeth, and relatively longer canines, than Night Monkeys.

Fights among captive tamarins were never allowed to continue for more than five minutes. Even during such short periods of time, however, the fighting individuals usually become quite exhausted, and occasionally severe wounds may be inflicted.

Overt attacks are relatively *very* rare among Rufous-naped Tamarins in the wild, much rarer than among *Callicebus moloch* individuals. The only observed attack performances by tamarins under natural conditions were brief rushes or chases, with or without Rasping vocalizations. Apart from one very exceptional incident, all these attacks involved individuals belonging to the same social unit. I never saw actual physical combat, serious wrestling and biting, in the wild.

This rarity is interesting in view of the obvious aggressiveness of tamarins in captivity. It seems to be due to several causes. The proximate causes are spacing factors. Individuals of the same group usually have

⁴ Throughout this paper, the initial letters of all certainly or probably ritualized patterns are capitalized.

plenty of room to retreat from one another in the wild. And individuals of different groups usually do not approach one another closely enough to permit fighting (see also page 7). The ultimate cause probably is that fighting is particularly dangerous among tamarins. It probably is more likely to produce exhaustion or injuries, or produce such results more rapidly, among tamarins than among titi monkeys or some other species of New World primates.

Thus the aggressive behavior of Rufous-naped Tamarins may seem to be "paradoxical." But it conforms to a widespread general rule, typical of many other species with particularly effective offensive weapons. Tamarins will use their weapons when "forced" to fight, but they usually manage to avoid fighting under natural conditions. In both respects, they resemble many other mammals and birds cited by Lorenz, (1952).

The escape behavior of adult and sub-adult *S. Geoffroyi* is more or less rapid retreat. This may be silent or accompanied by such vocalizations as Trills or Loud Sharp Notes (see below). As in the case of attack, it seems likely that the silent patterns are less ambivalent than the vocal ones. (Younger juveniles may respond to alarm by leaping upon an adult's back, in a typically infantile manner.)

One distinctive form of escape or partial escape behavior is a common reaction to "potential predators," such as man, gradually approaching from a distance (on the ground). When the members of a band of tamarins first become aware of the alarming stimulus, all the individuals usually begin to vocalize (see also page 28). They are very conspicuous at this time. As the source of the alarm comes closer, however, one individual after another will fall silent. Each individual also begins to run away as soon as it shuts up. Finally, in many cases, only a single individual is left vocalizing. Then it too falls silent and runs away. This behavior is obviously adaptive. The initial outburst of calling, and then the change from conspicuous vocalization to silence, may be confusing. And the last remaining individual certainly helps to "cover" the retreat of its companions. It concentrates the attention of the potential predator upon itself while the other individuals disappear unobserved. Similar behavior is characteristic of other more or less highly gregarious Platyrrhini which have large ranges or territories, e.g., *Cebus capucinus*, but not such species as *Callicebus moloch*. (Of course, the whole performance also is comparable

to the "distraction displays," or even "mobbing," of many birds.)

Saguinus Geoffroyi individuals alarmed by a bird flying overhead may roll under a branch (M. H. Robinson, personal communication), but they seldom or never dodge and hide behind a branch when a potential predator is approaching on the ground. In this latter respect also, they resemble the larger Platyrrhini, but differ from the smaller *Cebuella pygmaea* and may arboreal squirrels.

COPULATORY BEHAVIOR

As noted by Wislocki (1930 and 1939) and Enders (op. cit.), Rufous-naped Tamarins seem to have a definite breeding season in central Panama. The evidence for this is good, but rather heterogeneous. Wislocki found young embryos in the uteri of many females collected in January and early February. Most young probably are born in April and early May. In the course of the present study, I was never able to do much field work in these or the immediately adjacent months; and I never observed actual births. But large numbers of infants appear, quite suddenly, for sale as pets, in the markets of Panama City every May (personal observation).

As might be expected, there is some variation in the timing of breeding. Some of this may reflect individual differences in responsiveness to the same or similar stimuli. Another part may be due to the instability of the climate in central Panama. The onset and termination of the "wet" and "dry" seasons may differ, by a factor of several weeks, in successive years. The amount of rainfall during both seasons also is quite variable.

There are records of very early breeding. One infant conceived in captivity on Barro Colorado Island was born on 19 February. N. G. Smith (personal communication) saw one pair of very young infants in the wild on 29 March.

There also are records of late breeding. Three sets of infants conceived in captivity on Barro Colorado were born in late May and early June. Wislocki found advanced embryos in the uteri of some females collected in June. One female caught in the wild in an advanced stage of pregnancy gave birth to two normal young in late June. I observed one very young infant in the wild in July.

It seems probable, nevertheless, that the number of births usually decreases very rapidly after the usual

late April–early May peak. Fewer infants appear for sale in Panama in June than in May. Even fewer appear in July, and none appears later in the year. By August and September, when I was able to resume intensive field work during most years, only older young are present.

It has already been mentioned that I never saw copulations in the wild. Wislocki's data suggest, however, that they are most apt to occur, or most likely to be effective, in January. This is supported by evidence from the captive individuals on Barro Colorado Island. Individuals accustomed to captivity and kept in large cages with individuals of the opposite sex performed many apparently successful ("complete") copulations. They did so more frequently in January than in any other month of the year. (The same individuals, and even more characteristically other individuals kept in less optimal conditions, also were observed to copulate, or attempt to copulate, occasionally during every month of the year between September and July. But such behavior may have been more or less highly "aberrant.")

All this would suggest that the onset of normal or effective breeding behavior is "triggered" by the beginning of the dry season, which usually or often occurs during the last week of December or the first week of January in central Panama. (And this, in turn, may be an adaptation to ensure, or enhance the probability, that the birth of the young will coincide with the beginning of the rainy season, which more often than not occurs around the end of April.)

There may be two reasons why copulations were not observed in the wild during the course of the present study. In the first place, all wild individuals are more or less shy, and observation of captive individuals suggests that almost all forms of sexual behavior are inhibited by even slight alarm. Secondly, copulations probably are actually infrequent under natural conditions. Captive adults who have been kept apart from mature individuals of the opposite sex for a long time may perform a remarkably large number of copulations remarkably rapidly when finally given access to a suitable and receptive partner (I have seen a male copulate 15 times within an hour in such circumstances!). But this is very different from apparently more normal behavior. The captive animals which seemed to have formed the closest and most stable pair bonds, including the individuals which bred successfully, did not attempt to copulate more than once or twice during a 24-hour period, even at the height of the sexual season. Some

apparently well adjusted pairs may have copulated even less frequently.

In this respect, Rufous-naped Tamarins differ from *Callicebus moloch*, but probably resemble *Aotus*.

The actual copulatory movements of captive tamarins are rather simple.

Apparently successful copulations are usually, but not always, preceded by some display(s), at least extreme Upward Tail-coiling by the female (see page 48). In any case, the male eventually mounts the female from the rear; and sits behind and partly on top of her, clasping her tightly around the "waist" (just above or in front of her thighs) with his arms, and continuing to grasp the perch with his feet. He usually seems to insert his penis and begin pelvic thrusts almost immediately. These movements are irregular and not very conspicuous. Their number is variable but usually ranges from 3 to 20. Sometimes the male presses his face down into the fur of the female's back throughout all or most of the copulation. He may then also wrinkle his nose, partly close his eyes, and perform Tongue-protrusion movements (see Figure 15a) and occasional Head-flicks. The whole group of patterns can be considered a type of "Sexual Sniffing" (see also page 57). During some particularly prolonged and vigorous copulations, the male may eventually take his feet off the perch and begin to climb up the female's back! He always lets his tail hang more or less straight downward throughout the whole performance. The female usually sits quietly, in a rather hunched posture. More often than not, she lowers her head, bringing it forward and down, just as the male mounts, and then keeps it in this position. If she raised her tail in Upward Tail-coiling beforehand, she usually lowers and partly uncoils it as the copulation progresses. Typical copulation postures are illustrated in Figure 19.

The whole performance usually is rapid and brief. The male dismounts immediately after the last pelvic thrust. There is no elaborate post-copulatory display. Frequently, however, the male puts his hand down to scratch or massage his genitals, and/or bends his head down in an apparent attempt to lick the genital region, within a few seconds after the end of copulation.

Incomplete and obviously unsuccessful copulation attempts may take various forms. Sometimes a male simply mounts and dismounts without making any pelvic thrusts. An unwilling female may walk away when a male attempts to mount. Or she may simply sit and turn her head, to look at him over her shoulder. This seems to be a very effective way to discourage him.

It usually stops him dead in his tracks, or even induces him to retreat, at least temporarily.

The great majority of the copulations observed were heterosexual. But I also have seen homosexual mountings, with pelvic thrusts, among males, in the absence of a female, and among females, in the presence of an adult but sexually inactive male.

ALLOGROOMING (THE GROOMING OF ONE INDIVIDUAL BY ANOTHER)

This seems to be the only display of the species which is mediated primarily by the sense of touch (but see also page 18).

All or almost all other Platyrrhini have homologous patterns. But different species use them in rather different ways. Among adult *Aotus*, Allogrooming occurs very frequently in close association with copulations, but is rare or absent in other social circumstances. Among adult *Callicebus moloch*, by contrast, it is comparatively rare in association with copulations, but very common in many other nonhostile situations. In an earlier paper (Moynihan, 1967), it was suggested that the Allogrooming of adult Rufous-naped Tamarins may be almost as purely sexual as that of *Aotus*, although not necessarily copulatory. This statement still seems to be true, on the whole or as an average, as a description of the most "typical" patterns of the species; but it needs to be qualified even further. The Allogrooming behavior of *S. geoffroyi* is really quite complex.

It is comparatively very rare, *much* rarer than the corresponding behavior of *Callicebus moloch* or *Cebus capucinus*. I have never seen it in the wild, probably because it is inhibited by the slightest degree of alarm (just like the copulatory reactions).

It was, however, performed by many of the individuals kept in captivity, and in a variety of social situations.

It sometimes is performed by individuals who do not seem to have formed their bonds with one another. This type of Allogrooming certainly occurs throughout the year; i.e., both during and outside of the season of most frequent copulations. It usually is mutual, but never simultaneously so. First one individual grooms another; then they exchange roles. The former "groomer" becomes the "groomee" and vice versa. Roles may be reversed repeatedly. Very occasionally, one individual grooms another individual of the same sex. More often, a female grooms a male, or a male

grooms a female. I have seen at least one female groom two different males in rapid succession. As a general rule, during this type of Allogrooming, subordinate individuals tend to groom dominant individuals more frequently than the reverse and/or continue Allogrooming for longer periods of time. In this respect, these reactions resemble the only type of Allogrooming of *Callicebus moloch*.

Among Rufous-naped Tamarins, however, such performances are relatively less common than Allogrooming between mates. And the Allogrooming between mates is performed more frequently during the breeding, copulatory, season than at any other time of the year. But even this Allogrooming may be somewhat heterogeneous. It only occurs very rarely just before actual copulation. The great majority of performances of Allogrooming between mates, although characteristic of the breeding season, may be said to occur "apart" from copulation insofar as they are not performed immediately before or immediately after an overt copulation attempt.

To my eyes, the Allogrooming between mates apart from copulation is identical in form with that of non-mates. It also seems to be equally reversible.

Nevertheless, the two types of performance may be produced by different causal factors, different kinds of motivation. The rarer type between non-mates, may be an expression of some "general gregarious" tendency. The more common type, between mates, may be an expression of some sexual drive—but this can hardly be copulatory. Possibly it is an expression of some sort of "pairing tendency."

The very rare Allogrooming immediately before copulation is slightly more distinctive. In these circumstances, it is always the male who grooms the female. Possibly these performances are purely copulatory in the same way as the corresponding behavior of *Aotus*. (They may also be partial "substitutes" for copulation, being performed when the initiation of overt copulatory movements is delayed for one reason or another.)

The possible functions of Allogrooming, and its probable course of evolution within the Platyrrhini, have already been discussed elsewhere (Moynihan, 1967).

Twice, the Allogrooming of Rufous-naped Tamarins before copulation was seen to be accompanied, or interrupted, by wrestling. This was quite vigorous, but did not appear to be serious fighting. The wrestling animals apparently did not attempt to bite or strike one another.

All the actual Allogrooming movements of *S. geoffroyi*, in all situations, are quite similar to those of both *Aotus* and *Callicebus moloch* in form. All three species use both hands and teeth during Allogrooming. (In this respect, their Allogrooming differs from their self-grooming. The latter usually consists of little or nothing else but scratching with the hands or feet.)

All types of Allogrooming by *S. geoffroyi* seem to be very strongly and positively correlated with sunshine. They seldom or never begin unless the sun is shining quite brightly, and the individuals involved usually are fully exposed to the sunlight at the time. In some cases, however, grooming begun in sunshine may continue after clouds have come up.

All types of Allogrooming also have similar orientation. The groomer always pays most attention to certain special areas of the fur of the groomee, i.e., the rufous area of the back of the head and nape, and the brindled parts of the back and limbs. The white areas of the forehead and underparts usually are ignored.

An individual being groomed often raises the rufous hairs of the head and nape to a more or less extreme degree. Occasionally, these hairs are raised by one individual sitting next to another in what seems to be an attempt to "solicit" grooming. Apart from this (which may be considered a special display, the Rufous Ruffle, see also page 55), the methods used to invite grooming are very simple. An individual wanting to be groomed just approaches a companion, and sits or lies down, usually facing away in such a manner as to "present" its back to the companion.

OLFACTORY COMMUNICATION AND RELATED ACTIVITIES

Like both *Aotus* and *Callicebus*, *Saguinus* seems to have an acute sense of smell, and appears to rely upon this sense for much of its information about the outside world.

The usual initial reaction of any Rufous-naped Tamarin to a stranger, of its own or another species, or an unfamiliar object, is to sniff at it. When two previously unacquainted *geoffroyi* individuals encounter one another for the first time, they may sniff one another nose to nose, or one may sniff at the genito-anal region of the other, or (most frequently) the two individuals may place themselves in a mutual "nose to tail" position and sniff one another's genito-anal regions simultaneously. (This may provide visual as well as olfactory information. Not only is the base

of the tail rufous, but so are the hairs immediately surrounding the genito-anal region.)

Such simple behavior probably should not be considered ritualized per se. In a few particularly "exciting" social situations, however, otherwise typical sniffing movements may be combined with additional patterns which are unmistakably ritualized. These will be described separately on page 57.

Some more elaborate olfactory displays may be called "Rubbing." Various kinds of Rubbing patterns are performed by many species of New World primates. *S. geoffroyi* seems to have two main types. These have been mentioned in earlier publications (see, for instance, Moynihan, 1967; Epple, 1967; and Epple and Lorenz, 1967), but deserve to be described and analyzed in somewhat more detail.

The first type is done in a sitting position. An individual simply sits, presses its genito-anal region down against the substrate, and then rubs it back and forth, and/or from side to side, usually repeatedly. This pattern was called "Anal-Rubbing" in Moynihan (1967), but the term "Sit-rubbing" may be more convenient and appropriate. The Sit-rubbing of *S. geoffroyi* is basically similar to the only type of Rubbing observed to be done by *Aotus* in physical form although not in all other respects (see below).

The second type of Rubbing by Rufous-naped Tamarins may be called "Pull-rubbing." In this pattern, an individual lies down on its stomach, presses its genital region against the substrate, and then pulls itself forward with its hands. In order to get adequate leverage for pulling, the animal may have to raise its shoulders and chest off the substrate. Even then, however, the abdominal and genital regions almost always remain firmly pressed downward throughout the whole of the performance. Pull-rubbing does not intergrade morphologically with Sit-rubbing.

According to Epple (1967), similar-appearing Pull-rubbing is performed by several species of *Callithrix* (which she calls *Hapale*), one species of *Leontideus* (which she calls *Leontocebus*), and *Saguinus oedipus* (which she calls *Oedipomidas oedipus*).

The Rubbing patterns of *S. geoffroyi* are illustrated in Figure 2: Sit-rubbing in 2a, and Pull-rubbing in 2b.

Most Rubbing of both types by Rufous-naped Tamarins is done against branches. This was the orientation of all Rubbing observed in the wild (see also below). In captivity, however, individuals may rub against many other objects and surfaces, including the ground and the wire netting of their cages. Once,

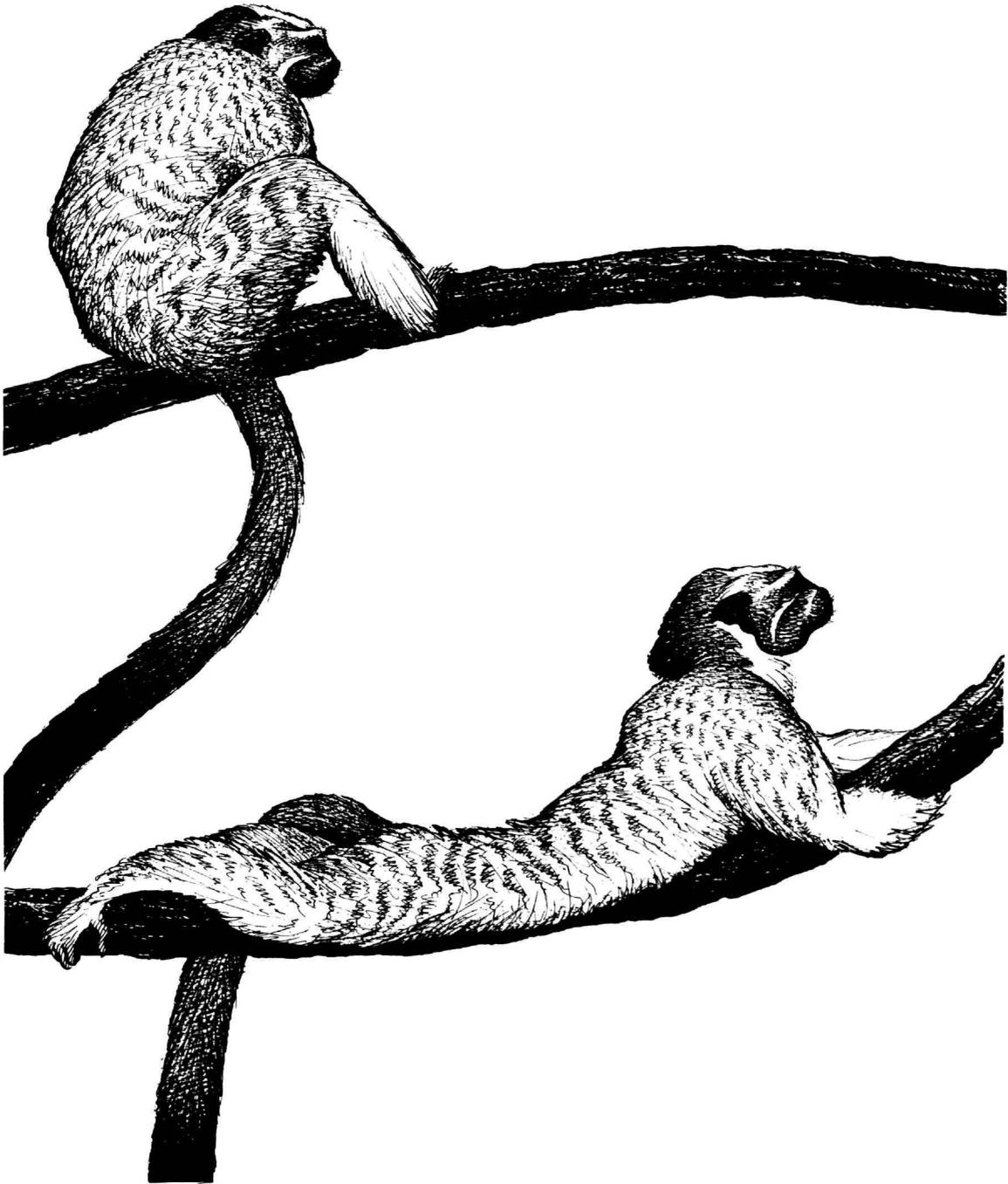


FIGURE 2.—Rubbing postures of adult Rufous-naped Tamarins, with Crown-smoothing: *a* (*top*), Sit-rubbing, with tail curved as in lashing; *b* (*bottom*), Pull-rubbing.

I saw an individual perform Sit-rubbing on the back of another individual. Presumably as an "artifact" of the conditions of captivity.

On branches, Rufous-naped Tamarins prefer to rub against small protuberances, such as knots, stumps of twigs, or projecting pieces of bark.

Both types of Rubbing are performed by both males and females.

Both patterns may serve to spread some odoriferous secretion(s) on the substrate. Wislocki (1936) has described glands in the genito-anal region which might produce such substances. It probably is significant, in this connection, that an individual may put its hand down to its groin, immediately after either typical Sit-rubbing or Pull-rubbing, to perform what appear to be scratching, massaging, and/or squeezing movements. These movements may accelerate the flow, or facilitate the spread, of secretions (see also below).

Epple and Lorenz (op. cit.) have described a variety of apparently secretory glands in the sternal regions of many different Platyrrhini, including one in *S. Geoffroyi*. They (and Epple, 1967) suggest that the pattern called Pull-rubbing here also spreads secretions from the sternal gland. This may well be true in many, perhaps most, cases. But the sternal gland seems to be less well developed in *Geoffroyi* than in many other species. And the "point of emphasis," the region pressed most strongly against the substrate, is far back of the sternum in all typical Pull-rubbing performances by Rufous-naped Tamarins. It also seems unlikely that much of the sternal gland substance(s) can be spread during the performances in which the shoulders and chest are lifted up.

Rubbing is performed very frequently by *S. Geoffroyi* individuals in captivity (probably more frequently than the corresponding patterns of *Aotus* or *Callicebus moloch* in comparable situations).

Most Rubbing occurs during disputes and other apparently hostile encounters. Both forms of Rubbing are common during the hostilities which usually break out when a "stranger" is introduced into a cage already occupied by one or more other individuals who have come to regard it as their "home." In these circumstances, the Rubbing is almost always performed by the "owner(s)," and almost never by the intruder. Both forms of Rubbing also occur, but less commonly, during disputes among individuals who are familiar with one another but on generally bad terms. In these circumstances, the Rubbing is more likely to be per-

formed by apparently dominant individuals than by apparently subordinate ones. Very occasionally, either one or both types of Rubbing may be performed by a very bold individual as a reaction to the approach of a human being.

Rubbing usually is accompanied by Crown-smoothing (see page 53), a hostile display, and follows or is followed by unritualized hostile movements. These may be either escape and/or attack, but most frequently the latter. Rubbing itself is usually silent; but it also may follow or be followed by vocalizations such as Loud Sharp Notes, Trills, and Twitters. All these vocalizations are partly or wholly hostile.

These facts indicate that Rubbing is produced by hostile motivation. Probably, it is produced by simultaneous activation of both attack and escape tendencies. Probably, the attack tendency is strongly preponderant during all or most Rubbing performances. But the escape component cannot be negligible. Crown-smoothing seems to express an appreciable amount of escape, and the escape tendency is stronger than the attack tendency in the vocalizations uttered immediately before and/or after Rubbing.

Probably, the actual strength of the attack and escape tendencies is quite different in different Rubbing performances. Rubbing occurs frequently during both brief, apparently low-intensity disputes, and prolonged, vigorous, and apparently high-intensity disputes. Sit-rubbing is the characteristic form during brief and not very energetic hostile encounters. Pull-rubbing is the characteristic form during the most prolonged and serious hostilities. Most disputes following the introduction of a stranger into a cage begin very actively and excitedly, and then gradually die down. When both forms of Rubbing occur during such a dispute, most of the Pull-rubbing is performed during the early stages and most of the Sit-rubbing later. These facts would suggest that Pull-rubbing is produced when both the attack and escape tendencies are stronger, on the average, than when Sit-rubbing is produced. But Sit-rubbing may also be performed by particularly aggressive individuals during some disputes which are of unmistakably high intensity. In such circumstances, it is performed very rapidly in brief pauses between attacks. Possibly, these aggressive individuals do this Sit-rubbing instead of Pull-rubbing simply because it takes less time (the preliminary "getting into position" is simpler), but it also is possible that all or most Sit-rubbing is slightly more aggressive, on the average, than Pull-rubbing. Sit-rubbing may

be performed when the *relative* strength of the attack tendency, compared with the escape tendency, is slightly greater than when Pull-rubbing is performed, irrespective of the *actual* strength of the two tendencies at any given instant.

Some Pull-rubbing by tamarin males certainly is accompanied by erection of the penis. Some by females probably is accompanied by erection of the clitoris. M. H. Robinson (personal communication) also has seen one case of erection during Sit-rubbing by a male. Such patterns may be considered forms of masturbation. But they do not seem to be correlated with activation of sexual drives in the same way as the Rubbing of *Aotus*. Neither type of Rubbing by *S. geoffroyi* is largely or completely confined to encounters between individuals of different sex.

The general form of the Rubbing patterns of Rufous-naped Tamarins, and the circumstances in which they occur in the conditions of captivity, would suggest that they should function as ways of "marking" territories, of proclaiming or advertising territorial ownership. But there are other indications that the situation is not so simple. The performance of Rubbing by one captive individual seldom induces a clear-cut immediate response by its cage mates. Individuals certainly do not usually sniff at, or avoid, sites where other individuals have Rubbed. (Once, I saw a male do Pull-rubbing at the exact same place where a female had performed a similar pattern a few seconds earlier, but the male's behavior may not have been a direct reaction to that of the female.) More important, Rubbing is performed only very rarely by wild individuals under natural conditions. I saw a few cases of Sit-rubbing in the wild, but no Pull-rubbing; and most of this Sit-rubbing seemed to be a reaction to me rather than to other tamarins.

The rarity of Rubbing in the wild must be correlated with the fact that groups of Rufous-naped Tamarins, under natural conditions at the present time, usually are able to repel one another and prevent "trespassing" by the use of vocal patterns, alone or in combination with visual information (see page 23).

As many other mammals of other orders "mark" their territories with olfactory information in order to advertise ownership, it seems very probable that the Rubbing of platyrrhine monkeys was originally evolved to subserve the same function (and/or is a direct descendant of a primitive mammalian pattern adapted to this function). At the present time, however, the Rubbing of *S. geoffroyi* would seem to be in process of

becoming obsolescent as a method of conveying information, at least by olfactory means. As a social signal, it seems to be nothing more than a "second-line reserve" method of territorial defense, only used in more or less strongly abnormal circumstances.

It seems possible, in fact, that even some of the Rubbing of captive individuals is less a signal or means of social communication than an "outlet" for thwarted motivation or a way of "relieving" frustration. The clearest examples of this phenomenon were provided by some animals being tested by M. H. Robinson on Barro Colorado. Dr. Robinson was interested in the tamarins' ability to recognize cryptic insects, and he conducted a series of experiments in which single individuals were released into cages in which various cryptic insects were hidden among twigs and leaves. Some of the tamarins took a very long time to discover the insects, and a few were completely unsuccessful during the time periods allotted for the experiments. Some of them performed Sit-rubbing and/or Pull-rubbing when first released into the experimental cages. These reactions may have been attempts to "claim" territories. But some of the individuals also performed progressively more and more Rubbing the longer they remained unsuccessful in finding the insects. And, at least in some cases, they stopped Rubbing when they finally did discover and eat the insects.

If this suggestion is correct, and the Rubbing of Rufous-naped Tamarins is in process of changing from a signal pattern to a method of relieving frustration, it is remarkable that the Rubbing movements are so complex, and conspicuous, in form. They certainly are at least as elaborate as the corresponding movements of other Platyrrhini. Possibly, relatively complex patterns are more suitable as outlets for thwarted motivation than are less complex patterns.

Some other platyrrhines, e.g., *Callicebus moloch*, occasionally perform movements which are more or less similar to the Sit-rubbing movements of tamarins immediately after defecation and/or urination in obviously non-hostile and non-sexual situations. In these circumstances, the movements appear to be purely cleaning patterns, and may not have special signal functions.

Saguinus geoffroyi itself may retain a trace of such cleaning behavior. At least, I have seen several captive tamarins perform what looked like typical Sit-rubbing movements, on two or three different occasions, immediately after defecation or urination, when they were not involved in overt disputes. But all the individuals

who performed such patterns had cage mates at the time; and it is impossible to be certain that their Rubbing was not motivated by some otherwise concealed feeling of hostility. It may also, of course, have been due to "postural facilitation."

In any case, it seems quite probable that the original signal version of Sit-rubbing was a derivative of a non-signal cleaning pattern.

If so, the Sit-rubbing and "pre-Sit-rubbing" movements of *S. geoffroyi* have subserved three very different functions in the course of evolution; i.e., cleaning, signaling, and channeling frustration. And they have done so with remarkably few changes in physical form. This is of some interest from a theoretical point of view. In Moynihan (1967), it was suggested that the tactile (Allogrooming) and acoustic signal repertoires of New World primates, unlike their visual signals, tend to be very adaptable (changeable) in function while remaining conservative in form. It would now appear that at least some of the olfactory signals are more similar to Allogrooming and vocalizations than to visual displays in this respect.

Pull-rubbing may have evolved as a simple exaggeration of the forward movements sometimes included in Sit-rubbing.

Incidentally, it should be noted that the typical Pull-rubbing of Rufous-naped Tamarins is almost perfectly intermediate, in form, between Sit-rubbing and the "Chest-rubbing" of *Callicebus moloch*. The latter may, in the course of evolution, have been derived from, or passed through a stage comparable to, Pull-rubbing.

Epple and Lorenz (op. cit.) show a photograph of a *geoffroyi* male performing a pattern which looks remarkably like the typical Chest-rubbing of *Callicebus*, i.e., the breast is pressed against a branch while the hindquarters are raised. In my experience, this sort of behavior is very rare among *geoffroyi* individuals. When it does occur, it appears to be abnormal, perhaps hurried, Pull-rubbing rather than a different, qualitatively distinct, signal.

The original connection between cleaning and specialized signal or outlet Rubbing may also be revealed by another type of performance by Rufous-naped Tamarins. Like many other Platyrrhini, these animals clean their faces, especially after eating messy food, by rubbing their "muzzles" along a branch. Usually, they turn the head from side to side as they do so, thus cleaning each side of the face in turn. Rather surprisingly, individuals occasionally perform identical or very similar movements during Pull-rubbing, even

when their faces are not dirty at the time. This is most likely to occur during obviously high-intensity disputes. The face rubbing in such circumstances appears to be due to some peculiar (see below) sort of "overflow" of rubbing motivation. One gets the impression that the individuals which behave in this way are "driven" by such a strong tendency that they will rub anything and everything available. In any case, the occurrence of such face rubbing during apparently ritualized Pull-rubbing suggests that the internal casual factors producing the two activities are (still) linked together in some way.

