

Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata**

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Abstract. The hypothesis that acoustic communication mediates spacing between groups of mantled howling monkeys, *Alouatta palliata palliata*, was tested experimentally in a Costa Rican forest. Previous work showed that reverberation increases with the distance sound propagates within the forest and thus could provide distance cues to monkeys. Two series of barks were therefore played back to test groups: the first series simulated the calls of a male withdrawing from the test group; the second series simulated the calls of an approaching male. In response, males approached the sounds of an apparently approaching male and withdrew from an apparently withdrawing male. Thus reverberation provided cues about distance to the howling monkeys. The direction in which the monkeys moved depended on the direction of movement simulated by the call sequence. Furthermore, the pattern of reciprocated movements, which exemplifies a form of the evolutionarily stable strategy 'Tit-For-Tat', helps to regulate relations between neighbouring males and hence spacing between neighbouring groups.

Long-range calls of primates have several adaptations to permit effective communication at a distance. These calls are often stereotyped, discrete and repeated, features which reduce the receiver's uncertainty about the acoustic characteristics of the signal (Cherry 1957; Quastler 1958; Marler 1965, 1973; Wiley 1983). The dominant frequency of these calls is usually between 100 and 1000 Hz, which ensures less attenuation than for higher frequencies (Marten & Marler 1977; Marten et al. 1977; Waser & Waser 1977; Wiley & Richards 1978; Richards & Wiley 1980; Waser & Brown 1984) and a higher signal to noise ratio than for calls outside this frequency band (Brown & Waser 1984). Animals use these calls most often during the early morning when temperature gradients within and above the forest create optimal conditions for long-range propagation of sound in the lower canopy (Waser & Waser 1977; Wiley & Richards 1978).

The loud vocalizations of howling monkeys, particularly mantled howling monkeys, *Alouatta palliata palliata*, have long been hypothesized as regulating intergroup spacing (Carpenter 1934,

1965; Altmann 1959; Chivers 1969; Baldwin & Baldwin 1976; but see Sekulic 1982a, b). The calls of this species are intense (often exceeding 90 dB, referenced to 20 μ Pa 5 m from the source; Whitehead 1985), emphasize frequencies below 1 kHz, and will therefore reliably propagate long distances to neighbours.

Those features of animal sounds that change predictably during propagation provide the receiver with information about the sender's location. Two types of information are necessary to establish the location of the caller: the azimuth and the distance. Information about the azimuth of the sound source is well preserved for most loud calls that primates make (Waser 1977b; Brown et al. 1978), because low-frequency sounds are less subject to scattering and absorption during propagation through the atmosphere (Waser & Waser 1977; Wiley & Richards 1978).

Ranging, judging the distance to a caller, could result from any one of three processes: degradation by reverberation, frequency-dependent attenuation and overall attenuation of amplitude (Wiley & Richards 1978). The temporal structure of plosive calls, like howler barks, is degraded by reverberation, particularly at distances between 50 and 100 m (Whitehead 1985). When the amount of reverberation varies with the distance from the signal source, the receiver could estimate the distance to the caller. In contrast, frequency-dependent atte-

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uation, the selective attenuation of higher frequencies during propagation, would probably not permit reliable ranging by howling monkeys. Thus, frequency-dependent attenuation of frequencies less than 1 kHz is slight for distances between 50 and 150 m. In addition, the ratio of amplitudes within frequency bands of a call to the respective bands of ambient noise is particularly subject to transitory variations in ambient noise (Whitehead 1985). Since the process requires the calculation of an average frequency-dependent attenuation, it would not function adequately as an instantaneous indicator of distance. In addition, the range of frequencies subject to differential attenuation is relatively narrow, and frequencies above 2 kHz are largely absent in excellent recordings of loud howler calls (unlike some bird vocalizations; see Greenewalt 1968; Hinde 1969). The third ranging process, judging distance by attenuation of the amplitude of the signal, is affected by irregular amplitude fluctuations resulting from micro-meteorological instability within or above the forest (Wiley & Richards 1978; Wiley & Whitehead, unpublished data). The wide variation in intensity of incoming signals limits the accuracy of any estimate of distance based solely on relative amplitude.

A synthesized tone similar in duration and frequency to a howler's bark had less reverberation at short distances in a tropical forest (50 m) than at longer distances (100 and 150 m). The magnitude of reverberation increased dramatically as the sound propagated over distances typical for the separation between neighbouring groups (Whitehead 1985; see also Waser & Brown 1986). Thus, howlers could distinguish near from distant callers solely by assessing the levels of reverberation. The experiments reported here test this possibility by means of field playbacks of reverberated and relatively unreverberated calls.

METHODS

Subjects and Study Area

The howling monkeys inhabited patches of seasonally deciduous forest and riverine evergreen forest, forms of lowland tropical dry forest (Holdridge 1967), on Hacienda la Pacifica, a cattle ranch near Cañas, Guanacaste Province, Costa Rica, Central America. La Pacifica has been the site of previous studies of howling monkeys (Glander

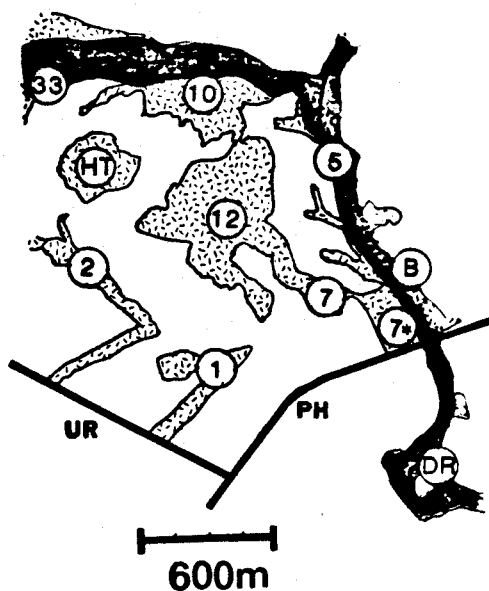


Figure 1. A map of the study area at Hacienda la Pacifica, Guanacaste Province, Costa Rica. Dark area = evergreen forest next to the Rio Corobici; speckled area = deciduous upland forest. PH = Panamerican Highway; UR = Upala Road. Areas between patches of forest are cultivated or fallow fields. The symbol '7*' locates group 7 during 1983; the symbol '7' represents its location during 1980.

