

**THE EFFECT OF THE LOCATION OF A SIMULATED
INTRUDER ON RESPONSES TO LONG-DISTANCE
VOCALIZATIONS OF MANTLED HOWLING MONKEYS,
ALOUATTA PALLIATA PALLIATA**

by

JAMES MATHER WHITEHEAD¹⁾²⁾

(Department of Biology, University of North Carolina, Chapel Hill, N.C., U.S.A.)

(With 14 Figures)
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Vocal communication among primates serves in part to maintain patterns of spatial distribution by means of signals which increase, maintain or decrease distance between groups (MARLER, 1968; KUMMER, 1971). Loud calls, often thought to influence spatial relationships of groups at long range, are found among numerous prosimians (PETTER, 1962; PETTER & CHARLES-DOMINIQUE, 1979), among new world species such as *Callicebus moloch* (MASON, 1968; ROBINSON, 1979, 1981), *C. torquatus* (KINZEY & ROBINSON, 1981, 1983), howling monkeys, *Alouatta palliata* (CARPENTER, 1934, 1965; ALTMANN, 1959; CHIVERS, 1969; EISENBERG, 1976), *A. seniculus* (SEKULIC, 1981, 1982a, b, c, 1983) and *Ateles fusciceps*

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²⁾ Present address: Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611-0301, U.S.A.

robustus (EISENBERG, 1976), among old world cercopithecines (GAUTIER, 1969) including *Cercopithecus ascanias* and *C. mitis* (MARLER, 1973), *Cercocebus albigena* (WASER, 1975, 1976, 1977a; WASER & WASER, 1977) *Papio* spp. (BYRNE, 1982), among old world colobines, *Colobus* spp. (MARLER, 1969, 1972; OATES & TROCCO, 1983), and *Presbytis entellus* (RIPLEY, 1967) and among the anthropoid apes, *Hylobates* spp. (CARPENTER, 1940; ELLEFSON, 1968; TENAZA, 1976; MITANI (1985b, c, d), *Symphalangus syndactylus* (CHIVERS, 1974, 1976), *Pan troglodytes* (MARLER & HOBETT, 1975) and *Pongo pygmaeus* (GALDIKAS, 1983; MITANI, 1985a; others in SEBEOK, 1977). These species normally inhabit dense forests where visual communication is impossible beyond short distances. In such habitats selection favors auditory modes of communication, especially over long distances.

The loud calls of mantled howling monkeys have long been considered candidates for signals that mediate intergroup spacing (CARPENTER, 1934, 1965; ALTMANN, 1959; CHIVERS, 1969; BALDWIN & BALDWIN, 1976). This study focuses on normative patterns of use of space as well as the association of group movement with the loud calls known as roars (the A series of calls in BALDWIN & BALDWIN, 1976). In addition the proposed effects of these loud calls on spacing are assessed by field experiments using sound playback of loud calls recorded from local, non-neighborly conspecifics. The experiments address two questions. First, does the location of a playback affect movements by test groups? The second question, based on the observation that females frequently join males in calling when one group encounters another, is: does the distinctive female accompaniment of roar choruses affect group movements? Finally, I relate the experimental results to the general question: what functions do the loud calls in howling monkeys serve?

Methods

Observations.

The study was conducted at Hacienda la Páccica, a cattle ranch 7 km west of Cañas, Guanacaste Province, Costa Rica during the wet seasons of August-December 1980 and May-September 1983. Eleven groups of howling monkeys, ranging in size from 5 to over 40 animals, occupied patches of evergreen and seasonally deciduous forest near the Rio Corobicí. During 1980 I and two field assistants collected descriptive information *ad lib* on the calls and patterns of movement of local groups. During June 1983, before any playback experiments, I and three assistants simultaneously monitored calls and movements of four groups for one month. Each morning an observer located a focal group before dawn, prior to the first continuous series of loud calls, and stayed with the group until the heat of the day, around 1130, when howlers normally rested. Observations resumed midafternoon at 1500, when group members normally foraged, and continued until the group had settled down for the evening, normally between 1700 and 1800.

Each observer noted the following activities during 15-min sampling periods: type and number of calls by males within the group; type and number of loud vocalizations from outside the group; azimuths of incoming loud vocalizations; behavioral contexts of the calls (broadly categorized as rest, move, feed, play) and azimuth and distance moved since the preceding sampling period. For simplicity we measured movements of the principal male of the group; the principal male is defined as the male that makes the majority of loud calls and is normally the alpha male. In practice the averaged movements by group members and by the principal male were virtually identical.

This study focuses on vocalizations that are candidates for signals effective in communication over a long distance, at least 400 m (WHITEHEAD, 1985). Calls comparable in sound level to howler's roars, around 90 dB at 5 m, attenuate to levels of ambient morning noise, 40-50 dB, between 400 and 1400 m from the source. Ambient noise

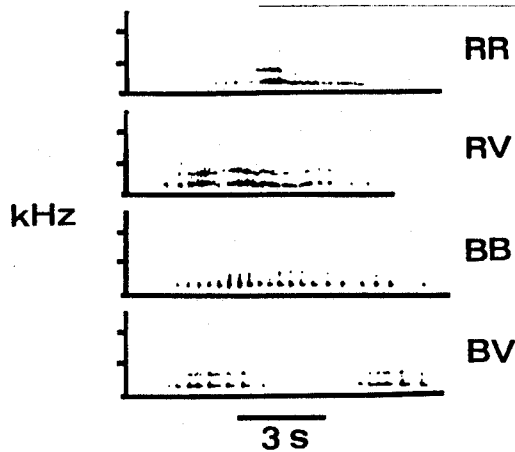


Fig. 1. Audiospectrograms of four categories of long distance vocalizations (LDV). See text for a detailed description of each type. The interval on the ordinate is 1 kHz. These LDV, all from the same male, were recorded at a distance of 10 m on 19 October 1980 with a Sennheiser MKH815 unidirectional microphone with a Nagra IVD taperecorder at 19c/s. RR, roar; RV, roar variant; BB, bark; BV, bark variant.

levels, crudely measured by the VU Meter of a Nagra IVD tape recorder, are similar to levels reported by WASER & WASER (1977) for an East African forest. This range of distances covers a radius of 1-3 neighboring groups about the vocalizer. Male howlers make four vocalizations loud enough to meet the criterion for long-distance communication (Fig. 1). Roars consist of a uniform sequence of notes (with maximum acoustic energy centered between 400-500 Hz) rapidly reaching a *crescendo* in intensity and followed by a *diminuendo* phrase of progressively shorter, less intense notes. The notes in this phrase are quite similar to the "oodle" (ALTMANN, 1959; BALDWIN & BALDWIN, 1976). The individual notes within the roar sequence often seem indistinct as if vocalized *legato* (EISENBERG, 1976; similar to *A. seniculus*, SCHON, 1986). A male making a full roar exhibits a posture and movements characteristic of these vocalizations: adopting a sitting or quadrupedal posture, roaring males orient their heads towards the canopy and with mouth forming a funnel-shape, produce the most intense note(s) of the roar; during the *diminuendo* phrase the male lowers his head in the sagittal plane and produces the terminal