(Face rubbing in these circumstances certainly is not a simple reaction to a change in the external stimuli confronting the performing animal. It is not a simple response to the fact that the face is brought close to the substrate during Pull-rubbing. Individuals do not usually perform face rubbing when they lie down in other circumstances. Nor is it a conventional "overflow activity" as the term is usually used by ethologists [see Bastock, et al., 1953]. In some ways, it resembles more the type of behavior frequently called "displacement activity." But the latter term is vague and possibly misleading [see comments in Moynihan, 1955a]. The application of the term to face rubbing during Pull-rubbing would be particularly misleading if the two activities are linked as suggested above.)

Although probably not always functioning as olfactory signals themselves, the more specialized Rubbing patterns may still (or also) play a variety of roles, or subserve several functions, in visual communication, at least occasionally.

Both Sit-rubbing and Pull-rubbing are more or less conspicuous to the eye, even when performed by themselves alone and in the simplest possible manner.

Some Sit-rubbing also is combined with visually conspicuous Tail-lashing. In this pattern, the tail is switched violently from side to side (see Figure 2a). This usually or always occurs when the Sit-rubbing movements themselves are lateral; but the tail movements definitely are *not* simple "mechanical" consequences of the body movements. I have seen Rufous-naped Tamarins perform vigorous side to side Sit-rubbing *without* conspicuous Tail-lashing. In some other species, e.g., *Callicebus moloch*, Tail-lashing occurs apart from Rubbing, by itself alone and/or in combination with other signal patterns. But the Tail-lashing of *S. geoffroyi* seems to be absolutely confined to some Sit-rubbing performances. In this respect, it resembles the Tail-lashing of *Aotus*.

The white underparts of many captive Rufous-naped Tamarins often are suffused with a tinge of yellowish-brown or brownish-orange. Sometimes this is quite bright, almost rufous. It appears to be a stain. It is quite variable, varying in the same individual at different times, and differing in different individuals. I think that this stain may be produced by the secretion(s) spread during Rubbing, especially Pull-rubbing. Individuals which perform a great deal of Pull-rubbing usually have more extensive and brighter stains of yellow-orange-brown than individuals which perform comparatively little Rubbing.

ACOUSTIC COMMUNICATION

Rufous-naped Tamarins have a moderate number of acoustic signals. All are largely or completely vocal. (There seems to be nothing comparable to the "Gnashing of teeth" of titi monkeys.) These vocalizations can be roughly divided into nine main types, some of which intergrade with one another through more or less continuous series of intermediates. Two major patterns may be considered "essentially infantile"; the others are "essentially adult."

Some brief citations in the published literature (e.g., Enders, *op. cit.*) might suggest that *S. geoffroyi* is a rather noisy species, but this seems to be only partly true of the population as a whole. The species is noisy only in certain circumstances. Wild adults may, sometimes, vocalize very conspicuously when they can see or hear a human observer or other potential predator, and when reacting to (or attempting to influence) other tamarins belonging to other social groups. But they tend to be very quiet indeed when they are not concerned with individuals of other social units and are not aware of being observed. On the whole, wild adult *geoffroyi* are very much less noisy than wild *Callicebus moloch*, or even *Aotus*. This probably is another adaptation to avoid attracting the attention of enemies in most circumstances (but see also pages 13 and 27).

The order in which particular vocalizations are listed below is not perfectly logical. It also differs from the order in which homologous and analogous patterns of *Aotus* and *Callicebus* were discussed in previous publications. It is used simply for practical convenience in description. The most important parts of the following descriptions will be illustrations of sound spectrograms. These will be supplemented by brief verbal summaries and comments which are essentially ac-

cessory. In general, verbal descriptions will refer to patterns as they sound in human ears. This may be deceptive in some cases. Rufous-naped Tamarins, like many other Platyrrhini, sometimes utter vocalizations which sound like single notes to human ears but which can be shown, by spectrographic analysis, to be "compound"; i.e., composed of several discrete units uttered in very rapid succession. Simply as a matter of convenience, however, I will refer to any group of sounds which seem continuous to my ears as "a note." If a note in this sense is really compound, the various units included will be called "components of a note."

- *Long Whistles*.—These are the most prolonged notes in the repertory of the species, with the possible exception of certain Long Rasps. They are relatively loud and "plaintive" in tone.

They are rather stereotyped in some ways. They can be uttered singly or in series of two, three, or four notes. But series of two or three notes are very much more common than either single notes or series of four. Series of two are slightly more common than series of three. Series may be repeated at frequent intervals, but never so rapidly that they "run together" and lose their individual identity. In all or most series, the first note is appreciably shorter than the succeeding ones. Thus, the sequence and arrangement of the notes would appear to have become almost as ritualized as the notes themselves.

A typical two-note series is shown in Figure 3. The last part of a typical three-note series is shown in Figure 4.

It will be seen that these patterns are really very complex, much more complex than they sound to human ears. Each note is composed of a very large number of separate "pulses" of sound. The "fundamentals" are rather low frequency (cycles per second) and very soft. It is the higher harmonics which provide the loudness. Apparently, the different harmonics of a single sound may vary in loudness independently of one another.

Figures 3 and 4 also reveal another peculiar feature of the Long Whistle. They seem to indicate that some of the notes are really composed of two partly independent series of pulses of sounds, partly overlapping one another. (This is particularly obvious at the beginning of the second note in Figure 3 and throughout most of the last note of Figure 4.) This may indicate that sounds are transmitted through two channels. The mouth always is wide open during Long Whistles. Possibly sounds also are emitted through the nostrils.

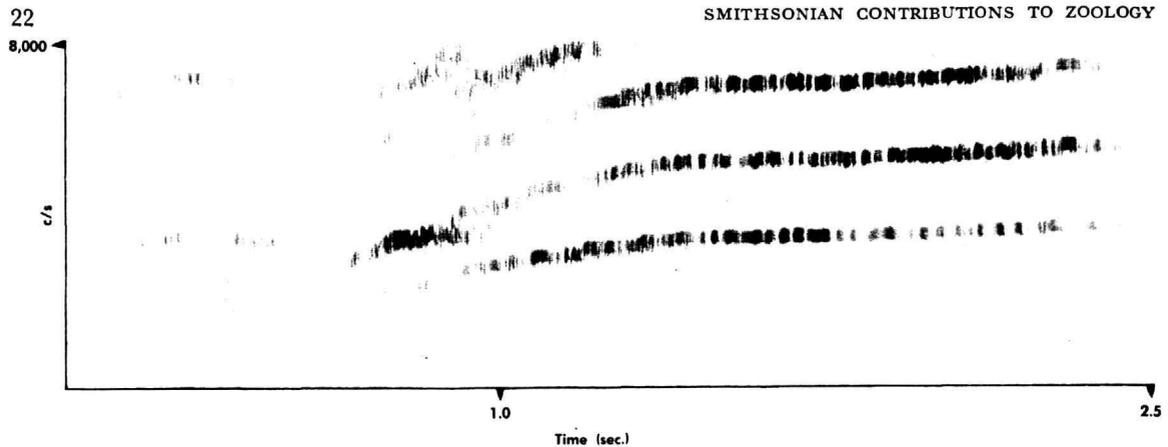


FIGURE 3.—A two-note Long Whistle series by an adult Rufous-naped Tamarin. All the Spectrograms illustrated in this paper were produced by a Kay Electric Company "Sonagraph" 6061 A. They were derived from recordings by a Nagra III NP, used with a Sennheiser MKH-104 microphone. This figure, and Figures 7 and 14, are based upon spectrograms made with a wide-band pass filter of 300 cps. All the other spectrograms illustrated were made with a wide-band pass filter of 600 cps.

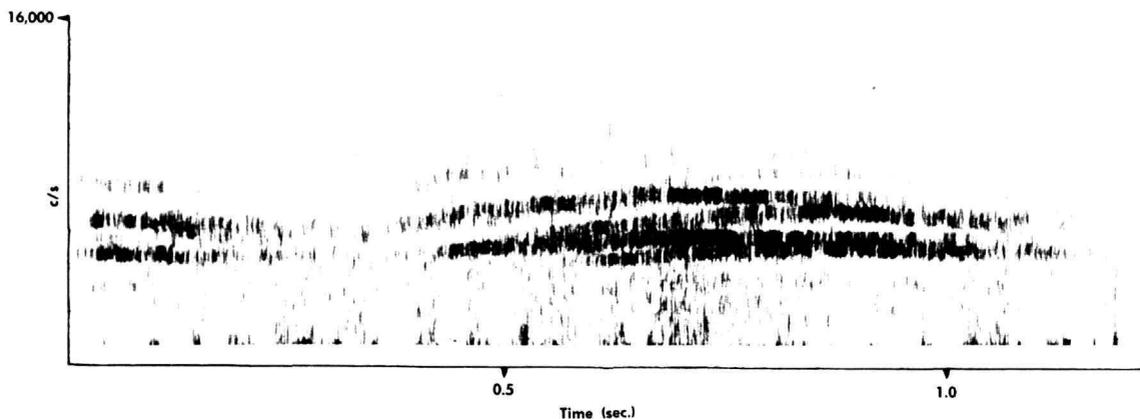


FIGURE 4.—The latter part of the second note and the whole of the third note of a three-note Long Whistle series by an adult Rufous-naped Tamarin. Some of the general "fuzziness" may be background noise or some other artifact, but certainly not all of it.

As might be expected, in view of their loudness, Long Whistles seem to be purely long-distance signals. They are uttered in a very peculiar and complex set of social and environmental circumstances.

They are uttered most frequently by individuals who have become separated from their usual companions; i.e., the other members of the same social unit (pair, family, or band). In the wild, a separated individual usually begins Long Whistles when, and as soon as, it realizes that its companions are no longer in sight. Captive individuals can be induced to utter

Long Whistles even when their usual companions are in full view, if they are prevented from rejoining the companions by some physical barrier such as a wire-netting screen. Long Whistles also are the first or only response of any normal adult individual kept in both physical and visual isolation in captivity when it hears a tape-recording of *any* sound of the species.

These facts would suggest that Long Whistles can function as "lost calls" or "location calls." They must reveal the location of a calling individual, and often indicate that it is alone.

The responses to Long Whistles by an isolated individual in the wild, under natural conditions, are rather varied. Usually, when the notes are being uttered by an individual who is a member of an established social group, the other members of the group go on about their business, perhaps uttering a few Long Whistles of their own in "reply" to the separated animal, but otherwise apparently unconcerned. In such cases, in the wild, the isolated individual sooner or later starts to search for, or runs to catch up with, its companions. It continues Long Whistles during these movements. But it stops them as soon as it finds and rejoins its companions. Occasionally, the isolated individual is particularly slow in beginning to search or follow. In these circumstances, the companions may eventually begin to search for it, and usually rejoin it after more or less of a delay. Again, the Long Whistles usually stop as soon as the group is reassembled. Such reactions would suggest that Long Whistles by one member of a group are more or less strongly attractive to some or all of the other members of the same group.

It is possible that Long Whistles also play a role in "pair formation" in certain circumstances.

Actually, as might be inferred from many preceding comments, I saw very little behavior which could be characteristic of an initial or other "early" stage of pairing in the wild. It is my impression that Rufous-naped Tamarins probably usually form pair bonds with a sibling or some other member of their own family group, and that such pair formation is a gradual process, accompanied by a minimum of conspicuous display. But I did see one individual (sex unknown) in the wild who was apparently unmated and quite solitary, and who uttered many Long Whistles for hours on end over a period of several days, while it roamed back and forth over its extensive home range or territory. A few days later, this individual was found to have acquired a companion, presumably a mate. Possibly, the mate had been attracted by the Long Whistles. In any case, once the pair was formed the Long Whistles were uttered much less frequently.

Long Whistles probably also subserve other functions in other circumstances. Certainly, they apparently are not always attractive. Sometimes, in fact, they may be just the opposite. They apparently can be used to maintain the integrity of territories.

The usual (and only acceptable) definition of territory is "any defended area." In many New World primates, defense of territory is obvious as such. It may take the form of actual attacks upon, or fights with,

neighbors and intruders. Or it may be effected by displays whose nature is unmistakably hostile. This does not, however, usually seem to be true of *S. geoffroyi*. As noted above, I never saw contact fighting, i.e., wrestling with biting and kicking, among tamarins in the wild. I saw only one encounter between individuals of different social groups in the wild which involved other hostile movements, some brief aggressive chasing back and forth. Even more remarkably, I never saw individuals of different social groups in the wild direct toward one another such unmistakably hostile vocalizations (which are characteristic of disputes in captivity) as Long Rasps, Broken Rasps, and Loud Sharp Notes. (All disputes in the wild which were accompanied by such notes, and the few other cases of obviously aggressive chasing, were among individuals of the same social group.)

I have, however, occasionally seen two or three different bands (or smaller social units) of tamarins remain for considerable periods of time (10 to 30 minutes) in trees only 10–100 yards apart, while some or all of the members of the different groups uttered numerous series of Long Whistles in steady and rapid succession. The notes obviously were directed toward individuals of the other group(s). The vocalizing animals usually looked straight toward the other group(s). And they continued to utter Long Whistles throughout the whole of the period of "confrontation," *even when* all the other members of their own group were gathered close around. Eventually, one or all of the groups retreated. And then the Long Whistles stopped.

This would suggest two things. One, Long Whistles can be released by factors other than physical isolation. And secondly, the Long Whistles of one individual can be definitely repellent to individuals of other groups in at least some circumstances.

The most interesting feature of such reactions is not that the repulsion of other groups, in effect the defense of territory, can be accomplished without overt fighting, but that the signals employed or involved, the Long Whistles, do not seem to be primarily hostile in motivation.

That the immediate causation of Long Whistles is essentially non-hostile is indicated by much of the evidence cited or referred to above. Long Whistles by isolated individuals really are very much more common than similar notes by individuals of different groups confronting one another. More important, it was possible to arrange a very great number of overtly hostile encounters of many different types among the indi-

viduals kept in captivity; and the overwhelming majority of these encounters were not accompanied by, or associated with, Long Whistles.

Of course, there were some problematic and probably ambiguous reactions. Thus, for instance, the one observed case of aggressive chasing among individuals of different groups in the wild was associated with Long Whistles—and no other vocalizations. In captivity, Long Whistles were observed to be uttered during one violent hostile encounter which developed after a stranger was introduced into a cage already occupied by a group of four. These Long Whistles were uttered while vigorous chasing and actual contact fighting were in progress, and were associated with many other unmistakably hostile vocalizations; but all or most of them were uttered by individuals who were not actually fighting with the stranger at the precise moment of utterance.

Both these individuals and the ones involved in less active “confrontations” between groups in the wild may have had very “mixed” feelings toward their “opponents.”

(I have also heard captive Rufous-naped Tamarins utter Long Whistles in apparent response to the approach of wild spider monkeys, *Ateles*, and anteaters, *Tamandua*; but captive primates often are not very discriminating in their reactions between their own and other species.)

On general methodological grounds, it would seem to be desirable to “explain” all performances of any given type of display, or any other behavior pattern for that matter, as direct consequences of the same causal factor(s) in all the circumstances in which the display or other pattern may occur. This is not always possible (viz., the Allogrooming described above). But it may be feasible in the case of the Long Whistles of Rufous-naped Tamarins. They may all be the results of thwarting some gregarious and/or pairing motivation, produced when the motivation is prevented from being expressed overtly, by joining, either by the interposition of some physical barrier (or ignorance of the location of other individuals) and/or the counteracting effects of some other simultaneously activated but “incompatible” type of motivation (such as feeding, escape, attack, or what have you).

The length of the series of notes in a typical Long Whistle performance obviously is correlated with the strength of the gregarious or pairing motivation and/or the strength of the thwarting. When many Long Whistles are uttered, the average number of notes

per series is higher than when fewer Long Whistles are uttered in the same length of time. (This is true only of typical Long Whistles. The general rule does not apply to performances which may be intermediate between typical Long Whistles and typical Twitters. See also below.)

The bivalent signal effects of *geoffroyi* Long Whistles, i.e., the attraction of members of the same group and the repulsion of members of other groups, are the same as those of the Songs of many species of birds. The Long Whistles probably are, in fact, strictly analogous to many bird Songs. Their relationships to patterns of other species of Platyrrhini are less obvious or, at least, more complex.

Some of the social circumstances in which Long Whistles are uttered are reminiscent of the “Hoots” of *Aotus*. The Hoots also are uttered by isolated individuals, apparently as a result of thwarting gregarious and/or pairing motivation. (Hoots have not been observed to be used to maintain the integrity of territories; but observations of Night Monkeys in the wild are so difficult that reactions of this type could be easily overlooked.) Hoots also resemble Long Whistles in being usually uttered in a series of two or three notes, each one of which is actually compound. These facts would suggest, very strongly, that the Long Whistles of *S. geoffroyi* are strictly homologous with the Hoots of *Aotus*.

The principal difference between Hoots and Long Whistles is pitch or frequency (cycles per second). The audible components of Hoots are *much* lower in pitch than the loud components of Long Whistles. But the importance of this difference should not be overestimated. As noted in Moynihan (1967), there seems to have been strong selection pressure in favor of raising the pitch, or maintaining the original high pitch, of all the vocal patterns of tamarins and marmosets. Simply because these animals are small, they probably are particularly vulnerable to predation. High-pitched sounds do not carry as far as low-pitched sounds. (The energy of a sound is lost in heating the air through which it passes, and sounds of higher pitch are used up more rapidly than sounds of lower pitch. Also, the relatively short waves of high pitched sounds will be more “scattered” by obstructions such as leaves and branches than the longer waves of low-pitched sounds.) Thus, high-pitched sounds are relatively less likely to attract the attention of potential predators, and this quality may be particularly valuable to tamarins and marmosets. In the case of *Aotus*, by contrast, there may

have been strong selection pressure in favor of low pitch, simply because the species is nocturnal, and has to rely upon vocalizations more nearly exclusively than all or most other New World primates. This may put a "premium" upon sounds which carry a long distance. (Possibly, the nocturnal habits of this species also make it less vulnerable to predation, at least predators approaching from a distance.) In any case, it is obvious that homologous vocal patterns have undergone major changes in pitch during the evolution of one or more groups of New World primates.

To human ears, individual Long Whistle notes also sound rather similar to both the Whistles and Screams of *Callicebus moloch*. This apparent resemblance is confirmed by analysis of sound spectrograms. Individual Long Whistles of Rufous-naped Tamarins are not very different from some Screams of *C. moloch* in basic structure. (They are less similar to *moloch* Whistles in structure, but there is other evidence that the latter patterns are closely related to Screams.) Nevertheless, it probably is significant that the Screams and Whistles of *C. moloch* are not usually arranged in short series like the Long Whistles of *S. geoffroyi* (or the Hoots of *Aotus*). They also occur in rather different sets of circumstances. The Screams of *C. moloch* (like the Long Rasps of Rufous-naped Tamarins) certainly are completely hostile. The Whistles of *moloch* probably are at least partly hostile. It is equally suggestive (in a different way) that individual Long Whistles of *S. geoffroyi* also sound rather like some Whistle patterns of other tamarins; i.e., *S. fuscicollis*, *Callimico goeldii*, and *Leontideus rosalia*. These also are partly or completely hostile and not usually arranged in specialized short series. Possibly all these patterns (including the Long Rasps of *geoffroyi*) are related phylogenetically. If so, the Long Whistles of *geoffroyi* probably are descended from a pattern originally produced by hostile motivation. (It seems likely that displays have changed from hostile to non-hostile, in the course of evolution, more frequently than the reverse, for obvious reasons. See also Moynihan, 1962.) If this assumption also is correct, then the Long Whistle patterns may represent an intermediate stage in evolution. They are almost exactly halfway between the Whistle and Scream patterns of many other Platyrrhini, on the one hand, and the Hoots of *Aotus* on the other hand. Possibly, the Hoots of *Aotus* passed through a similar stage in the course of evolution, probably before the species became completely nocturnal. (Some

of these patterns, and other related sounds, are also discussed on page 68.)

Although the Long Whistle performances of Rufous-naped Tamarins seem to be analogous to the Songs of many birds, they certainly are not homologous with the whole of the complex of vocal patterns of *Callicebus moloch* which has been called "Song." At best, they are homologous only with the Whistle phases of the (relatively few) Song performances of the latter species which include such phases.

(As an illustration of the difficulties which may be encountered in attempting to decipher the phylogenetic relationships and functional equivalence of the display patterns of different Platyrrhini, it may be mentioned that the most spectacular components of the majority of "complete" Songs by *C. moloch* are "Resonating Notes," and that these notes probably are strictly homologous with the "Resonant Grunts" of *Aotus* which probably do not function as Song.)

• *Twitters*.—These patterns are among the most characteristic of the vocalizations of adult Rufous-naped Tamarins. A typical Twitter performance consists of a series of moderately soft, rather high pitched, moderately short notes. The intervals between notes of a single series are quite variable, but usually not more (and often much less) than twice the length of a single note. The general effect, to the human ear, is usually quite rapid (almost "bubbling"). The number of notes per series also is variable. Probably the great majority include four to ten notes. Single notes essentially similar to the notes of series occasionally are uttered by themselves alone. It may be convenient to refer to both the single notes by themselves alone and the individual notes of series as "Short Whines." They all have something of the same plaintive quality as Long Whistles. Several Twitters are shown in Figures 5, 6, and 7. It will be seen that some of the notes in these series are almost flat, but that the majority rise in pitch. In some cases, the rise is steep. Also in some cases, the rise is preceded by a relatively brief descending phase. Very occasionally, a single note may first rise, then fall, and then rise again (see the second Short Whine in Figure 5).

(It may be necessary to add one more comment on terminology here. Series of Short Whines have been called Twitters in this paper because they belong to the class of sounds usually described as "twittering" in ordinary, every day, English speech. This usage must be distinguished from that of Andrew [1963], who uses the term in a restricted and rather special

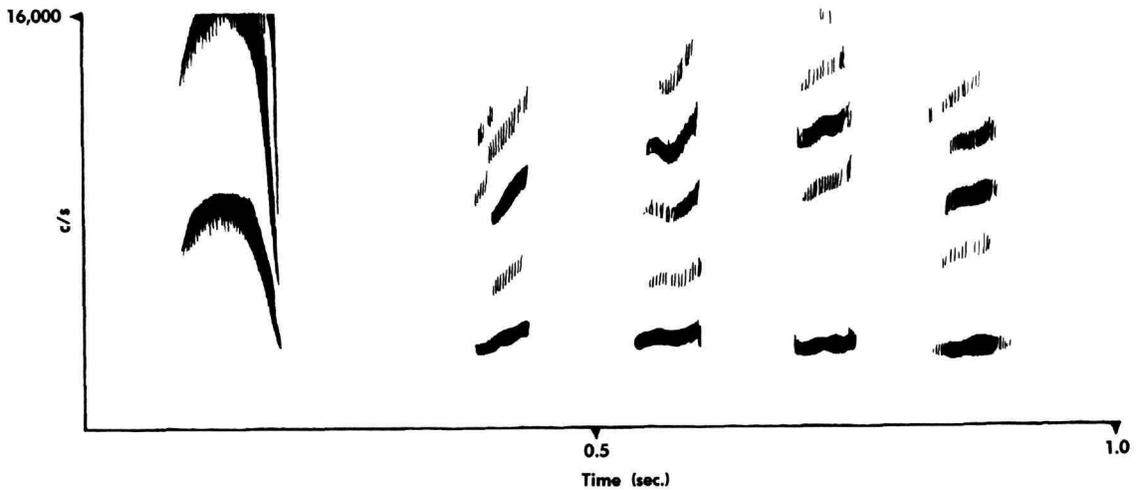


FIGURE 5.—A Sharp Note followed by four Twitter Notes (Short Whines) by an Adult Rufous-naped Tamarin. The Sharp Note may be intermediate between the typical Loud and Soft forms. All series of notes illustrated throughout this paper are "natural." Each series was uttered by a single individual. The intervals between successive sounds are those shown on the spectrograms.

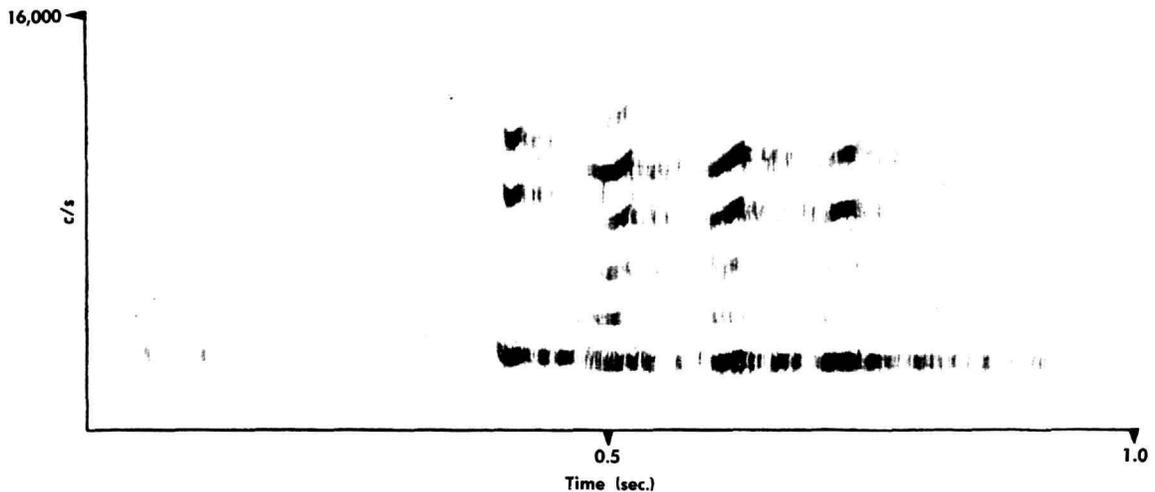


FIGURE 6.—A Twitter by an adult Rufous-naped Tamarin. The individual notes show a slight tendency to "run together." This may be an indication of relationship to (or intergradation with) Long Whistles.

sense. He defines "a Twitter" as a "high short call which ascends or descends steeply [or does both in a chevron]." Some of the Short Whines of Rufous-naped Tamarins conform to this definition, but others do not. And there are other patterns in the repertory of the species which conform much more consistently to Andrew's definition, but which are quite distinct from the Short Whines and do not sound at all twittering in

the ordinary sense of the word. Andrews also states that "Titters" are the "main type of vocalization" in all genera of tamarins and marmosets. Unfortunately, "Titters" in his sense include so many different types of vocalizations, some of them only distantly related, that the statement is essentially meaningless. Some other features of Andrew's account will be discussed on page 70).

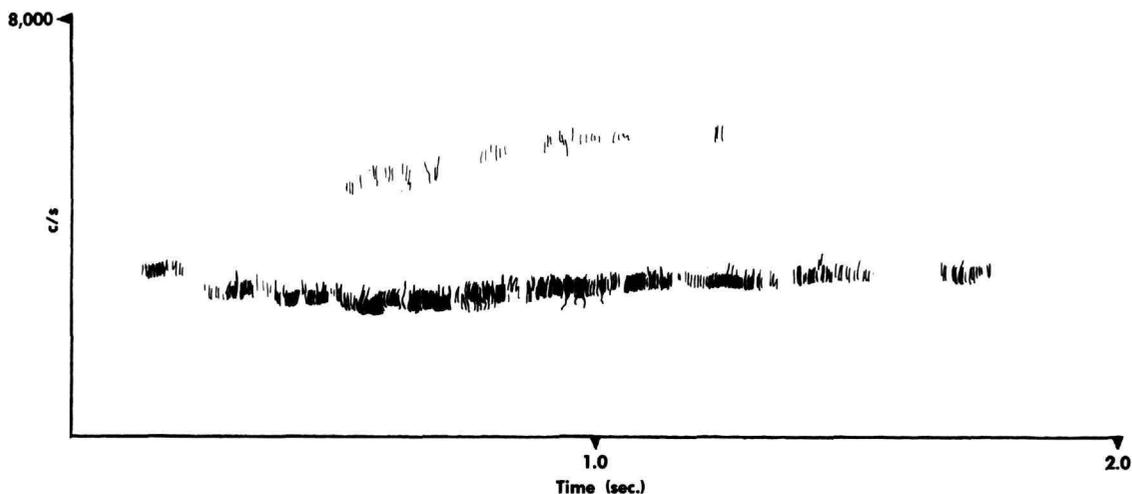


FIGURE 7.—A Twitter by an adult Rufous-naped Tamarin. The resemblance to Long Whistles is even stronger than in the preceding example.

The Twitters (as the term is used here) of Rufous-naped Tamarins are uttered in a wide range of social situations and probably are very highly ambivalent. They are uttered very frequently as reactions to potential predators; i.e., by wild individuals to the appearance of human beings and by both wild and captive individuals to other large mammals and hawks. They also are uttered by captive tamarins during some disputes among themselves. In both sets of circumstances, they often are closely associated with unmistakably hostile Loud Sharp Notes and/or Trills. Occasionally, they are combined with equally hostile visual signals such as Swaying, Crown-smoothing, and related or associated patterns (see below). All this would indicate that the Twitters themselves are at least partly hostile. Probably, the hostile motivation involved is purely or predominantly the escape tendency. Twitters occur relatively frequently immediately before, during, or after overt retreat, but relatively very seldom immediately before attack. On the other hand, there are very strong indications that many or all Twitters are also partly non-hostile. They are uttered by very tame, hand-reared, captive individuals as reactions to the approach of human beings from whom they expect to get food. In such circumstances, they appear to be a form of "greeting" (or even "food-begging"). The great majority of Allogrooming performances and copulation attempts are silent, but a few are accompanied by sounds, and Twitters and single Short Whines are among the least uncommon of such sounds. Twitters

also are uttered when captive individuals who are well acquainted with one another (and well adjusted to one another) move around their cages, in more or less close proximity, without any signs of overtly hostile movements. It will be remembered that Twitters resemble the apparently non-hostile Long Whistles in tone (see above). More important, they actually intergrade with Long Whistles with some appreciable frequency. (This intergradation may take either one of two forms. In some cases, a single note of a Twitter is unusually prolonged. In other cases, all the notes of a whole Twitter series tend to "run together" to form a long semicontinuous pattern which is quite reminiscent of some Long Whistles when analyzed on a spectrogram. Figures 6 and 7 illustrate this phenomenon to varying degrees.)

