Vocalizations of Howler Monkeys
(*Alouatta palliata*) in Southwestern Panama

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Abstract. This report presents an analysis of the vocal repertoire of howler monkeys (*Alouatta palliata*) observed during a field study in southwestern Panama. 26 types of vocalizations were identified and described, and sonagrams are presented for 21 of them. The vocal repertoire contained many nondiscrete calls that graded continuously into each other, and all of the calls appeared to fit into 5 or 6 broad families. A tape recording of the vocalizations described in this study is available.

Introduction

During the first research on the howlers (*Alouatta palliata*) of Barro Colorado Island (BCI), Carpenter [1934] identified more than nine different calls that were given in troop communication and coordination. In 1955, Altmann focused special attention on analyzing the vocal repertoire of the BCI howlers. He established clear descriptions of 13 calls along with their social significance [Altmann, 1959] and he obtained tape recordings of several of the calls [Altmann, 1966].

The present paper reports data on the vocal repertoire of *A. palliata* in a natural forest in southwestern Panama, 320 km WSW of BCI. The vocalization data were collected during a 10-week study on eight troops of howlers that occupied 15 ha of a continuous coastal forest of over 400 ha. The howlers habituated to being studied at distances of 7–15 m which made it possible to obtain detailed observations and good tape recordings of much of their communicative behavior.

Methods

The animals, study site and general methodology of the Barqueta study are described in detail elsewhere [BALDWIN and BALDWIN, 1972, 1973]. The present section will give a brief summation of that information plus a description of the additional procedures used in studying communication.

The study site was located on the Pacific coast in southwestern Panama, 4 km east of the mouth of the Escarrea River ($8°$ 19′ N. latitude; $82°$ 38′ W. longitude). The forest was bordered by an estuary of the Escarrea River on the north and by grasslands that were flooded in wet season on the south. Surrounded by water for most of the year, the site was effectively isolated from human disturbance. At the study site 8 km of trails were cut through 20 ha of the 400 ha forest. These trails permitted us to follow and study eight troops of howlers, two troops of squirrel monkeys *(Saimiri oerstedii)*, and one troop of capuchin monkeys *(Cebus capucinus)*. The eight troops of howlers contained 151 individuals and utilized 15 ha of the study forest. Six solitary howlers shared the same area and three unstudied troops bordered the eight study troops on the east and west.

The study was conducted between December 19, 1970, and February 25, 1971. A total of 513 h were spent in contact with the howlers. Vocalizations were recorded on an Uher 4000 Reporter L tape recorder at 19 cm/sec. All recordings were made with a nondirectional Uher M514 microphone. A parabolic reflector was not used. Because the Barqueta data corresponded reasonably well with the descriptive categories proposed by ALTMANN [1959], his numbering system was utilized and extended for cataloging the vocalizations heard during this study. Sound spectrographs were made from the tape recordings on a 6061B Sona-Graph (Kay Electric Co.).

The use of each call was recorded according to the social context, age and sex of the interacting animals. Individuals were categorized in the following groups: $infant_1$, $infant_2$, infant $_3$, early juvenile, late juvenile, adult female, subadult male and adult male [BALDWIN and BALDWIN, 1973].

Nonmixing troops. In order to describe intertroop relationships, it was necessary to establish the nomenclature 'mixing' and 'nonmixing' troops. Three of the eight troops studied could join, travel together and intermingle. They could form 'supertroops' of 38, 45, 47 or 65 animals, depending on which combination of troops joined. The relations among these three troops appeared to be friendly. None of the other troops in the study forest ever joined or traveled with other troops. All the troops that did not ever join or intermingle were defined as nonmixing troops vis-à-vis each other. The frequency of vocalizations exchanged between nonmixing and between mixing troops varied significantly.

Results

The following vocalizations were identified in the Barqueta study.

Roar or Howl, Type A₁

The roars of the adult males were the loudest calls given by the howlers and, under favorable conditions, could be heard for approximately 1 km
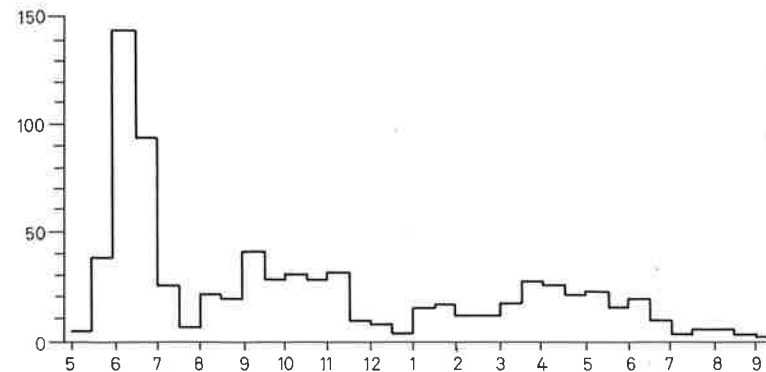
Fig. 1. The distribution of bouts of roar vocalizations (A₁) heard throughout the day (including the nearest 4–8 clearly audible troops).

through the forest. The calls could be heard for even greater distances across open spaces such as meadows and bodies of water. Roaring was most frequently heard in the mornings before sunrise and in intertroop confrontations during the daytime (fig. 1). Roaring was seldom done by one animal alone. Two or more males of a given troop tended to roar in unison, especially if accompaniment calls (B) were given by some of the older juveniles and adult females in their troop. The juveniles and adult females participated more often in the daytime intertroop confrontation calling than in dawn choruses. During the remainder of the paper these group calls will be identified as A–B group calls in which the dominant elements were A_1, A_2, B_1, B_2 and G_3 vocalizations, although there was occasional use of the A_3, C_1, C_2, E, G_1 and G_2 calls.

Because adult males tended to roar together, along with the accompaniment of older juveniles and adult females, isolated examples of roars given by a single male were not commonly heard. However, brief bouts of lone roars (fig. 2a) sometimes occurred during A–B group calling, when one male continued to be vocal during a pause in the activity of the other animals. During the study there was one morning on which a male spent more than 1 h giving roars and woofs (C_1) after he, a consorting adult female and a small juvenile became separated from their troop. The lone roar calls appeared to be the basic or fundamental form of roaring and did not exhibit as much variation as the roars during A–B group calls. Lone roars tended to consist of 1–4 exhaled syllables (usually 2 or 3) separated by shorter inhaled syllables which sounded like loud gasping for breath. The roars tended to be given at

a rate of one exhaled syllable per 1.0–1.5 sec. The roars frequently sounded like prolonged 'aw' or 'oh' tones, with the vocal energy concentrated in the range of 200–1,800 Hz and overtones sometimes as high as 6,300 Hz. At times the lone roars began or ended with a smooth transition to woofs (C_1), as is shown in figure 2b.

The rate and quality of the roars sometimes changed significantly at the end of a bout, grading into a distinctively different pattern which we called the 'roar terminus', $A_{1.1}$ (fig. 2c). The roar terminus came immediately at the end of normal roars and consisted of a very rapid series of roar-like syllables, usually of declining pitch. These rapid in-out pulses of air usually occurred at a rate of 3.5–4 times/sec, and they sometimes graded into oodle (E) calls with which they had structural traits in common. (There appears to be a continuum of calls from roars (A_1), to roar terminus ($A_{1.1}$), to a muffled roar terminus ($A_{1.1}$) to oodle (E).)

