A Preliminary Study of Vocal Communication in Wild Long-Tailed Macaques (Macaca fascicularis). II. Potential of Calls to Regulate Intragroup Spacing

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This study is a preliminary assessment of the potential of long-tailed macaque (Macaca fascicularis) calls to operate in systems of within-group spacing. Covariation in the rate of occurrence of calls with party spread, size, and activity among wild individuals of one group suggested that four classes of calls may function in intragroup spacing. Two of them are "clear" calls of long duration and pronounced frequency modulation. Calling rate increased with party spread for low- and high-frequency variants of these calls during resting and feeding, respectively, suggesting possible utility in maintenance of spatial relations over moderately long distances. A third "harsh" call was negatively correlated with party spread during foraging and may thus function to increase dispersion among foraging individuals. Another harsh call with a tonal onset was unique among all calls in the vocal repertoire in being more frequently performed by lone, isolated individuals than by macaques accompanied by others, suggesting a possible function in reestablishing contact that has been severed. The functional significance of these calls with respect to their acoustic structures is discussed. Macaques that use calls to regulate intragroup spacing can control communication distance and direction by their choice of acoustically different vocalizations. This choice may be affected not only by varying environmental constraints on sound transmission, but also by social and ecological factors such as intragroup competition.

KEY WORDS: vocal communication; vocal regulation of intragroup spacing; Macaca fascicularis.

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INTRODUCTION

Vocal systems of intragroup spacing have been difficult to elucidate in nonhuman primates in general and in macaques in particular. The most likely components of such a system in macaques are generally considered to be a set of narrow-spectrum calls referred to collectively as “clear” or “coo” calls. The functional significance of these acoustically varied calls is often asserted by observers who refer to them as “contact calls.” In the first substantive description of these calls among captive rhesus macaques, Rowell and Hinde (1962) suggested a spacing function only tentatively, and in the most detailed study of coo calls under natural conditions, Green (1975, p. 10) echoed this assessment by concluding that although they “had some element of contact or spacing-related function, . . . no overall pattern of use was clear.”

Demonstration of the functional significance of a call from observational data normally relies on the evaluation of three elements of call occurrence: (1) the nonvocal behavior or demeanor of the caller at the time the call is emitted, (2) the behavioral responses of individuals which hear the call; and (3) the context or causal stimuli accompanying performance of the call. These are all particularly difficult to specify for coo calls. For example, Green (1975) was able to identify the caller, respondent(s), and social situation for only 16% of all calls heard under the favorable observation conditions afforded by study of provisioned, terrestrial Japanese macaques. Obstacles arise because (1) coo calls are relatively quiet calls performed without gestures and little movement, which indicates something about caller demeanor but clearly hinders a functional analysis by making “it very difficult to tell which animal made them” (Rowell, 1972, p. 103); (2) coo calls do not usually elicit dramatic, overt behavioral responses from conspecifics that hear them, and in fact, it is generally unclear to whom the calls are directed; and (3) coo calls are typically associated with a wide range of contexts that seem to “have little in common” (Green, 1975, p. 10).

The study of vocal regulation of intragroup spacing in primates has generally focused on the so-called contact call. Vocalizations have typically been designated contact calls based on any combination of the following features: (1) a high rate of occurrence, (2) an emission pattern suggesting antiphonal “exchange,” (3) the relaxed demeanor of callers, (4) lack of obvious, immediate, nonvocal responses by conspecifics, and (5) variable contexts (Struhsaker, 1969; Pola and Snowdon, 1975; Gautier and Gautier, 1977; Snowdon and Cleveland, 1984; Masataka and Bihen, 1987). Using these criteria, virtually all long-tailed macaque “coo” calls indeed qualify as contact calls (Palominit, 1992). However, although one can argue that the causes and consequences of “contact calling” are apt to be subtle or ambiguous and that its temporal patterning is likely to be reminiscent of “dialogue,” crediting calls with a spacing function based on this evidence is clearly less satisfying than an actual demonstration of how the calls operate with respect to the spatial relations of individuals within the group, an effort that has only recently been undertaken (e.g., Robinson, 1982). This is especially important when the acoustic structure, and hence the efficiency in sound transmission, perception, and localization, of the relevant group of calls varies. Likewise, regulation of spacing in macaques is a complex process and calls that contribute to spacing mechanisms are likely to function in different ways. Thus, by subsuming a large number of intragroup vocal signals into one, somewhat ambiguous functional category, the term contact call misrepresents much of the behavioral, acoustic, and functional complexity and variability characterizing the use of calls within primate groups (Seyfarth, 1987).