Thus, all the evidence, taken together, would suggest that all or most Twitters are produced when the escape tendency and some friendly and/or sexual tendency are activated simultaneously.

From some points of view, it may be convenient to consider the Long Whistles, Twitters, and Short Whines as different "parts" of a single "complex" of patterns. This complex may be given the name of "Plaintive Notes."

Probably, all or most Twitter performances are low to moderate intensity; i.e., produced when all the activated tendencies are only moderately strong (at best). They are uttered relatively most frequently by animals which do not seem to be very excited. Thus,

for instance, a wild individual reacting to a potential predator which is nearby but stationary (and not making any threatening gestures) usually begins by uttering many Loud Sharp Notes and/or Trills as well as Twitters. Then, if the individual does not run away, and as it becomes accustomed to the presence of the disturbing stimulus, it gradually stops uttering the Loud Sharp Notes and Trills, while continuing the Twitters. As habituation proceeds even further, the Twitters also decline in frequency, until finally the animal relapses into silence. Similarly, of course, it is the Long Whistles and not the Twitters which are usually uttered by individuals which have become widely separated from mates or other social companions.

Short Whines uttered singly, by themselves alone, probably are produced by much the same type of motivation, combinations of the same tendencies, as the Twitters of several notes. But they probably are even lower intensity, produced when all the tendencies involved are actually weaker. They occur in much the same range of social circumstances as Twitters, but they are relatively much less common in the more "tense" or exciting situations, and relatively much more common in the less exciting ones. Thus, for instance, they are relatively rare during initial reactions to potential predators, but relatively very common when well adjusted cage mates are moving around together.

The Short Whines and full Twitters which are most plaintive in tone, or otherwise most similar to Long Whistles, probably are produced when the non-hostile motivation is relatively stronger (compared with the hostile motivation) than when less plaintive or less prolonged patterns are produced.

Although Twitters and Short Whines must be signals, they do not seem to be invariably precise and consistent "commands." When Twitters are uttered by one individual as a reaction to a potential predator, they may function as alarm or warning signals. They may induce immediate retreat by other members of the same social group or "trigger" the performance of "distraction" or "mobbing" patterns. In the latter case, the other members of the group usually gather around the first individual and utter more Twitters or, more frequently, Trills and/or Loud Sharp Notes, before drifting away, one by one, as described on page 13. In other circumstances, the Twitters do not seem to induce any overt movements, not escape nor approach nor anything else. Possibly, such Twitters may serve as another type of "contact pattern" or "location call," roughly comparable to Long Whistles in helping

to maintain the cohesion of a social group, but presumably effective only over shorter distances. In any case, as the Twitters seem to reflect or express the motivation (and perhaps other aspects) of a calling animal quite precisely, they must be capable of conveying this information to all or many other individuals within earshot. The information may be stored away "for future reference" even when it is not reacted to immediately.

As a partial summary, it may be said that most Twitters and Short Whines seem to be more "priming" than "releasing."

Some of their relationships to patterns of other species are fairly clear. Their plaintive quality, some of the circumstances in which they occur, and their mixed hostile and non-hostile motivation, are all more or less strongly reminiscent of the Moans of *Callicebus spp.* and both the Moans and Low Trills (which may be nothing more than rapid series of abbreviated Moans) of *Aotus*. Possibly they are largely homologous with all these patterns. But they differ conspicuously from both the *Callicebus* and *Aotus* patterns in some (other) aspects of form, especially in being much higher pitched. Thus, the physical differences between Twitters and Short Whines and the most nearly equivalent *Callicebus* and *Aotus* patterns is exactly parallel to that between Long Whistles and the Hoots of *Aotus*.

These suggested homologies are supported by other evidence; i.e., some aspects of timing. Thus, for instance, when Twitters and Loud Sharp Notes are uttered together, apart from other patterns, the usual sequence is one Loud Sharp Note followed by one Twitter series (see Figure 5). There is reason to believe that the Loud Sharp Notes (and the not very dissimilar Sneezing Sharp Notes) of *S. geoffroyi* are phylogenetically related to the Sneeze-grunts of *Aotus* and the "hostile sneezes" of *Callicebus moloch* (see page 42). Thus, it is interesting, and probably it is significant, that *C. moloch* individuals tend to utter Sneeze-Moan series, and that Night Monkeys utter both Sneeze-grunt-Moan and Sneeze-grunt-Low Trill series relatively frequently.

It would appear that the arrangement of some acoustic signals has been even more conservative than their form during evolution.

Of course, even if the Twitter and Short-Whine patterns of Rufous-naped Tamarins are largely homologous with the Moans and Low Trills of *Callicebus* and *Aotus*, this does not necessarily mean that they may not

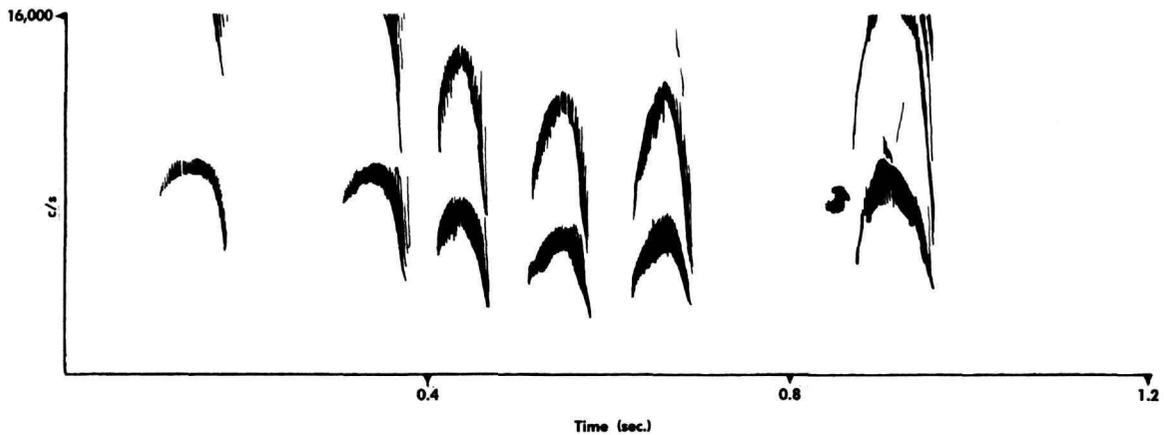


FIGURE 8.—A Trill by an adult Rufous-naped Tamarin. The third, fourth, and fifth notes of the series may be quite similar to individual Soft Sharp Notes.

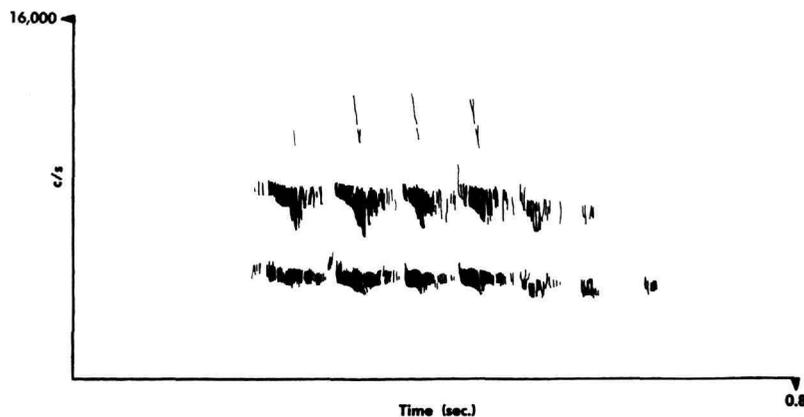


FIGURE 9.—A Trill by an adult Rufous-naped Tamarin. Some of the "fuzz" may be an artifact. But the notes of this series certainly are not absolutely identical with those illustrated in the preceding figure.

also be related to some other patterns of the same species; e.g., some of the high-pitched Squeaks of *Aotus* which are uttered in sexual situations. Although it is possible to trace homologies among the patterns of different Platyrrhini, the correspondence is not always perfectly one to one. See also below.

• *Trills*.—These patterns, and the next three cited below, may be considered parts of another "complex." This may be given the inclusive general name of "Sharp Notes." It seems to be roughly comparable to the Plaintive Note complex in scope.

The Trills are the most Twitter-like of the Sharp Note patterns. They are rapid series of short notes.

Usually, there are seven to twelve notes per series, but the individual notes do not sound at all plaintive to human ears. They also differ from Short Whines in sequence of changes of pitch. A single Trill note usually begins with a rise, or a nearly horizontal phase, and then falls. The emphasis always is on the terminal downbeat rather than the preceding upbeat. The transition between the phases of a single note is more or less abrupt. All typical Trills also are appreciably louder than typical Twitters. Several Trills are illustrated in Figures 8, 9, and 10.

Brief experiments with a "bat detector" indicate that some, if not all, Trill notes include loud ultrasonic

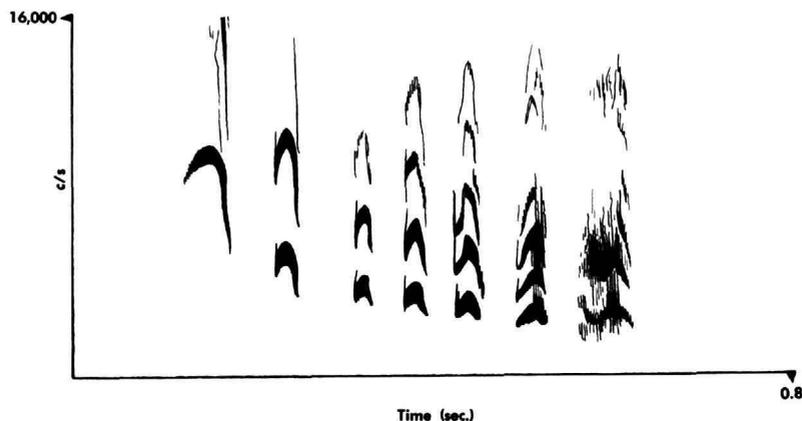


FIGURE 10.—Another Trill by an adult Rufous-naped Tamarin. The last two notes of the series would appear to represent intergradation with Rrasping patterns.

components, up to at least 24 kilocycles. (Probably such components are absent in Plaintive Notes.)

In a very few cases, the first “regular,” rising, phase of a Trill note is preceded by a very rapid and short “introductory” phase which is steeply descending. This is illustrated by several of the notes in Figure 10. These introductory phases may not have any functional significance. They certainly cannot be detected by the human ear. They may also be too brief to be heard by other animals.

Most Trills are obviously reactions to disturbing stimuli; i.e., potential predators. Some of the circumstances in which they occur have been mentioned above. Shy individuals in the wild frequently utter Trills when they see a human being. Both wild and captive individuals utter Trills when other large mammals pass by and birds of prey fly overhead. Trills may be accompanied by Swaying and (very occasionally) Head-flicks, and are uttered rather frequently immediately before, during, and/or immediately after retreat movements. All this would indicate that they are hostile. Unlike the Twitters, they probably are purely hostile. They are relatively much less common during intra-specific encounters. They may be quite absent during encounters or reactions among individuals which are familiar with one another. They are apparently never uttered as “greetings” or “food-begging” by captive individuals.

It has already been indicated that Trills probably are of higher intensity than Twitters on the average. They are never uttered by individuals which seem to be as little excited or disturbed as some individuals

uttering Twitters. Some Twitters certainly are produced when hostile motivation is weaker than in any Trills. Possibly, some Trills are produced when hostile motivation is (actually) stronger than in any Twitters.

The frequent association of Trills with overt retreat would suggest that they usually or always are produced when the escape tendency is stronger than the attack tendency. But the actual strength of attack motivation probably is not negligible. The retreats closely associated with Trills usually are not very rapid or prolonged. More important, Trills sometimes are closely associated with Rrasping sounds, which certainly include some aggressive tendencies (see pages 33 and 35). They may even intergrade with Rrasping sounds. One type of intermediate between the two classes of vocalizations is shown in Figure 10.

The function(s) of Trills probably are not very different from those of the Twitters which are uttered in interspecific hostile situations. They seem to be primarily warning or alarm notes (see also below).

• *Loud Sharp Notes.*—These notes may be uttered singly or in irregular, variable, and obviously unritualized series. Single Loud Sharp Notes are very similar to single Trill notes in basic form, but much louder and with higher ultrasonic components (more harmonics). In some cases, at least, they include loud components up to 45 kilocycles. The lower parts of two more or less typical Loud Sharp Notes are shown in Figure 11.

Such notes certainly are another type of alarm call. They are uttered as reactions to potential predators. Particularly as an initial reaction and/or when a preda-

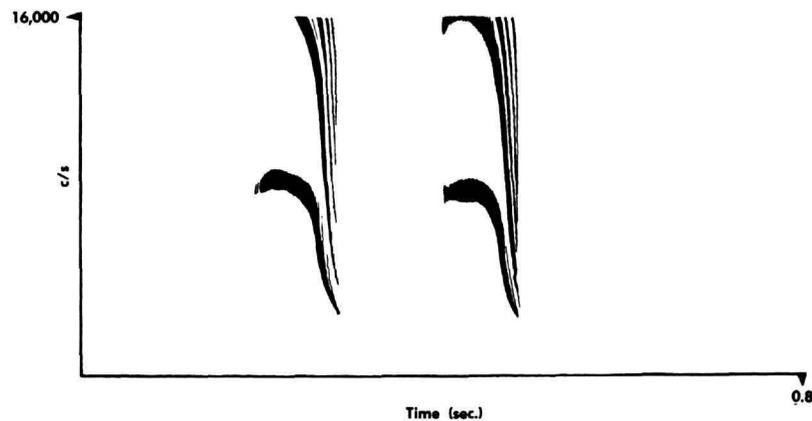


FIGURE 11.—The lower parts of two typical Loud Sharp Notes by an adult Rufous-naped Tamarin.

tor is very close (see above). They also occur during particularly violent intraspecific disputes. They usually are closely associated with escape movements, usually vigorous and rapid escape (“blind panic” during intraspecific fights). They may be combined with Swaying, Crown-smoothing, Head-flicks, and/or Tail-ruffling. They are extremely “contagious.” The sound of Loud Sharp Notes by one individual usually induces the utterance of similar notes by all other members of the same species in the immediate neighborhood. Once started, they may continue to utter such notes for ten minutes or more (a very long time for tamarins, which tend to be extremely “changeable” or rapidly variable in behavior). Loud Sharp Notes certainly are more contagious than either Twitters or Trills. They also stimulate escape movements by other individuals (relatively) more frequently than do either of the latter patterns.

Obviously, the Loud Sharp Notes are high intensity, produced by strong hostile motivation. And they probably are purely hostile. They are never closely associated with even partly friendly reactions among individuals of the same species. In these respects (also), they resemble Trills. But the relative strength of the escape tendency must be greater in Loud Sharp Notes than in Trills. Not only are Loud Sharp Notes frequently associated with particularly vigorous overt escape movements, but they seldom or never intergrade or alternate with Rasps. Possibly the actual strength of hostile motivation (as a whole) also is greater in some or all Loud Sharp Notes. Some individuals utter-

ing such notes seem to be more excited than any individuals uttering Trills.

The Loud Sharp Notes of Rufous-naped Tamarins probably are largely or completely homologous with the equally loud and almost equally abrupt alarm notes of many other Platyrrhini, e.g., *Cebus* spp. As noted above, they also seem to be related to several patterns of *Aotus* and *Callicebus moloch*. Some or all of the latter may not (usually) function as warning signals now; but they may have been derived from, or contributed to the development of, such patterns in the past. This subject is discussed in more detail on page 42 et seq.

Another point of comparative interest is considerably more problematic. Rufous-naped Tamarins seem to have more different types of vocal alarm signals than any other New World monkey whose behavior has been studied. This may be correlated with their apparent vulnerability to predation. But the exact nature of the relationship remains obscure. All I can suggest is that combinations of different types of signals may provide more precise information about the positions and probable intentions of potential predators, and/or may be more effective in attracting and retaining attention (of the predators and/or other tamarins), than even a multitude of variations on a single type of signal.

• *Soft Sharp Notes.*—Individual Soft Sharp Notes are essentially identical with both Loud Sharp Notes and individual Trill notes in basic form. They can be distinguished only by other features. They are comparatively very soft, much softer than typical Trill

notes, to say nothing of typical Loud Sharp Notes. (This is true at least in the range of frequencies, cycles per second, audible to human ears. Some, although certainly not all, Soft Sharp Notes include ultrasonic components up to 44 kilocycles. But these also may be softer than the equivalent parts of Loud Sharp Notes.) Some Soft Sharp Notes sound approximately as loud, in human ears, as many Twitters and single Short Whines; others may be even softer. They always are uttered singly or in short irregular series. These series are rather similar to series of Loud Sharp Notes, but probably are shorter, including fewer notes, on the average, and relatively rarer (by comparison with single notes).

Several of the individual notes shown in the illustration of a Trill in Figure 8 probably are (loudness excepted) very similar to the most common type of Soft Sharp Note.

Soft Sharp Notes certainly intergrade with Loud Sharp Notes (see Figure 5). They probably do so rather frequently. They may also intergrade with Short Whines, but I was never able to record an unmistakably intermediate pattern.

The significance of Soft Sharp Notes is difficult to determine, for practical reasons. Notes of this type certainly are uttered by individuals in the wild, but they are so soft that a human observer may fail to hear them. Thus, it is impossible to say anything very definite about their frequency, or the circumstances in which they usually occur, under natural conditions.

Captive individuals sometimes utter many Soft Sharp Notes while they move around their cages, as long as they are not engaged in more elaborate forms of social behavior, such as disputing or Allogrooming. This is reminiscent of the single Short Whines (see above). But Soft Sharp Notes differ from the Short Whines in being apparently non-friendly. Captive individuals sharing the same cage, and more or less well adjusted to one another, utter Short Whines both when they are close together and when they are far apart. But they usually utter Soft Sharp Notes only when apart.

Soft Sharp Notes must be very low intensity patterns. Possibly, they are produced by much the same type of motivation as Trill notes and/or Loud Sharp Notes, when both attack and escape tendencies are much weaker. One might expect that an individual of a vulnerable species would be slightly "nervous" whenever it moved around by itself, even in a familiar environment. Also, I have heard Soft Sharp Notes uttered in apparent response to usual loud noises outside the cages. Possibly, therefore, the Soft Sharp Notes are the lowest intensity alarm call of the species. They may also, at least occasionally, function as another type of contact note. (If so, their evolutionary history may have been somewhat comparable to those of the "Gulps" and Sneeze-grunts of *Aotus*. See below.)

• *Sneezing Sharp Notes*.—Both typical Loud and typical Soft Sharp Notes are quite "thin" and "clean." Both might be transcribed as "Tsit." But Rufous-naped Tamarins also emit notes which sound like "hoarse"

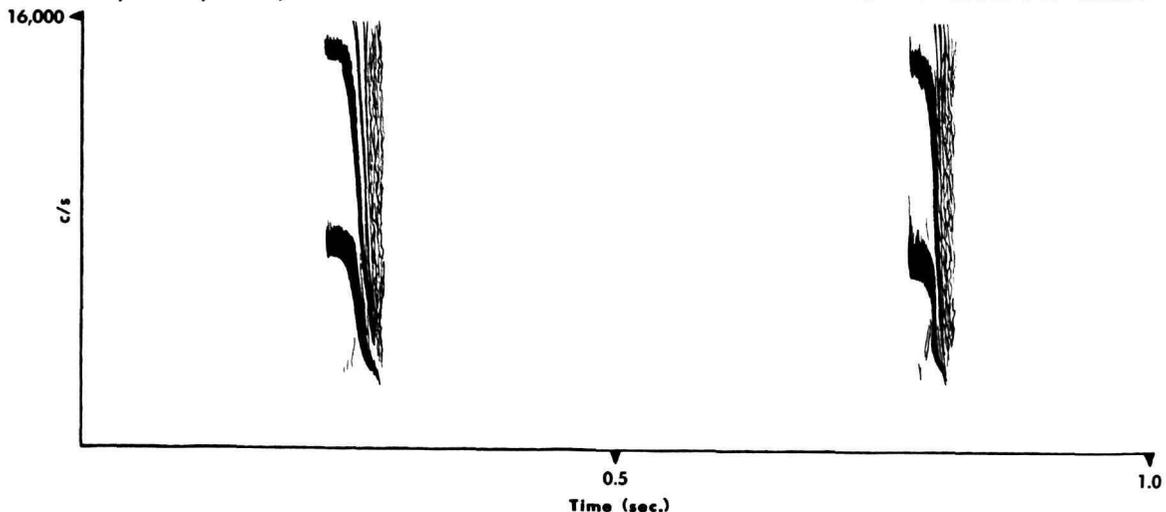


FIGURE 12.—The lower parts of two typical Sneezing Sharp Notes by an adult Rufous-naped Tamarin.

versions of Soft Sharp Notes. A single note of this type might be transcribed as "Tchuck." The actual sound is almost as reminiscent of the "ordinary" unritualized sneezes (which tamarins also perform in certain circumstances, see below) as of the other vocalizations. Two typical "Tchuck" notes are shown in Figure 12. It will be seen that both consist of two parts: first, a single clear sound, beginning horizontal and then descending abruptly, followed immediately by a thin column of "white noise." This second part is very similar to the Sneezes of *Callicebus moloch* in form (unfortunately, I do not have a recording of the ordinary sneezes of *S. geoffroyi*). Thus, it seems very probable that the "Tchuck" notes really are ritualized combinations of sneezes and Soft Sharp Notes.

Such Sneezing Sharp Notes certainly intergrade with typical Soft Sharp Notes. They also are uttered by captive individuals in much the same circumstances. (I did not identify them in the wild, but there is no reason to suppose that they do not also occur under natural conditions.) Possibly, all or most captive individuals were a little more obviously "nervous" when they uttered Sneezing Sharp Notes than when they uttered ordinary Soft Sharp Notes. In any case, it seems likely that both Sneezing and Soft Sharp Notes subserve much the same range(s) of functions.

• *Long Rasps*.—This pattern and the next are parts of another complex which may be given the name of "Rasping." Morphologically, the components of this

complex are the most distinctive of the vocalizations of the species. All the other notes and calls (with the partial exception of the Sneezing Sharp Notes) usually are clear in tone, to human ears. But the Rasping patterns are definitely and unmistakably harsh.

Long Rasps themselves are loud harsh screeches. Their actual length is variable, but the great majority are more or less prolonged. Figure 13 shows one of the shortest types, plus one of moderate (possibly average) length. It will be seen that each note is composed of a very large number of separate pulses of sound, and that the longer note is gradually ascending throughout most of its length.

Long Rasps intergrade with both Broken Rasps and (usually only in young individuals) Infantile Rasps.

They are uttered in a more restricted range of social situations than most other vocal patterns of the species. They are most common during extremely violent intra-specific disputes, when two individuals are actually wrestling with one another. In such circumstances, they may be uttered by the individual which begins the fight and/or by the individual which is attacked. They also occur occasionally during vigorous hostile chases. In which case, they usually are uttered by the pursued rather than the pursuer. Very rarely, they are uttered during less vigorous disputes over food, quite apart from chasing or contact fighting. One individual simply stands and screeches in the face of another. Finally, they are uttered by individuals caught and held

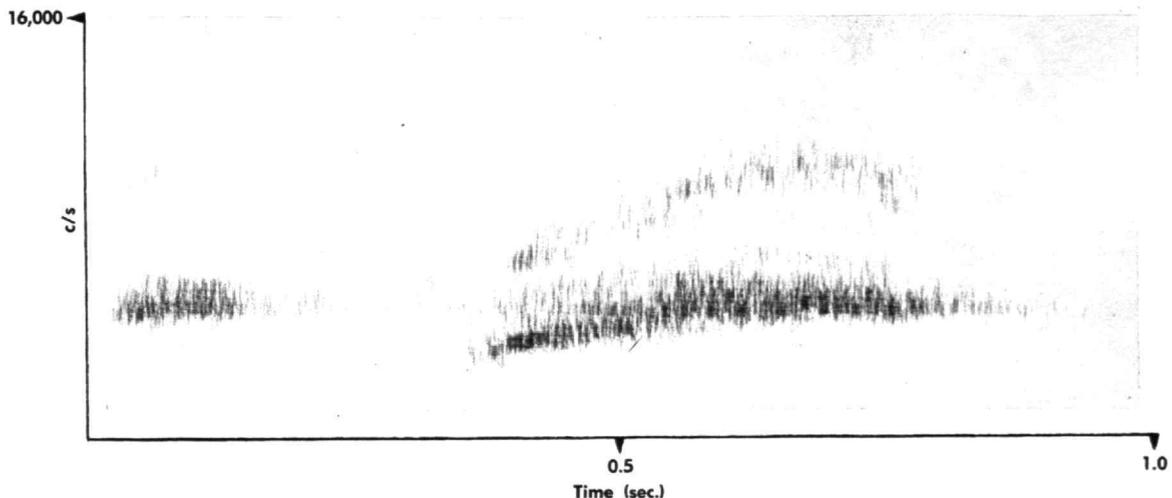


FIGURE 13.—Two "Long" Rasps by an adult Rufous-naped Tamarin. The first note is rather shorter than usual.

by human beings. Such individuals make violent attempts to escape, but they may also attempt to bite or hit their captors.

These facts indicate that Long Rasps are purely hostile, and high intensity on the average. Probably, the escape tendency is stronger than the attack tendency during all or most Long Rasp performances, but the attack tendency may be relatively stronger than in any of the Plaintive or Sharp Note patterns described above.

The signal effects of Long Rasps are difficult to identify, simply because they cannot be separated from those of the accompanying or associated movements and (other) visual signals. Possibly all or most Long Rasps are slightly intimidating; i.e., function as threat in the usual sense of the term.

The length of the Long Rasps, their motivation, and the circumstances in which they occur, would suggest that they are strictly homologous with the Screams of *Callicebus moloch* and *Aotus*.

They probably are less similar in form to the Screams of *C. moloch* than are the Long Whistles (see page 25). But the differences in form may be less significant (or less useful), in determining homologies, than the other similarities between the two patterns. Particularly as it is not difficult to see how the differences could be immediately adaptive.

The distinctive characteristics of the Long Rasps, in this context, are both their harshness and the fact that their loudest components are somewhat lower in pitch than many or most of the loudest components of the apparently homologous *moloch* pattern. This last feature really is quite remarkable. The Long Rasp is perhaps the only vocal pattern of the species which seems to be closely related to a *moloch* vocalization without being equally high, or higher, in pitch to human ears.

This apparent "discrepancy" may be correlated with the relative rarity of Long Rasps, and their virtual restriction to extreme emergencies. Selection pressure in favor of high pitch, to avoid attracting the attention of predators, may have been less severe in the case of the Long Rasps than for most other vocal patterns of the species. One might even suppose that attracting the attention of other non-predatory and non-aggressive individuals, both other Rufous-naped Tamarins and individuals of other species, might be positively advantageous in the circumstances in which Long Rasps are most likely to be uttered. An individual being chased, or engaged in a violent fight, might be relieved by the appearance of some other animal(s) which might distract its enemy or opponent. And, of course, the mere contrast with most of the other vocalizations of the species which is provided by the harshness of the Long Rasps may enhance their "attention getting"

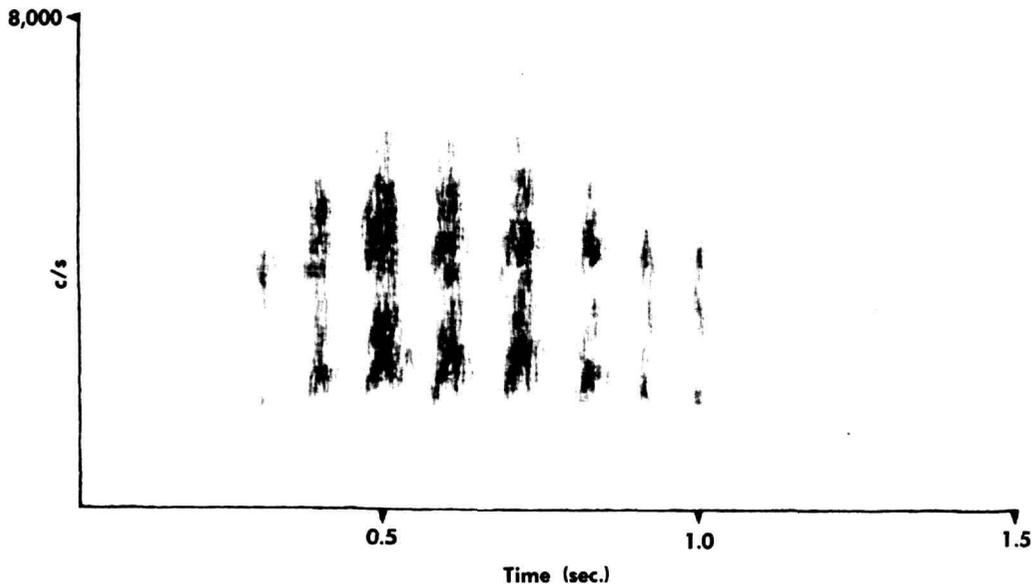


FIGURE 14.—A typical Broken Rasp by an adult Rufous-naped Tamarin.

power, and thus increase the probability of attracting distractors.

- *Broken Rasps*.—These are rapid series of short harsh notes. Each series sounds like a single Long Rasp which has been “broken up.” Figure 14 shows a typical series of this type.

Broken Rasps occur in much the same range of situations as typical Long Rasps, but they are even rarer on the whole. During fights, they are most likely to be uttered at the exact “moment of impact,” just as one individual leaps upon another.

The rhythm of Broken Rasp series is quite like that of the most rapid Trills. Broken Rasps also alternate and intergrade (see Figure 10) with Trills more frequently than do any other Rasping patterns.

These facts would suggest that they are produced by much the same type of motivation as Long Rasps, but are slightly higher intensity, on the average, and/or include a slightly stronger escape component.

They also may function as threat.