oodle-like phrase while rapidly quivering both head and torso. Roar variants (RV) lack one or more distinguishing features of the roars, such as the typical oodle-like terminal phrase or the characteristic rise and fall in intensity, beginning instead on an intense note and trailing off. Males making roar variants seldom adopt the posture and movements characteristic of full roars, instead often emitting the roar variants while in a resting position astride a branch. The rapid quivering of the body never accompanies roar variants. Barks are intense, uniformly rhythmic pulsatile vocalizations, 2-3/s, at a dominant frequency between 4-500 Hz, around 200 ms in duration (mean = 220.0 ms, SE = 4.9 ms, n = 20; barks taped with a Sennheiser MKH815 unidirectional microphone and a Nagra IVD tape recorder at 19c/s at a distance of 55 m; calls examined on a Unigon Angioscan audiospectrum analyzer, temporal resolution = 6 ms). Bark variants are distinguished from barks by a lack of uniform duration and intensity of the notes; the tempo of bark variants is syncopated, not regular. Observers in the field readily learned to assign calls to these four categories. Roars and roar variants, which correspond to A₁ calls in ALTMANN (1959) and the A series of calls in BALDWIN & BALDWIN (1976), were distinguished by the stereotypy of the roar vocalization in contrast to the variability of the roar variants. Likewise, barks and bark variants, both grouped in the vocal category C₁ of ALTMANN (1959) and the C series of barks or woofs in BALDWIN & BALDWIN (1976), were placed in separate categories based on the stereotypy of barks and the variability of the bark variants. The female accompaniment to roar choruses, quite different from the roars, normally consists of chirps and whimpers (vocalization G₁ and G₃, BALDWIN & BALDWIN, 1975, 1976), relatively narrow band frequency sweeps concentrated between 1-2 kHz. Although female mantled howlers make roar-like vocalizations (the B series of calls, BALDWIN & BALDWIN, 1976), observers could seldom detect, with one exception (Group 7) mantled howler females in the study population unambiguously contributing roar-like calls to choruses dominated by male roars and roar variants. In contrast female mantled howlers in other populations (BALDWIN & BALDWIN, 1976) and red howlers in the Venezuelan Llanos (e.g. SEKULIC, 1983) make loud calls similar to male roars more frequently.

To record the temporal associations of vocalizations from within and outside the focal group, observers used four categories: (1) a call from the focal group followed by 5 s of silence; (2) a call from the focal group followed within 5 s by a response from another group; (3) a call from another group to which the focal group responded within 5 s; (4) a call from outside the focal group that did not elicit a response from the focal group. Five seconds crudely approximates the time required for the sound to travel to the limit of detectability of the most intense roar, around 1500 m under favorable conditions (CARPENTER, 1934; pers. observ.).

Playback experiments.

Observers habituated test groups to their presence for at least three consecutive days and generally more than ten days prior to the first playbacks. Consecutive tests of one group were at least two weeks apart. On the afternoon before the day of a playback, the test group was located and observed for approximately three hours prior to dusk. The following morning, around 0430 prior to first light, an observer relocated the group, scored the morning chorus and charted the "vocal horizon". The vocal horizon is the distribution of types of loud calls and their azimuths about the focal group. Since groups and their neighbors generally occupy stable activity fields, the vocal horizon consequently remains relatively stable over time.

Around 0600, after the morning chorus, I placed a speaker at a distance 50 to 100 m (mean = 71.6 m, SE = 3.3 m, n = 25) from the test group and at an azimuth prominent within the vocal horizon. Tapes were played on a Uher Report L tape recorder or a Nagra IVD at 19 cm/s. Output was amplified by a Nagra/Kudelski DSM external amplifier which drove a Realistic 30 cm horn speaker. The speaker was secured atop an

8 m collapsible metal pole, held in position by a field assistant, and pointed in the direction of the test group. The frequency response of the speaker was essentially flat (± 5 dB) over the frequencies of interest (400-3000 Hz). The output levels of the playbacks approximated sound levels recorded from calling groups (mean Sound Level of playback at 5 m = 87.9 dB, SE = 0.90, n = 11; approximate sound level of group roars corrected to 5 m from the source = 91.0 dB, SE = 1.96, N = 12; sound levels measured with a Realistic 42-3019 Sound Level Meter, C-weighting, Fast Response setting, referenced to 20 Pa).

The playback tapes used were natural sequences of calls recorded locally. One tape of local males contained 14 roar variants and lasted 4 min. A second tape of several types of loud calls with female accompaniment contained 6 roars, 5 roar variants and 42 barks, and lasted 4 min 32 s. Recorded with a Nagra IVD tape recorder at 19 c/s and a Sennheiser MKH815 unidirectional microphone, the tapes were made during 1979 of groups that were not neighbors of any of the ones later tested.

Following playbacks, I recorded movements, vocalizations, including their behavioral contexts, in the manner described above. I maintained contact with the test group for at least 6 hours after the playback. In some cases, I located the group later in the afternoon to determine any shift in location at dusk.

To determine the location of a group, an observer recorded the distance and azimuth from easily recognized reference points on maps made from aerial photographs. Distances were measured by means of calibrated paces and a map of numbered trees within a part of the study area (GLANDER, pers. comm.); the accuracy of measured distances is within 10%. The distances reported here reflect the minimum distance between map locations and not distances, often reported in the literature, that animals travel along arboreal pathways between two points.

A scaled 40 x 40 m grid superimposed over the mapped locations of a group made possible an assessment of the intensity of use of space. Groups spent long periods of time in only a few areas within their range. MORISITA's indices (MORISITA, 1962; POOLE, 1974) based on distributions of quadrat use for 4 groups in contiguous forest are all significantly greater than 1 (Table 1). Doubling and redoubling of quadrat size did not significantly reduce the values of I_d (Fig. 2). The groups thus clearly made uneven use of quadrats and showed preferences for select patches of forest.

On the basis of this pattern, I divided the activity fields of groups (WASER & WILEY, 1980) into intensively and seldom used quadrats (Fig. 3). For data collected during group-days in 1980, a quadrat used more than once was considered intensively used; those occupied one time or less were seldom used. For the more extensive data collected in 1983, quadrats used during 1% or more of the sampling periods were considered intensively used; those used less than 1%, seldom used. Based on these criteria, the initial locations of groups exposed to playbacks and of playback speakers were assigned *post facto* to intensively used or seldom used categories. A playback from a speaker located in an intensively used quadrat is a Type H playback. A playback from a speaker in a seldom used quadrat is a Type L playback. All test groups occupied intensively used quadrats.

For statistical analysis of distances and angles moved in response to playbacks, I used non-parametric tests for categorical data (SIEGEL, 1956), because of small sample sizes and the constraints on movement posed by the narrowness of the riverine forest within the study area. Although the assignment of playback locations to either intensively used or seldom used quadrats is independent of the type of forest, *i.e.*, riverine evergreen or deciduous ($G_{adj} = 1.67$, $p > .05$), the potential for riverine forest to constrain movements in reaction to tapes excludes the use of more powerful bivariate parametric analyses of both angles and distances (BATSCHELET, 1981).

For estimates of the total number of quadrats used by a group, I employed a technique of maximum likelihood estimation of unused quadrats based on the assumption of a truncated lognormal distribution of the frequencies of quadrat use. The technique is described more fully in ROBINSON (1979), after BLISS (1966) and COHEN (1961).

TABLE 1. MORISITA'S indices of the intensity of quadrat utilization by four groups for three sizes of quadrats

Size of quadrats		Group number			
		5	7	10	12
N quadrats	(40 × 40 m)	90	30	84	138
I		2.25	1.69	1.97	2.20
F		30.62	36.92	14.50	13.68
p		<0.01	<0.01	<0.01	<0.01
N quadrats	(40 × 80 m)	45	16	42	71
I		1.84	1.25	1.47	1.65
F		41.84	26.59	14.66	16.85
p		<0.01	<0.01	<0.01	<0.01
N quadrats	(80 × 80 m)	23	8	21	36
I		1.52	1.20	1.41	1.41
F		51.47	46.44	25.00	21.72
p		<0.01	<0.01	<0.01	<0.01
N samples		2140	1558	1187	1719

Results

Normative use of space in 1983.