1975, 1980, 1981; Scott et al. 1976; Jones 1978, 1982; Glander & Clarke 1981; Clarke 1982). In this paper I report experiments, conducted between May and September 1983, on five groups that each contained one principal male. The principal male performed the majority of loud calling and was often the only adult male in a group. Three of the five groups occupied narrow stretches of riverine forest; the fourth inhabited patches of both riverine and upland deciduous forest; and the fifth group inhabited a small patch (ca. 8.75 ha) of deciduous forest separated from the riverine forest by ploughed or fallow fields (Fig. 1).

Normative Observations

During June and July 1983, four observers systematically recorded normative information on the movement and vocalizations of four groups: two of these groups contained one principal male (groups 5 and 7); and the remaining two (groups 12 and 10) divided periodically into subgroups which normally contained only one principal male. Each observer located his focal group before first light

and prior to the howler's first continuous series of loud calls during the morning, and then stayed with the group until activity declined during the heat of the day (around 1130 hours). Observations resumed in mid-afternoon at 1500 hours, when the howlers often began feeding, and continued until the evening, normally between 1700 and 1800 hours. Each observer noted the following activities during each 15-min period: type and number of loud calls from the focal group; type, number and azimuth of loud calls from outside the group; behavioural context of the calls (classified as resting, moving, feeding and playing); and angle and distance moved. Observers collected information on intergroup encounters whenever these occurred. The total duration of normative observations was 82 group-days, or 902 group-hours.

The loud calls of the howlers at La Pacifica resemble the features of two categories of vocalizations, roars and barks or woofs, described previously in the literature (Altmann 1959; Baldwin & Baldwin 1976; Eisenberg 1976). Because degradation by reverberation affects sounds with distinct onsets (i.e. rapid rise times) in a clearer manner than those with slow onsets, the calls were further subdivided into two categories (Fig. 2): roars and roar variants, corresponding to A_1 in Altmann (1959) and elements of the A series of calls in Baldwin & Baldwin (1976); barks and bark variants, corresponding to C_1 in Altmann (1959) and elements of the C series in Baldwin & Baldwin (1976). Roars were defined as a legato sequence of notes (Eisenberg 1976) with acoustic energy centred between 400 and 500 Hz; the sequence of notes increases in duration and intensity, followed by one note of maximum duration and intensity, and finally by a diminuendo of progressively shorter notes. The final phrase of the roar was similar to the 'oodle' call (Altmann 1959; Baldwin & Baldwin 1976). Roar variants lacked the typical oodle-like terminal phrase or the characteristic rise and fall in intensity, beginning instead on an intense note and trailing off. Barks were defined as intense pulses at a regular rate of 2–3/s. Each pulse had a dominant frequency between 400 and 500 Hz and a duration of about 200 ms (mean \pm SE = 220.0 ± 4.9 ms, $N = 20$; recordings made with a Sennheiser MKH 815 unidirectional microphone at a distance of 55 m; analysis on a Unigon Angioscan audiospectrum analyser with temporal resolution of 6 ms). Bark variants lacked the uniform duration and intensity of barks; the tempo

of series of bark variants was syncopated, not regular. Further analysis of carefully recorded vocalizations is required to establish whether these are graded or discrete calls. Observers learned to distinguish these modal forms of loud calls and to assign them reliably to the four categories while in the field.

The observers recorded the association between the vocal (or non-vocal) behaviour of the focal group and the corresponding behaviour of neighbouring groups by assigning the observations to one of four categories: (1) a call from the focal group followed by 5 s of silence; (2) a vocalization 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 another group to which the focal group did not respond within 5 s, a condition known as active silence. The criterion of 5 s crudely approximates the time required for sound to travel round-trip to the limit of detectability of the most intensive howler roars (ca. 800–1000 m; Carpenter 1934; personal observation).

Experimental Procedures

Recording the test tapes

To test the effects of reverberated calls on the movement by males, I selected the most plisive

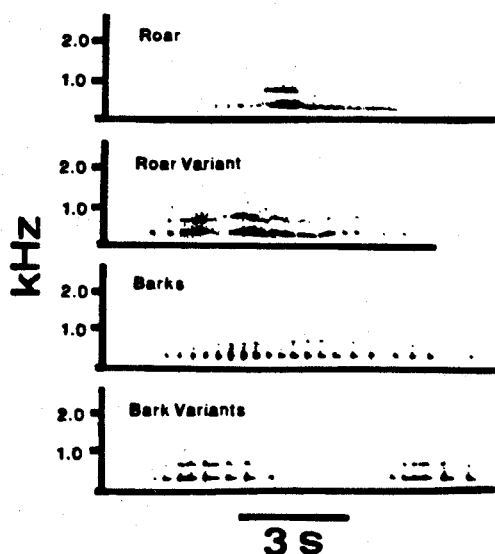


Figure 2. Audiospectrograms of four major long-distance vocalizations of *Alouatta palliata*. See text for a description of each vocalization.