- *Persistent Infantile Patterns*.—As noted above, tamarins raised in captivity tend to retain essentially infantile vocal patterns much longer than individuals which have grown up under natural conditions. More precisely, they tend to utter essentially infantile notes more frequently at later ages than do wild individuals. Sooner or later, however, even the most “backward” individuals usually stop uttering such notes as part of their “normal” repertory. This does not necessarily mean that they cease completely. I have heard captive adults, who have been behaving in an entirely adult manner for some considerable time, suddenly utter brief bursts of Infantile Squeaks and/or Infantile Rasps, when obviously badly frightened (see page 12) or in certain complex and extremely ambivalent social circumstances, such as particularly vigorous Allogrooming performances. Possibly, these “recrudescence” patterns function as some sort of “appeasement” and/or “deceptive” signals (see both page 38, and Moynihan, 1955b). If so, they may (also) be related to the Squeaks uttered by adult Night Monkeys in certain sexual situations.

- *General Comment*.—Before proceeding to other subjects, it may be useful to add some further comments on comparative aspects of the organization, articulation, and functioning of the vocal repertory of adult Rufous-naped Tamarins as a whole.

The only other Platyrrhini whose signal patterns have been analyzed in detail, in both captivity and in the wild, are *Aotus trivirgatus* and *Callicebus moloch*.

Many of the vocalizations of these two species certainly are homologous. They tend, however, to be used in very different ways. Intermediates among major types of vocalizations are common in *C. moloch*, but relatively rare in adult *Aotus*. Many vocal patterns of adult Night Monkeys are rather precise commands or releasers (i.e., they can be described quite legitimately in such terms as threat and appeasement). The same patterns tend to induce the same responses in all other individuals of the same species in a wide variety of circumstances. The comparable and/or homologous patterns of *C. moloch*, by contrast, are very much less precise as commands or releasers. Each pattern tends to produce different effects in different circumstances; i.e., a listener of the same species seldom reacts to a vocalization per se, but rather to the sounds interpreted in the light of other stimuli perceived earlier or at the same time.

With respect to these features, the acoustic signal system of adult *S. geoffroyi*, as a whole, may be considered almost exactly “half way” between extremes. Adult Rufous-naped Tamarins utter intermediates between major vocal patterns more frequently than adult *Aotus* but less frequently than *C. moloch*. Some of the vocalizations of adult *S. geoffroyi* are rather precise releasers and tend to produce the same effects in most circumstances, like the patterns of adult *Aotus*; while others are less precise or “imperative” as releasers, produce less consistent reactions, and apparently need to be combined with information from other sources, like the patterns of *C. moloch*.

Another way in which the adult repertory of *S. geoffroyi* seems to be intermediate between those of the other two species is the form or timing of associations between different patterns. Of course, Rufous-naped Tamarins frequently utter many different types of notes in more or less rapid succession. It has already been mentioned (see page 28) that Loud Sharp Notes usually precede Twitters when the two patterns are uttered together. When Trills are uttered also, the usual sequence is Loud Sharp Notes–Trill–Twitter. When Long Whistles are uttered in association with hostile notes, the usual sequence is Long Whistles–Trill–Twitter. These sequences are so much more common than any other combinations of the same patterns as to suggest that they are ritualized per se. *S. geoffroyi* has more ritualized “linkages” of this type than *Aotus*, but fewer than *C. moloch*. Moreover, none of the ritualized series of *geoffroyi* is as complex, including as many notes of different types of patterns, as

the most complex ritualized series of *C. moloch*, the so-called Songs.

Possibly, the Songs of *C. moloch* passed through a stage, in the course of evolution, roughly comparable to the series of *S. geoffroyi* in complexity. But the ritualization of sequences would appear to have proceeded independently in the two species. The patterns usually involved are either non-homologous, or occur in different places in the sequences, in the two species.

It will be noted that the ritualized series of vocalizations of adult *S. geoffroyi* begin with high-intensity patterns and end with the relatively low-intensity Twitter. Also, there is an alternation of more and less "aggressive" patterns. The Trill, which contains an appreciable attack component, is interjected between the high-intensity non-aggressive Long Whistle or Loud Sharp Notes and the low-intensity non-aggressive Twitter. This sort of "alternating decrease" probably is a very effective way of expressing highly ambivalent motivation. It seems to be characteristic of many groups of vertebrates; e.g., the Laridae (Moynihan, 1962). It is not, however, the usual arrangement in *C. moloch* Songs.

VISUAL COMMUNICATION

Adult Rufous-naped Tamarins have a larger number of visual displays than either *Aotus* or *C. moloch*.

The groups of patterns described below includes both unmistakable visual displays and a few other unritualized patterns which are comparable in some respects and/or homologous with displays of other species. They all appear to have been evolved, originally or primarily, to convey or control the transmission of visual information. Other patterns which probably originated or developed as adaptations to convey olfactory information, but which may also function as visual signals at the present time, have been described elsewhere (see page 20).

- *Some Body and Head Movements.*—Obviously alarmed or frightened Rufous-naped Tamarins may "freeze"; i.e., suddenly stop and stand or sit without moving for an appreciable length of time. Silent freezes may occur as a reaction to potential predators. Freezing also is performed by captive *geoffroyi* when introduced into a cage already occupied by other individuals of the same species. In these circumstances, the frightened individual usually freezes in a crouch posture, and often performs Crown-smoothing. This may be silent or accompanied by "recrudescence" Infantile Squeaks. A

typical crouch-freeze, with Infantile Squeaks, is illustrated in Figure 15*b*.

During both intraspecific and most interspecific encounters, an individual usually freezes just where it is when it first sees the alarming stimulus. Probably only during some responses to birds of prey (see page 13), is a tamarin very likely to take shelter, dodge below a branch, before freezing.

The freeze and crouch patterns of Rufous-naped Tamarins are not particularly stereotyped or exaggerated in form. They probably are not displays in the sense of the term used here (see page 11). But they certainly are involved in visual communication. And probably in quite opposite ways in different circumstances.

They must frequently be "anti-signals." They appear to be primarily adapted to prevent the release of reactions. Even though an individual performing these patterns may not be really concealed, it may well be less noticeable (and therefore less objectionable or appetizing) to a potential predator or opponent than it would be if it were doing something else.

On the other hand, the two patterns are quite distinctive, rather unlike anything else in the repertory of the species. Thus, when and if they should be observed, they may reveal a great deal about the state of the individual performing them.

Freeze and crouch patterns seem to be relatively very rare, or even absent, in *Callicebus moloch*, but they are not uncommon in *Aotus*. (The crouch was not distinguished as such in the account of *Aotus* in Moynihan, 1964, but it certainly is sometimes combined with both the simple freeze and Head-down patterns of the species.)

Another reaction of Rufous-naped Tamarins to potential predators is Swaying. (It is my impression that Swaying probably is much commoner than freezing, but I do not know how many freezing individuals may have been overlooked.) During Swaying, the body is moved repeatedly from side to side. The movements sometimes are very extreme, but the head always remains facing forward, while the performing individual fixates the disturbing stimulus. An individual may sit with both hands and feet firmly clasping its perch throughout the whole of a Swaying performance, or it may stand up on its legs (see also below), or it may lift its hands during the actual sideways movements and clasp the perch again between movements. In apparently high-intensity performances, the movements from side to side are moderately rapid, with little or

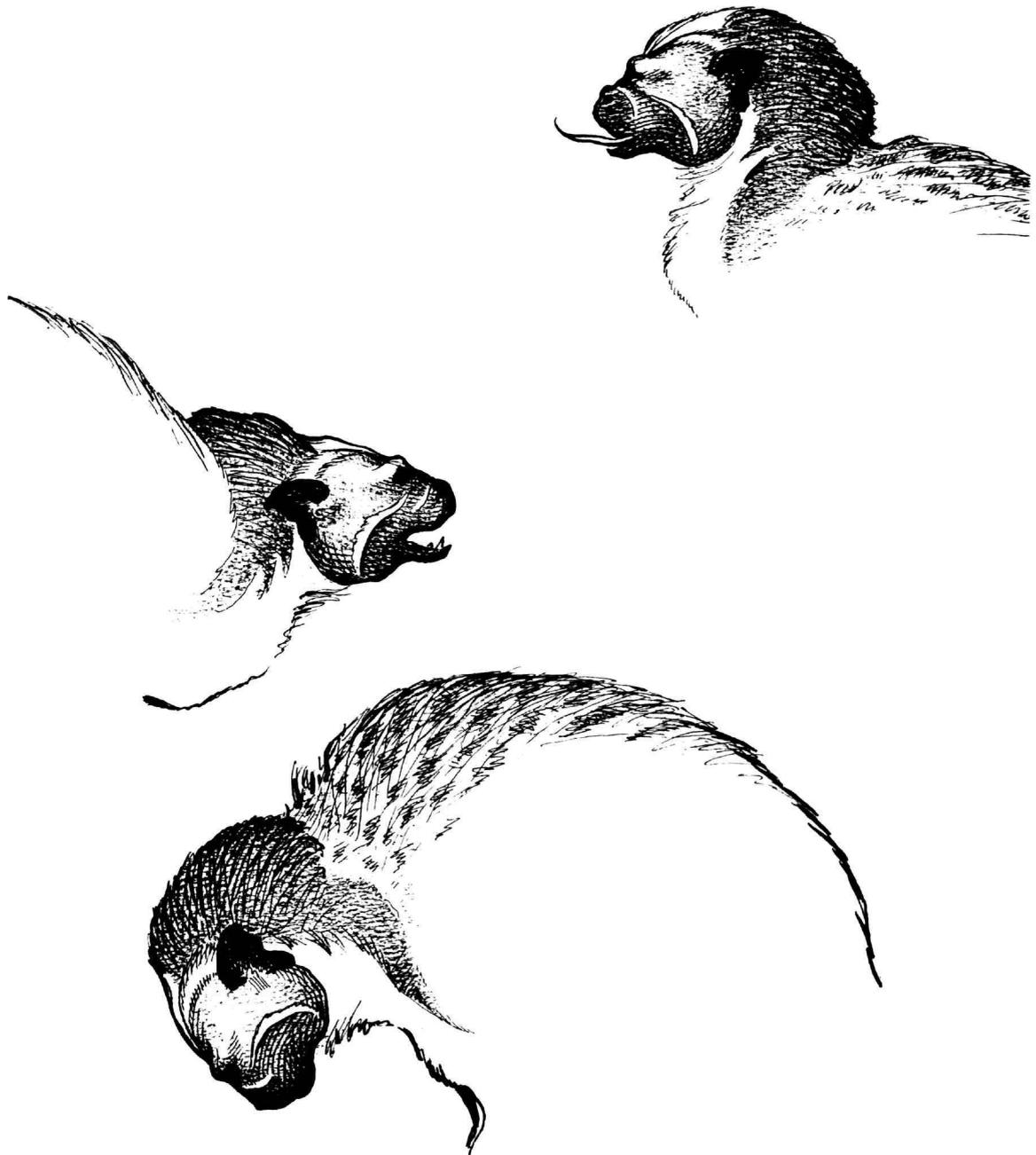


FIGURE 15.—Miscellaneous visual signals of adult Rufous-naped Tamarins: *a* (top), Tongue-protrusion, with some Nose-wrinkling and Eye-closing; *b* (center), crouch posture with Crown-smoothing (the mouth is opened as during the utterance of “recrudescant” Infantile Squeaks); *c* (bottom), head-down posture with Crown-smoothing.

nothing in the way of intervening pauses. In apparently low-intensity performances, by contrast, there may be relatively long pauses (the performing individual usually remaining tilted to one side throughout a pause).

Swaying may be silent or accompanied by Loud Sharp Notes, Trills, and/or Twitters. It frequently is combined with Tail-ruffling, and may also be associated with Crown-smoothing and/or Head-flicks.

It obviously is, at least in part, an expression of an activated escape tendency. Probably, the escape tendency is quite strong during all or most Swaying. Swaying is most common during initial reactions to the appearance of a potential predator, and disappears rapidly when habituation sets in.

Interestingly enough, it apparently never occurs during intra-specific encounters.

As noted in Moynihan (1967), Swaying is one of the most widely distributed of platyrrhine patterns. It seems to be common, exaggerated, and/or stereotyped enough in all species to be considered ritualized in all. But it may be more or less "highly" developed. The Swaying of *S. geoffroyi* is generally quite similar to that of *Aotus* in both form and frequency. It is somewhat less common and less exaggerated on the average than that of *Callicebus moloch*. The Swaying display probably subserves the same function(s) in all species. It must alert predators to the fact that they have been seen, and thus probably discourages them from giving chase. It may also act as a (supplementary) warning signal to other individuals of the same species.

S. geoffroyi shares another simple pattern with *Aotus*, *Callicebus*, and many other Platyrrhini. This is the head-down posture. As performed by Rufous-naped Tamarins, it is not very conspicuous, at least at a distance. The neck is bent and the head is lowered a little. This may be done while an individual sits still or walks slowly. In both cases, the performance usually is silent, but may be accompanied by Crown-smoothing (see Figure 15c).

The actual head movement is so slight that one hesitates to call the pattern a display. But there is evidence that it may be of social significance. In its typical form, at least, the posture is maintained for a considerable number of seconds, or even several minutes. And it is performed only during certain types of social encounters (see below). The comparative data also are interesting in this connection. The head-down

pattern of Night Monkeys is just as slight as that of Rufous-naped Tamarins, although performed somewhat more frequently; but the most extreme versions of the same pattern in *Callicebus moloch* are much more exaggerated, and almost certainly ritualized.

Thus, it may be convenient to discuss some aspects of the head-down of Rufous-naped Tamarins as if it were a display, irrespective of its precise status at the present time.

It probably is another alarm pattern, of some sort. It is seldom performed except before or during retreat, but it does not usually occur in the same situations as Swaying and it is much rarer on the whole. More important, it is almost or completely confined to intra-specific reactions. It occurs during a variety of obviously ambivalent encounters between cage mates, when the animals perform some overtly hostile movements, but still seem reluctant to fight. It may also be performed before or during Allogrooming, especially grooming among individuals which are not (yet) perfectly adjusted to one another.

This would suggest that it is produced by some combination of non-hostile motivation and the escape tendency (with or without some minimal attack component). Possibly it is lower intensity on the average, and/or contains relatively more escape, than such vocal patterns as Twitters and single Short Whines.

An individual assuming a head-down posture usually "faces" toward the other individual which released or induced the performance. Thus, the latter individual sees the posture from in front. It gets a particularly good view of the rufous nape patch (which is usually more or less hidden from the front in other postures). It also gets a good view of the white crown patch; but the white or whitish of the chest and upper arms is partly obscured by the lowered head. Thus, the general effect of the pattern is to present more rufous and less white than usual.

The quietness and inconspicuousness of the head-down of *geoffroyi*, and the circumstances in which it occurs, indicate that it cannot be an antipredator device or warning pattern comparable to Swaying or Loud Sharp Notes. Possibly, it usually functions as appeasement; i.e., directly reduces the strength of attack tendencies in the companions toward which it is directed, without simultaneously increasing their escape (or other) tendencies. (The existence of appeasing effects is always very difficult to confirm. But, at least it can be said that individuals which assume

head-down postures are not usually attacked immediately afterwards.)

One wild Rufous-naped Tamarin was observed to perform some peculiar patterns which may have been related to typical head-down postures. This individual reacted to my approach by uttering Trills and Twitters while performing Swaying with Tail-ruffling. All this was perfectly conventional. But, at the same time, the individual also "bowed" its head very rapidly and repeatedly. These downward movements (quite different from the lateral Head-flicks) looked like brief "intention movements" of assuming the head-down.

Possibly, a head-down component also was involved in the remarkable "slow scratching" performance of one captive individual described on page 43.

A spectacular Lie-back pattern was observed only during a few unusually prolonged and violent disputes between captive animals, when two individuals (see below) fought over particularly choice bits of food (grasshoppers) and one chased the other back and forth for minutes on end. Several times, the pursued individual became exhausted, or trapped in a corner of the cage. Each time, it stopped trying to escape. It then, either immediately or after a few seconds of violent wrestling, rolled or leaned over onto its back. It lay there motionless and silent, making no attempt to protect its exposed underparts. Rather astonishingly, this stopped attack by the opponent immediately, or prevented attack from developing. It appeared to inhibit all attempts to bite or hit by the opponent, even when the latter was standing right over the reclining individual. This pause endured for some seconds or minutes. Then, the reclining individual (having caught its breath or observed a possible route for further escape) turned over and started to run again. Sometimes this induced further chasing and fighting, with or without more Lie-back performances.

I think that Lie-back postures were assumed by only one of the individuals kept in captivity. (Certainly, they were not assumed by more than two.) But the pattern produced such remarkable and stereotyped effects that it can hardly have been a really individual peculiarity. Probably, it is a ritualized and "normal" part of the usual repertory of the species, but very high intensity and confined to extreme emergencies. Possibly the reason that I did not observe it more frequently is because such emergencies are very rare under natural conditions, and most fights among captive individuals were interrupted (by us) before they reached a sufficiently extreme stage.

To my knowledge, nothing similar to the Lie-back of *S. geoffroyi* has been observed in any other Platyrrhini.

The performance might inhibit attack either because it is threat or because it is appeasement. The few examples seen did not provide any direct evidence which would permit a choice between these alternatives. But it should be noted that the effectiveness of the pattern may be correlated with the fact that it reveals and emphasizes larger expanses of white or whitish coloration than any other display of the species.

The implications of this fact will be considered below (page 59), in connection with a general discussion of the functional significance of different colors.

Another somewhat problematic pattern is a stand-up posture. It has already been mentioned that Rufous-naped Tamarins occasionally stand up on their (hind) legs in order to get a better view of some distant animal or object, and also during certain hostile encounters. In both cases, the standing up seems to be quite unritualized per se; nothing more than a preliminary intention movement, a "preparation" for leaping, and/or an initial phase of leaping suddenly arrested by the effect of some counteracting stimulus (I have seen an aggressive individual stand up when its opponent assumed a Lie-back posture).

There are indications, however, that the simplicity of some stand-up performances may be the result of a rather complex evolutionary history. The best evidence was provided by a particularly aggressive and fearless adult male kept in captivity, in a very large outdoors cage. For a period of several weeks, this male showed a definite tendency to attack any human being who entered his cage. He would rush forward, usually silently but sometimes uttering vocalizations which included attack components, and then stop short, only a few inches or feet away from the human. He usually stopped in a stand-up posture, or assumed such a posture immediately after stopping, and then remained in the posture for some seconds. He also usually raised his whole pelage, in a General Ruffle (see page 52), during both the rush and the subsequent standing. His appearance at this stage is shown in Figure 20. After the rush and stand-up, he often performed a great deal of very rapid Sit-rubbing, just like some very aggressive individuals during intraspecific disputes. He probably was trying to "demonstrate" that the cage "belonged" to him.

There was nothing about his stand-up postures, in themselves, to suggest that they were basically differ-

ent from any other stand-ups; i.e., to suggest that they were anything more than locomotory intention movements. The accompanying General Ruffles, although undoubtedly significant in some respects (see below), probably were "accessory." (General Ruffles can be combined with different postures and movements in other circumstances, and the other stand-ups observed were not combined with General Ruffles.)

The real interest of this behavior is comparative. Many other Platyrrhini have a conspicuous, obviously ritualized, Arch posture. This is characterized by extreme raising and arching of the back (in much the same way as in the well-known hostile display of domestic cats). Both *Aotus* and *Callicebus moloch* have two principal variants of the Arch. In one, both hands and feet remain firmly grasping the perch. In the other, the hands are lifted, and the performing animal stands up on its feet alone. The stand-up postures of the male tamarin cited above were not accompanied by raising or extreme curving of the back; but they were quite similar to the standing Arch postures of *Aotus* and *Callicebus moloch* in all other aspects of form, such as the relative positions of head, arms, and legs. The Arch of *C. moloch* also is combined with a General Ruffle (*Aotus* does not seem to have any special Pilo-erection patterns in any circumstances). And there seem to be other resemblances in causation. The Arch patterns of *Aotus* and *Callicebus* occur in social situations which are comparable to those in which the male tamarin stood up; i.e., they are performed by more or less aggressive individuals during disputes of moderate or (more frequently) high intensity.

These facts would suggest that there is some phylogenetic relationship between stand-up and Arch patterns.

It seems likely, in fact, that the Arch postures were originally derived (by a process of stereotyping and exaggeration) from a locomotory intention movement more or less similar to a stand-up. (There probably was nothing else available, occurring at the right times and in appropriate circumstances, to be "seized upon" for ritualization when the development of an Arch display first became advantageous.)

But this does not necessarily mean that the stand-up pattern of *S. geoffroyi*, at least as shown by the aggressive male, is truly "primitive." The distribution of ritualized Arch postures among Platyrrhini is really very wide indeed. They are performed by species which are both different in ecology and only distantly related

to one another. Among the larger platyrrhines, for instance, they are characteristic of both *Pithecia monacha* and *Alouatta "pallata"* as well as *Aotus* and *Callicebus*. According to Epple (1967), they also are performed by many other species of tamarins and marmosets, including *Callimico goeldii*, *Leontideus rosalia*, *Callithrix jacchus*, *C. "leucocephala,"* and *C. argentata* (Epple refers the last species to the probably invalid genus *Mico*). This suggests that a ritualized Arch display is an ancient feature of the Platyrrhini, or a large part thereof, and that it must have been present in the repertory of the ancestors of *S. geoffroyi*. If so, then some of the stand-up postures of Rufous-naped Tamarins at the present time probably are secondarily simplified or dedifferentiated remnants of the more elaborate Arch. Such a process of simplification may be called "de-ritualization."

If these suggestions are correct, then the most remarkable feature of the history of the Arch display in the *S. geoffroyi* lineage is that it seems to have come full circle. The display seems to have decayed back into a form which cannot be very different from that of the original pattern from which it arose.

There are several reasons why all displays would be expected to decay eventually (see discussion in Moynihan, in press). But the de-ritualization of the Arch during the evolution of *geoffroyi* may have been facilitated or accelerated by a special factor. A conventional Arch of the usual platyrrhine type would not reveal or emphasize the characteristic color pattern of the species in a particularly advantageous way. Again, see page 59.

(The account of the Arch and stand-up patterns in Epple [1967] is unfortunately confusing. In one final comparative summary paragraph, she states both that all species of tamarins and marmosets perform Arches and that such patterns were never observed in *S. geoffroyi* and *S. oedipus*. She also shows a photograph of a Rufous-naped Tamarin allegedly performing "Katz-bucket-Drohen," a term which she applies to some of the Arch performances of other species. But the photograph appears to represent an initial or terminal phase of the stand-up with General Ruffle. And Epple's actual description of the behavior in another passage devoted to *S. geoffroyi* alone is not incompatible with the one presented here. Presumably the confusion in Epple's account is largely a matter of phrasing, due to the fact that she recognized that *geoffroyi* has a homologue of the Arch without having the Arch itself.)

The last pattern in this group of Rufous-naped

Tamarin performances is Head-flicking. It occurs more frequently than any of the others, with the possible exception of Swaying. In its typical form, a single Head-flick consists of two or three very rapid but extreme and conspicuous, and obviously ritualized, lateral movements. The head and face are turned first to one side and then back; or first left and then right (or vice versa) and then back. Sometimes the main movements are followed by very rapid but slight lateral "vibrations" of the head.

Head-flicking may be silent or accompanied by vocalizations. By far the most common vocalizations are Loud Sharp Notes. Usually there is one note per single Head-flick. The only other vocalizations ever heard to be uttered by adults during Head-flicking were a very few Soft Sharp Notes, (possibly) a few Sneezing Sharp Notes, a few single Short Whines, and (twice) Trills. (In this respect, adult *geoffroyi* are rather different from young individuals of the same species, which may combine Head-flicks with a greater variety of vocalizations. See page 66.)

Adults perform Head-flicking during both interspecific and intraspecific encounters. Wild individuals perform it as a reaction to potential predators. Captive individuals may perform it when a human being enters their cage, especially when attempts are made to catch them or they have been conditioned to expect to be caught. In both sets of circumstances, the Head-flicking is frequently, perhaps usually, accompanied by Tail-ruffling. Possibly, it is accompanied by Crown-smoothing equally frequently. Sometimes, as noted above, it is combined with Swaying. It usually is followed by overt retreat or escape movements. Apparently identical Head-flicking is frequently performed by captive individuals when they are released into cages already occupied by other individuals of the same species, especially when the newcomers and the "owners" of the cages are unfamiliar with one another. This Head-flicking also may be associated with Tail-ruffling, Crown-smoothing, and/or overt unritualized hostile movements. The latter may include some overt attack patterns, but attack after Head-flicking always is much less common than overt escape.

All this would suggest that Head-flicking is purely hostile. It should be mentioned, however, that captive individuals also perform Head-flicks in close association with a variety of other displays during Sexual Sniffing (see below). Males may even do so during the Sexual Sniffing which accompanies some copulations (see page 14). But all the situations in which such

behavior occurs probably are very highly ambivalent and may contain appreciable hostile components. Even during copulation, a male may be frightened, and possibly even irritated, by the close proximity or behavior of his companion (or as an after-effect of the maneuvering which may have been necessary to permit mounting). Thus, there is no reason to believe that the Head-flicking movements in such circumstances are not also (and only) expressions of hostile tendencies which are included in the complex motivation of the performing animals.

When Head-flicks are performed during reactions to potential predators, they are most frequent during the first stages of the reactions, when the performing animals seem to be most excited. Similarly, when they are performed during obviously hostile disputes among individuals of the same species, they usually are most frequent during the periods in which the general excitement seems to be greatest.

It seems very probable, therefore, that Head-flicking is still another high-intensity pattern in which the escape tendency is greatly preponderant. Possibly, Loud Sharp Notes with Head-flicks are higher intensity, on the average, than similar notes without Head-flicking. Swaying with Head-flicks may be higher intensity and/or contain a stronger escape component than Swaying alone.

I can say very little about the signal effects of Head-flicking movements, simply because they are impossible to distinguish from those of the accompanying acoustic and other visual displays. Possibly, all or most Head-flicks function as additional alarm or warning signals during interspecific encounters and as another form of appeasement during intraspecific encounters.

Perhaps their principal claim to interest also is comparative. Many New World monkeys give a brief lateral shake of the head when they sneeze. It has already been mentioned that Rufous-naped Tamarins perform "ordinary" sneezes in addition to uttering Sneezing Sharp Notes. These ordinary sneezes sound like soft versions of the corresponding human pattern. They seem to be cleaning or "comfort" patterns, a means of clearing the nasal passages. They are not associated particularly closely with any special type(s) of social behavior, and they appear to be quite unritualized, without any special signal function. Many, but probably not all, of the ordinary sneezes of Rufous-naped Tamarins are accompanied by head shakes of the usual platyrrhine type. These are comparatively very slight and inconspicuous, *much* less extreme than the typical Head-

flicks described above. (Possibly, some of the Sneezing Sharp Notes are accompanied by the same movements as ordinary sneezes. But, even in these circumstances, the movements are impossible to confuse with real Head-flicks.) Nevertheless, it seems quite possible that the ritualized Head-flicks were derived from the head shakes accompanying unritualized sneezes, in the course of evolution, by a process of exaggeration.

If so, the fact that Head-flicks are characteristically associated with Loud Sharp Notes in *S. geoffroyi* means that the species has *two* more or less stereotyped combinations of sneeze and Sharp Note patterns in its signal repertory.

This complicates comparisons with other species. For this reason, and also because brief references to more or less definitely related patterns of other species are rather scattered in the preceding pages, it may be useful to insert a partial recapitulation here, to summarize the sneeze-like and Sharp-Note-like patterns of *Saguinus geoffroyi*, *Aotus trivirgatus*, and *Callicebus moloch*, in the hope of clarifying the various resemblances and differences among them.

Saguinus geoffroyi adults have:

1. Ordinary sneezes. Non-ritualized. Without signal function.
2. Head-flicks. Probably ritualized derivatives of sneezing movements. So exaggerated in form that they must have signal function(s).
3. Loud Sharp Notes. Frequently but not invariably associated with Head-flicks. Primarily alarm or warning signals.
4. Soft Sharp Notes. Very closely related to Loud Sharp Notes, but not usually associated with any sneezing pattern or derivative thereof. Alarm and/or contact notes.
5. Sneezing Sharp Notes. Essentially stereotyped combinations of Soft Sharp Notes and the *audible* part of sneezing. Not usually associated with Head-flicking, the ritualized (visible) derivative of sneezing movements. Alarm and/or contact notes.

Aotus trivirgatus adults have:

1. Ordinary sneezes. Non-ritualized. Without signal function.
2. Sneeze-grunts. These sound like ritualized combinations of the audible part of ordinary sneezes and the "Gruff Grunt" vocalizations of the species. Gruff Grunts by (or in) themselves do not sound like anything in the repertory of *S. geoffroyi*. But the Sneeze-grunts are relatively loud, sharp, and brief. They also are associated with Moans and Low Trills, in series, in

much the same way that Loud Sharp Notes are associated with Twitters (which seem to be homologous with Low Trills). Thus, it is possible that the Sneeze-grunts include a component which is homologous with the Loud Sharp Notes. (This component probably is quite distinct, in origin, from the Gruff Grunt component. But it is just barely possible, in view of the fact that some homologues of high-pitched patterns of *S. geoffroyi* are low pitched in *A. trivirgatus* [see page 24] that the Gruff Grunts themselves are phylogenetically related, in whole or in part, to the Loud Sharp Notes.) The loudness, sharpness, and brevity of the Sneeze-grunts, all qualities which are reminiscent not only of Loud Sharp Notes but also some alarm patterns of many other Platyrrhini such as *Cebus* and *Saimiri*, would suggest that they may have originated as warning signals. But they apparently do not function as such now. At the present time, they seem to be contact notes.

4. Gulps. Not including any recognizable sneeze or sneeze-derived component, but rather brief and abrupt; functioning as contact notes at the present time; possibly related to Gruff Grunts; and, therefore, possibly having had a similar evolutionary history.

Callicebus moloch adults have:

1. Ordinary sneezes. Non-ritualized. Without signal function.
2. Hostile sneezes. Identical with ordinary sneezes in form, but apparently produced by hostile motivation (with the escape tendency preponderant). Tend to precede Moans in the same way as the Sneeze-grunts of *Aotus*. Signal function(s), if any, obscure.
3. Chuck Notes. Sound quite like Loud Sharp Notes. Possibly strictly homologous. Probably originated as warning signals; but functions apparently various at the present time, differing in different circumstances.
4. Chirrup. Sound like stereotyped intermediates between Chuck Notes and Moans (i.e., probably composed of all or most of the same elements as the Loud Sharp Note – Twitter, Sneeze-grunt – Low Trill, and Sneeze-grunt – Moan series of other species, but with the various elements "telescoped" together to such an extent that they have become simultaneous). Signal functions differing in different circumstances.