The total area of activity fields ranged between 4.5 ha for group 7 to 24.3 ha for group 12. The estimated percentage of the activity field not sampled during our observations ranged from 23.0-39.4%. Estimates of total activity fields were within the range expected from published values for *Alouatta palliata palliata* at relatively high densities, summarized in EISENBERG (1979) and CROCKETT & EISENBERG (1986).

The overlap between activity fields of neighboring groups ranged from 13.9-63.2%. Extensive overlap between activity fields of neighbors has also been noted for howlers on Barro Colorado Island, Panama (CHIVERS, 1969; SMITH, 1977), and in southwestern Panama (BALDWIN & BALDWIN, 1972). The percentage of a group's area entered exclusively by that group, the isolation field (WASER & WILEY, 1980), ranged from 36.8-86.1%. The highest value, 86.1%, resulted from sampling a group's area on one side only and is probably an underestimate. Another high value (80.7%), however, was obtained for a thoroughly sampled group (12) occupying a distinct patch of upland deciduous forest.

Clumped distributions of activity resulted largely from a group's selection of patches of particular trees; they returned to the same sleeping trees at night and also to favorite trees to forage on preferred plant parts (see GLANDER, 1981; WHITEHEAD, 1986).

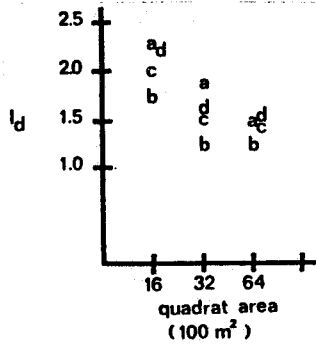


Fig. 2. MORISITA'S indices (I_d for quadrat use by three groups show that quadrat size does not alter the aggregated pattern of use of space. The indices were calculated from data collected during June 1983. a, group 5; b, group 7; c, group 10; d, group 12.1.

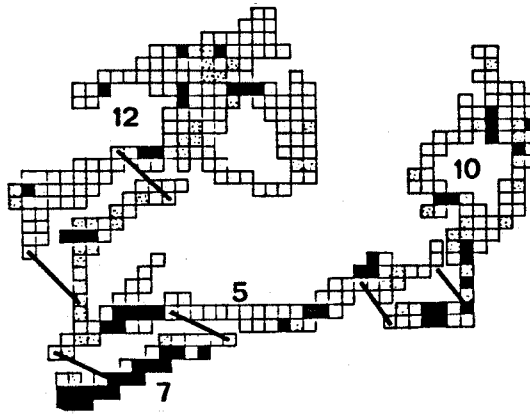


Fig. 3. Activity fields of four groups in contiguous forest in 1983. Each quadrat is 40 x 40 m. The clear quadrats were used less than 1% of the sampling periods; stippled quadrats, from 1 to less than 2%; and the dark quadrats, 2% or more of the sampling periods. Any quadrat used $\geq 1\%$ of the sampling periods is considered intensively used. Note the predominance of a few intensively used quadrats for each group, except group 7. For more details, see text. The heavy dark lines orient the superposition of the range maps for quadrats shared by neighbors.

Groups tended to move relatively short distances during the morning. During the 15-min sampling periods in which movement occurred, the average distance moved was 23.5 m (SE = 1.2 m, $n = 226$). A prominent move, defined as a move greater than 5 m which terminated in rest for longer than 5 min (WHITEHEAD, 1987) averaged 46.3 m (SE = 6.0 m, $n = 138$) and tended to last longer than one 15 min period of observation.

TABLE 2. Distances (m) groups moved between successive sampling days

		June	July	August
Group 5	Mean	137	224	206
	S.D.	141	255	157
	n	19	11	20
Group 7	Mean	92	111	79
	S.D.	98	108	97
	n	14	18	23
Group 12	Mean	213	303	175
	S.D.	167	146	105
	n	17	12	10

Differences between groups ($F = 10.532$) are significant ($p < 0.001$) but the difference between months ($F = 2.843$) and the interaction term ($F = 1.004$) are not significant ($p > 0.05$). S.D. = standard deviation; n = number of samples.

Groups differed significantly in the distance between locations on successive days (Table 2). Small groups tended to move less than large ones (Fig. 4). Large groups traveled between a large number of patches; small groups generally used fewer patches and returned to them more frequently.

The dimensions of the forest affected the azimuths of movements by groups. Groups 10 and 12, inhabiting extensive patches of forest, selected azimuths indistinguishable from a uniform (random) distribution (Rayleigh tests, BATSCHLET, 1981; Group 10, $r = 0.205$, $p > 0.05$; Group 12, $r = 0.050$, $p \gg 0.05$). In contrast, the two groups in narrow riverine forest customarily moved at angles significantly different from a uniform distribution (Group 5, $r = 0.417$, $p < 0.001$; Group 7, $r = 0.315$, $p < 0.01$). Thus, within extensive tracts of forest, large groups such as 10 and 12 tended to use numerous patches frequently; smaller groups, such as 5 and 7, occupying narrow forest by the river, tended to move in one direction in the morning and to return to sleeping trees in the opposite direction by dusk.

Mutual avoidance is one mechanism that could serve to maintain spacing between groups (BALDWIN & BALDWIN, 1976). CHIVERS (1969) presents evidence that *Alouatta palliata aequitorialis* in Panama move away from neighbors when on average 220 yards apart. A more quantitative method for demonstrating avoidance uses a model of random movement which serves as a null hypothesis against which actual rates of encounters may be compared (WASER, 1977a; WASER & WILEY, 1980). WHITEHEAD

(1987) calculate that the howlers at La Pacifica encounter neighbors at rate much lower than expected under WASER's model of random movement.

Additional evidence of intergroup avoidance comes from a comparison of quadrats shared by neighbors. If neighbors occupy the same quadrats and use portions of the forest jointly, and yet the rate of encounters is still much lower than expected from purely random movements, then the case for active avoidance is strengthened. Among the four groups thoroughly monitored during 1983, group 5 occupied an intermediate position between groups 7, 12 and 10. Group 5 used 50.0% of group 7's

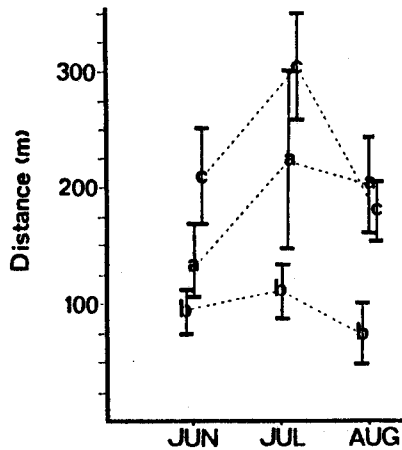


Fig. 4. Distances (± 1 SE) moved by groups within continuous forest on successive mornings during 1983. a, group 5; b, group 7; c, group 12.

quadrats, 13.9% of group 12's and 19.3% of group 10's. Since group 5 occupied substantial percentages of neighboring groups' ranges, the infrequency of encounters detected in 1983, 0.19/day, further reinforces the impression that neighboring groups are avoiding encounters, as well as avoiding entrance into shared quadrats when already occupied by vocal neighbors.

Normative use of vocalizations.

The temporal distributions of sampling periods for all loud calls (Fig. 5) and for each category of loud call made during the morning hours (Fig. 6) resemble ones in the literature (ALTMANN, 1959; BALDWIN & BALDWIN,

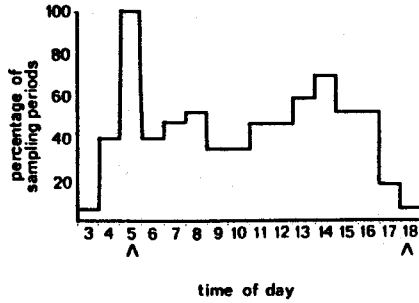


Fig. 5. Frequency distribution of long-distance vocalizations of all four types during 17 sampling days, 6 September to 13 October 1980. Thus around dusk observers heard any of the four loud calls on approximately 5% of the days. Carets indicate the approximate times of dawn and dusk.