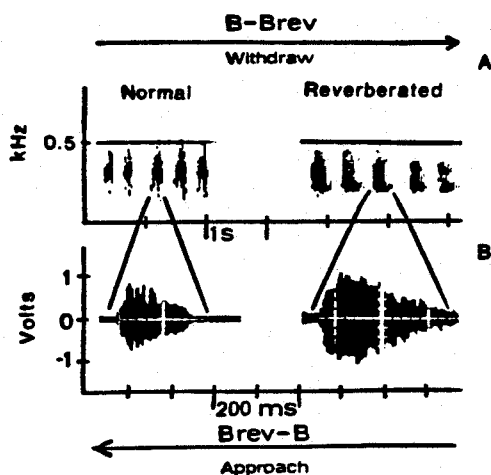


Figure 3. Audiospectrograms (A) and oscillograms (B) of barks. Clean barks (normal) and reverberated barks are shown. Each oscillogram shows amplitude as a function of the time for the bark indicated by bold lines. B-Brev = the Withdraw sequence; Brev-B = the Approach sequence.

howler call to produce a pronounced pattern of reverberation, and played back recordings of clean or relatively unreverberated as well as reverberated barks to free-ranging groups. In 1980, I recorded the clean barks from a local male (HT) at a distance of 10 m. This male was subsequently not used for playback experiments. For this recording I used a Sennheiser MKH 815 unidirectional microphone and a Nagra IVD tape-recorder at 19 cm/s. Later, I produced a recording of artificially reverberated barks by playing back and re-recording HT's barks in a room with non-parallel walls (a large attic). I re-recorded the barks at the same intensity, measured by the VU meter of the tape-recorder, as the original recordings. Viewing the reverberated pulses on an oscilloscope (Tektronix 502A), I altered the location of the microphone in order to match by eye the amount of reverberation shown on the oscilloscope to the amount caused by transmission through 100–150 m of forest (Reverberation Index greater than 0.25, see Whitehead 1985; for a different measure of reverberation, see Waser & Brown 1986). Figure 3 presents audiospectrograms and oscillograms of the clean and reverberated recordings of barks.

Field playbacks

For each trial, I played back one of two series of tapes. The first series, containing 90 s of clean

barks, as if from a nearby male, followed within 15–30 min by 90 s of reverberated barks, as if from a distant male, simulated a male moving away from the group. The second sequence, reverberated barks followed within the same interval by clean barks, simulated a male moving closer to the test group. I call these conditions the Approach sequence and the Withdraw sequence. The gain of the amplifier and the distance to the test groups were held constant within each series. For each trial I randomly selected the playback sequence, either Approach or Withdraw. Four of five test groups were exposed to both tape sequences; two of them were tested three times. On no occasion did the principal male move more than 5 m between the first and second tapes. The results of 12 playback trials are reported here.

Following Waser (1977a), I attempted to avoid habituating the monkeys to the test tapes by retesting a group only after a minimum of 5 days had elapsed. All playbacks commenced between 0605 and 0855 hours (mean time of onset = 0715 hours); the second tape ended no more than 32 min following the time of onset. The average distance between the test male and the speaker for all trials was 64.3 m (SE = 1.3 m) and thus was well within the range of distances over which reverberation increases substantially (Whitehead 1985). There was no significant difference between the group-to-speaker distances for the two experimental sequences (mean distance during Approach playbacks = 69.3 m; mean distance during Withdraw playbacks = 57.2 m; Mann-Whitney $U = 10$, $N = 5$, $P = 0.134$). Tapes were played on a Uher 4000 Report L or a Nagra IVD at 19 cm/s and amplified by a Nagra/Kudelski DSM external amplifier. The speaker was a Realistic 30.5 cm horn, secured atop an 8 m collapsible pole. A field assistant held the pole and pointed the speaker in the direction of the test group. The frequency response of the horn was essentially flat (± 5 dB) over the frequencies of interest (400–3000 Hz) and the output levels of the playbacks approximated sound levels (SL) of barking males (SL = 80.0 ± 1.2 dB at 5 m, $N = 29$; barks measured with a Realistic 42–3019 Sound Level Meter, C-weighting, Fast Response, referenced to 20 μ Pa, calibrated by a Bruel & Kjaer Sound Level Meter, Model no. 2209, to ± 1.0 dB).

For each experiment the test group occupied an intensively used quadrat of its activity space (quantitatively described in Whitehead 1985). To reduce the proximity of the speaker to the nearest neigh-

bours, I placed the speaker within the group's activity space as far from neighbours as possible. Later, I assigned the speaker location to either a seldom-used or intensively used quadrat of the group's activity space. Although I made no attempt to assess systematically the effect of the speaker location on group movement after the playback, the responses were consistently independent of the intensity of use of the speaker location. In contrast, the response to playbacks of roars depended on the location of the speaker (Whitehead 1985).

Vocal responses to playbacks were recorded, whenever possible, with a Sennheiser MKH 815 unidirectional microphone and a Nagra IVD tape-recorder at 19 cm/s or a Sony dynamic microphone and a Sony TC-55 cassette recorder. In all cases the test group was far enough from neighbouring groups that the test male's vocal response never initiated counter-calling from nearby groups.