5. *Callicebus moloch* also has several other vocalizations which seem to be related to the Gruff Grunts of *Aotus*, but which are even more distinct from any pattern of *S. geoffroyi*.

• *Apparently Irrelevant Acts*.—These are patterns which appear to be performed "out of context," the

sort of behavior which has been called "displacement" in the ethological literature.

The number and/or importance of such patterns would seem to vary considerably from species to species within the Platyrrhini. *Aotus* probably has no patterns of this type. All or most of the other species observed would seem to have at least one. This usually takes the form of movements or postures. (Among the few possible or probable exceptions to this general rule may be the hostile sneezes of *C. moloch* cited above. These would appear to be "displacement" in the conventional sense of the term.) In most species, the most common movements are self-grooming, and especially scratching. Apparently irrelevant scratching certainly occurs in *Saimiri* (Ploog, Blitz, and Ploog, 1963), *Cebus* spp., *Ateles* spp., *Alouatta* "*palliata*," and *Callicebus moloch*. In all these forms, it is performed in a more or less wide range of complex or "difficult" social situations, by individuals which are "frustrated" or thwarted for one reason or another. *Ateles* and *Alouatta* perform apparently irrelevant scratching comparatively very frequently, and usually in a stereotyped and ritualized form (different in the two genera). *C. moloch* performs such patterns much less frequently, but probably in an equally stereotyped way (although, again, the form is distinctive).

Saguinus geoffroyi may be partly intermediate between *Aotus* and some of the larger Platyrrhini with respect to the development of apparently irrelevant acts. Most individuals of this species certainly do not perform "unexpected" comfort movements in most situations of social stress. But this probably is not true of all individuals in all circumstances.

I saw one captive adult female repeatedly rub her back, and/or the side of her head and face, against the walls of her cage immediately after males failed to respond to her soliciting patterns, "invitations" to copulate. These movements appeared to be very similar to, or even identical with, "normal" comfort or cleaning patterns in physical form. They were remarkable only because the female did not have dirt on her back or face at the times.

Another captive adult female performed more conspicuous, distinctive, and perhaps even more problematic patterns. She was kept alone in a large outdoors cage. After several months of such isolation, first one male (a nearly full-grown juvenile) and then another (completely adult) were released into her cage and allowed to remain there. These introductions provoked a great many hostile reactions among all three individ-

uals, plus a variety of friendly or partly friendly, or even partly sexual, performances; but no immediate copulation attempts. During the first few days after the introduction of the males, the female repeatedly performed a remarkable complex of patterns which may be called "slow head-scratching." She always did this when neither male was particularly close. Sitting silently in a more or less hunched posture, probably a type of (or related to) the head-down (and similarly revealing the full extent of the rufous nape patch), and with her tail looped up between her legs (see page 45), she would scratch her head very, very slowly in an extremely "cautious" looking manner. These movements were quite different from the usual scratching movements of the species, and the same female in other circumstances, which are brisk and vigorous. The female usually began by scratching her white chin. Then she usually scratched her white crown. This is illustrated in Figure 16*b*. Occasionally, she omitted the chin-scratching. Also occasionally, she scratched her (white) forearm in addition to her chin and crown. Once, the chin-scratching was preceded by scratching of the belly or lower breast. But, to my knowledge, the slow scratching was never extended to any other part of the body or head. (This is another feature in which it differed from ordinary self-scratching in other circumstances.)

The fact that this peculiar behavior was closely associated with a great variety of both hostile and non-hostile reactions would suggest that it was an expression of highly ambivalent motivation, the result of a strong conflict between incompatible tendencies (a particular type of frustration).

Other males were introduced to other previously isolated females in a variety of cages of different sizes and shapes, at the same and at different times of the year, without ever inducing any similar performance.

This would suggest that the slow scratching of the one female was a real individual peculiarity. There is other evidence that points to the same conclusion. Unlike the equally spectacular Lie-back pattern cited above, the slow scratching was not obviously directed toward other individuals. Nor did it provoke any obvious, overt reaction by other individuals. This would indicate that it was not a species-specific display, not even a high-intensity display which might be expected to appear only rarely.

If so, the fact that an individual of the species can develop such a unique pattern is an interesting resemblance to *Cebus capucinus* (and probably other

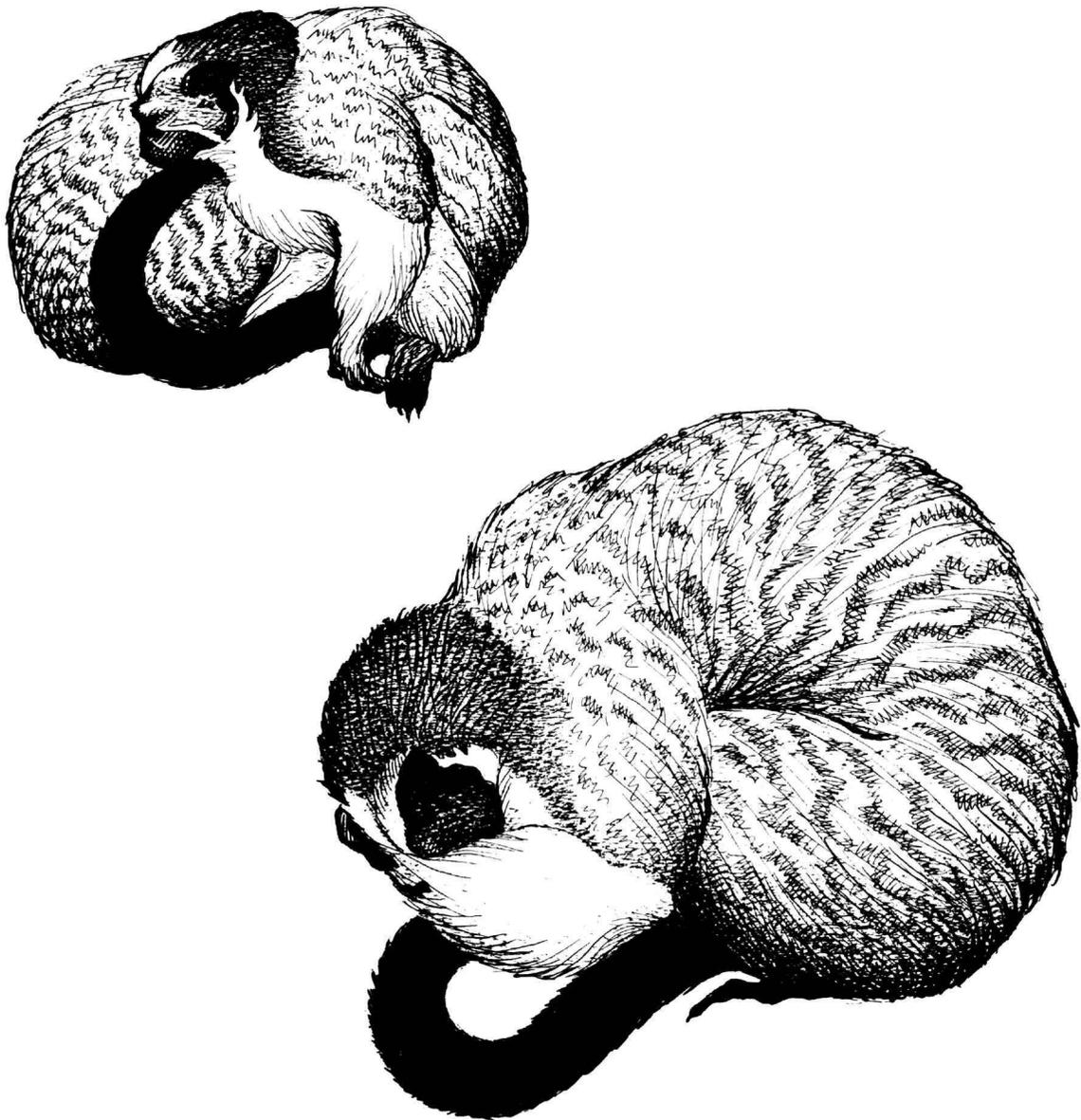


FIGURE 16.—Special postures and movements of adult Rufous-naped Tamarins: *a* (*top*), mates sitting close together, with the female having her tail Looped over the male's leg; *b* (*bottom*), posture assumed by a female during slow head-scratching, with Looped tail and (probably), a head-down component.

species of *Cebus*). Some *capucinus* individuals tend to develop special "nervous mannerisms" or "quirks" in captivity (M. Bernstein, personal communication). These are movements and postures which are not species-specific (or population-specific). Different individuals may develop different mannerisms, often involving different parts of the body. Many mannerisms seem to have been derived from ordinary grooming or scratching movements, but even these are modified in different ways by different individuals. (*C. capucinus* apparently does not have a common stereotyped form of "displacement" like *Ateles* and *Alouatta*. Conversely, it also seems likely, although it has not been definitely established yet, that *Ateles* and *Alouatta* do not tend to develop individual quirks in addition to their stereotyped performances.) As a group, the special mannerisms of *capucinus* individuals appear to be responses to a fairly wide variety of "conflict" or frustration situations. But each individual usually is quite consistent in using its own mannerism(s), in more or less the same form, in the same particular situation(s).

The performance of such mannerisms should reveal a great deal about the situation and motivation of a performing animal—to any other individual "prepared" to receive such information in such form. If quirks really were used in communication, and especially if individuals tended to learn them from one another, then they would be strictly comparable to the "artificial" learned sounds used in human languages. Unfortunately, it is still a dubious question whether or not *C. capucinus* individuals pay any significant attention to the quirks of their companions. But, in any case, whatever the function(s) of such patterns may be, the ability to perform a few quirks in exceptional circumstances, as shown by Rufous-naped Tamarins, probably represents an early stage in the evolution of the ability to perform a great many quirks in a wider range of circumstances, as shown by *C. capucinus*.

This type of similarity between *S. geoffroyi* and *C. capucinus* is rather surprising in view of the fact that the two species differ in ecology, and usually are organized in rather different social groups. (*C. capucinus* also seems to be much more "intelligent," in the ordinary sense of the term, than *S. geoffroyi*—and certainly has a much more "highly developed" brain, of more obviously complex structure.) It is at least conceivable, therefore, that the resemblance between the two species is an indication of special phylogenetic relationship. But *Saguinus* can hardly be as closely related to *Cebus*

as it is to some other genera. See also comments on page 75.

• *Tail Patterns*.—The tail probably is the most "expressive" organ of *S. geoffroyi*. It can be held and moved in many different ways, to convey different messages.

When running or leaping, a Rufous-naped Tamarin usually lets its tail "stream out" behind the body. The tail may be nearly straight, more or less horizontal and continuing the line of the back, or (more frequently) curved in a modified S-shape, horizontal or slanting downward at the base, then rising, and then curving downward at the tip. Figure 1 illustrates a very simple curve, with moderately extreme Tail-ruffling.

A standing or sitting individual sometimes lets the tail hang straight, vertically, downward. This is done when the individual is not alarmed, but is not prepared to relax. It is not usually combined with vocalizations, but is frequently followed by walking or running. It can hardly (by itself) be described as a movement, but it is potentially capable of transmitting the same message as the locomotory intention movements of many other species, and it may subserve the same function(s).

(The usual locomotory intention movement of *Calli- cebus moloch* is a raising [upward and backward] of the basal part of the tail. Rufous-naped Tamarins may perform similar-looking movements, but apparently only during some defecation, urination, and ritualized Rubbing performances. Such movements probably do not function as [separate] social signals in *geoffroyi*.)

When a sitting Rufous-naped Tamarin is prepared to rest or sleep, it brings its tail forward and upward. Usually, the tail is brought up between the legs. Occasionally, it is brought up alongside the body. Sometimes the tail is brought up very far, and the distal half left largely uncurled, so that it stretches up and across the whole front of the animal's body and head. This is a common occurrence in *Saimiri*, but is not usual in *Saguinus*. In most cases, a relaxed Rufous-naped Tamarin, having brought the tail up between the legs, allows the distal half to "settle" in a loose, often irregular or asymmetrical, loop. The extent to which the tail is visible, to an observer looking from the front or side, is quite variable, partly because the "bends" in the tail may occur in different places between tip and base. Despite this considerable variability, the pattern as a whole is exaggerated enough to suggest that it is at least partly ritualized. The Tail-looping of the slow-scratching female illustrated in Figure 16b may be as "typical" as any, in physical form, in itself. But most

Looping is not combined with either special quirks or other signal patterns. In particular, it is seldom or never accompanied by any raising of the hairs of the tail.

When mates are sitting side by side, one individual may Loop its tail over part of the body of the other. An example of this is illustrated in Figure 16*a*.

Presumably, Tail-looping always functions as a signal insofar as it indicates that an individual is undisturbed and is not planning to move. When one individual Loops its tail over the body of its mate, the performance also may provide some tactile stimulation. It seldom or never provokes any overt response by the mate, but the mere contact may help to strengthen pair bonds. In many circumstances, however, Tail-looping may be even more important in quite another way. The tail often is surprisingly conspicuous in the field when it is allowed to hang downward. There often is little or nothing else in the immediate environment which is of comparable length, nearly straight and vertical, and equally dark. (Most lianas and small branches are lighter, oblique or horizontal, and/or twisted or more irregular in shape.) Thus, the tail often is the first part of the body noticed by a human observer. Other potential predators probably react similarly. Of course, the conspicuousness of the tail is greatly reduced when it is raised and curved and partly hidden between the legs. It seems very probable, therefore, that Tail-looping also is a protective device. It may be a signal to other individuals of the same species, but it also seems to be a means of concealing a potentially dangerous sign stimulus from individuals of other species.

The remaining tail patterns may be more highly ritualized, as they are more stereotyped in some ways. They are not invariable in form, but the variations are somewhat more predictable.

The simplest is the Tail-forward. It can be performed by an individual while sitting, standing, or walking. The tail hangs downward, but is inclined forward and more or less curved at the tip. The actual angle of inclination and degree of curving differ in different circumstances. Two examples are shown in Figures 17*a* and 17*b*.

This obviously is another indication of alarm. It is a very common reaction of wild individuals to the appearance of a human observer, and it frequently is followed by overt retreat or escape movements. Probably, it is produced by a rather wide range of hostile motivation. Sometimes it is performed by individuals

which are absolutely silent and which retreat only short distances. At other times, it is performed by individuals which utter Loud Sharp Notes and/or Twitters. In such cases, it may be accompanied by Swaying and followed by rapid and prolonged escape. When Twitters are uttered, the Tail-forward may also be accompanied by a slight amount of Tail-ruffling, but otherwise the two patterns seem to be largely or completely mutually exclusive. Very excited individuals which utter many vocalizations tend to bring the tail farther forward under the body than do less excited individuals. Individuals which utter comparatively many Loud Sharp Notes tend to bring the tail farther forward than individuals which utter mostly Twitters. Individuals which have the tail far forward tend to retreat earlier, farther, and/or faster than individuals which have the tail only slightly forward. These facts would suggest that the more extreme Tail-forward patterns are expressions of stronger hostile motivation (as a whole), and/or relatively greater preponderance of the escape tendencies, than the less extreme versions of the same pattern.

All forms of the pattern probably function as additional warning signals to other individuals of the same species. Insofar as they modify the conspicuous verticality of a downward hanging tail, they may also be protective or concealing in much the same way as Tail-looping, although to a much lesser extent.

Another pattern may be called "Tip-coiling." This often looks like an exaggeration of part of one type of Tail-forward. The distal part of the tail (usually anything from one-fourth to one-half of the total length) is not only curved, but actually coiled. Sometimes all the coils are in one plane. In which case, the coiling usually is tight, and all the coils are touching. At other times, they may "sprawl" or fall sideways, to produce a "corkscrew" effect. (This is difficult to describe in words, but the two forms are illustrated in Figures 17*c* and 17*d*.) Tip-coiling probably is performed most frequently by individuals which are sitting or standing at the time. In these circumstances, the performing individuals usually let the uncoiled part of the tail hang straight downward. At least occasionally, however, what seems to be essentially the same pattern may be performed by an individual which is leaping or running. Then the longer part of the tail is allowed to stream out behind, in the usual way, but the tip is "tied up" in a tight little "knot."

The individuals which perform Tip-coiling often are unmistakably alarmed. This is another resemblance



FIGURE 17.—Special postures of the tail indicating alarm. From top to bottom: *a*, extreme Tail-forward; *b*, slight Tail-forward; *c*, one form of Tip-coiling; *d*, another form of Tip-coiling.

between Tip-coiling and the Tail-forward. But Tip-coiling seems to be relatively rare in the wild, under natural conditions, and relatively more common in captivity, especially when individuals are rather crowded together. In captivity, it usually is associated with many other signal patterns which contain appreciable escape components (e.g., Loud Sharp Notes, Twitters, Trills, Crown-smoothing), as well as overt escape and retreat movements; but most of the observed associations were not particularly helpful in revealing how the motivation and function(s) of the Tip-coiling might differ from those of the other signals. There is only a little evidence which may be more useful. The individual seen to perform (usually loose) Tip-coiling most frequently was a subadult kept in a small cage with two other individuals of approximately the same age, to whom it appeared to be slightly subordinate. This individual also tended to utter Infantile Squeaks and Infantile Raps relatively frequently, sometimes immediately before or during Tip-coiling. It may also be significant that the actual coiling part of the pattern is somewhat similar, in form, to the more extreme Upward Tail-coiling display, which is largely or purely sexual (see below). These facts might be interpreted to mean that Tip-coiling is produced by some combination of hostile (primarily escape) and non-hostile motivation, functions as a warning and/or appeasement or "deception" (see Moynihan, 1955b) display, and may have originated as a ritualized intermediate between the ordinary Tail-forward and Upward Tail-coiling.

The Upward Tail-coiling itself is the most elaborate of the special tail patterns. It always is performed, or at least begun, by an animal who is standing or sitting at the time. In its typical forms, it always involves the coiling of the whole of the tail. More often than not, an animal who performs the pattern has had its tail hanging downward beforehand. In which case, the Coiling may take either one of two forms. In the simpler of the two, the actual coiling movements begin at the tip of the tail, the rest of which continues to hang downward for the moment, and then continue upward toward the base, usually in more or less the same plane. The tail simply "rolls up" into a large coil immediately below and slightly behind the rear of the body and legs. In the more complex of the two forms, the whole tail is lifted upward, to stretch more or less horizontally backward behind the body, just before or just as the coiling movements begin. Again, the coiling move-

ments proceed from tip to base. But the process might be more correctly described as "rolling forward" than as "rolling up." Sometimes the "rolling forward" is not all in the same plane. The tail may begin to coil laterally (the broad plane parallel to the ground) and then continue vertically. The actual coiling itself always is very rapid, in all circumstances. Thus, the up-lateral-vertical sequence gives the impression of a sideways "flick" or "swish." This can be very noticeable; it is just the sort of movement which tends to attract the attention of even an inattentive observer. If an individual who performs Upward Tail-coiling has had its tail draped over or along a branch (rather than hanging down) beforehand, then the coiling movements will be more or less upward or forward depending upon the relative positions of the branch and the body of the performing individual. In any case, as soon as the coiling is complete, the animal usually slips the coiled tail forward between its legs, so that the main body of the coil rests on the substrate beneath the breast or belly. If the animal was sitting down beforehand, it has to raise its hind quarters in order to pass the tail forward. But it almost always sits down again immediately afterwards. Even if it was standing beforehand, it usually sits down within a few seconds after passing the tail forward. The sitting postures do not seem to be ritualized as such, apart from the position of the tail. The tail itself is seldom Ruffled at any stage during the performance. The coiling also usually is and remains very tight. As a result, the tail becomes very inconspicuous indeed as soon as it is passed underneath the body, even less conspicuous than when it is Looped. Not infrequently, it is quite invisible from the side. Having assumed a sitting posture with the tail coiled, an individual may remain in it for several minutes.

All this behavior usually is silent.

As a whole, at least in its typical forms, Upward Tail-coiling is "essentially" feminine. Females perform it very, *very* much more frequently than do males.

And, as mentioned above (page 14), Upward Tail-coiling by females apparently is the "normal" precopulatory display of the species.

It certainly seems to be an expression of copulatory motivation. Females which perform the pattern almost always are prepared to allow males to mount immediately. (I observed only a very few exceptions to this general rule, and they all occurred during obviously ambivalent encounters between males and females who were not well adjusted to one another. In all these

cases, the development of sexual behavior was interrupted by the outbreak of overt hostilities.)

Upward Tail-coiling was seen to be performed (or recognized as such) only among individuals kept in captivity. The fact that it is a "normal" part of the repertory of the species is indicated by several lines of evidence. It is quite common in captivity, in some situations. It also is more stereotyped, performed by more individuals in the same way, than would be expected of a learned quirk. Presumably, it was not seen or recognized in the wild simply because copulations were not observed in the wild.

A complete Upward Tail-coiling performance by a female usually is very attractive to a male. It frequently induces the male to approach the female, irrespective of whether or not he mounts her after the approach.

At the very least, such behavior by a female must indicate that she is receptive. Conceivably, it may also be used more "actively," as a soliciting pattern. Some or all of the components of the performance may actually stimulate, i.e., increase the actual strength of, the sexual tendencies of a male. The orientation of the pattern is somewhat variable. Females which are only weakly motivated (as shown by the fact that they allow only a few copulations afterwards) tend to perform Upward Tail-coiling wherever they happen to be when the spirit moves them, without attempting to orient the pattern in any special way vis a vis a male. But more highly motivated females definitely try to "present" their backs (and therefore also reveal and emphasize the tail movements) to the males. A female may even approach a male in order to do so. She may pass right in front of him and perform Upward Tail-coiling only a few centimeters in front of his face. (This may also provide olfactory information and stimulation.) A female performing Upward Tail-coiling with her back to a male sometimes looks over her shoulder, apparently to see what effect her behavior is producing. (This does not seem to be "discouraging" or intimidating in the same way as the similar movement during copulation itself, see page 14.)

(It will be noted that the behavior sometimes used to solicit copulation, apart from the accompanying tail movements, is not very different from the behavior sometimes used to solicit Allogrooming.)

Many or most females of long established pairs tend to perform the actual coiling parts of Upward Tail-coiling with a minimum of "fuss" or "ostentation," i.e., they usually do the simplest type of "rolling up." But

females of more recently established pairs, and especially females confronted with quite unfamiliar males, often perform particularly conspicuous lateral "swishes."

It seems possible, therefore, that Upward Tail-coiling is partly a double signal. The ultimate result of the performance, sitting with the tail coiled underneath the body, may indicate receptivity and nothing else. Perhaps the actively stimulating effect is produced only by the approaches and the "preliminary" coiling or rolling movements.

The form of Upward Tail-coiling is rather surprising in a sexual soliciting pattern. Offhand, one might have supposed that the position of the tail between the legs would block access to the female's genitalia. Obviously this is not the case, but the position of the tail can hardly facilitate the mechanics of the copulatory act. (It probably is significant, in this connection, that both *Aotus* and *Callicebus* females do not perform Upward Tail-coiling. If they do anything at all, they raise the base of the tail or move it to one side immediately before or during copulations. And it has already been mentioned that a female Rufous-naped Tamarin which has performed Upward Tail-coiling before copulation usually "relaxes" and lets the tail become partly uncoiled as the copulation reaches a climax. See page 14 and also Figure 19.) Thus, it is evident that Upward Tail-coiling has not been selected simply because the performance, in itself and apart from its signal functions, is particularly convenient. Here again, it seems likely that the concealment (from the eyes of a potential predator) of the otherwise all-too-visible tail has been a crucial consideration. Copulating tamarins probably are particularly vulnerable to predators (they cannot be very "wary" while their attention is engaged elsewhere). Thus, any protective or concealing device probably is particularly advantageous at such times. This may explain why *S. geoffroyi* has evolved Upward Tail-coiling, rather than something else, as a precopulatory display. The conspicuous part of the performance, the actual coiling, is very rapid and brief. And the remainder is as little conspicuous as anything could reasonably be expected to be in the circumstances.

Epple (1967) says that a female "saturates" her tail with urine during Upward Tail-coiling. But the females observed on Barro Colorado Island certainly did not urinate visibly at any stage of their performances.

Some other aspects of the timing and occurrence of the display may deserve to be noted in passing.

No matter how highly motivated she may be, an unmated female confronted with an unfamiliar male does not usually perform Upward Tail-coiling until she is certain that the male is sexually interested in her. Thus, the first copulation between previously unacquainted individuals may not be preceded by any special display. The male may take the female by surprise, and mount her without preliminaries. Such copulations sometimes appear to be completely successful. But all the subsequent copulations between the same individuals usually are preceded by Upward Tail-coiling of the usual types, irrespective of whether the first attempt has been successful or not.

Females which perform Upward Tail-coiling obviously are sexually "unsatisfied." They could be described as "frustrated." But it should be stressed that this frustration usually or always is due to the absence of consummatory stimuli, or the inability to perform the consummatory act in the absence of a suitable and willing partner, and *not* to any motivational conflict. A female usually stops Upward Tail-coiling immediately, or performs it in a highly modified form (see below), as soon as any hostile motivation is activated.

Granted that female Upward Tail-coiling is an expression of unsatisfied copulatory motivation, one might expect that it would cease, at least temporarily, even in the absence of any hostile behavior, immediately after a successful copulation has been performed. But this does not always seem to be the case. I have seen females perform the pattern immediately after prolonged copulation attempts in which the males made many pelvic thrusts in a well-oriented and apparently perfectly normal manner. Even when a female has partly uncoiled her tail at the climax of a copulation attempt, she may "re-coil" it again as soon as the male dismounts. This would seem to suggest two alternative possibilities. Either females frequently need several copulations in order to be satisfied (which seems unlikely in view of the usual rarity of copulations among well-adjusted pairs—see page 14). Or the satisfactions which they may derive from copulations are not provided, directly, by the movements of the males, but by some later (presumably physiological) changes within themselves.

Males were seen to perform, rather than respond to, Upward Tail-coiling on only two occasions.

Once, it was performed by an adult male shortly after he was released into the cage of an unfamiliar

adult female. Both individuals had been isolated for some weeks previously. They showed considerable overt hostility toward one another when first brought together. But the male also made intention movements of approaching the female in a manner which did not seem to be purely hostile. After some minutes, he pulled his tail up into a complete but *loose* spiral (*i.e.*, with the coils not touching one another), and held it behind his body, without making any attempt to bring it forward between his legs (see Figure 18a). Then he walked slowly backward toward the female, still maintaining his tail in the same position. Finally, he actually bumped into her. Whereupon she turned her head and stared at him. And he ran away immediately, uncoiling his tail as he went.

The other occasion was similar in some respects. An adult male was released into the cage of an adult female. But these individuals were not the same as those involved in the incident cited above, and they had had some previous acquaintance with one another. The male copulated repeatedly, and apparently successfully, with the female within a few minutes after being released. Then the female apparently became satiated. She stopped accepting the male. At which point, he began to perform a variety of Tail-coiling movements in rapid succession. They always began while his tail was hanging downward. Sometimes the Coiling was slight, hardly more than exaggerated Tip-coiling, and affecting only part of the tail. At other times, the whole of the tail was coiled, and even brought up between the legs; but the male never actually sat down after Coiling in the characteristic manner of females. The coils of his tail always were quite tight, usually touching one another throughout. Rather surprisingly, both the extreme and slight forms of Coiling often were accompanied by, or combined with, an appreciable amount of Tail-ruffling. Even more surprisingly, none of the performances provoked a direct, unmistakable, response by the female (although she did perform Rubbing from time to time).

The behavior of both these males would seem to be of the type which has been called "pseudo-female." The probable or possible significance of such behavior has been discussed by Morris (1955). Like the corresponding patterns of some other animals (birds and fish) cited by Morris, the Upward Tail-coiling of the male Rufous-naped Tamarins appeared to be produced by "arousal and subsequent thwarting of the sex (*i.e.*, copulatory) drive." Insofar as such behavior is "unexpected," it might be considered "displacement."

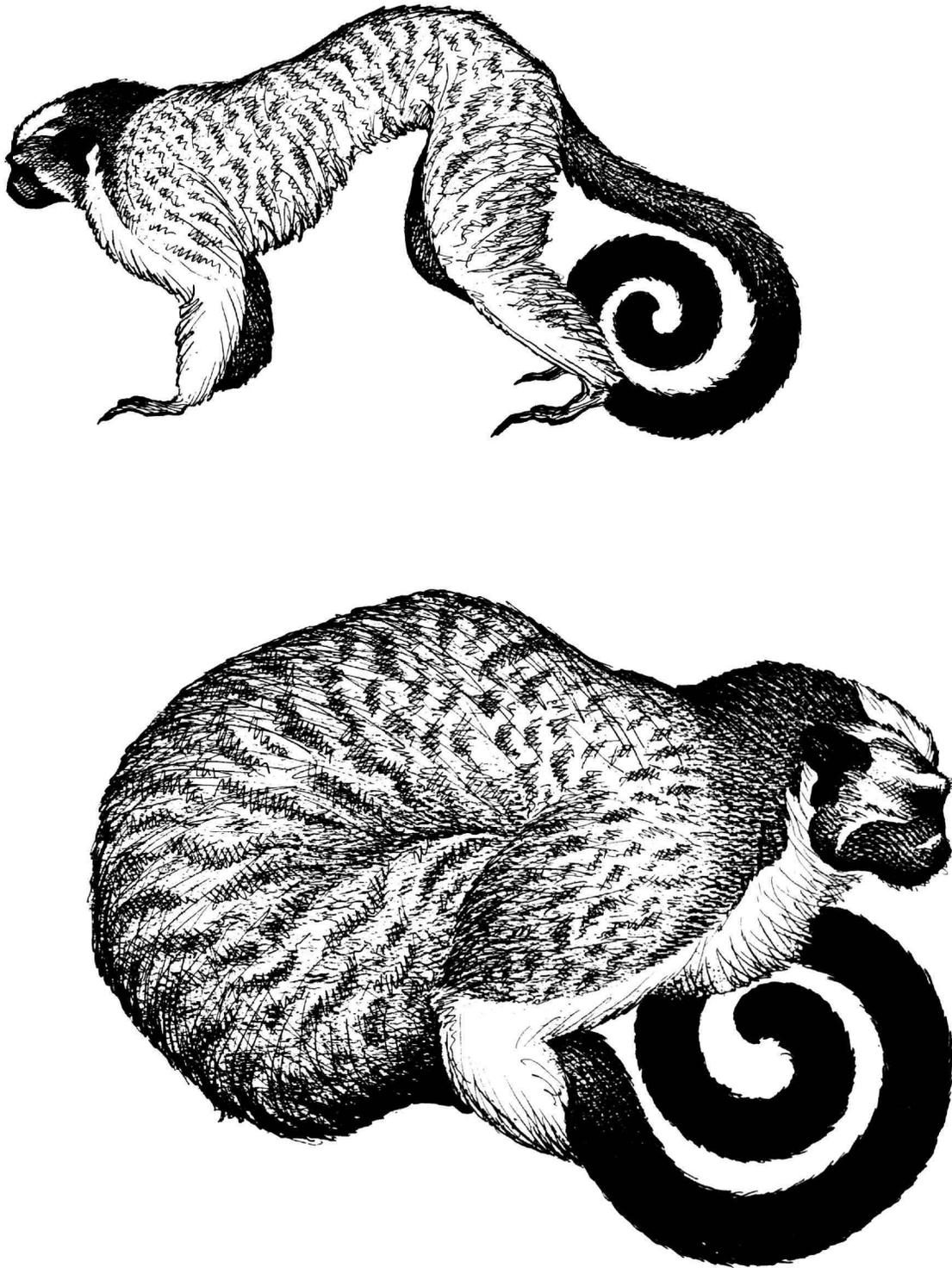


FIGURE 18.—Extreme but “loose” Upward Tail-coiling of adult Rufous-naped Tamarins: *a* (*top*), by male approaching a female; *b* (*bottom*), by a female, apparently soliciting or expecting copulation.