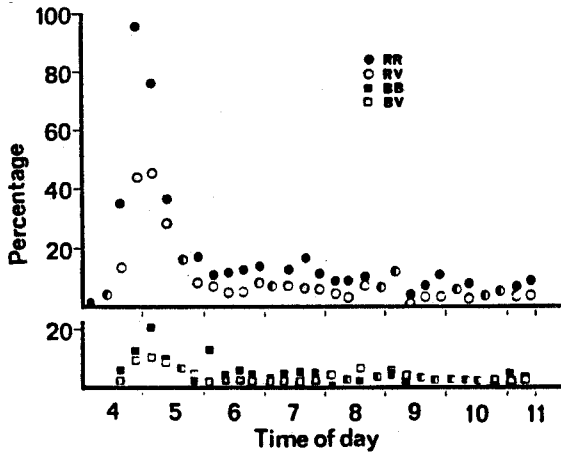


Fig. 6. Frequency distributions of the incidence of each category of loud call within sampling periods for four groups during June 1983. RR occurred during virtually every sampling period just prior to sunrise.

1976; CHIVERS, 1969, on *A. palliata*; HORWICH & GEBHARD, 1983, on *A. pigra*; SEKULIC, 1982b, on *A. seniculus*). There is a pronounced mode around sunrise and, for some vocalizations, a secondary mode in the afternoon.

Vocalizations before movement.

Between first light and the onset of movement (normally between 0700 and 0800 h), full roars were heard most and bark variants and roars with

female accompaniment least frequently (Fig. 7). Prior to moves when barks and bark variants were both heard, barks preceded bark variants in all cases (8/8, Binomial test, $p < 0.01$). When either barks or bark variants were heard, barks tended to occur more frequently (11/15, Binomial test, $p = 0.059$). Groups rarely refrained from calling or responding to neighbor's calls before movement.

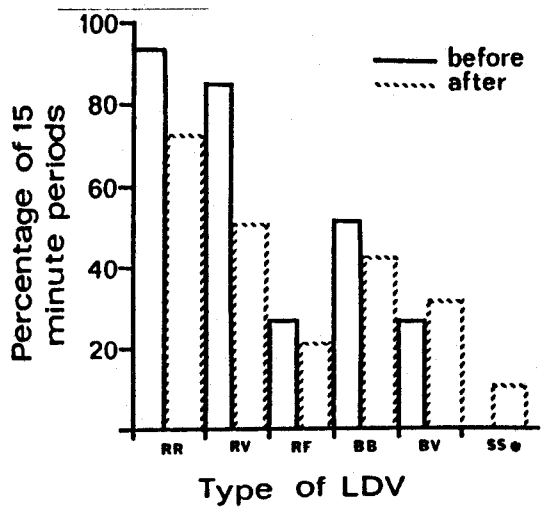


Fig. 7. The percentage of sampling periods during which focal groups produced loud calls before and after a prominent move (> 5.0 m) between 0430 and 1130 h in June 1983. RR, roars; RV, roar variants; RF, roar or roar variants with female accompaniment; BB, barks; BV, bark variants; SS*, silence within 5 s of a loud call heard from a neighboring group.

Vocalizations during movement.

During the 15-min sampling period in which the vocal group initiated movement, silence preceded movement in a majority of cases (35/52 = 67.3%). Of the remaining 32.7% of cases when loud calls occurred, 58.8% included roars, 41.2% barks and 17.6% roars with female accompaniment. The distance moved, when categorized as greater or less than 50 m, was independent of the presence or absence of loud calls during the same period ($G_{adj} = 0.02, p \gg .05$). The pattern of group calls did not vary with the eventual distance moved, and, in this context loud calls could serve to rally the group or to initiate movement.

Vocalizations after movement.

Vocal patterns were similar before and after moves except for the incidence of silence (Fig. 7). The number and type of loud calls are independent of their occurrence before or after movement ($G_{adj} = 1.13$, $p \gg 0.05$). In contrast, the distributions of types of loud calls as well as silence differ before and after movements ($G_{adj} = 18.56$, $p < 0.005$). Following 10 of 57 moves, groups maintained one of two forms of silence: active silence (WHITEHEAD, 1985) during 5 s after a loud call from outside the focal group (7 cases) and the complete absence of loud calls during a sampling period (3 cases). Active silence for 5 sec after a neighbor's call crudely approximates the time required for sound to travel to the limit of detectability, ca 1500 m (CARPENTER, 1934; WHITEHEAD, unpubl. obs.). Thus, though occurring after less than 10% of the moves, active silence, the active suppression of loud calls, appears to be an important alternative to vocal communication associated with movement. A similar phenomenon is evident among red howlers, *Alouatta seniculus* (EISENBERG, pers. comm.).

Combinations of different categories of loud calls co-occur in similar patterns before and after movement: (roars and roar variants) most often, followed by (roars, roar variants, barks and bark variants) and (roars, roar variants and barks). The prevalence of (barks and bark variants) sequence both before and after moves suggests a possible importance of bark-like calls in association with movement (WHITEHEAD, 1987). Bark-like calls commonly occur in unhabituated troops in response to human presence, or in response to intruders on the ground (EISENBERG, 1976; BALDWIN & BALDWIN, 1976; ALTMANN, 1959). Comparison of groups habituated to human presence to those not habituated suggests an association of bark-like calls with the novelty of human observers to the group. Both before and after moves, groups with a greater number of males used a greater variety of loud calls than small groups did. For example, the average number of types of loud calls by the 7 males in Group 12 (mean = 3.2, SE = 1.1) was significantly greater than from the 3 males in group 5 (mean = 2.1, SE = 0.7; Mann-Whitney $U = 43.5$, $p < 0.02$). Likewise large groups tended to use more kinds of loud calls after moving. For example, comparing the largest with one of the smallest groups, Group 10 used a significantly greater average number of types of calls prior to moves (mean = 3.1; SE = 1.5) than did Group 7 (mean = 1.6; SE = 1.5) (Mann-Whitney $U = 26$, $p < 0.05$). The number of males and the overall group size have significant effects on the

variety of vocal output and could thereby convey cues about group size to neighbors.

Experimental results.

Playbacks of loud calls simulate intrusions by vocal conspecifics, possibly perceived as strangers in the vicinity of focal groups. In this section I investigate two effects experimentally: the effect of the location of the simulated intruder; and the effect of roars with female accompaniment on group responses.

The location of the playback speaker influenced movements by groups within less than 30 min after playing tapes of roars with female accompaniment. Groups rapidly approached the speaker during a Type H playback from an intensively used quadrat. In contrast, they did not move or they withdrew slowly in response to Type L playbacks from seldom-used quadrats (Table 3). Type H playbacks of roars with female whimpers resulted in an average displacement from the original location of 58.3 m (SE = 10.4 m) in the direction within 10 degrees of the speaker. This distance is statistically indistinguishable from the normative average of prominent moves (46.3 m, SE = 6.0; $t_s = 1.99$, $p > 0.05$; SOKAL & ROHLF, 1981). Type L playbacks produced an average displacement after 30 min of 7.9 m slightly away and at an average angle of 136.5 degrees from the speaker. Fig. 8 contrasts the spatial responses to Type H playbacks with responses to Type L.