In seeking to derive an initial assessment of the potential of long-tailed macaque vocalizations to operate in mechanisms of intragroup spacing, this study is less concerned with specifying contact calls per se but focuses, instead, on covariation of call occurrence and overall dispersion of group members under different conditions. If a call is of use to macaques in mediating intragroup spacing, then aspects of its performance (e.g., calling rate) are expected to vary in some way with the spatial distribution of individuals. By focusing on group-level phenomena, this study is clearly a preliminary beginning of this kind of analysis. The potential of vocalizations to function in intragroup spacing is evaluated below by identifying covariation in call occurrence and group dispersion and by considering the acoustic properties of these calls with respect to sound transmission and spacing.

Long-tailed macaques are appropriate subjects for the study of vocal regulation of intragroup spacing in primates. These highly arboreal, frugivorous monkeys maintain extensive networks of long-term social relationships in multimale, multifemale groups of 8–50 individuals (Wheatley, 1978a; Aldrich-Blake, 1980; van Schaik, 1985). Group members may disperse over 500 m or more when subgroups form as monkeys leave sleep trees along a river in the morning, forage in dense riparian vegetation, and gradually move into primary forest farther inland where they exploit resources distributed in patches of widely varying size and abundance, primarily the fruit of an extensive variety of plants but also significant amounts of flowers, leaves, fungi, and arthropods (Kurland, 1973; Wheatley, 1978a,b, 1980; Aldrich-Blake, 1980; van Schaik et al., 1983a; van Schaik and van Noordwijk, 1986). These subgroups may fuse and divide repeatedly at various times during the day or remain separate until
the customary reunion at communal sleep trees along major rivers (Fittinghoff and Lindburg, 1980). This complex and dynamic socioecology, along with probable constraints on visual communication within the rain forest canopy (Aldrich-Blake, 1970; Gautier and Gautier, 1977; Waser and Waser, 1977), suggests that vocalizations may be useful components of systems regulating within-group spacing in long-tailed macaques. Previous work has provided a provisional vocal repertoire for these highly vocal monkeys and has also demonstrated variation in the rates of occurrence of the various intragroup calls suggestive of possible functional differences (Palombit, 1992). This study examines the spatial, social, and behavioral correlates of emission of these calls. As Jolly (1985, p. 216) has emphasized recently, "We are much farther from understanding these soft, variable primate calls than the simpler messages that can be hollered throughout the woods."

**METHODS**

**Study Site**

The research was conducted during April–June 1983 at the Mentoko Research Station, East Kalimantan, Indonesia. The study area is described in greater detail by Palombit (1992).

From June 1982 until June 1983, a large area of Borneo, including the study site, suffered a severe drought related to the El Niño Southern Oscillation (Berenstain, 1986; Leighton and Wirawan, 1986). The drought was most intense during February–April 1983, when numerous ground fires with flames ~0.33 m high also ignited. Although one such fire burned the understory vegetation of nonriparian forest over the entire study area in late April 1983, there were no active fires in the study group’s home range during the period in which data were collected. The drought ended as normal rainfall resumed in June 1983. The nonhuman primates of the Mentoko study area appeared to be among the vertebrates least immediately affected by the drought (Leighton and Wirawan, 1986). No deaths occurred in the study group of long-tailed macaques during and at least 4 months after the drought and fires, and a number of females gave birth the next year (Berenstain, 1986).