When males roared together or in A–B group calls, they often gave the basic roar described above, but they also produced a large number of variations on the basic roar. These roars were similar to the lone roars in that they consisted of loud exhaled 'aw' or 'oh' syllables which were separated by the inhaled syllables that sounded like loud gasping for breath. Also group roars often included transitions to and from woofs (C_1) and to the roar terminus ($A_{1.1}$). The variations on the basic roar qualities occurred along four general continua. (a) Group roars varied over a wider range of pitches, especially extending into the higher frequency ranges. Group roars often reached as high as 2 kHz at peaks of group activity. (b) Roar syllables were usually repeated more than the 1–4 times typical of lone roars. Group roars tended to contain 3–6 syllables, but the total range of repetitions was 2–14 syllables/bout. (c) The rate of syllable repetition also showed a wider variation, from 0.5–1.3 roars/sec. Dawn choruses often contained slow repetitions of roars, whereas intertroop confrontations often contained more rapid roars. (d) During group roaring the males showed a stronger tendency to make transitions to the other calls related with roars, that is to calls $A_{1.1}$, A_2, A_3, C_1, C_2, E, G_1, G_2 and N. When the troop members gave A–B group calls together, the bouts of calls from the separate individuals often overlapped to create complex combinations of sounds.

Most roaring occurred while the animals sat alone where they had been foraging or resting. When males gave roars, the neck was extended and the head lifted. In a few cases, males called while hanging by the tail. The females and juveniles also extended their necks while giving the roar accompaniment (B) calls, but to a lesser degree than males. Occasionally during A–B group

calling, several of the vocal animals (including females and juveniles) would run along the branches for short distances of 0.5–2 m while calling. When running did occur, there was a tendency for several individuals to run at the same time, as if influenced by social facilitation. While running along the branches during bouts of vocalizations, they occasionally came into physical contact and would touch or hold each others bodies.

There appeared to be a significant amount of social facilitation involved in producing A–B group roars. Either the males or the juveniles and adult females could introduce A–B calls. Before A–B group roars, it was common to hear many combinations of the following 'preroar' calls from the males and other troop members. Males often built up to roars by giving incipient roars (A_2); but woofs (C_1 and C_2), oodles (E) and whimpers (G_1 and G_2) were also common before group roaring. The juveniles and adult females often contributed significantly to the build-up of excitement that precipitated a full bout of male roars; they would usually begin with chirping whimpers (G_3) or occasionally incipient accompaniment calls (B_1).

After bouts of roars the males frequently made a smooth transition from roars into the roar terminus ($A_{1.1}$), incipient roars (A_2), woofing (C_1) and sometimes into incipient woofing (C_2). Occasionally, oodles (E) occurred shortly after bouts of roaring or during pauses between bouts. At times the hiccup (N) was heard during pauses in roars. Adult females and juveniles sometimes continued giving incipient accompaniment calls (B_2) or high chirping whimpers (G_3) after males had ceased roaring.

Dawn choruses. As is shown in figure 1, roars were given in the morning at dawn and, to a lesser extent, at various times throughout the day. There was no morning on which there was not a dawn chorus. The dawn chorus tended to begin at the earliest signs of light and was usually completed before sunrise. Occasionally, when there was strong moonlight, some troops would begin calling 15–30 min before the normal timing, but these 'early starts' were usually short-lived and involved only a few troops. After an 'early start' there was often a silent period before the general chorus began near the normal timing, and on these days the normal chorus tended to be shorter than usual. Although the total dawn chorus usually lasted 20–45 min, the animals of some troops vocalized for periods of less than 5 min/morning. Often the dawn chorus was mostly generated by only 1 or 2 highly vocal troops among the 4–10 that were heard on a given morning. Generally, the closer a troop was to a nonmixing troop, the more likely it was that one or both of the two troops would roar for prolonged periods, ranging from 20–45 min. When mixing troops were close together but were distant from nonmixing troops

at dawn, they tended not to engage in prolonged roaring. After the general morning chorus had died down, it was common to hear 1 or 2 males in the more vocal troops continue with woof calls (C) for 5–30 min, and occasionally, their whole troop would break into short bouts of roars during the woofing period. Usually one woofing male would not break out with roars unless a second or third animal joined him with incipient or full roars (A_2 or A_1) or incipient or full roar accompaniment (B_2 or B_1).

Daytime vocal interactions. At Barqueta during the day, roars were often given in the following situations: when nonmixing troops were nearby or approaching, when previously silent troops began to call, when airplanes flew over, when large birds flew close by, when dogs came nearby, during rains and strong winds, occasionally after midday naps, and at times 'spontaneously'. Research on BCI indicates that other stimuli can evoke roars. CARPENTER [1934] reported that thunder, lightning, predators, a fallen infant, and the proximity of humans can lead to roaring, and LUNDY [1954] reported roaring after the firing of a weapon. At Barqueta by far the greatest number of roars were precipitated by the proximity or approach of nonmixing troops. The most intense daytime exchanges of roars between troops occurred during confrontations, when two nonmixing troops came within 2–50 m and roared for periods that could be as long as 1 h or more. Mixing troops did not usually elicit prolonged roars from each other. The two peaks of daytime roars in figure 1 correspond to the periods in which troops were moving through the forests and were most likely to encounter other troops. Also, during quiet periods when the troops were spaced out, there were times when roar calls would be given by one troop, and other troops within hearing distance would call in response. Prolonged bouts of roars were most common when (a) there was a nonmixing troop within 50 m or visual contact; (b) neither troop retreated, and (c) there was social facilitation from other vocalizing animals. At Barqueta intertroop confrontations occurred approximately 5–15 times a week and ranged from 5 min to more than 1 h in duration.

Incipient Roar, Type A_2

Incipient roars had some of the same tonal qualities as roars, especially the 'aw' or 'oh' sound. They often occurred before bouts of full roars (A_1) as a vocal activity that could build in volume and grade smoothly into full roars when enough other animals joined in with any of the preroar calls. Thus, incipient roars occurred before, after and during pauses in the roars heard during dawn choruses, intertroop confrontations, rain, heavy wind, etc. Incipient roars were also heard at times when no roars were given. Often when

roar-evoking stimuli were present but apparently not salient, a few animals would give incipient roars, but they did not build to the full roar level. Incipient roars were also heard before and during troop progressions though they seldom became intense or led to full roars in progression situations, unless a nonmixing troop was encountered.

The incipient calls included several variations. The sound described by ALTMANN [1959] as a 'gruff, popping preface' appeared to be at one end of the continuum of variations. The other end of the continuum was a pure 'aw' or 'oh' tone that had no popping or gruff qualities. We found it useful to discriminate four points along the continuum.

$A_{2.1}$: Pure 'aw' or 'oh'. This clear call was the least frequently heard of the A_2 calls (fig. 2d).

$A_{2.2}$: Rough 'aw' (or 'er'). This was a slightly more rasping version of 'aw' than the previous call (fig. 2e).

$A_{2.3}$: Popped 'aw'. This sounded like a loud creaky door. The 'aw' quality was not obscured by the popping (fig. 2f).

$A_{2.4}$: Popping. The bursts of energy were so short and plosive that it was difficult to identify the 'aw' quality (fig. 2g).

The $A_{2.2}$ and $A_{2.3}$ calls were the most commonly heard of the A_2 calls. The 'aw' tones in A_2 calls tended to occur between 200 and 1,500 Hz, and the popping sounds were short, plosive sounds ranging from 50 Hz to 4–5 kHz. At times the males gave calls that were complex combinations of various A_2 signals. One of the more stereotyped patterns was a low pitched, medium quiet call (which sounded like a growl or groan) that sometimes lasted 1.8 sec. It usually began as an $A_{2.3}$ call near its highest and loudest point, then peaked and descended into a low, muffled $A_{2.2}$. There were other complex variations on A_2 calls. Our analysis could not determine whether any of the variations in the A_2 calls had special significance other than that identified for the whole A_2 category. All four of the basic A_2 variations could build in volume and lead directly to full roars. The woof calls (C), whimpers (G) and oodles (E) were also heard during periods of incipient roars, especially in periods of prolonged incipient roars that did not lead to full roars. It was common to hear incipient roars grade into prolonged woofing (C_1).