Tapes of roar variants resulted in similar responses within 30 min: Type H playbacks elicited approach and Type L withdrawal or no movement (Table 4). Type H playbacks of local roar choruses resulted in an average approach of 55.6 m (SE = 5.6), comparable to the normative values for prominent moves ($t_s = 1.66$, $p > 0.05$). Type L playbacks resulted in average movement of 13.2 m at 112.6 degrees from the playback speaker ($n = 7$) which is very similar to the response to the previous tape playback.

Analysis of groups' locations 6-11 hours after playback was possible only for experiments from seldom used quadrats. After Type L playbacks of a roar chorus with female accompaniment showed prominent movement away from the speaker (Table 5, Fig. 9) but no significant responses to tapes of roar variants alone. As female whimpers normally accompany intergroup encounters, movement away from the playback site of the former tape could reveal a tendency to avoid ongoing encounters. In contrast, the chorus of roar variants, a normal feature of

TABLE 3. Significant movement by test groups in response to Type H and Type L playbacks of roars with female accompaniment

Movements by test group	Type of playback	
	H	L
n approaches	6	0
n withdrawals or no significant movement	0	9

Fisher's exact probability, $p < 0.001$.

TABLE 4. Significant movement by test groups in response to Type H and Type L playbacks of roar variants

Movements by test group	Type of playback	
	H	L
n approaches	2	0
n withdrawals or no significant movement	0	7

Fisher's exact probability, $p < 0.028$.

all morning choruses, represents a less powerful vocal stimulus to which groups tend to respond mildly without avoidance.

Vocal response to the tapes.

Test males make more loud calls in response to Type H than to Type L playbacks. The probability of each type of loud call during the playback exceeded by far the probability in the absence of playback (Fig. 10a-b). Comparison of the numbers of loud calls during and after playback (Fig. 11a-d) demonstrates the efficacy of Type H playbacks in stimulating calling, especially roars, roar variants and barks. Roars and barks were heard significantly more frequently during Type H than during Type L playbacks. For example, test groups barked more frequently after Type H playbacks of roars with whimpers than after Type L playbacks (Mann-Whitney $U = 10$, $n = 6, 9$; $p < 0.05$). Males also responded with more barks and bark variants after a Type H than a Type L playback of local roars plus whimpers (Mann-Whitney $U = 9$, $n = 6, 9$; $p < 0.05$).

Type H and L playbacks evoked different rates of vocalizing during and after the presentation of the tape. Males, in response to roars with female whimpers from a intensively used quadrat, made fewer roars during the tape than during the subsequent 30 min (Wilcoxon Matched-

TABLE 5. Locations of test groups, expressed in x, y coordinates, 6-11 hours after playbacks from seldom used areas

N	Conditions	S	(SE)	ts	p	Y	(SE)	tx	p
7	MM	47.5	68.1	0.7	NS	7.4	49.0	0.15	NS
11	MF	7.9	29.4	0.3	NS	-76.4	33.0	2.32	<0.05

The Y-component of movement is along the axis between the playback speaker and the original location of the group. MM = tape of male voices only; MF = tape of males with female accompaniment.

Pairs Signed-Ranks $T = 0$, $p = 0.05$). In addition, males barked more frequently after a Type H playback of roars with whimpers than during it (Wilcoxon Matched-Pairs Signed-Ranks $T = 0$, $p = 0.025$). The vocalizations of test groups presented with tapes of roar choruses were quite variable; males made any of the four major loud calls during or within 30 min following the tape. Finally the numbers and types of loud calls were not significantly associated with the specific playback presentation (Friedman 2-way analyses of variance, $p > 0.05$). Thus neither tape used in playbacks uniformly elicited a specific form of loud call more than the other.

Discussion

Most groups of mantled howler monkeys respond in a site-dependent manner to experimental playbacks of roars. They approach simulated intruders in an intensively used part of their activity field; they do not approach and in some cases move away from simulated intruders in seldom used quadrats. Here I discuss the multiple contemporaneous functions served by loud calls, the functional flexibility within an animal's lifetime and within the putative evolutionary history of *Alouatta*. Finally I comment on the meaning of site-dependent spacing for howlers and other species, and point out limitations of this study.

Functions of long distance vocalizations.

WASER (1977) discusses seven possible functions of loud primate calls. This study provides evidence in support of five of these functions. First, loud calls affect intergroup spacing (Table 6). At close range (<50 m) all loud calls, along with visible distinctiveness of the caller (*e.g.*, facial scars), make individual identification or categorization (*e.g.* adult male)

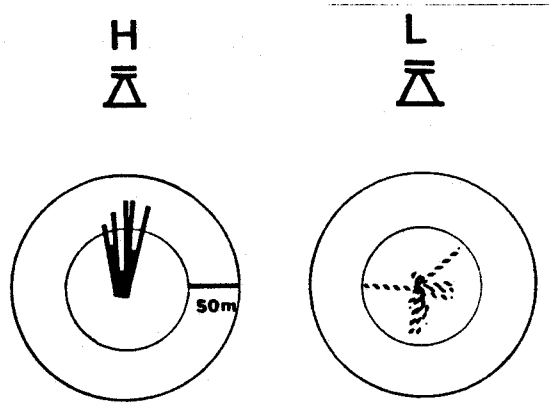


Fig. 8. Circular histograms of movement within 30 min in response to all playbacks from intensively used and seldom quadrats respectively. Solid bars, responses to Type H playbacks; striped bars, responses to Type L playbacks. The bars depicting response to the speaker in an intensively used quadrat (Type H) actually cover a sector of 5° but are spread out here for clarity.

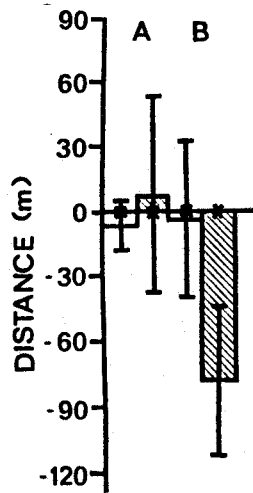


Fig. 9. Distances moved (± 1 SE) in response to Type L playbacks after 30 min (the clear histograms) and after 6-11 hours (hatched histograms). Only the component of the move towards or away from the speaker (positive and negative values, respectively) is presented in this figure. X, median distances. A, playbacks of only male calls; B, playbacks of male LDV with female whimpers. The distances moved 6-11 hours after playbacks of males with female accompaniment are significantly different from 0 ($t_t = 2.32$, $p < .05$).

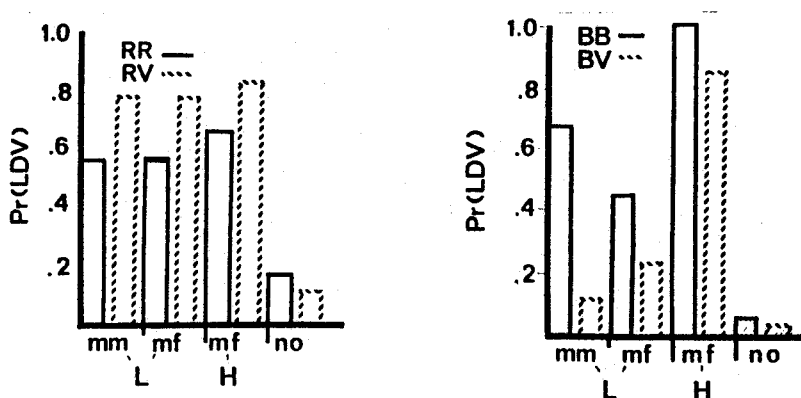


Fig. 10a. The probabilities of roars RR (solid lines) and roar variants RV (broken lines) within 30 min after playbacks. The hatched areas depict the probability of a call occurring between 0630 and 0700 in the absence of playbacks. Abbreviations: mm, tape of male LDV only; mf, tape of male LDV with female accompaniment, largely whimpers; no, normative observations; L, speaker located in a seldom used quadrat; H, speaker in an intensively used quadrat.