The lack of vocal data from nondrought periods makes it impossible to determine the actual effect(s) of the drought on vocal behavior. It is clear from Berenstain’s (1986) observations that two aspects of macaque behavior highly relevant to vocal communication, namely, activity profile and group cohesion were influenced by the drought, but not in any consistent direction. One expects that the ecological and bioenergetic disruption caused by a drought would affect the activity profile of the macaques (and hence, perhaps, their predisposition to vocalize). During May, the proportion of time spent resting was indeed higher than normal, as macaques fed very little and primarily on low-quality herbaceous items (Berenstain, 1986). But an “outbreak” of lepidopteran larvae and coleopteran grubs in June provoked a dramatic reversal in this pattern as time spent resting fell sharply and active foraging for these insects increased. Thus, over the entire study period, the effect of the drought on the activity profile of the macaques was not unidirectional. Finally, drought-induced depression of vocal behavior is more likely for high-energy vocalizations (such as the “krahow” loud call) or for calls associated with “expensive” activities such as reproduction, which may account for the absence of copulation calls during the study period.

Changes in group cohesion caused by the drought (Berenstain, 1986) were likely to affect the use of calls that regulate spatial relations. Group cohesion was generally reduced during May and June, as individuals within the group or subgroups were more widely dispersed in the period immediately following the fire than in previous prefire months. This change might be expected to promote greater vocal regulation of spacing. On the other hand, the increased visibility and luminosity afforded by the reduction in canopy foliage during the drought might be expected to permit more visual monitoring of conspecifics and thereby reduce the use of calls for spacing. Subgrouping was somewhat more frequent during May than in most, but not all, prefire months. Conversely, subgrouping was relatively low during June as macaques fed on insect larvae and grubs. Thus, while it is clear that the drought and fire influenced the activity and social dispersion of macaques of the study group, there are no clear indications of any particular direction in these effects.

**Study Animals and Observations**

The Mentoko study group comprised 17 well-habituated and individually identified macaques: 3 adult males, 5 adult females, 1 subadult male, 6 juveniles (5 of which were male), and 2 male infants.

Problems inherent in monitoring the vocal behavior of the subjects (Palombit, 1992) required that vocal behavior be measured at the level of the group or subgroup and that conceptual emphasis therefore be on the potential of vocal signals to regulate intragroup spacing. All calls heard during 5-min sample periods for a given subgroup of macaques were counted and classified (Struhsaker, 1975; Byrne, 1981). Following the
Table I. General Vocalization Categories of the Long-Tailed Macaque Vocal Repertoire (from Palombit, 1992)

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Clear&quot; (or &quot;coo&quot;)</td>
<td>Narrow-spectrum vocal categories:</td>
</tr>
<tr>
<td>&quot;HLM&quot; coos</td>
<td>High frequency, long duration, frequency modulated</td>
</tr>
<tr>
<td>&quot;HIS&quot; coos</td>
<td>High frequency, short duration</td>
</tr>
<tr>
<td>&quot;LLM&quot; coos</td>
<td>Low frequency, long duration, frequency modulated</td>
</tr>
<tr>
<td>&quot;LS&quot; coos</td>
<td>Low frequency, short duration</td>
</tr>
<tr>
<td>&quot;HEM&quot; coos</td>
<td>High frequency, long duration, &quot;extended&quot; frequency modulation</td>
</tr>
<tr>
<td>Whimpers</td>
<td></td>
</tr>
<tr>
<td>&quot;Harsh&quot;, wide-spectrum vocal categories</td>
<td></td>
</tr>
<tr>
<td>&quot;Kra-(o)&quot;</td>
<td>Common &quot;kra&quot; noise</td>
</tr>
<tr>
<td>&quot;Kra-(o)&quot;</td>
<td>Aroused &quot;kra&quot; noise</td>
</tr>
<tr>
<td>Bark</td>
<td></td>
</tr>
<tr>
<td>&quot;Krahoo&quot;</td>
<td></td>
</tr>
<tr>
<td>Alarm 1</td>
<td></td>
</tr>
<tr>
<td>Alarm 2</td>
<td></td>
</tr>
<tr>
<td>&quot;Harr&quot;</td>
<td></td>
</tr>
<tr>
<td>Scream</td>
<td></td>
</tr>
<tr>
<td>&quot;Khreert screech&quot;</td>
<td></td>
</tr>
<tr>
<td>Squeal</td>
<td></td>
</tr>
<tr>
<td>&quot;Wraagh&quot;</td>
<td></td>
</tr>
<tr>
<td>Copulation calls</td>
<td></td>
</tr>
<tr>
<td>Ad hoc collapsed vocal categories</td>
<td></td>
</tr>
<tr>
<td>All vocalizations</td>
<td>HLM, HIS, LS, LLM, and HEM coos and whimpers</td>
</tr>
<tr>
<td>Clear calls</td>
<td>All calls listed above &quot;Harsh&quot; except copulation calls</td>
</tr>
<tr>
<td>Harsh calls</td>
<td>Barks, screams, and harr vocalizations</td>
</tr>
<tr>
<td>Agonistic harsh calls</td>
<td></td>
</tr>
</tbody>
</table>