But it may also have special signal function(s). Although the performances described above did not appear to be effective, it is conceivable that similar behavior by males in other circumstances might stimulate the sexual tendencies of their partners (i.e., function in some or all of the same ways as the equivalent behavior of females).

More or less exaggerated and stereotyped forms of loose Tail-coiling also were seen to be performed only twice. Once by the male cited above, and once by the female of a well-established pair. This female and her mate had been kept together for a long time. They were seen to copulate once or twice a day for several days in a row. Then the male seemed to lose interest. On the following day, the female was seen to go to a branch on which copulations had occurred previously, pull up her tail in a complete loose spiral, put it between her legs, and then sit down with the coils protruding in front. This is shown in Figure 18b. It appeared to be as attractive as more conventional performances. The male ran to the female as soon as she sat down, and placed one hand upon her back. But then again his energy failed.

As the illustrations indicate, loose Upward Tail-coiling is remarkably conspicuous when viewed close up. It is not, however, at all conspicuous when viewed from a distance, when the concentric coils seem to disappear, like the stripes of a zebra.

• *Pilo-erection and "Smoothing" Patterns.*—Adult Rufous-naped Tamarins seem to have six or seven more or less distinct patterns of raising or depressing hair.

One is a General Ruffle, raising all or almost all the hair of the head, body, limbs, and tail. As noted above, this may be superimposed upon the stand-up posture of a very aggressive male (illustrated in Figure 20). It may also be combined with a variety of other patterns. It is sometimes performed, or assumed, by individuals engaged in violent and obviously aggressive chases and fights. In these circumstances, it usually is maintained throughout the whole of an encounter; i.e., combined with all the vocalizations, locomotory and fighting postures and movements which may be performed by the aggressive individuals, irrespective of whether or not stand-up postures are included among them. I also have seen General Ruffles assumed by a captive male and female performing Tongue-protrusion with Head-flicks, and uttering Soft Sharp Notes and/or Infantile Squeaks, immediately after being introduced to one another and just before begin-

ning to chase and fight; and by another captive male and female during silent sniffing and Tongue-protrusion immediately after a violent dispute.

All these facts would suggest that General Ruffles are produced when the tendency to attack is very strong. Probably when other tendencies also are strong, but somewhat less so than attack.

Possibly General Ruffles usually or always function as threat. They must, at least, increase the apparent size, and therefore "impressiveness," of the performing individuals.

A pattern which may be called Crown-raising is much less spectacular. In its typical form, it entails raising the white hairs of the "blaze" on the forehead and forepart of the crown to the maximum extent possible, while raising the rufous hairs of the nape only moderately (perhaps not at all in some cases) and leaving the hairs of the body and limbs unruffled. When an adult performs the pattern, the white hairs of the "blaze" look very much like those of the young animal illustrated in Figure 21. (The young itself may or may not be displaying. See below, page 61.)

During at least some Crown-raising performances by adults, the hairs of the white stripes across the cheeks also are raised (brought forward), but this is noticeable only when viewed very close up.

All the Crown-raising, in fact, is so inconspicuous from a distance that I cannot be sure that I did not overlook it quite frequently (see also page 60.) I did see it performed by wild adults, as a reaction to potential predators, in combination with Loud Sharp Notes, Swaying, and Tail-ruffling. I also saw it performed by many captive adults, usually rather aggressive individuals engaged in disputes in less vigorous and/or less prolonged hostile encounters than those in which General Ruffles occurred.

This would indicate that adult Crown-raising is purely hostile. Possibly it is produced by much the same type of motivation as the General Ruffle, when all the tendencies involved are weaker on the average. The individuals which perform it in captivity often seem to be slightly intimidating to their companions. Perhaps the pattern itself functions as threat, a rather less frightening or impressive threat than the General Ruffle.

Crown-smoothing is the "opposite" of Crown-raising in form. All the white hairs of the forehead and crown are smoothed down flat, while the rufous nape hairs



FIGURE 19.—Copulation postures of Rufous-naped Tamarins. The female has partly uncoiled her tail.



FIGURE 20.—General Ruffle by an adult male Rufous-naped Tamarin in a stand-up posture.

and the rest of the pelage of body and limbs are maintained in an ordinary unritualized position. This Crown-smoothing also is difficult to distinguish at a distance. But it obviously is common and performed in a considerable variety of circumstances. It is most frequently combined with overt retreat and escape movements and intention movements. Occasionally, it may be performed by individuals advancing toward others. Sometimes such advancing individuals show clear signs of aggressiveness. But they always appear to be simultaneously alarmed to some extent, even though the alarm is not relatively strong enough to overcome the tendency to approach. In almost all circumstances, Crown-smoothing is closely associated or combined with other signals in which escape is prominent; e.g., Trills and other patterns of the Sharp Note complex, Infantile Squeaks, Tail-ruffling, crouch and head-down postures, and some Rubbing performances. See Figures 1, 2, 15*b*, and 15*c*.

If the Crown-raising which emphasizes the white areas of the head functions as threat, it seems likely that the Crown-smoothing which reduces the apparent size of the white areas functions as appeasement.

Another related pattern which might be considered "opposed" to Crown-raising is the Rufous Ruffle. In this pattern, all the rufous hairs of the nape are raised, while the white hairs of the face and crown are either smoothed down or maintained in an unritualized position, and the rest of the body and limb pelage (also) remains "normal." As indicated on page 16, an individual may do this in an apparent attempt to induce grooming by a companion. It seems to be rare in other social situations. I noticed only one conspicuous example apart from Allogrooming. This was performed by a captive male immediately after being introduced into the cage of an unfamiliar female. She was mildly aggressive, and the male obviously was both attracted to and frightened of her. He retreated, apparently reluctantly, whenever she advanced toward him. He uttered Long Rasps whenever she came particularly close. He also performed Rufous Ruffles during his retreats, both when silent and when vocalizing.

Certainly, the Rufous Ruffle cannot be primarily aggressive. It may be largely due to some combination(s) of a tendency to escape and some friendly and/or sexual motivation. It may function as another appeasement pattern and/or a releaser of friendly or sexual reactions.

The remaining patterns of this group involve the hairs of the tail.

Tail-ruffling is one of the most common displays of the species. In its typical form, it consists of raising all the hairs of the distal part of the tail (most of the black part) to a more or less extreme extent. This is illustrated in Figure 1. Typical Tail-ruffling is a very frequent reaction to the appearance or approach of a potential predator. In such circumstances, it may occur by itself alone, or be superimposed upon otherwise unritualized retreat or escape movements, or be combined with almost any one or several of the other display patterns expressing some degree of alarm (as well as other tendencies), including Twitters, Trills, Sharp Notes, Swaying, and/or Head-flicks. It also may be combined with either Crown-smoothing or Crown-raising, or both in rapid succession. It seems to be somewhat less characteristic of intraspecific reactions. But I have seen it combined with, at least, Twitters, Loud Sharp Notes, Head-flicks, and even sniffing with Tongue-protrusion, during some encounters between male and females in captivity.

Tail-ruffling performances certainly are associated with Twitters much more frequently than with any other ritualized signal.

All this would suggest that a tendency to escape usually is predominant during Tail-ruffling, but the escape must usually or always be accompanied by some slight activation of friendly and/or sexual motivation.

Tail-ruffling itself must be low intensity. It is performed more frequently than either Twittering or Crown-smoothing, and in an even greater variety of circumstances. All the tendencies involved in the production of Tail-ruffling must be very weak indeed.

It might, in fact, be supposed that Tail-ruffling was nothing more than "low-intensity Twittering," produced by the same tendencies, in the same proportions, but at a lower level of strength; however, this probably is not correct. Not only can Tail-ruffling occur without Twittering, but Twittering can also occur without Tail-ruffling. It seems likely, therefore, that there are qualitative as well as quantitative differences between the causal factors of the two displays. Presumably, there is a slight difference in the relative strengths of hostile and non-hostile tendencies. Possibly the Tail-ruffling contains or expresses relatively more friendly and/or sexual motivation (*viz.*, the captive male which combined Tail-ruffling with Upward Tail-coiling, described above, page 50).

Rufous-naped Tamarins probably also have distinct Tail-fluffing and/or Tail-smoothing displays. The tails

of at least some individuals certainly appear to be "thicker," without being obviously Ruffled, at some times more than at others. The difference, however, is so slight, and so difficult to distinguish at a distance, that I could never analyze it properly.

• *Facial Expressions.*—All tamarins and marmosets are notoriously "poker faced" (for fairly obvious reasons, see Moynihan, 1967). But *S. geoffroyi* may have a slightly greater range of facial expressions and related patterns than some other species.

Perhaps the simplest expression is a slight opening of the mouth, without making special lip movements or revealing or emphasizing the teeth in any conspicuous way. This occurs during some vocalizations. It can also be done silently. When silent, it usually is maintained for several seconds or even minutes. Presumably as an unritualized intention movement of vocalizing and/or biting.

Actually, the appearance of the mouth, and the movements of the lower jaw, are rather different during the utterance of different types of notes and calls. The mouth is opened more or less widely during Long Whistles, Long Rasps, Infantile Rasps, and at least some Infantile Squeaks (see Figures 15*b* and 21), and closed after every note of these types, even when they are uttered in series. It also is opened widely during Trills and some intermediates between Trills and Twitters. During these performances, the lower jaw vibrates up and down in rhythm with the notes, but the mouth is not closed between the successive notes of a single series. Sometimes the tongue also goes in and out (but not very far out) in rhythm with the notes. When the mouth is open, the fleshy pink color of the tongue and the lining of the mouth may be rather noticeable. Typical Twitters and Short Whines, on the other hand, usually or always are uttered with the mouth nearly or completely closed throughout, without any visible revelation of pink. Thus, it seems quite possible that one tamarin could tell what its companions were saying, as long as they were in sight, even if they were not audible. Such a situation is not very likely to occur in nature. But the visual information must at least supplement the acoustic, and may perhaps enhance its effectiveness.

One captive male was seen to open and close his mouth repeatedly, without uttering a sound audible to my ears, much more rapidly and frequently than usual. Unfortunately, he was not in good health at the time, and his behavior was difficult to interpret. Some other Platyrrhini give similar performances as

regular displays, but the behavior of this male may have been aberrant for his own species. Possibly he had simply "lost his voice" as a result of illness. Or, he may have been exhibiting an individual quirk comparable to the others cited above.

Andrew (op. cit.) mentions one facial expression of *S. geoffroyi* (which he too calls *Oedipomidas spixi*); i.e., a "marked grin." He says that it accompanies "twitters" and a "rasping screech." (See page 70, for the probable identity of these sounds according to the terminology used here.) In another passage of the same paper, Andrew described the "grin" accompanying "screeches" as "low." Elsewhere, he implies that the expression accompanying "twitters" is similar. By his definition, a "low grin" should consist of the drawing back of the corners of the mouth and nothing else.

My own experience would suggest that such drawing back, although possibly evident in almost all vocalizations given with the mouth open, is almost always very slight. It certainly is much less well developed in *S. geoffroyi* than in some of the larger New World primates.

There seems to have been only one exception among the Rufous-naped Tamarins kept in captivity on Barro Colorado Island. M. H. Robinson (personal communication) says that one individual "showed its fangs" (drew back the corners of the mouth far enough to reveal the canines) almost continually for the first few days after it was brought into the laboratory. The general effect was so unusual that the individual was immediately named "Dracula." By the time that I saw it a couple of weeks later, the peculiar pattern had almost disappeared. Presumably it was another individual quirk, and a rather fugitive one.

The most complex of the facial expressions involve, or are closely associated with, a very conspicuous display which may be called Tongue-protrusion.

It has already been mentioned that the tongue may be flicked in and out, slightly, during some vocalizations. Apparently identical movements may be performed by both male and females during Allogrooming (by the groomers), immediately before and/or after feeding, and even when simply looking at areas or sites where they are accustomed to feed. In many of these latter cases, the animals appear to be "tasting," or anticipating the taste of, some aspect of the environment.

But real Tongue-protrusion, as the term is used here, is much more exaggerated. In its complete and typical form, the tongue is extended just about as far

as it can go. Usually the tip is curled upward. This is illustrated in Figure 15a. Sometimes the tongue is held motionless for several seconds. At other times it may be vibrated up and down very rapidly. This may be the highest intensity version of the performance.

Extreme Tongue-protrusion may intergrade with the simple flicking in and out associated with feeding and some vocalizations. The tongue can go in and out more or less rapidly and be protruded to varying extents.

Both the extreme and intermediate forms of the display are almost always silent. But they usually are accompanied by other ritualized components. The nose is usually "wrinkled up" and the eyes are half closed. And an individual performing Tongue-protrusion almost always gives many Head-flicks. When the tongue goes in and out more or less regularly, there may be exactly one Flick per protrusion. More frequently, the synchronization is less perfect. There often are several Head-flicks while the tongue is maintained in the extended position. Or the Flicks may occur both during and between extensions.

As a whole, the real Tongue-protrusion display can be said to be characteristically masculine. During the course of the present study, it was seen to be performed by males very much more frequently than by females.

It was a very common reaction of captive males when confronted by unfamiliar individuals of their own species, strangers of either sex and almost any age. In these circumstances, it often was combined with sniffing, apparently as a complex form of "investigation" or even "greeting." A male would approach a stranger and sniff at it, either face to face or nose to tail, and perform Tongue-protrusion (with accompanying Nose-wrinkling, Eye-closing, and Head-flicks) throughout the period of sniffing. This often was preceded by Rubbing with Crown-smoothing by the male, and followed by more of the same and/or overt attacks and fighting.

Occasionally, a male would perform Tongue-protrusion, with Nose-wrinkling, Eye-closing, and Head-flicks, without bothering to approach the stranger. More than one male was seen to do so when he was at least 10–15 feet distant from the releasing stimulus. Perhaps such performances were accompanied by some sort of "long distance" sniffing.

Typical sniffing with Tongue-protrusion and associated patterns sometimes continued for several minutes, or was frequently repeated, when the stranger

was an adult female. But it usually disappeared rather rapidly when the stranger was a male and/or a juvenile.

Similar patterns were performed by males during copulations, while their faces were pressed down into the fur of the females' backs.

It is, in fact, this combination of Tongue-protrusion with Nose-wrinkling, Eye-closing, and Head-flicks which was subsumed under the heading of "Sexual Sniffing" in several passages cited above. The whole combination must be very closely related to the patterns of many other eutherian mammals which have been called "*Flehmen*." See Andrew (op. cit.).

Neither *Aotus* nor *Callicebus* has anything strictly homologous with Tongue-protrusion itself. But, according to Epple (1967), similar patterns are exhibited by *Leontideus rosalia*, *Callimico goeldii*, and species of *Callithrix*. This is interesting from a comparative point of view (see page 74). The Tongue-protrusion of tamarins and marmosets probably also is closely related to the series of rhythmic tongue movements which are the usual precopulatory displays of both male and female *Alouatta palliata* (Carpenter, 1934).

There are several types of variations in the performances of Rufous-naped Tamarins in addition to those already mentioned.

Real, extreme, Tongue-protrusion is performed by females occasionally. Thus, for instance, I saw one female perform silent Tongue-protrusion just like the male with whom she was engaged in mutual nose to tail sniffing at the time. Another female was seen to perform more or less similar movements during an apparently unsuccessful copulation attempt, when she was resisting the male (M. Bernstein, personal communication).

(Epple [1967] cites several other possible examples. But I am not sure that she always distinguished between the ritualized Tongue-protrusion display and the less extreme, possibly or probably unritualized, "tasting.")

Several times, wild tamarins were seen to perform Tongue-protrusion in apparent response to the approach of a human being. I think that these displays were accompanied by much less well developed Nose-wrinkling and Eye-closing than the corresponding patterns of captive animals in partly or wholly sexual circumstances. Certainly, at least some of the Tongue-protrusion by the wild individuals was not combined with Head-flicking. One captive adult male also did Tongue-protrusion directly to me when I entered his

cage. This was associated with Head-flicks, but (again) with little or no Nose-wrinkling and Eye-closing.

The wild individuals uttered Trills and Twitters before and after their Tongue-protrusion. The captive male uttered Trills, Short Whines, and Infantile Squeaks before and after his similar performance. And the female resisting copulation actually uttered a peculiar muffled, rhythmic noise, possibly a modified version of Broken Rasps, *during* her Tongue-protrusion. (It may be added, in this connection, that a captive juvenile once performed Tongue-protrusion in close association with Infantile Squeaks, Infantile Rasps, Long Rasps, and Broken Rasps, when caught and held in the hand for some minutes. This was done without Eye-closing, Nose-wrinkling, or Head-flicks.)

Obviously the extreme Tongue-protrusion display with associated patterns is very highly ambivalent, perhaps one of the most highly ambivalent behaviors of the species. And all or most of the tendencies involved must be relatively quite strong even in the least high-intensity versions.

The activation of hostile motivation is revealed by the associations with partly or completely hostile calls, Rubbing and Crown-smoothing, and even overt fighting, as well as the occasional performances toward potential predators. Copulatory motivation must be strong in the patterns performed by males during copulations. This and/or some other sexual tendencies probably are involved in the "greetings" between males and females. Sexual and/or friendly tendencies may be present in the performances directed by males toward other males or juveniles.

The various patterns probably also are heterogeneous in another sense. As noted above (page 41), the accompanying Head-flicks may be purely hostile. The Nose-wrinkling, with the Eye-closing which seems to be linked to it (see also below), may be almost purely sexual, or at least more strongly sexual than the tongue movements themselves.

Three times, I saw captive individuals put their heads together and partly "interlock" their jaws. This always was silent. It always occurred in very ambiguous, but at least partly hostile social circumstances. It appeared to be a very inhibited and/or ritualized form of mutual biting; but it never produced any visible injuries, and it may have been accompanied by some sort of mutual "tongue play."

It is mentioned here only because some comments by J. K. Hampton (personal communication) would

suggest that similar performances may be more common in *S. oedipus*.

Rufous-naped Tamarins have another pattern which probably functions as a special signal. The Eye-closing associated with Tongue-protrusion may entail some lowering of the "eyebrows," but this is usually or always slight. Occasionally, individuals of the species may lower the eyebrows much more vigorously, to produce an extreme Frown, quite similar to the corresponding human pattern in appearance. This may be purely hostile. I have seen it performed, with Crown-raising, by a captive adult male who was making intention movements of attacking me. His Frowning also was accompanied by a partial closure of the eyes, a sort of "squinting," but there was little or no trace of Nose-wrinkling and certainly no Tongue-protrusion. (Thus, it would seem to be advisable to distinguish sharply between this squinting and the "real" Eye-closing as the latter term is used in this paper.) Exaggerated Frowns, probably with squinting, also may occur with many or all General Ruffles. Possibly they are another form of threat.

Epple (1967) cites Frowns by both *S. geoffroyi* and *S. oedipus*. She says that they are accompanied by protrusion of the lips. I did not notice this myself. The protrusion of the lips cannot be as conspicuous as in *Ateles*, *Cebus*, or *Callicebus moloch*.

Rufous-naped Tamarins do not seem to flatten and erect the ears during hostile reactions in the same ways as the species of *Callithrix* described by Epple (1967). Unlike most species of *Callithrix*, they do not have elongated "ear tufts" of black or white hair. But they may bring their ears forward during some Sexual Sniffing performances. I do not think that this can be considered an independent display.

• *Significance of Colors*.—Most of the more aggressive displays of *S. geoffroyi*, usually functioning as threat, are performed facing more or less directly toward opponents. This must reveal and emphasize the white on and around the face. And the amount of visible white is increased by special movements and postures and/or pilo-erection in such aggressive patterns as the stand-up (with General Ruffle) and Crown-raising. This would suggest that white may be intimidating per se. If nothing else, individuals should learn that a parade of white often precedes attack.

The rufous of the nape, genital region, and base of the tail, by contrast, is emphasized in a variety of friendly and/or sexual displays; and also in appeasement. This would suggest that rufous itself may be

“positively non-hostile.” At least, an individual performing a pattern emphasizing rufous probably is attempting to indicate that it would prefer to avoid overt hostilities if possible.

The brindled black and yellow of the back and outer parts of the limbs may be effectively neutral.

Certain inferences can be drawn from these assumptions.

The Lie-back posture, with its extensive revelation of white, should be intimidating.

The ultimate cause of the disappearance of the Arch display during the evolution of *S. geoffroyi* probably was that it emphasized the neutrally colored back instead, or even at the expense, of the white on the underparts. Arch displays are aggressive, and function as threat, in all the species in which they are known to occur at the present time. The Arch of the ancestor of *S. geoffroyi* presumably was similar. One can easily imagine that such a behavior pattern would become much less effective as soon as white coloration became intimidating and was concentrated on parts of the body which the pattern did not emphasize. (And selection probably did not favor the development of white on the back, because it would render individuals too nearly continually conspicuous, and therefore vulnerable, to predators, especially flying birds of prey.)

The closely related *S. oedipus* is quite similar to *geoffroyi* in both behavior (see page 66) and many morphological features, but it has relatively more white (a very large “top-knot” or mane) and no visible rufous on its head. Thus, one would expect that individuals of one form would interact with individuals of the other form rather less easily and efficiently, on the average, than either would with other individuals of its own form (see also page 67). If so, then there probably would be selection pressure against hybridization between the two forms, when and if it should ever occur in the wild.

GENERAL COMMENT ADULT SIGNAL REPERTORY

Adult Rufous-naped Tamarins certainly have more types of visual displays, and use them more frequently, than *Callicebus moloch* individuals which are approximately equally diurnal and live in rather similar-looking vegetation. To some extent, this seems to be a real replacement or substitution. Rufous-naped Tamarins perform visual displays in some circumstances in which *C. moloch* individuals would be expected to perform acoustic displays. Conversely, *C.*

moloch individuals perform acoustic displays in some circumstances in which Rufous-naped Tamarins would be expected to perform visual displays. This seems to be another illustration of a general rule among primates, which has already been summarized as follows:

... vocalization is the principal means of communication in the order as a whole. It probably is actually or potentially the most efficient method of communication between individuals of all species. It probably has been selected against, in some species, only because it is equally or more efficient in communicating information to the ‘wrong’ individuals (of the same or other species) as to the ‘right’ individuals (Moynihan, 1967).

The wrong individuals are easily identifiable in the case of the Rufous-naped Tamarin. As has been mentioned repeatedly, individuals of this species seem to be particularly vulnerable to predation. Certainly much more so than *C. moloch* individuals. And vocalizations are much more likely to be noticed by a predator, especially at a distance in forest and scrub, than are visual displays, especially such patterns as pilo-erection and positioning of the tail.

In spite of the difference in relative importance of visual and acoustic displays, it seems likely that the total number of all specialized signals, mediated by all senses, is roughly comparable in *S. geoffroyi* and *C. moloch*. Both species have rather extensive repertoires of qualitatively distinct ritualized patterns (“major” displays in the sense of Moynihan, in press) plus many other ritualized patterns which can best be described as only quantitatively distinct. In the case of *C. moloch*, most of the latter are intermediate between major displays (usually vocalizations). In adult *S. geoffroyi*, most of them are combinations of major displays; for example, one or more vocalizations combined with one or more pilo-erection or smoothing patterns, special positions of the tail, and/or movements of the body or head. Adult Rufous-naped Tamarins probably have approximately 32 major displays (give or take a half dozen). By combining these in various ways, and modifying the forms of particular components of combinations according to circumstances (especially strength of motivation), they can, and obviously do, produce huge numbers of recognizably different signals. I could not always distinguish between the signal valences of some complex combinations which were only slightly different in form. But such patterns certainly could encode slightly different “messages” (in the sense of the term used by W. J. Smith, 1965). And for logical (meth-

odological) reasons, the student of behavior must assume that they actually do so.

The display repertory of adult *C. moloch* seems to contain a rather large amount of redundancy. Different displays seem to transmit essentially similar messages to the same receivers. The approximately equally large repertory of adult *S. geoffroyi* also must include some redundancy, but probably not nearly as much.

Many of the display performances of adult *geoffroyi* are less obviously unified or "cohesive" than are those of *moloch*. I often found it difficult to grasp what a single Rufous-naped Tamarin was both saying and doing, with different parts of its body, at the same time. Many combinations of displays of the species do not seem to have any general *gestalt* as a whole. This would suggest that different components of the combinations may be designed for, adapted to be perceived by, different recipients, which also seems reasonable in many particular instances. Consider, for example, an individual which utters Loud Sharp Notes and performs Swaying with Tail-ruffling and Crown-smoothing as a reaction to the appearance of a potential predator. The notes and Swaying may be adapted to tell the predator that it has been discovered. The notes also may inform other potential prey, individuals of other species (which might be induced to mob the predator) as well as other Rufous-naped Tamarins, that there is danger in the neighborhood. And the Crown-smoothing and Tail-ruffling may reinforce the warning for other tamarins of the same social group as the performer, individuals who are likely to be fairly close by, at least in sight, more often than not.

Thus, one of the reasons why so many Rufous-naped Tamarins display performances are so complex (compound) may be that they have to work in many different ways. A single performance probably must be designed to transmit one or more messages along different channels, to different distances, and often in different directions, all simultaneously.

Behavior of Infants and Young Juveniles

Like the female of all or most other species of tamarins and marmosets, female *S. geoffroyi* usually conceive and presumably usually bear two young at a time (Wislocki, 1939), but both members of a set of twins are seldom raised successfully in the wild in the Panamanian region under present conditions. In my experience, it is very rare to see two infants or juveniles of the same size, apparently of the same age, in a

group of wild *geoffroyi*. And all or most of the few examples seen were in relatively large groups, and may well have been the offspring of different mothers. Thus, it would appear that one of a set of twins usually dies shortly after birth under natural conditions. (Wislocki also cites several cases of one of a pair of fetuses being resorbed before birth.) The "extra" individual of every set of twins usually seems to be nothing more than "reinsurance," a possible replacement for the other member in case of disaster, or an added but highly speculative "bonus," only to be cashed (reared) in years when the environment is particularly favorable.

(The limiting factor may be food. Several sets of twins born in captivity on Barro Colorado Island were raised successfully by their own parents. Both they and their mothers were provided with super-abundant food and a greater choice of things to eat than would be likely to be encountered in the wild.)

Some aspects of the behavior of young Rufous-naped Tamarins and their parents have already been described by Epple (1967) and others. The following account will not attempt to duplicate these descriptions. It will include a little miscellaneous background information plus analyses of certain infantile signal patterns.

My own observations of young Rufous-naped Tamarins were fairly detailed in some respects and extremely summary or incomplete in others. I saw very little of the behavior of newly born or very young infants in the wild, but I did observe large numbers of older infants and juveniles, one-third to three-quarters grown, in such areas as Ancon Hill and the Forest Reserve. Some thirteen young were born alive in captivity on Barro Colorado Island during the course of this study. Of these, I watched three (one single individual and one set of twins) intensively at irregular intervals. Many other young which were not born on Barro Colorado, but some of which were obtained at very early ages, were hand reared in the laboratory and studied more nearly continuously.

APPEARANCE

The coloration of newly born young is quite distinctive. The areas of the body which are brindled in adults appear to be nearly or completely pure black. The rufous of the nape is already well developed, and always relatively much more conspicuous than it usually is in adults. The white crown patch, on the

other hand, is very insignificant. It consists of only two thin streaks (meeting in front of the rufous to form a V). It is not very white either, more of a dirty light gray. Most of the underparts with white or whitish fur in adults are nearly naked in newly born young, and the bare skin of these areas is an inconspicuous, medium dark, pinkish gray. Only on the sides of the neck are there small patches of light gray hair.

This coloration is obviously adaptive. Hostile white is reduced (and reaches its minimum when an infant is sleeping or resting quietly, when it usually keeps its head pressed down into the fur of the adult on which it is riding). Non-hostile rufous is always at a relative maximum. Both features should help to avert attack by adults, either by parents (who might be irritated or alarmed by their new dependent) or by other members of the same social group.

By the time that the young are approximately one month old, they are much more similar to adults in appearance, although still easily distinguishable (see Figure 21). Their peculiar features are concentrated



FIGURE 21.—A young juvenile Rufous-naped Tamarin uttering Infantile Squeaks.

on the head. The white crown is fully developed. It is, in fact, even more conspicuous than in adults. It is relatively larger and often broader, and the hairs of the crown are usually or always erect or semi-erect. (This probably means that older infants and young juveniles do not have distinct Crown-raising and Crown-smoothing displays, but see page 52.) The faces of young animals at this stage also are covered with rather dense coats of light gray hairs. As a result, they look a great deal "fluffier" than adults. In this

respect, of course, they resemble the young of many other mammals, species of other orders as well as other primates.