Fig. 10b. The probabilities of barks BB (solid lines) and bark variants BV (broken lines) within 30 min after playbacks. Abbreviations as in Fig. 10a.

possible. For example, in one group calling males became silent when a calling group member nearby came into sight; in contrast they continued calling towards a vocalizing non-group male (pers. obs.). At intermediate distances (50-100 m) barks and resultant reverberations convey the azimuth and coarse cues about the distance to the vocalizer (Whitehead, 1987). At distances greater than 100 m, loud calls convey the azimuth of the caller and possibly coarse cues about distance resulting from frequency-dependent attenuation (WILEY & RICHARDS, 1978).

In addition to male calls, some female calls might affect spacing between groups. Higherpitched female whimpers propagate distances much greater than 100 m (pers. observ.). The experiments with sound playback suggest that whimpers with roars, often accompanying a confrontation between groups, appear to stimulate avoidance by other groups within earshot (Fig. 9). In contrast, playbacks of female whimpers alone often elicit male loud calls, generally roars, and approach by males (unpubl. expts.). Females may whimper and induce resident males to call loudly to forestall approach or elicit avoidance by migrating males.

WASER's second function of loud calls, the coordination of intragroup cohesion, finds support in the reduced interindividual distances observed

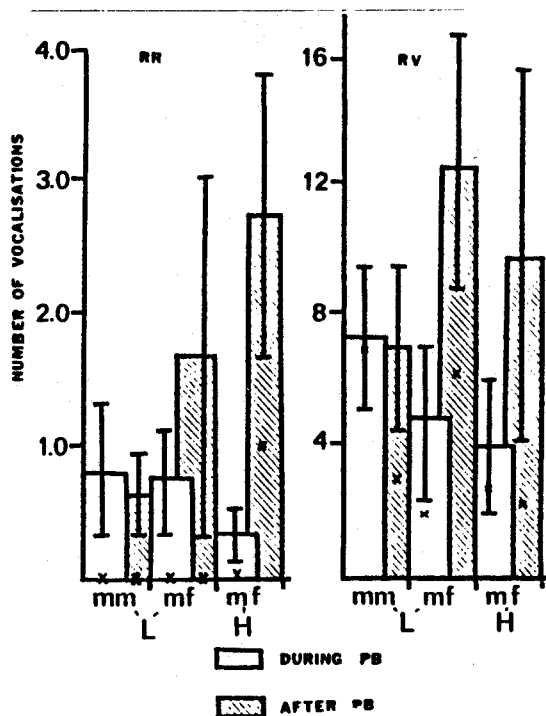


Fig. 11a, b. The numbers of roars and roar variants (± 1 SE) during and after playbacks. Abbreviations: H, speaker located in an intensively used quadrat; L, speaker in a seldom used quadrat; mm, tape of roar variants; mf, tape of roars with female accompaniment. X, the median value in each category.

during some playback trials. This effect, most consistently present during the APPROACH sequence (WHITEHEAD, 1987), was less evident during the playing of the other tapes.

The third function, broadcasting of information about the location of resources, is supported by the clumped use of space by *pallata* and the close correspondence between calling and activity fields. Howlers tend to call most frequently from intensively used quadrats and do not move to special calling locations. A howler towards callers will undoubtedly find an edible resource. Loud calling near the location of long-lasting resources (e.g., *Ficus* spp., Moraceae) might provide cues to neighbors about the location of these valued resources. However, information about the location of short-lived resources (e.g., flowers of *Tabebuia neochrysantha*, Bignoniaceae), which a resident group would harvest before a stranger could arrive, might be useless to eavesdroppers.

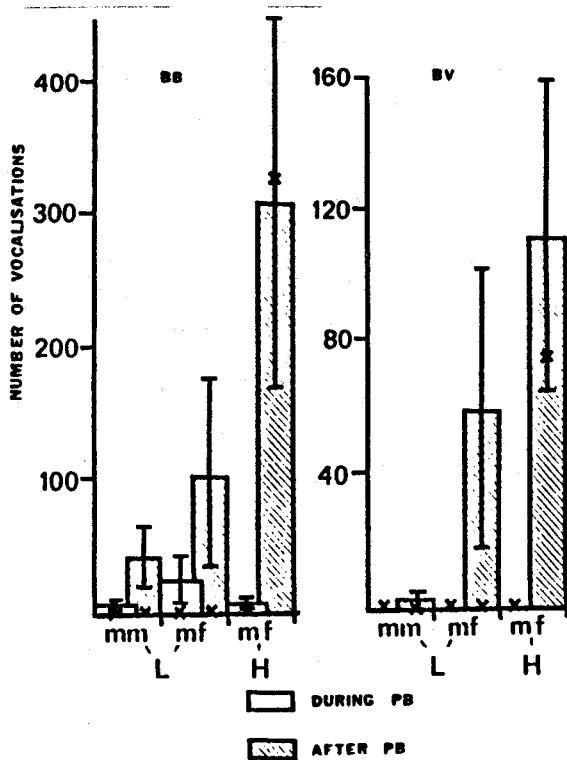


Fig. 11c, d. The numbers of barks and bark variants (± 1 SE) during and after playbacks. Abbreviations as in Fig. 11a, b.

The fourth function of loud calls, the attraction of reproductive partners, is exemplified by a brief history of one local male, Bandido, who started a new group in 1980 with just one female. By 1983 he had acquired 2 more females from neighboring groups, probably by advertising his position to dispersing females (GLANDER, 1980).

One anecdote from the 1983 field season illustrates how this might have occurred. A juvenile female became separated from her group and, instead of heading downriver where group members were eating mangos (*Mangifera indica*, Anacardiaceae), she moved upriver while giving a lost call ("hunh-wheeze"; similar to vocalization type K, "wrah-ha", BALDWIN & BALDWIN, 1976). On the other side of the river, Bandido paralleled her course upriver and roared and barked in her direction. The antiphonal calls of the lost female and the calling male continued until she had first traveled upriver about 1 km and then returned

TABLE 6. Cues provided and behavior elicited by loud calls at different distances from the caller

Approx. Range	Communication modality	AZI	Cues DIST	Provided <MOVED	I.D.	Behavioral response
< 50 m	visual/vocal	X	X	X	X	confront or greet
50-100 m	vocal (barks)	X	X	X		reciprocal approach/ withdrawal
> 100 m	vocal (roars)	X				location-dependent

Abbreviations: AZI = azimuth; DIST = distance; <MOVED = direction of movement; I.D. = individual or categorical identity.

downriver to reunite with her group. There were no trees suitable for crossing the river in this stretch, so we cannot know what might have happened had contact between the two animals been possible. BALDWIN & BALDWIN (1976) describe a similar observation of a male barking to a lost female consort.

WASER's fifth function, the initiation and subsequent direction of group movements, also proposed by GAUTIER (1969) for West African cercopithecines, is supported by the calling patterns associated with subsequent movement, discussed in WHITEHEAD (1987). The precise mechanisms by which group members direct movement, however, remains unclear.

The function of loud calls depends in part on the ontogenetic status or "ontogenetic trajectory" (WILEY, 1981) of the individual member of the social group. For male howling monkeys, three trajectories are possible. First, a young male can join a queue behind other males within his natal group and await accession to breeding status. The son of the dominant male in group 7 replaced his father as primary breeding male (GLANDER, 1975, pers. comm.). Within this trajectory the young male adopts the calling patterns functioning within his natal group. The second trajectory, more likely when the queue for accession to breeding status is already long, is to leave and attempt to start a new group. Bandido exemplifies this ontogenetic trajectory. This path is made possible by the trait, unusual among mammals, of both sexes migrating within *Alouatta* (GLANDER, 1980; RUDRAN, 1979; CROCKETT & EISENBERG, 1987). Loud calls by males allow migrating females to locate the male. They permit establishment of new groups without confrontation with established social units, necessary and desirable traits for a successful colonizing species (EISENBERG, 1979).