Preliminary vocal repertoire provided by Palombit (1992), 13 wide-spectrum "harsh" call categories were distinguished. Six ad hoc classes of narrow-spectrum "clear" calls were also defined operationally on the basis of acoustic differences in duration, fundamental frequency, and frequency modulation (Palombit, 1992). Table I lists these 19 vocal classes of the vocal repertoire, for which descriptions of acoustic features, contexts, and callers are given by Palombit (1992).

Additional data collected during each 5-min sample include the following.

Party Dominant Activity. At the beginning of each sample period, the activity of the majority of individuals was recorded. Definition of party activities was based on a system employed by Berenstain (1986, p. 258) on the same study group: (1) resting — party is stationary; (2) feeding — food intake on "sources yielding a high rate of return, such as patches of fruits, seeds, flowers, young foliage, stems, shoots, and insects"; (3) foraging — "active search and some low return-rate feeding" on dispersed food items, primarily insects; and (4) travel — more or less directed movement of the party in a certain direction. Communication with two simultaneous observers facilitated assessment of activity.

Party Spread. Subgroups of long-tailed macaques are normally quite discrete, but this was particularly so during most of the present study when the level of subgrouping and the dispersion of subgroups were more pronounced than usual (Berenstain, 1986). Thus, if macaques were not within the sample party, they were far enough from me that the probability of scoring their calls was small (communication with observers following other subgroups on various occasions supported this assumption). The samples in which this was ambiguous are excluded from the analysis.

The relative locations of all members of the small study group or, more often, the even smaller subgroup were generally well-known during 5-min sample periods since I worked at all times with two other experienced observers monitoring other behaviors of the same monkeys. At the beginning of each 5-min sample period, we estimated group spread by first noting the distance separating the two monkeys farthest from each other. The length of a second spread axis perpendicular to and bisecting this one was also estimated. The average values of these "spread" axes during sample periods were 30 ± 15 m (range = 2-100 m) and 20 ± 10 m (range = 1-50 m) (N = 195). The lengths of these two axes were positively correlated.
with one another (*r* = 0.59, *P* < 0.001), suggesting that changes in party spread may be relatively homogeneous in space, at least as far as this maximal measure of it is concerned. These two measures are multiplied together to give one index (in m²) referred to as “maximal party spread,” or simply “party spread.”

**Party Size and Composition.** This is the number of adult males, adult females, subadult males, juveniles, and infants constituting the sample party. A wide range of party sizes was sampled (Fig. 1). The average party size was 8.6 ± 4.7 animals (X ± SD; *N* = 195), which corresponds with the value for parties of the same subspecies of long-tailed macaques in Sumatra (van Schaik et al., 1983b). Party size and party spread were positively correlated with one another in this study (*r* = 0.54, *P* < 0.001, *N* = 179) as also occurs among African cercopithecines (Struhsaker and Leland, 1979).

I exclude from the analysis any 5-min sample periods during which marked changes in any of the above nonvocal measures occurred or during which rain fell. These 5-min sample periods were always separated from each other by intervals of 25 min in order to increase their statistical independence (Byrne, 1981). In the present analysis, I use 195 5-min sample periods distributed across more than 100 daylight hr (0600–1800).