These features also must be adaptive. The increased white may help to avert attack, because it is intimidating. Intimidating characters might be expected to be also irritating in some circumstances. But this is not usually evident among the threat patterns of Rufous-naped Tamarins. In any case, juveniles may be able to take more risks than newly born infants, and/or whatever irritating qualities may be inherent in white coloration may be contradicted or nullified by fluffiness.

RELATIONS WITH PARENTS

It is generally supposed (see, for instance, Hill, 1957, and Sanderson, 1957) that infant and young juvenile marmosets and tamarins are carried by the male parent most of the time when they are not being suckled by the mother—at least after the first few days after birth. This also was true of several infant Night Monkeys and one infant *Callicebus moloch* born and raised by their parents in captivity on Barro Colorado Island. But the division of labor was slightly different in the case of infant Rufous-naped Tamarins born and raised in similar circumstances. These infants were carried by their mothers and fathers with approximately equal frequency, and they spent considerable time on their mothers quite apart from feeding. Epple (1967) says that infants also may be carried by other (presumably adult) members of the same social group. Possibly some of this behavior is an artifact of captivity. Possibly infant Rufous-naped Tamarins are carried longer and/or more often by their fathers in the wild, where adults range over wider areas and are in less constant close proximity to one another.

(As might perhaps have been expected, however, a single female can rear twins successfully in the conditions of captivity even in the absence of an adult male.)

An infant being carried by a parent can move about quite actively on occasion, crawling over different parts of the parent's body (see below), but these bursts of activity tend to be brief. Most of the time, the infant remains nearly immobile, apparently asleep or resting. During the periods of calm, the infant usually rides high on the parent's back, often in a diagonal transverse position (i.e., arranged in such a way that its own head is just behind and to one side of the

adult's head). It clutches the adult's fur with both hands and feet, and keeps its tail firmly pressed against, or partly coiled around, the adult's body.

My own observations of captive animals suggest that infants are carried nearly continuously for approximately one month after birth. But they certainly are capable of moving around independently of adults almost from the very beginning, and they may do so, very briefly and occasionally, even during the first week of life. These excursions rapidly become longer and more frequent during the second month. By the end of this period, an infant usually is moving independently all the time. (This schedule is similar to, although not exactly identical with, the one reported by Eppler, 1967.)

The process is reversed in only one set of circumstances. As noted above, juveniles may leap onto a parent's (at least an adult's) back when alarmed.

Even when not disturbed, young juveniles usually stay within a few inches or feet of their parents during the first few weeks after beginning to move independently, but older juveniles associate much less closely. In the wild, parent-young bonds may have become very inconspicuous indeed by the time the young are half grown.

Adults carrying infants usually pay surprisingly little obvious attention to their burdens. They tend to move more cautiously (slowly) when carrying than when not, but they seldom manipulate or even look directly at the infants.

An infant usually moves to the breast to suckle by its own unaided efforts. It does so by moving up and over the mother's shoulder, and then crawling down to a nipple. Having reached its goal, it may turn around and suckle head upward. Then it returns to the mother's back by the same route. The mother usually is sitting down during suckling, in a perfectly ordinary posture with Tail-looping. The infant may be partly supported by the mother's thighs or knees, but only rarely does she lift a hand to provide additional support or guidance.

Presumably infants have to learn which parent gives milk. I have seen very young infants try to suck on their fathers' nipples.

Infants usually have to transfer from one parent to the other on their own. A parent who seems to have become tired of carrying just sits down. It may do so where it happens to be at the time, or make a special effort to join its mate. If it does not go to its mate, the latter usually comes to it, sooner or later. Then

the two adults sit side by side. Often facing in opposite directions. At which point, the infant(s) may or may not crawl from one adult back to the other.

I could not detect any other "commanding" signal, such as a special call, which initiated or accelerated transfers.

Obviously, different infants can react differently to the same external stimulus. When twins are involved, as in some of the captive animals, one infant may transfer while the other does not.

I never saw a parent lend a helping hand during a transfer which was proceeding more or less normally. If an infant should fall, however, a parent usually will grab it. Once grabbed, the infant clammers back to the parent's back under its own power.

INFANTILE VOCALIZATIONS

The most common displays of young Rufous-naped Tamarins are the Squeaks and Infantile Rasps which have already been mentioned several times above.

Infantile Squeaks are illustrated in Figures 22, 23, 24, and 25. It will be seen that they are quite diverse in form. All the variants are at least fairly brief, but some are much shorter than others. On the whole, they are perhaps most reminiscent of Short Whines. It is always possible, nevertheless, to distinguish between the two patterns. Infantile Squeaks usually or always show (on spectrograms) fewer harmonics than Short Whines. They also are descending in pitch. In most cases, the descent is much slighter and more gradual than in Sharp Notes. And even the most abrupt Infantile Squeaks do not include the initial rising or horizontal phase which is typical of most Sharp Notes. When Infantile Squeaks are uttered in series (see below), the temporal patterning of notes is never the same as in either Trills or Twitters. All or most Infantile Squeaks are approximately as loud as most Twitters; i.e., softer than Loud Sharp Notes or the majority of Trills. They also have, to human ears, a very characteristic nasal, "complaining" quality. (They could be described as even more whining than the Short Whines.)

Infantile Rasps are illustrated in Figures 24 and 25. They do not look very different from Long Rasps on spectrograms, but they seem to be more even, "steadier," in pitch. Many of them also are much shorter than any Long Rasps (without being obviously "fragments" like the "syllables" of Broken Rasps). They are quite loud and harsh, but they also

have much the same nasal and complaining quality as the Infantile Squeaks.

Infantile Squeaks sometimes are uttered singly, or in short homogeneous series which do not include any other types of notes. This may also be true of Infantile Rasps. But it is much, *much* more common for the two patterns to occur together, in rapid succession, in the same series. The two types of notes may even intergrade during some series. See Figures 22 and 23. Both usually are uttered with the mouth wide open. This is shown in Figure 21.

Both patterns, when performed by young animals, seem to be "distress" notes, expressions of "dissatisfaction," and rather generalized as such. They are uttered by infants and juveniles who are uncomfortable or unhappy in almost any way—e.g., too hot, too cold, wet, falling down, in pain, thirsty, hungry, or isolated, or lost—but perhaps only when the animals cannot relieve the situation, remove or get away from the source of the discomfort, by their own unaided efforts. (Like young Night Monkeys, young Rufous-naped Tamarins who are just beginning to become dissatisfied usually start to move, and these initial movements often are quite silent. Usually, it is only when the first movements do not procure satisfaction that the animals begin to vocalize.)

The principal or only casual difference(s) between Infantile Squeaks and Rasps would seem to be degree of discomfort and/or strength of frustration. The two patterns may occur in the same types of situations, but Squeaks obviously are lower intensity than Rasps. They are uttered more frequently than Rasps. And a young animal who is uttering many Rasps usually is unmistakably more unhappy and/or thwarted than an animal which is uttering only Squeaks. This may be illustrated by the example of an infant which is hungry but cannot find, or reach, a source of food. After some preliminary fruitless movements, it utters one or two brief Squeaks. As it gradually becomes hungrier, it utters series of notes, including at least one long Squeak as well as shorter variants, plus one Rasp. When it becomes hungrier still, it utters longer series including two or three Rasps. The Rasps themselves also tend to become longer. During this progression, the infant may make increasingly vigorous "searching" movements. And as the series become longer, they also tend to become more frequent, following one another at ever shorter intervals.

Young animals raised by their parents, in captivity as well as in the wild, utter distress calls much less fre-

quently than infants and juveniles raised by human beings in the laboratory. Presumably the young associated with their parents are much less frequently dissatisfied.

It seems probable, however, that other factors may also be involved in producing the peculiar behavior of hand-raised young. Of course, all these young always suffer from lack of normal companionship. But they seem to make partial adjustments to this lack quite easily and rapidly. They usually stop making obvious escape and continuous searching movements within a few days after being brought into the laboratory, as long as they are well provided with such things as food, milk, water, suitable ambient temperatures, woolly towels to grasp, and sleeping boxes. And yet they usually or often utter Squeaks and Infantile Rasps almost incessantly. Certainly, they tend to vocalize much more frequently than the young of most other genera of New World primates in similar circumstances. It is hard to escape the impression that a good deal of this vocalization is simply the result of boredom (which might, after all, be considered another form of distress).

This explanation does not contradict the suggestion made on page 12. Hand-raised young Rufous-naped Tamarins utter Squeaks and infantile Rasps relatively and comparatively frequently at *all* stages of juvenile development. Granted that this is partly due to the fact that human beings are not completely satisfactory as substitutes for real parents, and that hand-raised young are often bored, it is still quite possible that the *prolongation* of frequent infantile vocalization into the later stages of the development of such animals is also partly a consequence of their peculiar relationship with their human keepers. Human beings may not be very good parent substitutes, but they remain *in loco parentis* much longer than real parents.

It should also be stressed that prolongation of infantile behavior is just as characteristic of all other New World monkeys raised by humans as of Rufous-naped Tamarins. But this does not affect the fact that hand-reared Rufous-naped Tamarins utter infantile vocalizations more frequently at all stages of development than do comparable individuals of most other species.

The primary function of the distress calls of young Rufous-naped Tamarins probably is to attract the attention of parents (and possibly other adult members of a band) and induce them to satisfy the needs of the young.

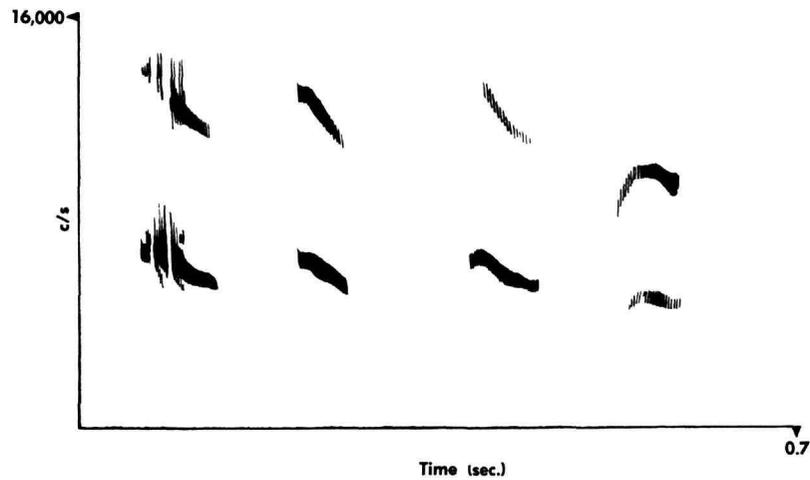


FIGURE 22.—Vocalizations of a young Rufous-naped Tamarin. The first note is intermediate between an Infantile Rasp and an Infantile Squeak. The other three notes are more or less typical Squeaks.

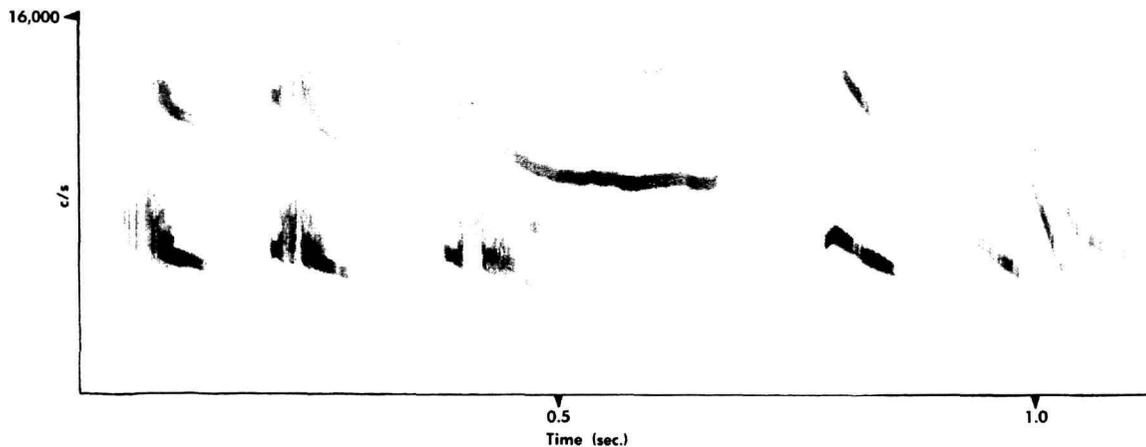


FIGURE 23.—Vocalizations of a young Rufous-naped Tamarin. More Infantile Squeaks and intermedates between Squeaks and Infantile Rasps.

The precise effects of particular infantile vocalizations are not always easy to detect in the wild under natural conditions. But certainly parents will catch falling young which are uttering Squeaks and/or Infantile Rasps. An adult which has left its partly independent young behind, while moving through trees or scrub, may stop or even turn back if the young begins to utter distress calls. This permits the young to rejoin the adult. And a mother may allow the young to suckle after rejoining in such circumstances.

It probably is significant that there is considerable

individual variation in the arrangement of different distress notes. All the accompanying illustrations are derived from recordings of a single young individual (less than half grown at the time). They indicate that this individual usually uttered Infantile Rasps before Squeaks when both types of notes were uttered in a single series. Other young usually uttered Squeaks before Rasps.

This sort of variation may facilitate individual recognition.

The situation may be summarized by saying that

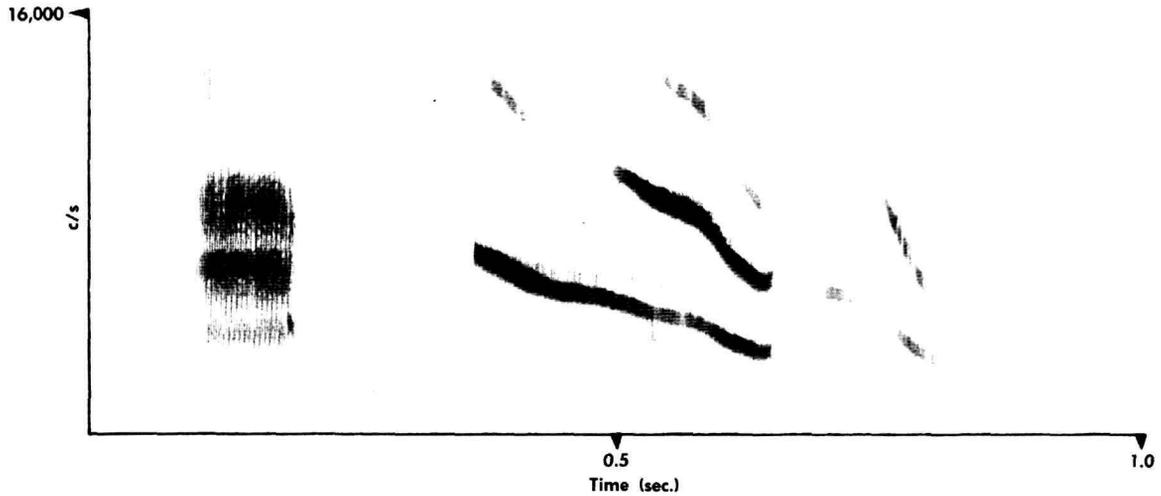


FIGURE 24.—Vocalizations of a young Rufous-naped Tamarin. A brief Infantile Rasp followed by a prolonged Infantile Squeak.

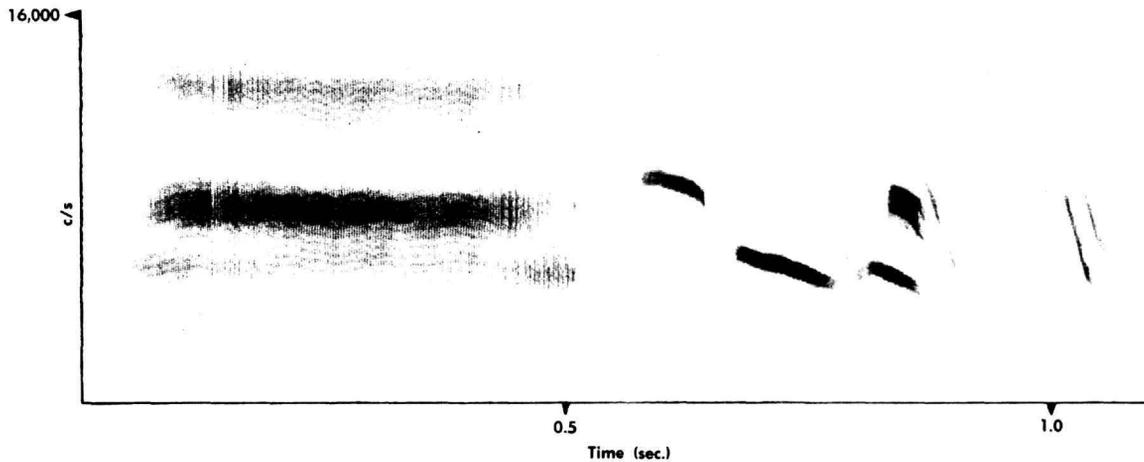


FIGURE 25.—Vocalizations of a young Rufous-naped Tamarin. A prolonged Infantile Rasp followed by one (or one and a half) Infantile Squeak(s).

association between Infantile Squeaks and Infantile Rasps certainly is stereotyped (ritualized) per se, but the form of the association is not.

Squeaks and Infantile Rasps can be supplemented by other vocalizations. It has already been mentioned (page 11) that young individuals can perform many typically adult patterns. I have heard captive young who were one to two months old (still very small) utter Long Whistles, Twitters, Trills, Loud Sharp Notes, Soft Sharp Notes (and possibly Sneezing Sharp Notes), Long Rasps, and probably Broken Rasps, on

a few occasions. Sometimes these patterns were uttered by themselves alone. At other times, they were incorporated into series of Infantile Squeaks and Rasps. They all occurred in circumstances which suggested that their motivation was similar to, or identical with, that of the same patterns when performed by full adults.

There also is some intergradation between typically adult and typically infantile vocalizations. Infantile Rasps seem to be particularly likely to intergrade with Long Whistles and Long Rasps. Squeaks may be

most likely to intergrade with Twitters (Short Whines) and Soft Sharp Notes.

(It may have been noticed that I have suggested that both Long Whistles, and in some circumstances, distress notes may function as "lost calls." This does seem to be true. When both types of patterns are uttered by young, the distress notes seem to be of lower intensity than Long Whistles. A separated infant or juvenile usually begins vocalization by uttering distress calls, and then switches to Long Whistles if its isolation continues.)

The fact that *S. geoffroyi* has a fairly distinct repertory of infantile vocalization is interesting from a comparative point of view. Young *Aotus* also have distress notes which are characteristically infantile. These probably are related to the infantile vocalizations of Rufous-naped Tamarins, but they are rather different in some aspects of form. Most conspicuously, they do not include notes of harsh or rasping quality. As a whole, the infantile repertory of *Aotus* seems to be more similar, in morphology, to the complex of high-pitched vocalizations of *Callicebus moloch*, but the *moloch* patterns seem to be almost equally characteristic of both adults and young. Of all the species of other genera that I have observed at some length, only *Pithecia monacha* (very different from tamarins in some other ways) seems to have both clear and rasping special infantile distress notes.

OTHER PATTERNS

It is not easy to determine exactly when young Rufous-naped Tamarins first became capable of producing other display patterns, simply because they seldom have occasion to do so under normal conditions. Some patterns certainly appear, or are performed frequently, earlier than others. I have seen Head-flicking, Tail-ruffling, Tail-forward, Tip-coiling, and Sit-rubbing performed by very young individuals in captivity. Many other signal patterns gradually "drift in" during the later stages of childhood and adolescence. Even distinct Crown-raising and Crown-smoothing may appear before full maturity is attained. The only major hostile or friendly display which I have not seen performed by a subadult individual is the General Ruffle, and juveniles probably are too weak and/or timid to engage in the very high-intensity disputes to which General Ruffles seem to be confined.

Most of these nonvocal patterns are essentially identical, in form and other respects, with those of

full adults as soon as they appear. The only obvious exception is provided by the Head-flicks, which may be combined with a much greater range of calls and notes (including distress notes, Twitters, Long Rasps, and Broken Rasps) when performed by (hand-raised) young than when performed by adults.

Young monkeys of many species are more or less "playful" (play may be difficult to define theoretically, but it is usually easy to recognize—see also comments in Loizos, 1967). The most typical forms of play in young Rufous-naped Tamarins are chases and wrestling bouts, with adults as well as other young, which do not culminate in the vigorous biting and striking of "real" fights. *S. geoffroyi* infants and juveniles perform such patterns approximately as frequently as young Night Monkeys, less frequently than young *Callicebus moloch*.

SIGNALS OF OTHER SPECIES OF *SAGUINUS*

A few other forms of the genus have been observed more or less briefly and casually.

Saguinus oedipus, the closest relative of *geoffroyi*, is the best known. Some of its behavior patterns have been described by Epple (1967 and 1968), Epple and Lorenz (op. cit.), and Andrew (op. cit.). All the published accounts imply (or state) that many of the displays of *oedipus* (at least ritualized movements, postures, and vocalizations) are nearly identical with those of *geoffroyi*. They suggest that the behavior of the two forms may be (even) more similar than their color patterns. This also is my impression. I kept a single adult male *oedipus* in captivity on Barro Colorado Island for almost a year in late 1958 and 1959. During most of this period, he was kept in an outside pen with three to five *geoffroyi* individuals (all adult except one). In these circumstances, he was seen to perform both nose to nose and nose to tail sniffing (with the Rufous-naped Tamarins), stand-up postures (to me), Swaying, Head-flicking, and Tongue-protrusion. He also was heard to utter Twitter-like notes (and possibly a few Squeaks and/or Soft Sharp Notes), Trills, Loud Sharp Notes, Long Rasps, and Broken Rasps. All these patterns were very reminiscent of the corresponding performances of *geoffroyi* in form, and occurred in roughly comparable social situations, although not always with the same frequency (but see also below). I might add that Epple (1968) describes another pattern of *oedipus* which may be strictly homologous with the Long Whistle of *geoffroyi*; and

Epple and Lorenz (op. cit.) state that *oedipus* also performs Rubbing (apparently Pull-rubbing).

It probably is very significant, therefore, that the male *oedipus* kept in captivity on Barro Colorado was the "odd man out" in the group of Rufous-naped Tamarins with which he was confined. He slept in the same box with the other animals at night (although there were alternative sleeping quarters available), and did not fight with the others any more than they fought among themselves. But he tended to "keep his distance" during the day, often remaining on the edge or outskirts of the group. He appeared to be followed and joined by the Rufous-naped Tamarins, and to follow and join them, rather less frequently on the average than they followed and joined one another. (This partial segregation was particularly remarkable because some other kinds of specific discrimination seem to break down in captivity. See page 24).

A third form of the genus is *leucopus*. This has always been recognized as a good species, but it shares a number of morphological characters (not including type of color pattern) with *geoffroyi* and *oedipus*, and may be not very distantly related. (Hershkovitz, 1966, places all these forms among the "bare-faced" tamarins.) I observed a single *leucopus*, a male on the threshold of maturity, in the New York Zoo for several hours on two successive days in November of 1958. This animal had been born and raised in captivity, but was being kept in a small cage by himself (after an illness) at the time. He was seen to perform many elaborate Tongue-protrusion displays, apparently as reactions to my approaches. The Tongue-protrusion movements themselves were quite like those of *geoffroyi* and *oedipus* in form. To my surprise, however, they usually were accompanied by a peculiar sound, a sort of "Muffled Chattering" of variable loudness. This was quite different from anything I ever heard uttered by Rufous-naped Tamarins (but it may, conceivably, have been related to the sound which M. Bernstein heard uttered by a female *geoffroyi* performing Tongue-protrusion during an unsuccessful copulation attempt, see page 57). The *leucopus* male, also uttered Short Whines (possibly organized into brief Twitter series), Soft Sharp Notes, Loud Sharp Notes, Long Rasps, Broken Rasps (quite distinct from the Muffled Chatter), Infantile Squeaks, and Infantile Rasps. All were quite similar to the corresponding patterns of *geoffroyi* in sound, except the Long Rasps which were much more nasal, i.e., more like Infantile Rasps in tone.

Another group of species of the genus *Saguinus* is even less like *geoffroyi* in appearance than is *leucopus*. It probably includes all the forms which Hershkovitz (1966) calls "hairy-faced 'white-lipped' tamarins" plus some others; and it seems to be essentially equivalent to (although certainly not absolutely identical with) Hill's (op. cit.) "genus" *Tamarinus*. Most of the animals of this group are largely black and rufous, and have black faces with white muzzles, and sometimes more or less well-developed white moustaches.

As might be inferred from the preceding passage, the classification of the forms of this group is still rather chaotic. To my knowledge, the last published revision is by Hershkovitz (1966). This is only partial, and unfortunately Hershkovitz does not cite the evidence for most of his conclusions (viz., page 1). But he does recognize, and list diagnostic characters for, three species: *S. graellsii*, *S. nigricollis*, and *S. fuscicollis*.

I saw several individuals of this group on various occasions during the course of the present study. By sheer chance, they all appeared to have been representatives of the species defined by Hershkovitz.

Six adult individuals (including both males and females) and one juvenile (more than half grown) were kept in captivity on Barro Colorado Island for almost two weeks in August 1964. They were obtained from an animal dealer in Iquitos, Peru. They certainly all belonged to the same subspecies, apparently a form of *fuscicollis sensu* Hershkovitz.

As a precautionary measure, in case there should be more revisions or changes in the taxonomy of the group in the future, it may be useful to insert a brief description of these animals. They had black heads, ears, and faces, with white muzzles. The white was interrupted only by black on the top of the nose and by a series of vertical black stripes on the chin just below the mouth. (The latter were really remarkably conspicuous. The alternation of black and white areas on the chin gave the impression of enormously large teeth, which can hardly be coincidental. It may be very intimidating.) The white hairs of the muzzle were much longer ("fuzzier") in the juvenile than in the adults. There was a not very extensive area of rufous behind and around the black face and ears. The hands and feet were black, but the other parts of the limbs were rufous as were most of the underparts. Most of the back was brindled black and yellow. Most of the tail was black. All the individuals were appreciably smaller than Rufous-naped Tamarins of apparently similar ages.

These animals may have arrived on Barro Colorado Island in a diseased condition. They all died at the end of two weeks as a result of something which looked like "fulminating" Leishmaniasis. During the first few days, however, they were very active and apparently well adjusted, and they performed many display patterns.

All the individuals were seen to perform Swaying.

They also uttered many calls. Most of their vocalizations were higher pitched than the corresponding patterns of *geoffroyi*, possibly in correlation with smaller body size.

The juvenile uttered many Infantile Squeaks and Infantile Rasps. Both types of notes seemed to be identical with those of *geoffroyi* in every respect except pitch and, possibly, loudness or firmness of tone. They sounded even "thinner" and slightly "reedy."

Both the juvenile and the adults uttered Short Whines, Trills, Loud Sharp Notes, and Long Rasps. These vocalizations also, at least by themselves, were hardly distinguishable from the corresponding patterns of Rufous-naped Tamarins except by pitch.

But a few other aspects of the acoustic signal system were considerably more interesting. The Short Whines apparently were never organized into stereotyped series like Twitters. I never heard any Broken Rasps. Their absence may be correlated with the presence of another kind of display.

The adults often uttered more or less prolonged Whistles. At first hearing, these sounded quite like Long Whistles of *geoffroyi*, but further analysis revealed appreciable differences. The *fuscicollis* patterns were not usually organized in two or three note series. They were not plaintive in tone. Most of the individual notes were strongly rising in pitch. Some of them even "broke off," halfway through, in such a way as to suggest that they had moved up completely into the ultrasonic range. Almost all the *fuscicollis* Whistles also occurred in circumstances which were unmistakably hostile. They frequently intergraded with Long Rasps.

They must, in fact, have been produced by much the same type of motivation as Long Rasps, but they appeared to be rather lower intensity on the average. Thus, for instance, an individual picked up in the hand usually uttered many Long Rasps and struggled and fought violently at first. Then it would gradually relax (start to "give up"), struggle less violently, and also switch to Whistles. This would suggest that the intensity of motivation in the Whistles of *fuscicollis* may be much the same as in the Long Rasps of *geof-*

froyi, and that the intensity of motivation in the Long Rasps of *fuscicollis* may be much the same as in the Broken Rasps of *geoffroyi*.

It has already been mentioned that the Long Rasps of *geoffroyi* probably are homologous with the so-called Screams of many other species of Platyrrhini, including *Aotus* and *Callicebus moloch*. The latter patterns are basically similar to Long Rasps in almost all respects except for the fact that they are not (or not very) harsh. But, simply because they are clearer in tone, they are even more similar to the Whistles of *fuscicollis*. This would suggest that the Long Rasps and Whistles of *fuscicollis* are both descended from the same ancestral patterns, the Whistles having remained more primitive in form. If so, then the retention of a hostile Whistle display is a feature in which *fuscicollis* has remained more primitive than *geoffroyi* (and probably more similar to other tamarins such as *Leontideus rosalia* and *Callimico goeldii*).

At this point, it may be useful to pause and recapitulate. There have been so many references to various Whistles and Rasps, Squeaks and Screams, and related or associated vocalizations, in the preceding pages that it may be convenient to provide a partial summary, an outline of some of the differences and resemblances among the patterns of the different species cited and discussed.

1. *Aotus trivirgatus* has long, clear, high-pitched scream patterns. These are uttered by both adults and young. They seem to be purely hostile, and high intensity on the average, when uttered by adults. In the rather different vocal repertoires of infants, however, they are associated and often intergrade with high-pitched Squeaks and High Trills, in what can be called a Squeak complex. The Squeaks of infants seem to be generalized distress notes. The Screams of infants, which are essentially identical with the adult patterns in form, also seem to be distress notes, higher intensity than Squeaks, more often than not, at least in the first stages of infancy. But some of the infantile Screams may (also) be hostile, and the proportion (although not necessarily the actual number) of hostile Screams must increase rapidly as an animal matures.