The third trajectory is to gain access to breeding females through a contest with the dominant male in an established group. The agonistic function of loud calls of *seniculus* within this ontogenetic trajectory is thoroughly discussed by SEKULIC (1981, 1982a, b) and by CROCKETT & SEKULIC (1984). Thus the function of the loud calls depends on which ontogenetic trajectory a male selects; no doubt males may adopt more than one trajectory within a lifetime. Future studies employing experimental removal of animals might determine how rigidly the functions of long-distance vocalizations are fixed after selection of an ontogenetic trajectory. For example, can a male, remaining within his natal group, alter his pattern of calls to function as a beacon to migrating females? Experimental translocations of young males (*e.g.*, JONES, 1982) could be used to address this question.

Spacing in an evolutionary perspective.

EISENBERG (1979) characterizes *Alouatta* as a "hardy colonizer" based on its wide distribution in the Neotropics and the diversity of forest types it inhabits. The history of Neotropical biota during the Pleistocene has been influenced by alternating wet and dry periods (SIMPSON, 1971; SIMPSON & HAFFER, 1979). These varying conditions would create strong selection for some form of behavioral flexibility to promote adaptation to a diversity of tropical habitats under changing climatic conditions. Evidence for behavioral flexibility of *Alouatta palliata* and perhaps other congeners as well is available in three areas: foraging, intergroup relations, and spacing. The foraging of howling monkeys is quite selective (GLANDER, 1981). The type of mechanisms for maintaining selectivity (MILTON, 1981; WHITEHEAD, 1986) involve continual monitoring of the preferred resources and learning of select phenophases, especially leaves, from social partners. These mechanisms are sufficiently flexible to function at any point within the range of *palliata*. Thus, aside from providing a more parsimonious explanation of feeding selectivity than local adaptations, they explain dynamic adaptations to variations within the flora and its phenology.

The behavioral mechanism underlying intergroup relations is based in part on the evolutionarily stable strategy "Tit-For-Tat" (WHITEHEAD, 1987). Howlers meet the criteria for contestants in this game: they have sufficient memory of previous events, possess the ability to recognize individuals, and interact repeatedly (AXELROD & HAMILTON, 1981; AXELROD, 1984). Tit-For-Tat, while making possible periodic evaluation of neighboring males, is based on the history of intergroup relations.

Thus a flexible interaction rather than a fixed process governs intergroup relations.

The third evidence of behavioral flexibility in howlers is their spacing patterns. The howler spacing system allows both site-dependent responses to intruders as well as a form of territorial defense of small rich patches of forest. This flexibility enhances a species' success in colonizing changing environments.

Faced with competing species, like the spider monkey *Ateles*, howling monkeys must in addition possess a spacing system capable of effectively solving ecological problems at lower population densities than would occur without competitors (EISENBERG, 1979). Possibly the requirements of the spacing system are in conflict at different population densities: to regulate intergroup distances at high densities, normally through avoidance, and to locate conspecifics at low densities by means of accurate approximation. I propose the following scheme as the basis for understanding the functional significance of loud calls in howling monkeys. At high population densities, the spacing system, through roars and roar variants, makes available to neighbors information about the azimuth and possibly the distance to a calling group. Movement coupled with barks (WHITEHEAD, 1987) allows matched neighbors to reciprocate movements. Intrusions into neighbor's favored areas result in confrontations and mutual assessment. But under normal circumstances, groups rarely encounter each other, a result of site-fidelity plus reciprocated avoidance.

At lower population densities, caused either by the presence of competitors, by sparser resources, or by normal variations in population densities, possibly as a result of epizootics (COLLIAS & SOUTHWICK, 1952), different ecological requirements obtain. For example, in Santa Rosa National Park, Guanacaste Province, Costa Rica, *Alouatta palliata* occurs at lower density and calls less frequently in the presence of *Ateles geoffroyi* and *Cebus capucinus* (FREESE, 1976; pers. obs.), than when alone, as in this study. A similar pattern occurs among congeners: in central Suriname at the Ralleighvallen-Volksberg Nature Reserve, *A. seniculus* (MITTERMEIER, 1977) occurs at densities much lower than *A. palliata* in western Panama (BALDWIN & BALDWIN, 1972) or in western Costa Rica (GLANDER, 1980). In contrast to the commonplace occurrence of morning choruses by the red howler in the llanos of Venezuela (SEKULIC, 1982b), *seniculus* is heard calling infrequently within the more diverse primate community in Venezuela (e.g. in P. N. Guatopo, EISENBERG, pers. comm.) and in central Suriname (pers. obs.). Clearly the adaptive func-

tions of howling must differ under these conditions. Howling by males can serve as a beacon to neighbors living under conditions of low density. Providing azimuthal information to neighbors permits orientation of both sexes of howling monkeys in the process of migrating between groups at low densities and helps mediate intergroup avoidance at high densities (GLANDER, 1980; RUDRAN, 1979). In the process of colonization, loud calls acting as beacons provide migrating females (*e.g. solitarias*) with the cues necessary to move towards males starting groups *de novo*, which, though a relatively infrequent event in *palliata* (pers. observ.) and *seniculus* (CROCKETT & EISENBERG, 1987) under normal circumstances, achieves greater importance during a period of population expansion. During colonization calling by males from established troops announces the presence of dominant males at one location and may facilitate the selection of vacant areas by migrant males.

The howler's site-dependent spacing system in relation to other species.

In their review of spacing behavior in animals, WASER & WILEY (1980) emphasize the importance of site-dependent agonism as a behavioral mechanism of spacing. The most striking feature of the playbacks from intensively used areas is the vigor of the response by the howlers: rapid approach and powerful, prolonged vocalization. The response is in distinct contrast to normative behavior of howlers at La Pacifica, as well as descriptions in the literature of a rather peaceful, sedentary monkey (*e.g.*, CARPENTER, 1934). The playbacks of roars reveal a tendency, seldom observed in unmanipulated groups, to challenge or attempt to dominate vocal intruders (for a discussion of similar agonism in *seniculus*, see CROCKETT & POPE, in press).

The tendency to challenge vocal male intruders, probably a rare event between groups, has two implications. First, countercalling affords neighboring males the opportunity for mutual assessment, a necessary requirement for the maintenance of reciprocity in intermale spacing relations. The callers in howling monkey groups are often the same males for as long as five years (pers. observ.). Thus neighboring males can interact repeatedly with one another over an extended period of time, conditions which can favor the establishment of some form of reciprocity. Memory of a neighbor's tendency to repulse vigorously intruders in an intensively used area could form part of the behavioral mechanism producing the observed pattern of intergroup avoidance (WHITEHEAD, 1987). Second.

the howler's familiarity with their activity space, coupled with distance-judging mechanisms, permits accurate assessment of intrusions by strange conspecifics. As selective folivores, the howlers have doubtless evolved sophisticated mechanisms to track and map the phenological condition of the forest. The dry seasonal forest of western Costa Rica provides the howlers with food that is seasonally quite variable in its identity and location (GLANDER, 1975; FRANKIE, BAKER & OPLER, 1974; pers. observ.). Test groups within 100 m of favored areas attempt to dominate vocal intruders. However, playbacks from favored areas at a greater distance do not produce a vigorous approach (unpubl. observ.). The howlers' response to vocal intruders can be viewed as a result of evaluating the cost of travel to a distant patch, the cost of possible confrontation, and the benefit of the resource sought. Additional playbacks from locations of known, favored resources (e.g., *Ficus* spp., Moraceae) from a variety of distances to test groups could clarify the relationship of resource quality to the distance at which a vocalization elicits movement.