Given that long-tailed macaques spend over 50% of their time at canopy heights below 20 m (Rodman, 1978; Aldrich-Blake, 1980) and that vocal behavior was measured from below the center of mass of the group, members of the sample party were, on average, no more than approximately 20–25 m (± 15 m) from me during sample periods. Thus, members of the sample party were generally close enough to me that the natural bias for the scoring of louder calls was probably not inordinate, except for those of extremely low sound pressure.

I conducted multiple regression with each of the call types and “other” scored during sample periods acting successively as the dependent variable, and party size and party spread as the independent variables. Of the 19 call classes listed in Table I, 17 are used as dependent variables: copulation calls are excluded from the analysis because they did not occur during the research period (Palombit, 1992), and the two alarm call types are analyzed together as the composite “alarm calls.” The dependent variable for each multiple regression is specifically the number of signals of each call type heard during each 5-min sample period divided by the party size at that time (this quotient controls for the correlation between party size and party spread and, secondarily, provides a rough estimate of the average individual calling rate). A total of 2359 calls was heard in all sample periods combined. Sample periods in which party size = 1 (i.e.,

### Table II. Results of Multiple Regression Analysis for Each Vocalization Type Treated as the Dependent Variable

<table>
<thead>
<tr>
<th></th>
<th>R²</th>
<th>Party size</th>
<th></th>
<th></th>
<th>Party spread</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>s²</td>
<td>β</td>
<td>s²</td>
<td>β</td>
<td>s²</td>
</tr>
<tr>
<td>Overall (<em>N</em> = 178 samples)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLM coos</td>
<td>0.071**</td>
<td>-0.290***</td>
<td>0.071</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LLM coos</td>
<td>0.092***</td>
<td>-0.242**</td>
<td>0.050</td>
<td>+0.299***</td>
<td>0.076</td>
<td></td>
</tr>
<tr>
<td>HS coos</td>
<td>0.033*</td>
<td>-0.162*</td>
<td>0.022</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LS coos</td>
<td>0.053**</td>
<td>-0.244**</td>
<td>0.051</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whimper coos</td>
<td>0.066**</td>
<td>-0.258**</td>
<td>0.056</td>
<td>+0.196*</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td>Rest (<em>N</em> = 65 samples)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLM coos</td>
<td>0.124*</td>
<td>-0.355**</td>
<td>0.118</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LLM coos</td>
<td>0.399***</td>
<td>-0.299**</td>
<td>0.084</td>
<td>+0.636***</td>
<td>0.380</td>
<td></td>
</tr>
<tr>
<td>LS coos</td>
<td>0.095*</td>
<td>-0.313*</td>
<td>0.092</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whimper coos</td>
<td>0.174**</td>
<td>-0.405*</td>
<td>0.087</td>
<td>+0.370*</td>
<td>0.128</td>
<td></td>
</tr>
<tr>
<td>“Wraagh”</td>
<td>0.233***</td>
<td>-0.269*</td>
<td>0.068</td>
<td>+0.473***</td>
<td>0.210</td>
<td></td>
</tr>
<tr>
<td>Feed (<em>N</em> = 66 samples)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLM coos</td>
<td>0.088*</td>
<td>-</td>
<td>-</td>
<td>+0.366*</td>
<td>0.087</td>
<td></td>
</tr>
<tr>
<td>“Kra-(a)”</td>
<td>0.117**</td>
<td>-</td>
<td>-</td>
<td>+0.366*</td>
<td>0.087</td>
<td></td>
</tr>
<tr>
<td>Alarm</td>
<td>0.171**</td>
<td>-</td>
<td>-</td>
<td>+0.488***</td>
<td>0.154</td>
<td></td>
</tr>
<tr>
<td>Forage (<em>N</em> = 19 samples)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>“Kra-(c)”</td>
<td>0.286*</td>
<td>-</td>
<td>-</td>
<td>-0.389***</td>
<td>0.105</td>
<td></td>
</tr>
<tr>
<td>Travel (<em>N</em> = 25 samples)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLM coos</td>
<td>0.292*</td>
<td>0.529**</td>
<td>0.168</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>“Kra-(a)”</td>
<td>0.296*</td>
<td>0.529**</td>
<td>0.259</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Given are the standardized partial regression coefficients (β), semipartial correlations (s²), and multiple R² for each vocalization yielding a statistically significant overall F test.