High Roar Coda, Type A_3

During dawn roaring, in troops that were vocally very active, there were times when a single male would switch from the normal roars to a sustained pure, high tone with a fundamental pitch near 500–520 Hz and overtones to 2.6 kHz. This call was heard on only eight mornings in which it was repeated
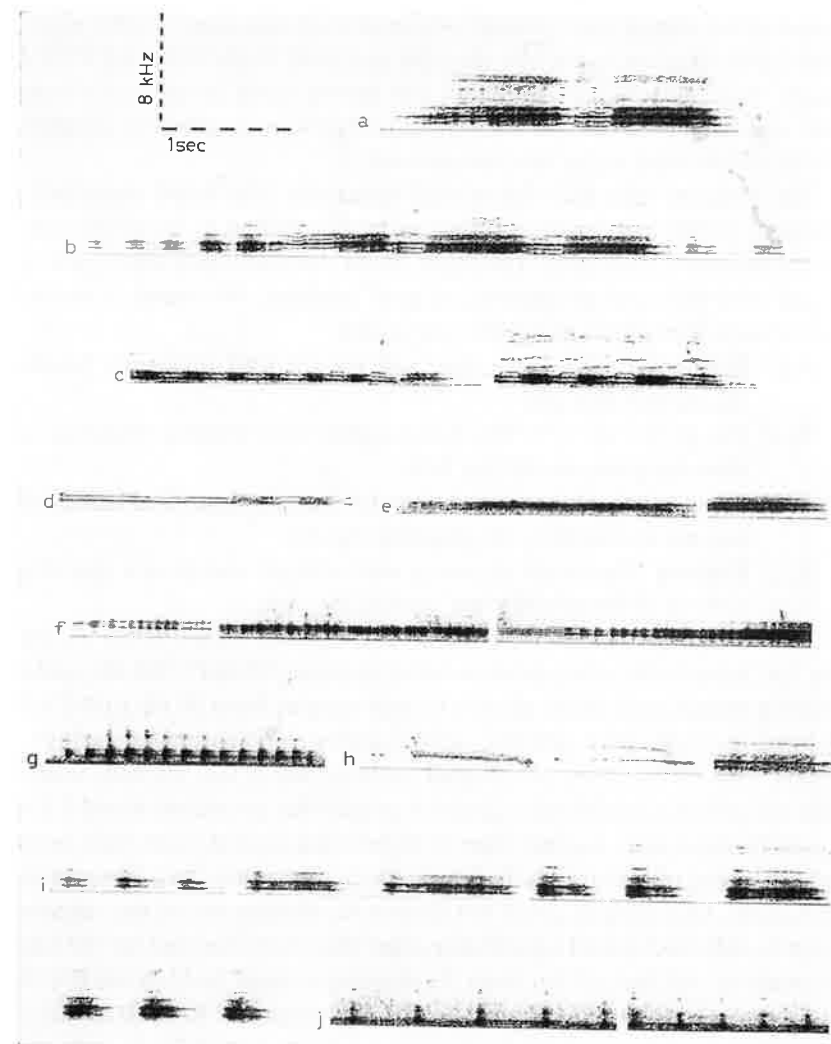
Fig. 2. a Roar (A$_1$) with two exhaled syllables separated by an inhalation syllable. *b Woofs* (C) before and after a 3-syllable *roar. c Roar terminus* (A$_{1.1}$) showing variations. *d Incipient roar* (A$_{2.1}$) ends with two brief bursts of A$_{2.2}$. *e Incipient roar* (A$_{2.2}$). *f Incipient roar* (A$_{2.3}$) contains some popping noises; it occurs between A$_{2.2}$ and A$_1$ in a typical preroar pattern at right. *g Incipient roar* (A$_{2.4}$) shows strong popping noise. *h Roar accompaniment* (B$_1$) shown alone twice, and superimposed on the end of male roars at the right. *i Male woof* (C$_1$) showing common variations (see also *b*). *j Incipient female woof* (D$_2$) was a quiet call and easily obscured by background noise. *k Oodle* (E) (brief vertical noises are twigs snapping). *l Eh* (F) showing variations. *m Whimper* (G$_1$). *n Male emphatic whimper* (G$_2$).
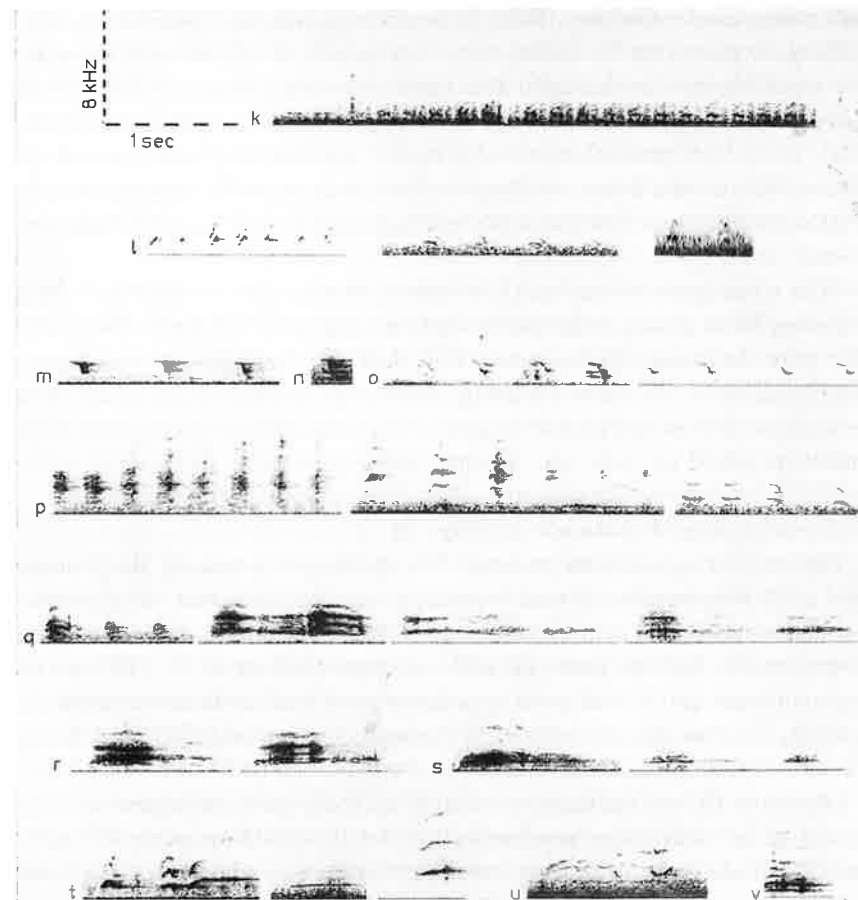
o Chirping whimpers (G₃). *p* Heh (I) showing variations. *q* Caws (J). *r* Transition calls with both *caw* and *wrah-ha* qualities. *s* Wrah-ha (K) typically contained two syllables (left), but could contain a third closing syllable (right). *t* Two *yelps* followed by three *screeches* (L). *u* Infant 'squeaky door' vocalization was the longest of the infant squeak and bark calls (M). *v* Hiccup (N) by an adult male.

numerous times at peaks of vocal activity. Like ALTMANN [1959] we could not identify any special significance for the call.

Roar Accompaniment, Type B₁

Older juveniles and adult females often gave B₁ vocalizations at times when the adult males were giving roar vocalizations (A₁), especially in daytime

intertroop confrontations. These roar accompaniment vocalizations were difficult to record and describe, since they usually occurred while the males were making their louder calls. The accompaniment call sounded like a high pitch, loud 'er', 'aar' or 'chaar' (fig. 2h). It could be given in 1-sec long syllables that clearly bore resemblances to the males' 'aw' roar (A_1) and sounded like the howling of small dogs; or they could be given in short, staccato syllables that sometimes sounded like a terrier's bark [as CARPENTER, 1934, described them].