Criterion for a prominent movement

I noted the direction, length and duration of the first prominent movement in response to each playback. A prominent movement was defined as any movement greater than 5 m, by the principal male, beginning during the second tape and ending with the monkey's resting for more than 5 min. The average duration of a prominent movement was 2.91 h: 2.48 h for Approach playbacks and 3.52 h for Withdraw playbacks (Mann-Whitney $U=11$, $N=5, 7$, $P<0.05$). Prominent movements were virtually identical to the movement of other group members. Distance was measured by using calibrated paces or by calculating distances between numbered trees from a detailed map of part of the study area (Glander, personal communication; accuracy within 10%). Angles were measured with a Suunto compass to within 5° . Non-parametric statistical tests were from Siegel (1956) and Sokal & Rohlf (1981), circular statistics from Batschelet (1981).

RESULTS

General Responses

In response to the Approach playbacks, prominent movement was towards the location of the speaker; in response to the Withdraw playbacks, prominent movement was away from the speaker

(seven approaches and zero withdrawals to the Approach sequence; five withdrawals and zero approaches to the Withdraw sequence; Fisher's exact probability test, $P<0.0026$, two-tailed). The two movement vectors are significantly different (Hotelling's two-sample test, $T^2=16.8$, $P<0.025$; Fig. 4).

Test males generally showed rapid orientation towards the speaker when a playback began; for example, the modal latency of orientation was 1 s to both playback sequences. Otherwise, the range of behavioural responses to the playbacks was broad: in response to reverberated barks presented first, one male (H) oriented slowly towards the speaker, yawned, and then looked in a different direction; in contrast, another male (BSTK) responded to the unreverberated barks by urinating, defaecating, moving higher in the tree and counter-calling with the taped barks. During one trial the test male (H) appeared to sleep through the first tape of reverberated barks, clearly audible to an observer on the ground 12 m below him. Less than 30 min later, he awoke within 5 s of the start of the tape of clean barks, rapidly moved 25 m towards

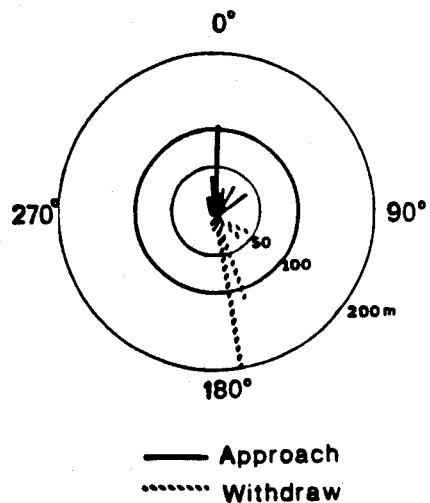


Figure 4. The length of prominent movements and angles of response to two playback sequences: the Approach sequence (reverberated barks followed by clean barks) and the Withdraw sequence (clean barks followed by reverberated barks). Each bar represents the results of one playback sequence. In all cases the speaker was approximately 60 m from the test male at a bearing of 0° .

the speaker and began making low barks (vocalization C₂, Baldwin & Baldwin 1976) until the tape stopped.

Distance Moved

During the normative observations, prominent movements averaged 55.7 m (SE = 10.8 m, $N = 138$) between the hours (0715–1015) when the experiments were later performed. The mean length of a prominent movement during the experiments was not significantly different from the normative mean (experimental mean \pm SE = 61.0 \pm 4.40 m, $N = 12$; $t_1 = 0.49$, $P > 0.05$; Sokal & Rohlf 1981). The mean distance moved after the Withdraw sequence (Fig. 4) was significantly greater than the normative mean (mean \pm SE = 84.0 \pm 13.4 m; $t_1 = 2.63$, $P < 0.01$, $N = 62$). In contrast, mean prominent movement during the Approach sequence did not differ from the normative value for movement during the morning (mean \pm SE = 44.6 \pm 4.34 m; $t_1 = -1.03$, $P > 0.05$, $N = 62$). Latency and duration of movement in each playback sequence were statistically indistinguishable (mean \pm SE latency to prominent movement after the Approach sequence = 60.7 \pm 26.2 min; mean \pm SE latency after the Withdraw sequence = 93.0 \pm 12.3 min; Mann-Whitney $U = 9$, $P = 0.101$, $N = 5, 7$; mean \pm SE duration of movement after the Approach sequence = 32.6 \pm 10.1 min; mean \pm SE duration of movement after the Withdraw sequence = 51.0 \pm 19.3 min; Mann-Whitney $U = 13$, $P = 0.265$, $N = 5, 7$).

The average angle of movement in response to the Approach playback, based on a range from 0° (direct approach) to 180° (direct avoidance), was 18.1° (SE = 3.1, $N = 7$); the corresponding angle of response to the Withdraw playback was 149.0° (SE = 5.7, $N = 5$). The distribution of angles moved following all playbacks was indistinguishable from the normative angles of movement (Kuiper's two-sample test, $K = 836.6$, $P > 0.05$). The distribution of angles moved by both experimental and non-manipulated groups differed from a uniform circular random distribution (Rayleigh's test, $r = 0.1297$, $P < 0.02$). This non-randomness of movements resulted from the narrowness of riverine forest. The two groups (groups 5 and 7) that spent the most time in the narrow riverine habitat (Fig. 1) moved non-randomly during the morning (Rayleigh's test, $r = 0.417$, $P < 0.001$ for group 5; $r = 0.3145$, $P < 0.05$ for group 7; all angles doubled

to reveal bimodal distributions), whereas the distribution of movements within broad patches of deciduous forest (groups 10 and 12) was indistinguishable from a uniform circular random distribution (Rayleigh's test, $r = 0.205$ for group 10, $r = 0.050$ for group 12, for both groups, $P > 0.05$).