The Squeak complex *Aotus*, as a whole, is comparable to the Infantile Squeak - Infantile Rasp complex of *Saguinus geoffroyi*. Some or all of the patterns involved probably are partly or wholly homologous. See also below. And the two complexes further resemble one another in being radically transformed, largely declining, with age. In the case of *Aotus*, only

the Squeaks and Screams normally survive into adulthood. And both types of vocalizations are uttered by adults only in rather restricted circumstances.

Aotus does not have any really harsh rasping sounds.

But it does have a distinctive Hoot display. Which usually takes the form of two or three moderately long, clear, but low-pitched notes. This seems to be entirely non-hostile, a signal to attract companions (mates or parents). At least when uttered by adults, the Hoots do not seem to be particularly closely related to, or associated with, either Screams or Squeaks.

2. *Callicebus moloch* also has long, clear, high-pitched Screams.

They are part of a complex of high-pitched patterns which also includes Squeaks, Whistles, and Trills. All of these patterns seem to be essentially hostile. And they all seem to be nearly or completely as characteristic of adults as of young.

Callicebus moloch does not, in fact, have any sort of complex of vocalizations which could be described as primarily infantile. The species differs from both *Aotus* and *Saguinus geoffroyi* in this respect.

It seems probable, nevertheless, that the Squeaks of *moloch* are strictly homologous with those of Night Monkeys. They are really very similar in form. The Screams of *moloch* are slightly more distinctive in form, but may be equally strictly homologous with the corresponding patterns of *Aotus*. Interestingly enough, the Whistles of *moloch* look (on sound spectrograms) even more like the Screams of *Aotus*. These Whistles may be homologous with either typical Screams or intermediates between Screams and Squeaks of *Aotus*. This apparent superfluity of homologues is not really anomalous. The Whistles of *moloch* often appear to be low-intensity versions of the Screams, and high-intensity versions of the Squeaks. And they certainly intergrade with both.

The Trills of *moloch* also may be strictly homologous with the High Trills of *Aotus*.

Callicebus moloch individuals do not utter harsh rasping sounds.

Nor do they utter stereotyped series of two or three non-hostile notes to attract mates, parents, or other social companions.

3. *Saguinus geoffroyi* does have Rasping patterns. They occur in much the same situations, and seem to subservise the same functions, as the Screams of *Aotus* and *C. moloch*. They may be strictly homologous with

the latter, but they are rather strikingly different in some, not all, aspects of form.

Other patterns show similar ambiguous relationships. The Infantile Squeaks of Rufous-naped Tamarins may be partly or completely homologous with the Squeaks of both *Aotus* and *Callicebus moloch*, but again are rather different in form. The Trills of Rufous-naped Tamarins also have some features in common with the Trills of *C. moloch* and the High Trills of *Aotus*, but not enough to prove that they are perfectly homologous in the strictest sense of the term. Possibly the notes incorporated into the high-pitched Trills of all three species have a more or less remote common origin. But the components of the Trills of *S. geoffroyi* are distinctive enough to suggest that they may have been organized into series independently.

Saguinus geoffroyi does not have any long, clear, high-pitched Scream or Whistle pattern which is unmistakably hostile. What it does have is the special and non-hostile Long Whistle display. This sounds as if it had been formed by organizing Screams or Whistles like those of both *Aotus* and *C. moloch* into the temporal arrangement of the Hoots of *Aotus*.

4. *Saguinus fuscicollis* has some of the same Rasping patterns as *geoffroyi*. Unlike *geoffroyi*, however, it also has (presumably retained) long, clear, high-pitched Whistles which are hostile in motivation.

Saguinus fuscicollis certainly has a special primarily infantile vocal repertory. This seems to be essentially identical with that of *geoffroyi* in form. Presumably the various components are related to patterns of *Aotus* and *C. moloch* in exactly the same way(s) as are the corresponding patterns of *geoffroyi*.

The most enigmatic sounds uttered by the adult *fuscicollis* on Barro Colorado Island were Rattles. These were soft and relatively low pitched (for a tamarin). They were quite common, obviously lower intensity and/or less completely hostile than the Trills. They may have "taken the place" of the Twitters of *geoffroyi* in some sense. But they sounded very much like Rattles uttered by saki monkeys, *Pithecia monacha*. (It will be remembered, in this connection, that *P. monacha* individuals are the only other monkeys, apart from other tamarins of the genus *Saguinus*, which I have heard utter both clear and rasping infantile distress notes. The significance of such resemblances can only be assessed after *Pithecia* itself has been studied more intensively.)

Two individuals, an adult female and a subadult male, which were (tentatively) identified as *Saguinus graellsii* also were kept on Barro Colorado Island for a couple of weeks in November 1958. They were observed only very briefly, but a few display patterns were noted. One or both individuals performed Sit-rubbing, and uttered Infantile Squeaks, Short Whines, Trills, Loud Sharp Notes, and Long Rasps. Four individuals of another form of this group were observed in the National Zoo in Washington, D.C., at irregular intervals during both October and November 1958. They were identified (by the zoo authorities) as *Saguinus nigricollis*. They were adult or subadult but I did not check their sexes. They were seen to perform Sit-rubbing, and heard to utter Short Whines, Trills, Loud Sharp Notes, and brief stereotyped series of short notes which may, conceivably, have been Twitters. Almost all the observed displays of these presumed *graellsii* and *nigricollis* seemed to be very similar to the corresponding patterns of both *geoffroyi* and *fuscicollis*.

It seems probable, therefore, that the signal system of *geoffroyi* is at least fairly typical of the genus *Saguinus* as a whole.

FURTHER COMPARISONS

The preceding descriptions and partial summaries may be completed by a final comparative analysis, paying special attention to the morphologies of entire repertoires and to certain other genera which have not yet been mentioned very frequently.

Previous Descriptions of *S. geoffroyi* Vocalizations

Some of the additional genera which must be considered have been observed by other students. As would be expected, each student has used slightly different terms. Visual displays usually can be identified in (or through or behind) any form of description. But the human language and sensory equipment being what they are, it is much more difficult to interpret verbal descriptions of vocalizations. This difficulty may be inescapable. But some of the students of other genera have also observed *S. geoffroyi*. Comparisons of their descriptions of this species with the one given above may provide a standard by which to assess their accounts of other species. And also, of course, an opportunity to explain certain apparent contradictions or discrepancies in different accounts of *geoffroyi* itself.

Some of the defects of the general discussion of tamarin and marmoset behavior in Andrew (op. cit.) have been mentioned on page 26. In addition to his general comments, Andrew describes (without illustrating) two vocalizations of *geoffroyi*. Some of the details presented would suggest that the patterns which he identified as twitters in this particular species were series of Infantile Squeaks and that those which he calls "rasping screeches" were Infantile Rasps. The *geoffroyi* individuals whom he observed probably were infants and/or older animals which had retained, or reverted to, infantile behavior in the conditions of captivity.

Epple's (1968) account of the vocalizations of *geoffroyi* is much longer and more extensive, but seriously misleading in several respects. The reasons why her analysis is so poor are not always obvious. One factor seems to have been that she studied *Callithrix jacchus* much more thoroughly than any other marmoset or tamarin, and then "extrapolated" recklessly from this one species to the others. She recognizes the same categories of vocalizations, and gives them the same names, in *geoffroyi* as in *jacchus*. Unfortunately, however, it turns out that the organization of vocal patterns is quite different in the two species. This will be discussed below.

The particular patterns of *geoffroyi* cited by Epple include:

1. "Te" notes. Epple implies (without actually stating) that these are the most common and/or characteristic of the vocalizations of infants. She does not provide any illustration of them, when and as they are uttered by infants, but all or most of them must be the same as the notes called Infantile Squeaks in this paper. Epple seems to have missed the fact that they usually are uttered in stereotyped series with rasping notes. She implies that they usually are uttered singly by young infants. She does say that a young animal just starting to move independently uttered long series of "variable, faint, and high-pitched sounds," but she adds that the notes did not have a distinct rhythm. This is almost certainly wrong, or at least very atypical of the species.

She also says that similar notes are uttered by adults. She calls the adult patterns "monosyllabic calls given in close visual contact" and "monosyllabic calls in loose visual contact and when disturbed." She gives two drawings of sound spectrograms of the latter. They are very different in appearance. One probably represents a (perhaps slightly aberrant) Twitter. The other is a perfectly typical series of Infantile Squeaks.

Epple's animals may well have been retarded in the same way as those studied by Andrew. It is remarkable, nevertheless, that she nowhere recognizes the real distinction between Twitters (Short Whines) and Infantile Squeaks, either when uttered by young or by adults.

2. "Monosyllabic calls given in isolation." This is illustrated by a drawing of a spectrogram which seems to represent a three-note Long Whistle performance; perfectly typical, but rather abbreviated.

3. "Trills given in high excitement." These seem to be Trills in the sense used here, but Epple's drawing of a sound spectrogram of the pattern is very crude, omitting part of the relevant detail.

4. "Squeals given in submission." This is illustrated by an excellent photograph of a spectrogram which reveals that the pattern is an Infantile Rasp. (I do not understand how such a harsh note—and the features producing harshness are just as evident in Epple's spectrogram as in any of mine—could be described as a Squeal.) As noted above, Epple does not mention that Infantile Rasps usually are combined with Infantile Squeaks in stereotyped ways. She does, however, state that there is a similar but slightly different adult pattern, presumably the Long Rasp.

5. "Chatters given when angry." This must be the Broken Rasp, but it is accompanied by a drawing of a sound spectrogram which is very crude and incomplete indeed.

6. "Mobbing calls" or "Tsik" notes. The verbal description of these patterns suggests that they are Loud Sharp Notes, but the accompanying drawings of spectrograms are peculiar and puzzling. They show sounds like the Loud Sharp Notes illustrated in this paper, but with *much* longer introductory phases. I am at a loss to explain this difference. Possibly the patterns illustrated by Epple were ambivalent (some combinations of Long Whistles and Sharp Notes might be expected to produce the same effect on spectrograms). It may also be significant that some of the other species kept by Epple produced similar sounds. Possibly some of her Rufous-naped Tamarins were learning patterns from individuals of other species?

7. "Warning calls." As described by Epple, this category is hardly identifiable. All I can suggest is that it may represent some type of extreme Sharp Note.

Signals of Marmosets

Here the most important evidence is provided by Epple's work on *Callithrix jacchus*, summarized in her 1967 and 1968 papers (and in a third paper published under the name of Epple-Hösbacher, also in 1967) as well as in Epple and Lorenz, op cit. This may be supplemented, and partly checked, by information from other sources, including a rather detailed account of the same species (again ascribed to "*Hapale*") by Le Roux (1967), an anecdotal description by Fitzgerald (1935), some brief observations of my own on a few captive adult *jacchus* (observed in the London and Paris zoos in 1959 and 1961), and the results of a longer but still incomplete study of the related *Cebuella pygmaea* in captivity on Barro Colorado Island.

Most of the olfactory and visual displays of *jacchus* which were seen by Epple have already been cited above. They include Sit-rubbing, Pull-rubbing, Arch Postures with a general Ruffle, Frowns, Flattening and Raising of the Ears and Ear-tufts in threat, an "*Angsthaltung*" which consists of a forward movement of the ears and tufts, and Tongue-protrusion.

I saw slight Swaying performed by both the London and Paris individuals. Le Roux shows a drawing of what seems to be more exaggerated Swaying. He also describes a simple "looking away," like that of *Callicebus moloch*, and suggests that it may be a very low-intensity expression of alarm.

The animals in the Paris zoo performed an apparently ritualized Baring of the Teeth pattern. The lips were separated in front, without being drawn back at the corners, while the jaws remained almost or completely closed. The net result was to reveal the teeth, especially the lower incisors, as a white patch in the center of the blackish face.

This was essentially identical, at least in form, with the Baring of the Teeth by *Callicebus moloch* individuals. It was quite different from both the simple opening of the mouth which is typical of all *Saguinus geoffroyi* and the "fang showing" of the one aberrant individual described on page 56 (or any "grins" performed by the individuals observed by Andrew).

Sometimes the Baring of the Teeth by the *jacchus* individuals was quite silent. At other times, it was combined with soft rattling noises.

Some of the latter performances were accompanied by partial eye-closing. This probably was not the true Frown of the species. It certainly was different from the Frown of *Saguinus geoffroyi*. It was not brought about

by conspicuous lowering of the eyebrows. Thus, it was much more reminiscent of the "real" Eye-closing display of *geoffroyi*. And also a somewhat similar pattern of *Callicebus moloch*. As performed by the *Callithrix jacchus* individuals in Paris, it was not accompanied by either Nose-wrinkling or Tongue-protrusion.

Both Le Roux and Fitzgerald show photographs of Baring of the Teeth and Eye-closing by *jacchus*. Le Roux also provides excellent drawings of different intensities of the two patterns.

Cebuella pygmaea seems to have a special facial expression composed of similar elements. (See Figure 6 in Moynihan, 1967.)

Perhaps the most conspicuous of the ritualized visual (or visual and olfactory) signals of *Callithrix jacchus* is what Epple calls "*Genitalpräsentieren*." Rather surprisingly, this seems to be purely hostile. A performing animal faces away from its opponent(s), raises its tail (in the form of a question mark) and reveals its genito-anal region. A photograph of Epple-Hösbacher shows that all the hairs of the whole tail may be raised at the same time, in a sort of extreme Tail-ruffling. Possibly other parts of the pelage also are raised. This Genital-presentation may be characteristic of all marmosets. Epple says that it is performed by *Callithrix argentata* and *C. "leucocephala"*, and it certainly occurs in *Cebuella pygmaea* (it was called simply "presentation" in Moynihan, 1967).

Extreme Tail-ruffling also is performed by *jacchus* in other situations. Le Roux indicates that it can be combined with what seems to be an exaggerated Tail-forward. The tail is actually pulled up between the legs, but apparently not Looped or Coiled. This seems to express high-intensity alarm or fear.

Epple, Le Roux, and Fitzgerald all record Allogrooming by *jacchus* individuals. The usual version seems to be identical with that of most other New World primates in physical form. More significantly, it seems to be a "general social" or gregarious pattern. This is another resemblance to *Callicebus moloch*.

Epple also describes a peculiar display or complex of displays by *jacchus* individuals immediately before copulation attempts. The essential feature is a Licking of the partner, especially around the face and the foreparts of the body. This may be alternated with "combing" of the partner's pelage, using the incisor teeth. Both patterns may be preceded by sniffing, Tongue-protrusion, and a possibly distinctive "Lip-smacking."

Le Roux confirms the occurrence of sniffing and Licking in these circumstances.

It seems overwhelmingly probable that the Licking and combing, at least, are closely related to, presumably derived from, more ordinary forms of Allogrooming. If so, their morphological peculiarities are significant. To my knowledge, *jacchus* is the only species of Platyrrhini recorded to have such extremely different types of Allogrooming, or derivatives thereof, in general social and sexual situations. (The differences between sexual and apparently gregarious Allogrooming in *Saguinus geoffroyi* are matters of frequency and orientation rather than basic form. See page 15.) It also seems likely that the condition of these patterns in *jacchus* is highly specialized.

The vocalizations of *jacchus* described by Epple may be summarized (and partly homologized) as follows:

1. "Phee" notes, "monosyllabic calls given in close visual contact," "monosyllabic calls given in loose visual contact and in distress," and "monosyllabic calls given in isolation." These are illustrated by drawings of sound spectrograms. Both the drawings and the accompanying verbal descriptions would indicate that they are strictly homologous with patterns of the intergrading Squeak - Whistle complex of *Callicebus moloch* (and equivalent to the "*trilles et sifflements*" of Le Roux, which are just as reminiscent of the same *moloch* sounds). If this interpretation is correct, then the patterns of this category probably are related to the Squeaks of *Aotus* and (perhaps less closely or directly) to the Infantile Squeaks of *Saguinus geoffroyi*. But Epple's account would imply that they are approximately equally characteristic of young and adult *jacchus*. When uttered by infants, they may be generalized distress notes. When uttered by adults, they seem to be purely or largely hostile. This latter point is somewhat obscured, in the actual account, because some of the names given to the patterns are deceptive. Epple does say, however, that even the "monosyllabic calls given in isolation," when uttered by adults, are given by individuals who can hear others, and "are often accompanied by threat signals such as arch-postures and genital presenting." This would seem to be conclusive evidence that the "monosyllabic calls given in isolation" by *jacchus* are more like the Whistles of *Callicebus moloch* (or *Saguinus fuscicollis*) than like the Long Whistles of *S. geoffroyi*. It also, of course, indicates that the patterns of *geoffroyi* and *jacchus* to which Epple applies this name are not identical or even functionally equivalent (see page 71).

As an example of how confused Epple's descriptions can become, it may be mentioned that she implies (in

fact actually states) that Arch and Genital-presenting postures accompany the "monosyllabic calls given in isolation" (Long Whistles) of *S. geoffroyi*, although she also says elsewhere—and this time quite correctly—that neither posture is assumed by this particular species!

2. "Titters." According to Epple, these occur in three versions in *jacchus*: infantile, juvenile, and adult. The juvenile version seems to be perfectly intermediate between the other two.

All the versions may be partly or wholly homologous with what I have called Titters in *geoffroyi*, but they are rather different in form(s). Each note of a series rises much more strongly and steeply in the *jacchus* performances than in those of *geoffroyi*. The rising phase of each note is followed by a brief descending phase in the Titters of infant *jacchus*. The descending phase seems to be quite absent in the corresponding performance of adults. At least, it is not shown in the drawing of a sound spectrogram of the pattern presented by Epple. This would suggest that the adult performance may also be closely related to the Sharp Note patterns of *S. geoffroyi* (and many other species) and the "Chuck" Notes of *Callicebus moloch*.

The soft rattling noises which I heard uttered by the captive individuals in the Paris zoo may have been some form(s) of Titters. If so, they confirmed the impression conveyed by Epple's spectrograms. The *jacchus* patterns sound very different from *geoffroyi* Titters to human ears, and presumably also to the ears of other animals.

3. "Rhythmical calls given in close visual and bodily contact." Epple does not illustrate this pattern, and her description is vague (she suggests that the sounds are "like the faint chirping of birds"). This *might* represent something like another (fourth) type of Twitter.

4. "Squeals given in submission." These are illustrated by a photograph of a sound spectrogram of a single note which is certainly a Rasp of some sort. It looks most like the Infantile Rasp of *S. geoffroyi*, but Epple (again) implies that the pattern is typical of individuals of all ages.

This brings up more problems of interpretation.

Epple does not suggest that these Rasps and the "Phee" Notes are often associated with one another in stereotyped series. This would seem to indicate that *jacchus* does not have a specialized Infantile Squeak – Infantile Rasp complex like *geoffroyi*. Possibly Epple's account of *jacchus* is correct in this respect, even

though her account of the corresponding behavior of *geoffroyi* is not. I never heard any unmistakable Infantile Squeak – Infantile Rasp series uttered by the *jacchus* in the London and Paris zoos. And the distress notes of infant *Cebuella pygmaea* seem to be all Squeak (or other clear sounds) and no Rasp, like those of *Callicebus moloch*.

Le Roux, on the other hand, cites a pattern, the "*cri plaintif*," which may also be homologous with the Infantile Rasp of *geoffroyi*, and he states that it definitely does tend to occur immediately after a "*trille*" or a "*sifflement*." This must produce series like Infantile Squeak – Infantile Rasp sequences, but Le Roux's account would not suggest that such series are particularly infantile in *jacchus*.

Thus the whole subject is left up in the air. All one can say is that some clear sounds of *jacchus* are quite similar to some high-pitched notes of *Callicebus moloch*, and may or may not be incorporated into separate infantile and adult complexes.

5. "Tsee tsee tsee . . ." calls "given in aggressive threat." Epple's description of these notes is accompanied by a drawing of a spectrogram. This looks quite unlike anything normally uttered by *geoffroyi*. It could, conceivably, be related to some Squeak and/or Sharp Note patterns of other species. In the form described by Epple, however, it seems to be very distinctive, perhaps diagnostic of *jacchus* (although further investigation may show that it is shared with other marmosets).

6. "Chatters given when angry." These are illustrated by a drawing of a spectrogram. If the drawing is at all adequate, these "chatters" also are distinctive, but it will be remembered that Epple applied the same name to the Broken Rasp of *geoffroyi*, and gave a very poor drawing of the latter. Possibly the two supposed "chatters" are related but not identical.

It might be added, in this connection, that Le Roux's account of the various rapid rhythmic calls of *jacchus* cannot always be reconciled, in all details, with Epple's descriptions. And some of his drawings of spectrograms also are obscure. But his account confirms the existence of marked differences between some of the *geoffroyi* and *jacchus* patterns of this general type.

7. "Crackles" and "coughs." These may be very abbreviated Rasps. They are hostile, used as "mobbing" calls and in aggressive threat.

8. "Tsik" notes. Epple's verbal description would suggest that these are Loud Sharp Notes, but the ac-

companying sound spectrogram shows a prolonged pattern. On the evidence presented, it is impossible to determine if this is a distortion or not (see also above, page 71).

9. "Warning calls." Like the patterns of *geoffroyi* to which Epple gave the same name, these are essentially unidentifiable.

10. "Screams." These are high-intensity patterns, produced when the escape tendency is predominant. Epple does not illustrate them and, again, her verbal description is somewhat vague. But my own observations of the *jacchus* individuals in the London and Paris zoos would indicate that the Screams of this species are clear in tone, sounding more like the Screams of *Callicebus* and *Aotus* than like the Long Rasps of *Saguinus geoffroyi*.

Epple's brief comments on the vocalizations of *Callithrix "leucocephala"* and *C. argentata* are not very useful, except insofar as they suggest that the two species are as similar to *jacchus* in these respects as in others. It may be mentioned, however, that the drawing of what Epple calls a "Trill" of *argentata* is remarkably reminiscent of the most Trill-like Whistles of *Callicebus moloch*. This may be of some comparative significance. It also suggests that the supposed "Trills" of *argentata* are not strictly homologous with the Trills of *Saguinus geoffroyi* (see also page 69).

Final Comments

Some of the implications of the preceding survey are rather puzzling.

There are many resemblances among many displays of all New World primates. This is as true of *Callithrix* and *Saguinus* as of most other genera. There also are certain broad features or general aspects of display behavior which seem to be common to all marmosets and tamarins. Some of these are cited and discussed in Moynihan (1967). They include the predominance of high-pitched vocalizations, the restricted variety of facial expressions, and the (perhaps compensatory) development of diverse sets of pilo-erection and smoothing patterns.

It is at least conceivable, however, that these features are nothing more than superficial or immediate adaptations. Like some of the morphological characters shared by the same animals (e.g., clawlike nails, the loss of third molars in most genera, and the smoothness of the cerebral hemispheres), they could be adaptations to

small size and/or some of the consequences or correlates of small size.

Unfortunately, attempts to interpret the real significance of these general features are not helped very much by more detailed analyses of individual displays. Point by point comparison of patterns described above would seem to reveal the following:

1. Some displays are characteristic of either tamarins or marmosets, but not both. Genital-presenting is a notable example. But the category may also include such patterns as Licking and Upward Tail-coiling before copulation.

2. Some displays which are shared by species of both groups, i.e., Sit-rubbing and the General Ruffle, also occur in some or all other Platyrrhini.

3. Still other features which are shared, e.g., some vocal elements, are arranged in different ways in the two groups.

Of all the more complex and distinctive individual displays, probably only Tongue-protrusion and Rasps really suggest that tamarins and marmosets are more closely related to one another than either is to other groups of New World primates. Only some tamarins and marmosets are known to have both patterns, but this is by no means conclusive. Rasps may take different forms and/or subserve different functions in different species. They also seem to be shared with *Pithecia*. Tongue-protrusion seems to be shared with *Alouatta*.

The differences between the signal systems of marmosets and tamarins are perhaps rather surprising. They are more extensive than might have been expected in view of the fact that all the species conform to a rather uniform morphological type and (as far as is known) have similar ecologies and social structures.

Perhaps further studies of other species will reveal that some have display behavior which is intermediate between *Saguinus geoffroyi* and *Callithrix jacchus*. My incomplete study of *Cebuella pygmaea* would suggest, however, that its signal system is even less like that of *geoffroyi* than is that of *jacchus*. Very brief observations of *Callimico goeldii* would suggest that its behavior is distinctive rather than intermediate, and more different from *jacchus* than from *geoffroyi*. (This also is the impression conveyed by Epple's account of the species in her 1968 paper.)

The situation becomes even more complicated when *Callicebus* and *Aotus* are considered. The contrasts and similarities between these two genera would seem to be strictly comparable to those between *Saguinus* and *Callithrix*. *Aotus* and *Callicebus* resemble one

another in body proportions and some other anatomical features. (So much so that they have been placed in the same subfamily or tribe by some authors. For instance, Simpson, 1945.) They also share a number of more or less general features of display behavior; e.g., the inclusion of both high- and low-pitched notes in the adult vocal repertoires. Many of their individual displays certainly are homologous, but many of these are shared with many other Platyrrhini. And other displays of the two genera are quite different. Only a few of their more complex signals; e.g., Tail-twining and long "Song-like" series of Resonating Notes or Resonant Grunts, are both distinctive and similar enough in the two genera to suggest a special relationship.

In actual fact, as mentioned repeatedly above, there may be as many or more resemblances between the signal repertory of *Saguinus Geoffroyi* and that of *Aotus* as between the latter and the corresponding repertory of *Callicebus moloch*, but the special similarities are quite different in the two cases. The features common to *Aotus* and *Saguinus Geoffroyi* include predominantly sexual Allogrooming, Tail-lashing only during Sit-rubbing, stereotyped series of two or three long notes to attract mates or companions, comparatively frequent performance of freeze and crouch patterns, and similar forms of Swaying and head-down postures.

These similarities are all the more remarkable because the two species have rather different social structures, and one is diurnal while the other is nocturnal.

Saguinus Geoffroyi seems to show few or no significant special resemblances to *Callicebus*.

But *Callithrix jacchus* may. *Callithrix* and *Callicebus* seem to share Baring of the Teeth, "general social" Allogrooming, and some very similar forms of vocalization.

On the other hand, *Callithrix jacchus* shows few or no significant special resemblances to *Aotus*.

Thus, the situation can be outlined as follows:

1. *Saguinus* resembles both *Aotus* and *Callithrix*, but in different ways. The special features it shares with *Aotus* are not the same as those it shares with *Callithrix*.

2. *Callicebus* also resembles both *Aotus* and *Callithrix*, again in different ways. The special features it shares with *Aotus* are not the same as those it shares with *Callithrix*. Nor are the special features which it shares with *Aotus* and *Callithrix* the same as those which *Saguinus* shares with the same genera.

3. *Callithrix* resembles both *Saguinus* and *Callicebus* in different ways.

4. *Aotus* also resembles both *Saguinus* and *Callicebus* in different ways. The special features shared by *Aotus*, however, are not the same as those shared by *Callithrix*.

It may be premature to attempt to draw phylogenetic conclusions from data of this type. Obviously, there must have been considerable parallelism or convergence, of behavioral and/or morphological characters, during the evolution of some or all of these genera. Such as they are, the known data might suggest that marmosets and tamarins are independent derivatives of a more typically monkey-like stock (animals of larger size and more completely omnivorous or even frugivorous diet), or that *Callicebus* and *Aotus* are independent derivatives of some common tamarin-marmoset stock. In the absence of useful information from the paleontological record, these possibilities can be checked only by further studies of other living forms.

SUMMARY

Saguinus Geoffroyi, the Rufous-naped Tamarin, is fairly widely distributed in parts of Panama and northern Colombia. Individuals of the species have been observed in the wild, in central Panama, and some aspects of their behavior have also been studied in the laboratory.

The species is rather small, for a monkey. It is most characteristic of dense scrub and not very tall forest, often second growth, in areas of moderate humidity. Individuals tend to remain near, but not exactly at, the edges of such habitats. They are diurnal, almost completely quadrupedal, and come down to the ground only occasionally. They eat a variety of foods, including much vegetable matter, but probably prefer insects when available. They give every indication of being preyed upon frequently.

Under present conditions in the wild in Panama, they may occur singly or in groups of two to nine individuals. Each single individual or group seems to have its own territory. Territories usually are quite large. The animals move rapidly when active. It probably is typical for each individual or group to move through all or most of its territory at least once a day. There is relatively little trespassing.

The social and ecological relations between Rufous-naped Tamarins and other (non-predatory) animals,

at least one other mammal and many birds, are complex and probably highly specialized. They may involve several forms of social mimicry. Competition between the tamarins and some other species also is reduced by differential timing of activities. The advantages and disadvantages of such arrangements may help to explain the geographical distribution of the species and the genus.

The communication system of adult Rufous-naped Tamarins is composed of a few tactile and olfactory patterns, a moderate number of different types of vocalizations, and even more kinds of visual signals. Most of the latter are gross movements of the head and/or body, pilo-erection and smoothing patterns, and special ways of holding and moving the tail. The importance, or preponderance, of visual signals in the adult repertory of the species may be an adaptation to avoid attracting the attention of predators. Postures and movements probably are not as conspicuous at long distances, in forest and scrub, as are sounds. The vocalizations include both "clear" and harsh rasping notes, but all are more or less extremely high pitched. This may be a similar adaptation. High-pitched sounds do not carry as far as low-pitched sounds.

Some of the vocalizations of adult Rufous-naped Tamarins intergrade frequently; others do not. Some of them usually seem to be quite precise releasers; others may provide little or nothing more than information for future reference. Different types of signals are combined in almost endless permutations, probably because it usually is advantageous for a single performance to transmit one or more messages, along different channels, to different recipients, all at the same time.

Among the distinctive features of the species are individual "quirks." These look like displays. Some of them may function as signals, but they do not seem to be species-specific.

Young animals utter well-differentiated distress notes.

Brief observations of some other species of *Saguinus* (*oedipus*, *leucopus*, *fuscicollis*, *graellsii*, and *nigricollis*) suggest that many of the displays of *geoffroyi* are typical of the genus as a whole.

The phylogenetic implications of the signal system of *Saguinus* are perplexing. *Saguinus* certainly resembles both *Aotus* (the Night Monkey) and *Callithrix* (typical marmosets), but in different ways. It does not show any special similarities to *Callicebus* (titi monkeys). Nor does *Callithrix* show special similari-

ties to *Aotus*. *Callicebus* does resemble both *Callithrix* and *Aotus*, although not in the same ways as *Saguinus*. Obviously, there must have been parallelism or convergence, of behavioral and/or morphological characters, during the evolution of some or all of these genera.

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