The older juveniles and adult females gave roar accompaniment calls in the same kinds of situations that evoked the roars (A_1). Generally, they called less than the males which suggests that their threshold for responding may be higher than the males'. During intertroop confrontations, peak vocal periods came in waves, and at the peaks sometimes 25% or more of the troop members would be vocal and moving rapidly from perch to perch.

Incipient Roar Accompaniment, Type B_2

Before, during and after periods of A_1 and B_1 group roaring, the juveniles and adult females often gave either of two other vocalizations, incipient roar accompaniment (B_2) or high chirping whimpers (G_3). The incipient roar accompaniment had the same 'er' and 'aar' tone qualities as the full roar accompaniment, but it was given at a lower pitch and lower sound intensity. This B_2 call was not as common as the high chirping whimper (G_3) during periods of juvenile and adult female excitement.

Both the B_2 and G_3 calls could build up from quiet, infrequent vocalizations to full roar accompaniment (B_1), and this build-up often seemed to facilitate male roars, even from males that had previously given no incipient or 'preroar' vocalizations. When the males began to roar, the juveniles and adult females would usually switch from B_2 and G_3 calls to the full roar accompaniment (B_1). The incipient roar accompaniment was never heard, except in times closely associated with A_1 and B_1 group calls.

Male Woof or Bark, Type C_1

ALTMANN [1959] described this call as a bark. To us the word 'woof' more accurately conveyed the tonal qualities of the call (fig. 2i), and throughout this paper the call will be referred to as woof. The call was sometimes given in loud forms that could be heard for 200–400 m, but there were continuous variations from loud to gentle woofs and finally to incipient woofs (C_2). Often woofs had a guttural tone quality that closely resembled the 'aw' or 'oh' tone of roars (A). The second sonagram in figure 2i shows double woofs with

strong 'aw' qualities which closely resemble roar syllables. Another dimension
of variation was the pattern of repetitions; the call tended to be given in
clusters of 1–4 repetitions or in long, continuous, evenly spaced sequences.
Continuous woofs averaged 2.0–2.5 woofs/sec, but they could be given as
fast as 3.4 woofs/sec.

Woofs were often given in stimulus situations which were similar to those
which evoked roaring (A_1), except that the stimuli were usually less intense,
less dangerous, or apparently less salient. The fact that woofs often occurred
before, during pauses in, and after bouts of roaring also suggested a relation-
ship with roars. Between periods of all roars and all woofs, there were often
stereotyped patterns of syllables, like 'roar-roar-roar-roar-woof-woof' that
were repeated for several minutes at a time. As is described in the following
paragraphs, woofs were also given in a variety of situations where roars
were not.

Adult males gave woofs in response to some within-troop social situations.
First, after a male threatened or frightened an adult female and the latter
gave 'hehs' (I), the male might give 2–10 sec of woofs. Apparently, when the
female was more vocal, physically active or nearby, the male was more likely
to woof. Second, infants that were separated from their mothers usually gave
'caws' (J) until they could locate or cuddle with their mothers. When an adult
male came within 1–2 m of a cawing infant or vice versa, the male often gave
gentle woofs for several seconds or until they began separating. It appeared
as if the infant's distress was communicated to the male. Third, the woofing
of one male sometimes led to a second or third male's beginning to
woof. At times this may have been coincidental as different males became
attentive to an environmental stimulus; but within troop communication,
alerting or social facilitation definitely occurred in some circumstances.
Nevertheless, contagion occurred less frequently with woofs than with
roars.

Prolonged woofing between nonmixing troops occurred when troops were
as close as 75–200 m, but apparently were not heading toward each other.
A bout of spontaneous roars from one troop often led to 1–2 exchanges of
roars between the troops, then prolonged woofing from one or both troops
which could last up to 1 h or more. Usually, one or both troops moved away
and avoided closer contact. When troops were at 200 m or more, short ex-
changes of roars, then woofs often occurred. Whereas the proximity or ap-
proach of a nonmixing troop usually led to prolonged confrontation roars,
more distant and less intense stimuli led to brief roars, prolonged woofing
and troop avoidance.

During troop progressions, the males made a variety of vocalizations; quiet incipient roars (A₂), quiet woofs (C), oodles (E) and whimpers (G) were the common progression calls, but almost all the other male calls were heard from time to time during progressions. (Adult females and young often gave whimpers (G), 'caws' (J), 'wrah-ha' calls (K), and occasionally other calls during periods of troop travel). As SOUTHWICK [1962, 1963] noted, these progression calls were often noisy enough that nearby troops could have heard and avoided each other without direct confrontations. Also, the vocalizations may have facilitated troop coordination in travel or aided lost individuals in relocating their troop.

When a troop suddenly came across a solitary howler, one or more of the troop males (and at times juveniles) ran toward the lone animal and woofed. The lone animal invariably fled rapidly, and troop males seldom pursued the lone individual further than 50 m. Woofing continued until the lone animal was out of sight. Even males that were not involved in the chasing often woofed. At times 2 or 3 males and often some juveniles engaged in what apparently was mobbing; after detecting something in the thickets or on the forest floor, the mobbing animals ran toward the stimulus and the males woofed for 30–120 sec before returning to the troop.

Woofing also occurred during periods of wind and rain. When males slipped and fell to the undersides of branches or when branches broke or cracked under their weight, the males often woofed for 5–30 sec until they recovered from the slip and resumed travel. When humans surprised the howlers by suddenly appearing at 5–15 m, the monkeys often whimpered (G) and males sometimes woofed. The males were more likely to woof if they were foraging near the ground, hanging by the tail, or forced to travel directly over the humans. This relatively mild response to the proximity of humans differs significantly from the long and intense woofing and roaring responses reported by CARPENTER [1934] and ALTMANN [1959]. There was, however, a troop adjacent to the west side of the present study forest that woofed and roared whenever they saw us.

After dawn roaring, it was common to hear 1 or 2 males in the forest continue to woof for 5–30 min, although the other males in their troops seldom joined them. Occasionally, a male would woof for several hours after sunset, and, at times, other males would woof with him or join in a bout of roars. We could never clarify why these single males persisted in such long bouts of solitary woofing. Sometimes the males may have woofed themselves to sleep, as ALTMANN [1959] described. Woofing was also heard at various times throughout the night.

Incipient Male Woof or Bark, Type C_2

The quietest woofs often graded into an incipient form. Incipient woofs were heard in troop progressions, when a nearby squirrel broke a branch, when distant troops roared, and when the observers stayed too close (5–7 m). The call sounded like a muffled 'unf-unf-unf' and was made with the mouth closed or nearly closed. This call could also grade into whimpers (G) and vice versa.

Female Woof or Bark, Type D_1

The female woof was heard very rarely. On a few occasions, for unknown reasons or when we accidentally came very close to adult females (5–7 m), they gave woof calls. They had a plosive burst, were higher than the male woofs, and did not contain the guttural qualities of male woofs. No other animals were observed to respond when a female made this call.

Incipient Female Woof or Bark, Type D_2

The incipient female woof was heard more often than the female woof (D_1). Once, during a long male-female consort relation, the female came up very close to the male and gave several quiet 'uf' or 'unf' sounds (fig. 2j). The male made no response as the female sat near him. Occasionally, adult females gave quiet low, guttural incipient woofs that were fast and rhythmical, averaging 2–3 syllables/sec. The evoking stimulus could not be determined, unless it was the presence of the observers. Other animals made no visible response.