Did the type of forest patches affect the distance groups moved following playbacks? In general, the type of forest was not associated with differences in the distance a group normally moved. Whether in riverine or deciduous forest, both single and multi-male groups tended to move approximately the same distance during the hours sampled (Kruskal-Wallis test, $H = 4.46$, $P > 0.05$, $df = 3$).

Vocal Responses

Howling monkeys called loudly in response to playbacks. The relative probabilities of each long-distance vocalization occurring during playbacks markedly exceeded the normative probabilities of calling during the morning (Fig. 5).

During most trials the males behaved consistently during the playing of the two tapes. For example, if a male vocalized loudly during the first tape, he called during the second; likewise, a silent response to both tapes in an experimental sequence was also scored as a consistent response (consistent responses on 11 of 12 trials; binomial test, $P = 0.006$, two-tailed).

Individual males, however, did not show a consistent pattern of response during and immediately following playback of the tapes. Four of five males, tested more than once, permitted comparison of responses to both tape sequences. A comparison of the consistency of individual males in silent versus loud responses (Table I) showed that the tendency to vocalize during or after each tape was not a tendency of individual monkeys. Likewise, there was no order effect: the position in the sequence of tapes did not elicit a consistent response. These findings reduce the likelihood that test monkeys responded to the artificially reverberated tape by consistently giving an alarm response.

In contrast, the two playback sequences elicited different rates of vocal responses during prominent movements as compared with the time to the onset of a prominent movement. Comparison of the rates of specific calls with the experimental conditions reveals an association (Friedman chi-squared = 8.775, $P \leq 0.014$). The small sample size and frequency of ties limit more detailed evaluation

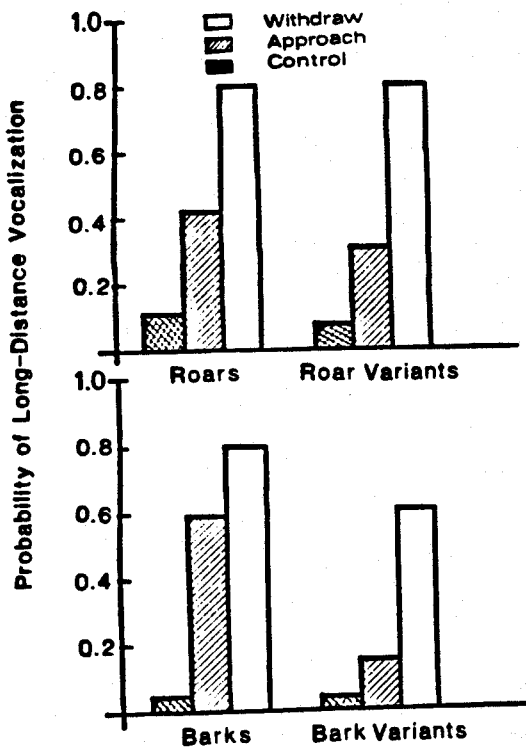


Figure 5. The probabilities of roars, roar variants, barks and bark variants in response to Approach and Withdraw series. Normative probabilities (Control) are based on the number of sampling periods between 0600 and 0630 hours when loud calls of each category were scored on 62 group days of observation. The normative probabilities of each of the long-distance vocalizations are less than experimental values.

Table I. Consistency in vocal behaviour by four male mantled howling monkeys during playbacks*

Male	During first tape	After first tape	During second tape	After second tape
H	-	-	-	+
B	+	-	-	+
BSTK	+	+	+	-
S	-	-	+	+

* '+' represents consistent behaviour during or after both presentations of the first or second tape (clean or reverberated barks) to males tested twice. For those tested more than twice, any lack of correspondence was scored as a '-'. Thus neither the order of presentation of the tapes nor the identity of the test male ensures a consistent response to playbacks.

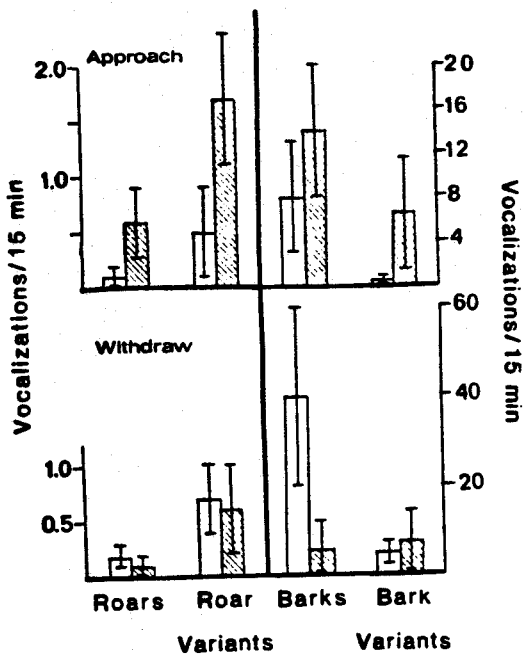


Figure 6. Rates of long-distance vocalizations in the number of loud calls/15 min (± 1 SE) before and during movement in response to playback. The open histograms indicate vocal responses after the sequence of playback tapes but prior to prominent movement; the hatched histograms show vocal responses during movement.

of simple hypotheses. However, a complex pattern emerged from inspection of the data: during the Approach sequence the rate of calling during prominent movement was greater than prior to movement; and during the Withdraw sequence the rate of calling was less during prominent movement than prior to prominent movement. This complex hypothesis is upheld for roars (seven of eight cases with four ties; binomial test, $P=0.035$) and for roar variants (eight of 10 cases with two ties, $P=0.011$), but not for barks (six of 10 cases with two ties, $P=0.377$) and bark variants (six of eight cases with four ties, $P=0.145$). Following the Approach sequence, the rates of all types of long-distance vocalization increased during movement (Fig. 6). In contrast, males moving after the Withdraw sequence were relatively quieter than they were prior to movement. The single exception is the relatively higher rate of bark variants during movement. Chivers (1969) and Baldwin & Baldwin