Vocal responses to playbacks resemble vocal behavior observed before and after normal group movements. Males vocalize loudly in response to playbacks, especially from intensively used areas. Males remain relatively quiet while the simulated intruder in an intensively used area vocalizes; males roar and bark frequently during and after their rapid approach to the playback speaker. The use of barks and bark variants in response to playbacks is similar to vocalizations heard during normal group movements; both these loud calls may convey specific cues about distance which affect neighbors' movements (WHITEHEAD, 1987).

The site-dependent responses, shown in this study, are consistent with playbacks by SEKULIC (1981, 1982a, b) with *A. seniculus*. She played tapes of roars from seldom-used areas shared by neighboring groups; thus, SEKULIC's playbacks, consistent with Type L playbacks, evoked primarily vocal responses and no detectable alteration of intergroup spacing. Gibbons have provided evidence of site-dependent spacing, demonstrated experimentally by MITANI (1985d) who did not find an association between the specific playback locations and resources, either important food resources or sleeping sites. In contrast, evidence for site-independent responses to loud calls has been found for an Old World primate, *Cercocebus albigena* (WASER, 1975; WASER, 1977) and for wolves, *Canis lupus* (HARRINGTON & MECH, 1979, 1983). Most interesting are studies by ROBINSON (1979) and KINZEY & ROBINSON (1983) which document different spacing patterns in congeners, *Callicebus moloch* and *C. torquatus*. Whether these contrasting patterns are evidence of different spac-

ing systems manifest among congeners or of a unitary spacing system responsive to different ecological conditions are questions worth exploring. The howlers of La Pacifica provide evidence of the latter, a unitary spacing system: they respond to widely dispersed resources with a spacing pattern based on site-dependent responses to intruders (this study) and reciprocity between neighboring males (WHITEHEAD, 1987); where resources are concentrated and activity fields unusually small, however, howler males tend to defend favored quadrats that function as boundaries. Comparison of spacing systems of other members of the *Alouattinae* will help to probe the substance of these spacing mechanisms.

Limitations of this study.

The vegetation on Hacienda la Pacifica, forty years ago a continuous stand of seasonally deciduous and evergreen riverine forest, is now an anthropogenic mosaic of fields and forest. Nevertheless, the physiognomy of the local forest is similar to less disturbed vegetational formations in the same region (*e.g.* Parque Nacional Sta. Rosa) and in northern South America (*e.g.* the *llanos* of Venezuela). Howlers, as "hardy colonizers" (EISENBERG, 1979), have proven successful inhabitants of both discontinuous and continuous types of forest. La Pacifica's howlers have revealed a variety of adaptations to local forest conditions, quite different from Barro Colorado Island, the site of Carpenter's original study.

Within the patchy forest, it has proven difficult to validate the distances at which CHIVERS (1969) found reduction, maintenance or increase in intergroup separation. Such intergroup distances (220 to 350 yards) at La Pacifica often occurs across fields rather than through continuous forest. This study, as well as WHITEHEAD (1987), have shown avoidance, but of a different sort than proposed by CHIVERS.

An additional difficulty in the interpretation of this study depends upon the playback techniques. Often during playbacks the vocalizing respondents established an antiphonal coordination with the taped calls. After a short interval, the coordination broke down, owing possibly to the fixed sequence and intercall intervals on the tape; and subsequently the test group vocalized less intensely and less frequently. Possibly the decline in frequency of calling resulted from the technical limitation imposed by the rigidly linear sequence of calls recorded on the tape itself. If true, the analysis of call frequencies during and after playbacks should be treated with great caution. Consequently, I have treated them as relative measures rather than as absolute rates.

One technique for increasing the verisimilitude of playbacks is illustrated by a test of the following hypothesis. Howlers might gauge the distance to neighbors by the latency between their own and neighbors' roars. A calling male perceiving a "short" (e.g., 500 ms) interval between his call and his neighbor's might respond differently than to a longer intercall interval. This possibility, suggested by some field observations, has received support from preliminary playback experiments. A protocol designed to test this hypothesis might employ a voice-activated circuit, band-pass filters and possibly a portable microcomputer with digitized vocalizations in memory. Thus greater verisimilitude could result from enhancing the interactive capabilities of the playback apparatus.

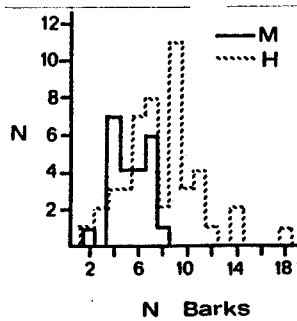


Fig. 12. Frequency distributions of the number of barks in bark trains during intergroup encounters by the dominant males in groups 5 (M) and in group 7 (H).

The tapes used in playbacks were from local groups not used in this study. The tapes were selected to avoid the possibility that responses depend on individual recognition by voice. Individual identification in long-distance communication is problematical for two reasons. During long-distance propagation individually distinctive features might degrade (RICHARDS & WILEY, 1980). Examination of audiospectrograms of different males' calls has not revealed obvious identifying features, though the possibility remains that each male possesses a distinctive sequence of calls. Preliminary investigation of one possible feature, the modal numbers of barks made by individual males, shows considerable overlap between males (Fig. 12; see WHITEHEAD, 1985). In addition, playbacks of local and Panamanian howlers fail to show differences in vocalizations and movement (WHITEHEAD, in press) which implies that the howlers do

not distinguish loud calls, possibly due to degradation of the acoustic structure during long-distance propagation. Likewise, among gibbons, *Hylobates muelleri*, MITANI (1985) finds no evidence from sound playback of individual identification by loud calls. Howlers probably identify individuals by distinctive calls that propagate only short distances. Besides, non-acoustic cues could insure the identity of callers: callers staying in one area for a long time could communicate their identity by any call, once a receiver associates a regularly used location with a particular caller. The vocal horizon provides spatial fixes on familiar neighbors each morning.

Summary

Mantled howling monkeys, *Alouatta palliata palliata*, of Guanacaste, Costa Rica, respond in a site-dependent way to experimental playbacks of choruses of loud vocalizations. Groups of howling monkeys increase their rates of calling and approach simulated vocal intruders located in often-used patches of forest. In contrast, they call less than previously and do not approach simulated intruders in seldom-used areas. These monkeys adjust their responses to simulated intruders depending upon the quality of local patches of forest. Various additional factors determine the functions of loud calls of howling monkeys: the distance to a receiver, the "ontogenetic trajectory" (WILEY, 1981) of the caller, the density of calling groups and possibly the existence of an ongoing confrontation.

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Resumen

En el oeste de Costa Rica entre los monos aulladores o congos guanacastecos, *Alouatta palliata palliata*, las respuestas a los gritos fuertes reproducidos por una grabadora, o 'playback', dependen del lugar en el que se sitúe la bocina de la grabadora. Los grupos de congus aumentan la tasa de gritos y se acercan inmediatamente a los vecinos aparentes cuando estos se sitúan en lugares muy usados por los grupos. En contraste, cuando la bocina se sitúa cerca de árboles poco usados, los monos gritan muy poco y permanecen en el mismo sitio al menos media hora. Las respuestas de estos monos dependen de la calidad de los recursos dentro de los cuadrantes forestales de donde se originen los sonidos conspecíficos. Las funciones de los gritos son determinadas por otros factores como: la distancia al receptor, el tipo de vida ('ontogenetic trajectory' de WILEY, 1981) de los machos adultos; la densidad de población de monos; y la incidencia de luchas entre grupos vecinos.