Oodle, Type E

The adult male's rapid 'oodloodloodloodl' calls described by ALTMANN [1959] sounded like a mechanical modulation of a rich, low tone (fig. 2k). They consisted of a rapid series of in-out pulses of air, with 3.3–7.5 exhaled syllables/ sec. The oodle sequences tended to last 1–4 sec and were not usually repeated close together. These calls had some similarities with the roar terminus ($A_{1.1}$), except that they were faster and in a muffled tone. The fact that an intermediate between the oodle and roar terminus was heard (in the form of a muffled roar terminus) further demonstrates the structural relatedness of these calls.

The oodle was a moderately common call, heard 20–50 times a day. During pauses in dawn roaring, males often gave oodles as their louder vocal activities tapered off. Oodles were given before, after and during lulls in intertroop confrontations. They also occurred before and during troop progressions and as 'spontaneous' calls at other times during the day. In general the oodles

were heard in situations in which the males also gave incipient roars (A₂) and woofs (C), though the oodle was the least frequently given of these calls. It could not be determined whether there was a particular stimulus configuration that evoked the oodle or whether it was merely a lower probability response to the same general stimuli that could also evoke incipient roars and woofs. The relationships that incipient roars, woofs, and oodles have to full roars and the roar terminus suggest that all three of these calls are related to roar situations, except that the evoking stimuli are less intense or apparently less salient than the stimuli that evoke full roars.

Eh, Type F

A very quiet call was occasionally heard from infants of all ages (stages 1, 2 and 3). The sound rarely carried more than 10–15 m. The call was variously described in our field notes as 'eh', 'ah' and 'ǎ', and at times it was heard after a series of quiet 'hehs' (I). It was given by infants who were off their mothers and exploring the environment. ALTMANN's [1959] observations suggested that the 'eh' may serve as a 'locator signal' that provides the mother with information on the location of her infant and on the fact that the infant is not in distress. In the present study the 'eh' was sometimes given by the exploring infant, as ALTMANN described. Also, the 'eh' was at times given as an infant returned toward or sat next to its mother, and it may have increased the probability that the mother would open her arms to accept the infant into the ventral-ventral cuddle position which sometimes included nursing.

Two lines of evidence indicate that the 'eh' is the least intense call on a continuum of anxiety calls ranging from screech (L) to 'heh' (I) to 'eh'. First, there are structural similarities among the calls. 'Ehs' often sounded like quiet 'hehs' (compare figures 2l and 2p), and they were frequently repeated in a series similar to a series of 'hehs'. Second, after an animal was threatened or frightened, it usually gave 'hehs' and occasionally, these graded into 'ehs' before the animal became silent. These data indicate that the 'eh' may reflect a mild degree of alarm or anxiety. The fact that most 'eh' calls were heard from infants during exploration or return to the mother may indicate that exploration or not being able to regain immediate contact with the mother are mildly anxiety-producing. MASON [1968, 1971], ROSENBLUM [1971], and others have demonstrated that infant rhesus monkeys do become overaroused during prolonged exploration; after the overarousal begins to become aversive, the infants attempt to return to their mothers for arousal-reducing contact.

Whimper, Type G

In the present study a variety of sounds that all graded continuously together were labeled whimpers. The following considerations suggest that more accurate descriptions of the structure and use of these calls are necessary in order for various researchers to categorize them reliably. (1) Whimpers have not been extensively described in the literature; (2) ALTMANN [1959] reported that whimpers were given only by immature animals, and (3) some of the grunt calls described by others could be what we identified as whimpers (especially low pitch male whimpers). The following paragraphs will attempt to clarify what were identified as whimper calls in the present study.

Three types of whimpers were identified: the basic whimper pattern, G_1; male 'emphatic whimpers', G_2; female and juvenile high chirping whimpers, G_3.

The basic whimper calls (G_1) were given by infant₃'s, juveniles and adults in a variety of situations. Whimpers often occurred singly or in a series (fig. 2m), and series lasting longer than 1 min were not infrequent. Rhythmic series of whimpers had structural elements in common with quiet continuous woofs (C_1) and continuous incipient woofs (C_2), and apparently males could make smooth transitions among these three calls. The rate of continuous whimpers varied considerably. The pitch of male whimpers varied from low, almost guttural to quite high tones, whereas the pitch of infant, juvenile and adult female whimpers was more consistently in high ranges only. One loud type of male high whimper was called an 'emphatic whimper' (G_2); it had 'aw' qualities typical of roars (A), and it sometimes occurred when males were building up to bouts of roaring (fig. 2n). Juveniles and adult females could produce a short, high pitch whimper (G_3) that sounded like a chirp (fig. 2o). These calls often occurred before bouts of A–B group roaring, and they frequently graded into roar accompaniment vocalizations (**B**). These facts suggest that whimpering may be related to A and B vocalizations.

Whimpers occurred in at least six types of situations. First, adult males often whimpered (G_1 and G_2) during troop progressions. Juveniles and adult females also whimpered (G_1 and G_3) during troop travel, but they tended to whimper less than adult males. Travel whimpers were intermixed with quiet incipient roars (A_2), quiet woofs (C), oodles (E), 'caws' (J) and 'wrah-has' (K). In rapid progressions whimpers often reached their loudest and could be heard up to 100 m in less dense areas of the forest. These loud calls sometimes signaled nearby troops of each other's presence and may have led to the convergence of mixing troops and to either confrontations or avoidance among nonmixing troops. Sometimes, when a progression terminated as a

troop arrived at a feeding area, the whimpering continued for 5–10 min before tapering off.

Second, increased whimpering occurred at the first sign of two nonmixing troops, beginning to approach each other before a confrontation. Whimpers built up to stronger intensity and more frequent occurrence as troops approached. In males, whimpers (G_1) could lead to emphatic whimpers (G_2) or directly to roars. They could also lead to incipient roars (A_2) or woofing (C) which could in turn lead to roars. In females, whimpers (G_1) could lead to chirping (G_3) or to the roar accompaniment (B). During pauses in confrontation roars, there were often whimpers, and at the end of confrontations some animals continued to whimper intermittently for 2–45 min (especially when neither of the two troops retreated very far after the confrontation). Thus, whimpers tended to occur in the lower levels of confrontation excitement for males, females and juveniles.

Third, when mildly startled, surprised, threatened or pestered, juveniles and adults often gave whimpers (predominately of the G_1 form). When an animal walked across a branch that snapped or broke under its weight and the animal slipped or fell, it tended to whimper (although adult males sometimes woofed, C). Once, when a juvenile fell 10 m into low brush, it whimpered for 30 sec before beginning to climb back into the trees. Occasionally, when capuchin monkeys *(C. capucinus)* came within 5–10 m of the howlers, the howlers whimpered (and some males gave incipient roars, A_2). When a troop was surprised by the proximity of another nonmixing troop or of a solitary howler, 10–50% of the troop members usually gave whimpers. Once, when a solitary animal accidentally came into a tree where a troop was taking a midday siesta, the troop suddenly began giving whimpers and many of the troop members defecated while the lone animal turned and hastily retreated. The whimpers ceased after 2 min, when the solitary animal was out of sight. When an animal mildly threatened, startled or frightened another member of its own troop, the latter animal often whimpered. (Extreme threats and startling usually led to yelp or screech responses, L, and moderate threats usually led to 'hehs', I.) Often, when one animal lunged at or displaced another, the displaced animal gave yelps or screeches that graded into 'hehs' which in turn graded into 'ehs' (F) or whimpers (G_1), then silence. When humans startled the howlers by suddenly appearing at distances closer than 7 m after a silent approach, the nearest monkeys usually whimpered (though males sometimes woofed, C). When the monkeys were startled while 1–3 m from the ground, they usually ran up 0.2–2 m and whimpered. This startle response often alerted other adults who were further from the startle stimulus.