Table II. Calling rates ($N/15$ min) of groups near or distant from each other

Distance to nearest neighbouring group	Type of vocalization			
	Roar	Roar variant	Bark	Bark variant*
Far				
$\bar{X} \pm SE$	2.9 ± 0.3	4.3 ± 1.1	77.7 ± 23.5	42.9 ± 12.2
N	80	9	13	14
Close				
$\bar{X} \pm SE$	2.5 ± 0.3	4.5 ± 0.8	162 ± 65.5	270 ± 92.6
N	63	32	16	11

* The rate of bark variants is significantly greater when groups are close ($r' = -2.43$, $P = 0.034$, Sokal & Rohlf 1982). The other rates of vocalizations are not significantly different.

(1976) also found an increase in loud calls, particularly barks, of *Alouatta palliata aequitorialis* associated with withdrawal.

Vocal Behaviour at Normal Intergroup Distances

Is the change in the rates of some loud calls, as shown in playback experiments, evident in normative observations? To examine this question, I compared the numbers of calls and distances moved during normative observations on days when the initial distance to the nearest neighbouring group was below the mean (469.6 m, $SE = 34.2$ m, $N = 17$) with days when distances were above the mean (647.9 m, $SE = 44.2$ m, $N = 16$). Of all loud calls, rates of bark variants (Table II) from the nearby groups were significantly greater than from the groups farther apart. Thus, bark variants might serve as distance-increasing signals between groups closer together than normal. The rates of barking were not significantly different, although nearby groups tended to bark more. Baldwin & Baldwin (1976) also noted the association of barks with movement in *Alouatta palliata aequitorialis* in Panama.

Vocal activity following prominent movement took one of two forms: announcement of the group's location by loud calling, or concealment of the location by silence. A salient feature of vocal behaviour after movement was the incidence of active silence, defined as the absence of loud calls from the focal group within 5 s of calls originating from outside the group. The number of sampling

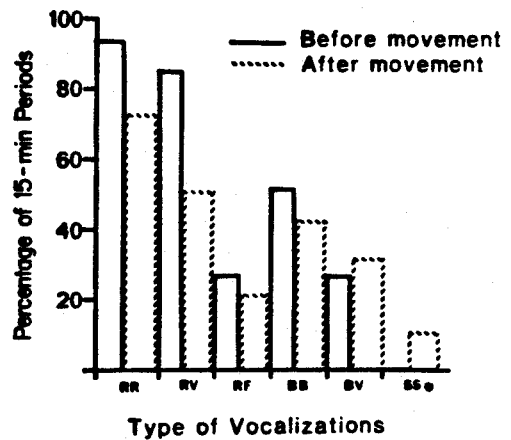


Figure 7. Percentage of sampling periods in which long-distance vocalizations occurred before or after prominent movement by the focal group. RR = roars; RV = roar variants; BB = barks; BV = bark variants; RF = roars or roar variants accompanied by female whimpers. SS* = active silence by the focal group for the first 5 s following a long-distance vocalization from a non-focal group.

periods in which a long-distance vocalization occurred before prominent movement was not statistically different from the number after prominent movement ($G_{adj} = 7.87$, $df = 5$, $P > 0.05$). In contrast, the number of sampling periods containing loud calls plus active silence before prominent movement was significantly different from the number after movement (Fig. 7; $G_{adj} = 18.56$, $P < 0.05$). Groups tended to maintain active silence following prominent movement.

When both barks and bark variants preceded prominent movement, focal males barked first during 11 of 15 sampling periods and made bark variants first during only four (binomial test, $P = 0.059$). Of the bark-like calls, only barks alone preceded movement, never bark variants (eight of eight occasions, binomial test, $P < 0.01$). After a prominent movement, barks were more likely to precede bark variants (11 of 13 occasions, binomial test, $P < 0.011$). Barks after movement were slightly less likely to precede bark variants than before (seven of 10 sampling periods; binomial test, $P = 0.172$). Calling males thus tended to announce their presence during the morning chorus and prior to movement. When barks occurred, they generally preceded bark variants.

Intergroup Encounters

What happens on the rare occasions when neighbouring groups of howling monkeys come close together? During 3.5 h of taped vocalizations of six intergroup encounters in 1983 (average intergroup distance less than 50 m), roars, roar variants and barks occurred during a majority of 5-min sampling periods; bark variants occurred during only a few sampling periods. Although many groups involved in encounters contained more than one male, only one male normally gave the majority of loud calls. None of these encounters, however, was observed from the beginning, and the recordings lack calls occurring prior to the close approximation of the groups.

Vocalizations between groups within sight, in contrast to those only within auditory range, include female accompaniment in the form of chirps and whimpers (G vocalizations, Baldwin & Baldwin 1976). These calls are higher in pitch (1–2 kHz) than the male-like roars (B vocalizations, Baldwin & Baldwin 1976) that females sometimes make. Roaring females were noted in only one single-male group at La Pacifica (personal observation).