(Infants tended not to react when other animals gave the startle response, and juveniles reacted inconsistently.) If humans stayed near the startled monkeys, whimpers lasted from 1–3 min in habituated troops and longer in unhabituated troops. There were times when animals in troop progressions crossed directly over the observers, and when the crossing was lower than 7–10 m, the monkeys often whimpered while above us, and occasionally, they defecated or urinated shortly after crossing.

Fourth, whimpers commonly occurred during more active play among infant₃'s, juveniles, and adult females. More active play consisted of face-to-face orientation, open mouth grins or grimaces, swatting or pawing with the hands and pulling or holding with the hands and feet. Sometimes the players ran or changed positions quickly. Play often included pauses and terminated with the retreat of one or more animals. It is possible that play whimpers indicated either excitement or perhaps mild anxiety evoked by rough activity.

Fifth, when adults 'greeted' each other, they sometimes whimpered. Greetings consisted of one animal approaching and embracing the other by putting its arms around the second animal's shoulders or body. In some cases both animals would sit, embrace each other, and whimper intermittently up to 1.5–2.0 min. Mouth-to-mouth orientations, elements of play, urination and urine smelling sometimes occurred during greetings. Since greetings usually took place when 2 or 3 mixing troops joined to form a supertroop, it is possible that greetings occur as a consequence of the general excitement of having 2 or 3 troops traveling together, or as a consequence of animals making friendly approaches to others that they did not often see. Thus, the whimpers in this context could reflect excitement or friendly approach, but this does not exclude the possibility of anxiety or uneasiness in such situations.

Sixth, whimpers occurred in some mother-infant interactions. Infant₃'s and early juveniles sometimes fell from the trees. Mothers did not respond to fallen juveniles; however, they did respond to fallen infants. If the mother was nearby, she often moved to look for or at her infant, and she tended to whimper for 2–30 sec until the infant resumed travel. No infants (or early juveniles) were ever seen to be injured in these falls. When infants became separated from their troops, they tended to give 'caw' calls (J) until they relocated their mothers, and the mothers sometimes whimpered in those instances when they approached to retrieve the infants. It could not be determined to what degree the whimpering facilitated the coordination of the mother and infant.

In summary, whimpers occurred in a variety of situations. Predominantly, the situations appeared to be related to certain aversive conditions: startle,

fear, falls, first sign of confronting nonmixing troops, mild threats, rough play, etc. It is possible that whimpers were also associated with mild general arousal, excitement or mild positive affect, since the calls did occur during play, travel excitement and greeting. It may be misleading to assume positive affect, however, because even in the apparently positive approach interactions there might be mild aversive components related to proximity, rough play, or rapid travel.

Grunt, Type H
From ALTMANN's [1959] description of the grunt call, we can only assume that he was referring to moderately quiet, low pitch calls which we at first labeled as 'grunt', 'groan', and 'growl' calls while in the field. Later spectrographic analysis revealed that all of these calls were either on the continuum of A_2 calls or they were complex combinations of those calls. Therefore, we conclude either that we did not hear the grunt call that ALTMANN [1959] was describing or that his grunt call is actually subsumed under the category of A_2 calls.

'Heh' or Cackle Laugh, Type I
This call was heard frequently during agonistic interactions between members of the same troop. In its loud form, this call sounded like a series of 'heh-heh-heh-heh' syllables. In quieter forms, the call could sound like quiet, panting 'eh-eh-eh-eh-eh' syllables. The syllables of both loud and quiet forms tended to be repeated 2–6 times/sec. Although ALTMANN [1959] described this call as a cackle laugh, only on a small number of occasions did the call appear to us to have these tonal qualities. Therefore, we prefer to describe the call as 'heh'. As ALTMANN observed, there was a wide range of pitch and tonal qualities in this call when heard in different situations and from different age animals (fig. 2p).

The vocalization was usually given by a smaller animal (i.e., an adult female, juvenile, or infant[3]) when a larger animal (usually an adult male or adult female) lunged at, swatted at or rapidly displaced it. These situations often occurred (i) during rough play involving at least one adult; (ii) after a smaller animal pestered or came too near a larger animal, or (iii) when a larger animal displaced or threatened a smaller one for no apparent reason. Typically, the threatening animal faced and lunged 0.2–1 m toward the second animal, while both animals made open mouth grins or grimaces. The two animals were usually 0.3–1.5 m apart, and occasionally, one or both animals pawed or swatted at the other. After the first animal made 1–3 lunges, the

second animal usually backed away and gave a series of rapidly repeated calls that lasted 2–10 sec. The series usually sounded like 'HEH-HEH-Heh-heh-heh-heh', with the sounds being at first loud and of high pitch and then progressively quieter and of lower pitch. More intense bouts were often begun with a yelp or screech (L), and sometimes the 'hehs' tapered off into 'ehs' (F) or whimpers (G). At times the threatening animal also gave 'hehs'. On one occasion, when an infant[3] could not follow its mother across a very large gap, the infant gave a yelp (L) followed by 'hehs' immediately after the mother jumped. Thus, while the call was usually a response to a social threat, it could occur in nonsocial situations where there was a sudden onset of aversive conditions.

As ALTMANN [1959] points out, the metallic cackling tones reported by COLLIAS and SOUTHWICK [1952] are probably the cackle laugh or 'heh' call (I). Whereas COLLIAS and SOUTHWICK suggest that the call may be a threat, the Barqueta data indicate that the threatened animal was more likely to give the call than the threatener.

Additional Vocalizations

At Barqueta several vocalizations were identified that have not been described previously for howlers. These vocalizations are labeled J through N as an extension of the categorization begun by ALTMANN [1959].

Caws, Type J

The 'caw' calls were given by infant[3]'s when they were lost from their mothers or when their mothers would not accept them for contact. There was a great deal of variance in these frequently heard infant calls (fig. 2q). The 'caws' were commonly given in a series of three syllables in which the first was emphasized, and the second was inhaled: 'CAW-(caw)-caw'. The number of syllables in bouts of 'caw' calling varied from 1–5 and almost any syllable could be emphasized. One plosive 'caw' at times sounded like a puppy's bark. 'Caws' varied from quiet to very loud, and loud 'caws' could be heard for 75–125 m through the forest, depending on foliage density and wind conditions. Bouts of cawing were repeated as frequently as every 3 sec or as infrequently as every 30 sec. Lost infants often cawed 15–30 min, and sometimes 60 min, before their mothers retrieved them or they found their mothers. When retrievals did occur, the mother could have been responding to either the 'caws' or the infant's absence. When infants did relocate their mothers, however, they usually stopped cawing, ran to the mothers and nursed at the first opportunity. Older infant[3]'s and early juveniles were sometimes shunned

by their mothers for as long as 1–2 h. These animals traveled and rested with the troop, and at times they gave quiet 'caws'.

Some 'caws' by older infants and early juveniles (fig. 2r) contained the acoustic qualities of both the 'caw' (J) and 'wrah-ha' call (K). The 'wrah-ha' was typically given by adult females when they became separated from their troops. Hence, the 'caw' and 'wrah-ha' appear to be related in form and usage. There was, however, much more variance in the structure of the 'caws' than of the 'wrah-has'.

Wrah-ha, Type K

Mothers of dependent infant$_3$'s and occasionally other adult females gave the 'wrah-ha' call when they became separated from their troops. There was a moderate amount of variance in the call, in both intonation and intensity (fig. 2s). The first syllable was almost always the louder, and the second appeared to be an inhaled tone. Occasionally, there was a third tone that followed the main two syllables. The sounds of 'wrah-ha', 'bu-ha' or 'brah-ha' could often be heard for 70–100 m through the forest.