DISCUSSION

Vocal Mediation of Intergroup Avoidance

Observers of howling monkeys from Carpenter (1934) to Altmann (1959) have commented on the rarity of contact between neighbouring groups in the forest. Waser (1977a; see also Waser & Wiley 1980) adopted a more quantitative approach by formulating a null hypothesis of random movement with which actual rates of encounters between social units can be compared. Random movement, as in an ideal two-dimensional gas, results in an expected frequency of encounters

$$Z = 8 (\rho) (\gamma) (\sigma) / \pi$$

where ρ = the density of groups, γ = the velocity of a group, $\sigma = d + s$, where d = the distance at which an encounter is said to occur, and s = the diameter of a group. For rates of movement, densities and detection distances like those for howlers at La Pacifica, expected rates of encounters fall between 0.51 and 2.55 encounters/day. Expected rates of encounters increase with the rate of movement (Fig. 8). The mean rate of group movement is 0.575

km/day (Glander 1975). During the 1983 field season we observed 14 encounters between two groups during 72 field days. The observed rate of encounters was 0.19/day, 2.5 times less than the lower limit of the estimate based on random movement. Further refinements of Waser's model would doubtless produce a smaller, but nevertheless significant, estimated rate of encounters based on random movement. Thus groups of howlers encounter one another at rates much less than predicted by chance. A similar conclusion results from calculations for a population of *A. seniculus* (Sekulic 1982b) whose actual rate of encounter ($Z = 0.40$) is markedly less than that predicted for random movements ($1.70 < E(Z) < 3.39$).

The degree of overlap between neighbours' activity fields further reinforces the impression of intergroup avoidance. The activity field of group 5 overlaps with those of three contiguous groups: 13.9% with group 12, 19.3% with group 10 and 50.0% with group 7. Much of this overlap occurs in quadrats that are intensively used by one or both groups. Thus, neighbouring groups share the use of some quadrats but normally occupy them at different times and without confrontation.

In their review of animal spacing systems, Waser & Wiley (1980) emphasize that avoidance of an opponent, in addition to threat and attack, could serve as a behavioural mechanism regulating the use of space. Carpenter (1934) first proposed the hypothesis that loud calls of howling monkeys mediate 'territorial' behaviour between groups of howlers on Barro Colorado Island, Panama. Working on the same island, Chivers (1969) found that groups of howling monkeys tended to avoid nearby neighbouring groups. The experimental results presented here show that male howlers do avoid each other on the basis of vocal cues alone.

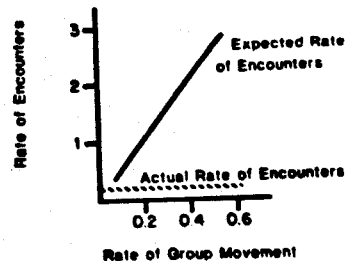


Figure 8. Expected and actual rates of intergroup encounters as a function of the rate of movement (km/day).

The howler males move away from the source of calls of a retreating male. This response minimizes the cost of intergroup chases and of injuries which accompany confrontations. Furthermore, the energy constraints imposed by folivory (Milton 1980, 1982) increase the effectiveness of selection for any change that reduces the energy costs of intergroup encounters. Avoidance of neighbours coupled with stable reciprocity could result in temporarily stable buffer zones between adjacent activity fields.

Reciprocation Between Moving Males

Reciprocation of patterns of movement by neighbours is a form of the evolutionarily stable strategy 'Tit-For-Tat' (Axelrod & Hamilton 1981; Axelrod 1984). The evolution of intergroup reciprocity fits the model of a reiterated game of Prisoner's Dilemma (Maynard Smith 1982). The defining condition for payoffs of Prisoner's Dilemma is the inequality $T > R > P > S$ (Rapoport & Chamah 1965), where T is the benefit derived from defecting when an opponent cooperates, R is the mutual reward for cooperation, P is the cost of intermale contests, and S is the sucker's loss from cooperating with a defecting opponent. Howling monkeys satisfy this inequality in the following ways. T is the benefit of unhindered access to forest vacated by a retreating male. T is greater than R , the benefits of two cooperating animals that share resources. R , in turn, is clearly greater than P , the cost of intermale contests which can be prolonged and can result in injuries (personal observation). Finally, P is greater than S , the uncontested loss of nearby resources that results from continuous retreat from a neighbour. S could be quite substantial because familiarity with local trees is critical to diet selection of howling monkeys in this region (Glander 1981; Whitehead 1986). Thus the Prisoner's Dilemma can serve as a model for repeated interactions between howler neighbours.

A robust solution for the Reiterated Prisoner's Dilemma is the strategy Tit-For-Tat (Axelrod & Hamilton 1981). Tit-For-Tat is an evolutionarily stable strategy which does at least as well as, and often much better than, any invading mutant strategy. Maynard Smith (1982) proposed three requirements, all met by howling monkeys, for the evolution of cooperation between groups employing Tit-For-Tat. First, groups must interact repeatedly. Howling monkeys counter-call daily with

neighbours; around 70% of calls made during the morning chorus overlap with neighbours' calls. In addition, many groups in Costa Rican forests remain neighbours for years (Glander, personal communication; personal observation). Second, members of local groups must recognize each other as individuals or otherwise interact with a few social partners. Ample evidence from laboratory and field studies (e.g. Cheney & Seyfarth 1980, 1982; Seyfarth & Cheney 1982) supports the belief that primates are capable of individual recognition. Third, each animal must be able to retaliate against failure to cooperate by another. This study shows that howlers are able to retaliate by approaching calls of an apparently approaching male and thereby risking an encounter and injury. Thus the experimental demonstration of reciprocated patterns of movement reveals an underlying pattern of evolutionarily stable cooperation between groups based on a form of Tit-For-Tat.