When an infant$_3$ could not make a crossing and keep up in a troop progression, its mother sometimes stopped to wait for the infant or she returned to retrieve the infant. If the mother became separated from the troop, she was likely to begin calling. Some mothers began to call as soon as they left the troop, and others began only after they had located their infant. In the former case the mother's vocalization might have aided the infant in locating its mother, but we have no evidence to show that infants did benefit from hearing the 'wrah-ha'. When a mother began to give 'wrah-ha' calls, she usually sat in one place or moved only short distances at a time. The calling could last up to 1 h or more, until there were vocalizations from the mother's troop that revealed its location. The call was a reliable indicator of the mother's condition of being separated from the troop and having few or no cues about its location. The call may be an adult version of the 'caw' vocalization (as the data above suggested), and, like the 'caw', it may reflect a state of isolation and distress.

When the mother heard roars or other loud calls from her troop, she either gave fewer of the calls or completely stopped calling and began to travel toward the troop. (Whimpers G often replaced 'wrah-ha' calls as the mother progressed toward the troop.) There was no evidence that the troops vocalized as a direct response or answer to 'wrah-ha' calls, but it is possible that the calls might have caused an undetectable increase in the likelihood that troop

animals would vocalize. Apparently, the calling mothers had to wait until their troops gave a sufficiently loud vocalization before the mothers could locate their troops. Almost all troops did vocalize from time to time, however, and no mother (accompanied only by her infant) was ever observed to be separated from her troop for more than 1.5 h.

Yelp and Screech, Type L

Various calls were given that sounded like yelps or screeches (fig. 2t). The calls were sufficiently infrequent and given in such similar situations that it was not possible to determine whether these were two distinct calls. In addition there appeared to be significant variance in both calls. The yelp tended to sound like the yelp of a dog when it is suddenly hurt. The screech sounded like a loud high 'EEEeee'. Both yelps and screeches were relatively loud calls that could sometimes be heard 50 m through the forest. They were heard only 17 times during the study and were given by infant$_3$'s, juveniles and adult females. In most cases they occurred after a large animal startled, lunged at or swatted at a smaller animal. Thus, the yelp and screech appeared to be responses to sudden, intense fright. They were often followed by a series of 'hehs' (I), and the calling animal usually retreated from the threatening animal. On three occasions an infant$_3$ gave a yelp or screech followed by 'hehs' when its mother made a long jump that left the infant stranded (as described under call I, above). This use indicates that these calls may be given in response to sudden fright situations other than social threat.

Infant Squeak and Bark, Type M

Infants gave a variety of quiet calls that could be heard only at close distances. At times it was difficult to categorize these calls; therefore, we offer only a tentative analysis. The most common of these two infant calls was a squeak which was given by infants of all three age classes. Most squeaks were short, repeated calls, but occasionally squeaks lasted 0.8–1.5 sec and sounded like squeaky door hinges (fig. 2u). The two main contexts in which the call was given implicate mild distress, and that perhaps the squeak may be related to an infant form of whimpers (G) or to a low intensity version of the screech (L). When an infant was off its mother's body and the mother began to move, the infant often gave squeaks and hurried toward her. The mother usually responded by pausing, permitting the infant to crawl onto her body, then resuming travel. Infants were more likely to squeak when the mother moved rapidly, when she was approaching a wide crossing point, or when there were general troop progression activities among several nearby animals. Also, when

older animals played roughly with infants, the infants often squeaked while trying to escape or avoid the larger players.

A second quiet call that may be related to the infant squeak is a more plosive call that sounded like a puppy's bark. The call was given with a variety of tonal qualities and intonations. It was sometimes given when an infant was played with roughly by larger animals, but the bark was less common than the squeak in this situation. Only a small percentage of the time (approximately 5%) did mothers retrieve squeaking or barking infants from rough play. At times infants gave barks when startled by other animals. Twice, when infants could not gain access to their mothers' nipples because the mothers were sprawled on branches, the infants gave solitary barks, and the mothers sat up to permit nursing.

Hiccup, Type N

Adult males occasionally made a sound that resembled the human hiccup. It usually occurred during pauses in roar activities, but no special significance was identified (fig. 2v).

Discussion

Families of Vocalizations

The vocalizations heard at Barqueta appear to fit into six (perhaps five) major families, based on similarities of structure and usage (fig. 3). Grouping the calls into families emphasizes the relatedness of many of the calls and demonstrates which calls form graded series with each other. Almost none of the calls qualified as discrete, nongraded signals.

By far the most complex family of calls consisted of roars and their derivatives. The main group of roars (Ia) was all based on the 'aw' or 'oh' syllable heard in incipient roars (A_2), full roars (A_1), high roar coda (A_3) and roar terminus ($A_{1.1}$). The incipient roars (A_2) contained four variations that could be discriminated by the amount of 'popping' that was imposed on the 'aw' or 'oh' tone.

The derivatives of the main roar group (Ib) shared less in common with each other than each did with some aspect of the roars. The oodle (E) had little acoustic similarity to incipient roars (A_2), but it occurred in similar low arousal situations. The oodle was clearly related structurally with the roar terminus ($A_{1.1}$), and the animals produced a continuum of calls from A_1 to $A_{1.1}$ to E. The hiccup (N) appeared to be an incidental call that was most likely to occur when males had been roaring. The roar accompaniment (B_1
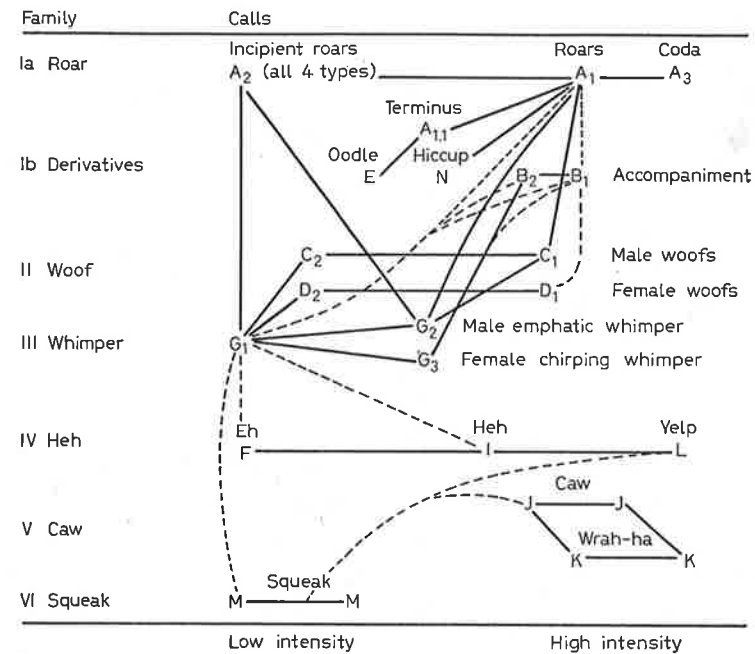
Fig.3. Given the numerous ways in which the calls could grade into each other and the various structural similarities among calls, it was possible to group the calls into basic 'families'. Solid lines indicate the presence of strong relationships in structure and/or usage. Broken lines represent weak, indirect or questionable relationships between calls. Within each family the calls on the left were typically given in response to low intensity situations, and those on the right to high intensity situations.

and B_2) calls of older juveniles and adult females were closely associated with and paralleled the male roar (A_1 and A_2) calls in usage and structure.

The calls of family II included male woofs (C_1 and C_2) and female woofs (D_1 and D_2). These vocalizations varied from quiet 'unf' sounds to full, loud calls. The loud male woofs often graded into roars or occurred in alternating sequences with roars. Because woofs could be loud calls, they may have served spacing functions similar to the calls of the roar family. However, woofs also appeared in mobbing, times of distress, encounters with lone animals, intra-troop agonistic interactions, and in troop progressions.

The calls of family III included three forms of whimpers and these were related to the first two families. Quiet whimpers (G_1) often graded into various roar calls (A and B) and woofs (C and D). Male emphatic whimpers (G_2

often graded directly to full roars (A_1), and female high chirping whimpers (G_3) had the same relationship with roar accompaniment calls (B_1).

Thus, the first three families of calls were highly interrelated. The remaining three families of calls did not appear to be closely related to other families. Family IV contained three calls that appeared to reflect anxiety or fright. The loudest calls were the screech or yelp calls (L) in which sudden fright was most obvious. The screech was, at times, immediately followed by 'hehs' (I) and 'ehs' (F) as the caller calmed down after being frightened. 'Heh' calls (I) were frequently heard in less intense agonistic interactions. The 'eh' (F) appeared to indicate the lowest level of arousal in this family of calls. Even the 'eh' calls of exploring infants or infants, that were waiting to be accepted by their mothers, may fit this interpretation.

Family V contained the 'caw' (J) and 'wrah-ha' (K) calls which indicated the state of being lost or separated. Similarities in tone and usage suggested that these calls were closely related. Infants tended to give 'caw' calls and adult females 'wrah-ha' calls. Interestingly, older infants and early juveniles sometimes gave a type of call that showed both 'caw' and 'wrah-ha' qualities (fig. 2r). Thus, the differences between the calls may reflect changes in the vocal apparatus due to maturation.

Family VI, which contained a variety of infant calls (M), was especially difficult to analyze. These infant vocalizations (namely, infant squeaks and barks) were usually heard in times of mild distress. The symmetry of figure 3 and the possible relatedness of some infant barks (M) with single 'caws' (J) suggest that the squeak calls may belong at the low intensity end of the 'caw' family. However, more intense squeaks may grade into screeches or yelps (L) of family IV. Also, there were relationships between squeaks and whimpers (G). It is possible that the squeak calls could be subsumed under one of the previous three families, reducing the number of families to five.

The Role of Roars in Intertroop Spacing

The roars heard at Barqueta occurred in four types of circumstances:

(1) Roars were at times given spontaneously. At dawn, after waking from a midday nap and in other periods of relaxation, there were incidents when an otherwise tranquil-looking male would suddenly put his head back and roar; and often he would be joined quickly by the A and B calls of his troop mates. MARLER [1968, p. 429] has noted that spontaneity in producing loud calls is characteristic of signals that maintain intertroop distance. Troops that are well adapted to dividing up space by mutual avoidance may be expected to vocalize before they accidentally encounter each other. If the function of

the calls is 'to maintain the *status quo,* they can have no complete dependence on external triggering situations'. They must be given before troops come into contact with each other. The spontaneous roars announce the location of a troop to any other troops within 1 km or more radius.

(2) Roars were given in response to low pitch noise, such as the drone of airplane engines, rain, wind, thunder and the roars of other howlers[1]. This may relate to communication both between and within troops. When one troop gave roars, either spontaneously or for other reasons, other troops up to 300 m away were likely to 'answer' almost immediately. Thus, in the quiet of the day, a series of roars might begin in one part of the forest and lead to contagious roars from other troops in the forest. This mechanism tended to reveal the location of most of the troops and could clearly operate in facilitating intertroop avoidance. Concerning communication within troops, perhaps a portion of the social facilitation effect noted within troops was due to the fact that, hearing the low pitch sounds of one male roaring, increased the probabilities that other males would roar too. However, the fact that howlers would not always roar when troopmates roared indicates that social facilitation is more complex than merely reflex-like responding to an eliciting low pitch tone. Probably the remaining two factors affect the likelihood that one animal would join in and support the calls of another.

(3) Danger stimuli evoked roaring. Predators, dogs, a fallen infant, the proximity of humans, the firing of a gun, etc. can elicit roars. The differences between the BCI data and the Barqueta data indicate that howlers can learn different danger associations in different environments. In some areas howlers roar at humans, but in other areas they do not [CARPENTER, 1934; this report]. Roaring at danger stimuli may disrupt the activities of some predators or drive them off; however, at Barqueta roars sometimes attracted potential predators, such as dogs and humans, rather than repelling them.

(4) At Barqueta, when two nonmixing troops were within 50 m or visual contact, there was a tendency for one or both of the troops to roar, and the troop that eventually retreated first usually roared more than the other troop. In general, a troop that had been using an area would be more likely to withdraw from the area than a new troop that was moving toward it, and the first troop usually roared more than the incoming troop. At Barqueta, roaring

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[1] POLEY [1972] experimented with various stimuli to see if he could elicit roars from a single adult male *Alouatta caraya* in the Duisburg Zoo. The drumming sound of water hosed onto wooden perches in the cage proved very effective. The water sound was of the same pitch as the howler's calls. This was the only sound that POLEY found which would elicit the roars.

between nonmixing troops was associated more strongly with retreat than with approach. On BCI CHIVERS [1969] also noted that roaring was most frequent before a troop retreated from other troops. Troops tended (i) to move away from each other when they came closer than 200 m, and (ii) to roar most frequently before retreating from other troops [CHIVERS, 1969, p. 73].

These four response patterns cover all of the cases of roaring identified at Barqueta. The first two types – spontaneous calls and answer calls – account for dawn choruses and most midday exchanges at a distance. The latter two types – danger roars and confrontation between nearby troops – could also start a contagious chain of midday roars among several troops. These situations all fit a model of howler spacing at a distance via avoidance mechanisms. The facts that howlers woof (C) when moving toward targets of mobbing, but that they roar when not moving toward the target again suggest that roars may be more strongly associated with avoidance or withdrawal than approach.

The data from BCI also support the avoidance hypothesis. SOUTHWICK [1962, 1963] noted that the frequent vocalizations that howlers make at dawn and during troop progressions seem to help troops avoid each other more successfully than less vocal monkeys (such as rhesus) do. CHIVERS [1969] rejects the territorial hypothesis and describes the troops as spacing away from each other by avoidance. At Barqueta, morning choruses may have aided the troops in avoiding some confrontations, but the high density of troops made it likely that when avoiding a nonmixing troop on one side, a given troop was likely to run across a second nonmixing troop on another side. This helps explain the high number of daytime confrontations at Barqueta.

Summary

This paper presents an analysis of the vocal repertoire of howler monkeys *(A. palliata)* from a field study in southwestern Panama. 26 types of calls were identified and described; sonagrams are presented for 21 of them. By making finer discriminations among the variations of some of the calls (such as the compound A_2 calls; 'hehs', I; 'caws', J; or 'wrah-has', K), the total number of calls could reach 30 or more. On the other hand, by focusing on general patterns rather than fine discriminations, about 15 basic calls stand out, and these fit into 5 or 6 broad families. Many of the calls heard at Barqueta are similar to those that have been identified on BCI. However, the present study discriminates on five new vocalizations and eight new variations on calls that were not previously specified in ALTMANN's [1959] schema. Also, there were differences in the frequency and usage of several signals. These differences appear to be the consequences of two factors. First, the

Barqueta animals could be studied and tape-recorded at the relatively close distances of 7–15 m. Proximity greatly facilitates the discrimination of the structure and usage of vocal patterns. Second, since intertroop confrontations occurred 5–15 times a week, there were repeated opportunities to study the complex use of calls that occurred in conjunction with troop roaring.

Future studies may be able to determine whether or not dialects or local variations in howler communication exist. To facilitate comparative studies on vocalizations, a tape recording of the calls described in this study is available from the authors or from the Laboratory of Ornithology, Cornell University, Ithaca, N.Y. [BALDWIN and BALDWIN, 1975].

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