Why do confrontations occur at all if mutual cooperation, as in Tit-For-Tat, should result in mutual avoidance? There are two possible reasons. First, the rate of encounters depends on ecological conditions, such as the availability of resources; the rate is highest when preferred resources are concentrated. For example, during July and August 1983, when the mangos (*Mangifera indica*, Anacardiaceae) were ripening, the number of encounters was significantly higher than during June and September, when the mangos were unripe or had been shed (one encounter in June and September and 15 encounters during July and August; binomial test, two-tailed, $P < 0.001$). Distances to nearest neighbours during mango ripening were also significantly less than before or after (chi-squared approximation of Kolmogorov-Smirnoff test for unequal sample sizes; chi-squared = 12.66, $df = 2$, $P < 0.01$). A formal approach to defining ecological boundary conditions in which Tit-For-Tat is a successful behavioural strategy for organisms that repeatedly interact has been taken by Brown & Caraco (unpublished data) and Caraco & Brown (in press). Second, the Prisoner's Dilemma requires matched opponents and the consequent symmetry of payoffs for each participant. Perfect symmetry is probably rarely found in nature. The existence of coalitions among male howling monkeys (Jones 1978, 1982), as well as in social groups of many other primates, reduces the likelihood of opponents being evenly matched. Periodic deviations from Tit-For-Tat may then serve as opportunities

for assessment of opponents, much like the parallel walk of red deer *Cervus elaphus* (Clutton-Brock & Albor 1979; Clutton-Brock et al. 1982) or the extended vocal bouts between red howlers *Alouatta seniculus* (Sekulic 1982a, b). Encounters between groups provide information about opponents and reinforce patterns of intergroup relations. When well matched, each opponent should adopt the best strategy, Tit-For-Tat.

The maintenance of reciprocity through protection against cheaters could be the function of mobile males. Among grey-cheeked mangabeys, *Cercocebus albigena*, certain males that rapidly approach the source of loud calls (Waser 1976) could protect against possible cheating by checking on the location of nearby callers. Howlers, on the other hand, generally remain in a cohesive group when responding to calls, whether real or played back. On some occasions, however, males disappeared from the resident group, only to reappear close to a neighbour or a playback site (Whitehead 1985). As these disappearing males were not principal males, observations of their behaviour were incomplete. In addition to protection against cheaters, the assessment of neighbours by non-principal males could affect changes in male dominance within a group.

Reverberation, Deception and Honest Signalling

The traditional view that natural selection acts to increase the efficiency of information transfer between the signaller and receiver has recently been called into question. Dawkins & Krebs (1978) proposed that natural selection acts to improve a signaller's ability to increase its fitness by manipulating conspecifics and 'exploiting other animals as tools' (Krebs & Dawkins 1984, page 382). The response to a signal can result in an increase or a decrease in either the signaller's or the receiver's fitnesses; manipulative communication enhances the signaller's fitness at the expense of the receiver's fitness (Wiley 1983).

Reverberation during the propagation of barks creates a cue for ranging that the sender cannot control. Barks, with their abrupt onset and termination, facilitate the listener's detection of reverberations. To a receiver, a clean bark can only imply a caller nearby. Clean barks are therefore a form of honest communication of information about distance.

Howlers could use calls other than barks to manipulate conspecifics. Bark variants, resembling reverberated barks in note morphology though not in temporal pattern, could be used along with barks to manipulate receivers into withdrawing. This hypothesis, readily tested by field experimentation, is supported by two observations. First, the sequence of barks followed by bark variants, which frequently occurred both before and after normal movement, mimicked the Withdraw sequence of playbacks. Second, a male in a moving group can benefit from causing nearby silent males to leave the proximity of his group. Because spatial overlap between neighbouring groups is extensive, between 13.9 and 63.2% of the activity fields (Whitehead 1985), movement by a group into an area of overlap would best be accompanied by a sequence of calls which induces undetected males to withdraw.

Howlers could also withhold information about their location by remaining silent. While numerous animals withhold calls as an alarm signal (Marler 1965), active silence following movement by Costa Rican howlers suggests a function of disguising an animal's location. Silence by howlers in other sites, pointed out by Chivers (1969), Richard (1970) and Klein (1974), could serve the same function. Neighbours intrude on each other's foraging areas as long as they remain silent; territorial residents aggressively exclude any vocal intruders from their activity field (Waser & Wiley 1980). The use of silence to cover up a male's location could complement deceptive vocalizations that induce withdrawal; both practices must be considered in any explanation of the effects of long-distance calls on the use of space and intermale relations in *Alouatta palliata*.

Degradation of signals by reverberation could also affect communication of ranging information in other forest primates. For example, responses of *Callicebus moloch* (Robinson 1979, 1981) to playbacks depend on the distance to the speaker; playbacks to nearby test groups (30–80 m) could provide the titi monkeys with a less degraded signal than those to groups farther away (80 to greater than 100 m). The pulsatile 'whinny' of *Ateles* spp. (Eisenberg 1976) or the trilled 'roar' of *Colobus guereza* (Marler 1972; personal observation) are candidates for providing cues about distance. In contrast, degradation of long-distance vocalizations might not be the cue for withdrawal from playbacks by grey-cheeked mangabeys, *Cercocebus albigena*. Reverberation in the forests of central

Africa inhabited by mangabeys, if similar to reverberation in Costa Rican forests, appears not to provide adequate cues for ranging at distances at which mangabeys normally begin withdrawal (ca. 100–150 m; Waser 1976, 1977a). Other processes involving environmental effects on auditory communication or the rapidly approaching male could function to maintain intermale relations and intergroup distances in this species.

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