*0.01 < *P* ≤ 0.05.

**0.001 < *P* ≤ 0.01.

*** *P* ≤ 0.001.

**** *P* = 0.13 (see text).

an individual is isolated from the entire group) are not included in the analysis, since by definition there is no party spread in this case. They are examined independently with respect to the “wraagh” call. An overall regression is conducted using the data from all samples. Subsequent regressions concentrate successively on data for each of the four general activity categories.

All statistical tests are two-tailed.
Table III. Results of Multiple Regression Analysis Using the Five “Collapsed” Call Categories as Dependent Variablesa

<table>
<thead>
<tr>
<th></th>
<th>Party size</th>
<th>Party spread</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2$</td>
<td>$\beta$</td>
</tr>
<tr>
<td>Overall (N = 179 samples)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All calls</td>
<td>0.056**</td>
<td>-0.526</td>
</tr>
<tr>
<td>Clear calls</td>
<td>0.088***</td>
<td>-0.314***</td>
</tr>
<tr>
<td>Rest (N = 65 samples)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All calls</td>
<td>0.180**</td>
<td>-0.415***</td>
</tr>
<tr>
<td>Clear calls</td>
<td>0.022***</td>
<td>-0.394***</td>
</tr>
<tr>
<td>Fce (N = 66 samples)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>None of the dependent variables yields significant overall F</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forage (N = 19 samples)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>None of the dependent variables yields significant overall F</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Travel (N = 25 samples)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agonistic harsh</td>
<td>0.296*</td>
<td>0.555</td>
</tr>
</tbody>
</table>

a Given are the standardized partial regression coefficients ($\beta$), semipartial correlations ($se^2$), and multiple $R^2$ for each call yielding a statistically significant overall F test. Dependent variables are (1) all calls; (2) clear calls; (3) harsh calls; and (4) agonistic harsh calls. $\beta$ and $se^2$ are given only for those dependent variables yielding significant overall F scores for the regression.

* $0.01 < P \leq 0.05$
** $0.001 < P \leq 0.01$
*** $P \leq 0.001$

RESULTS

The statistically significant standardized partial regression coefficients ($\beta$), the semipartial correlations ($se^2$), and the multiple $R^2$ for each call yielding a statistically significant overall F test are given in Table II. Table III provides the same information for regressions using the four collapsed call categories of Table I as separate dependent variables.

Party Size and Calling Rate

The four most commonly heard clear calls, i.e., low long modulated (LLM), low short (LS), high long modulated (HLM), and high short (HS) coos (Palombit, 1992), and whimpers were the only calls individually correlated with party size for all samples combined: as party size increased, the rate of calling per animal decreased for these calls. This pattern was upheld for the most part during periods when resting was the dominant group activity except for the occurrence of high-frequency, short-duration (HS) coos. Calling rate was not correlated with party size during feeding or foraging for any call type. Of the clear calls, only high extended modulated (HEM) coos were correlated with party size during travel when, in contrast to previous patterns, the rate of calling for HEMs increased with increasing party size.

Calling rate was not correlated with party size for any of the 11 harsh call categories analyzed when data for all activities are combined (i.e., the “overall” case in Table II). When analyzed with respect to activity, only two harsh calls yielded significant regression coefficients with party size: the “wraagh” calls, negatively correlated during resting, and the “kra-(a)” calls (i.e., aroused “kra” noises), positively correlated during travel.

Party Spread and Calling Rate

The occurrence of considerably fewer calls was correlated significantly with party spread. For all data combined, calling rates of only LLM coos and whoops were correlated, both positively, with party spread. This pattern was more prominent during resting (as reflected by the size of the standardized partial regression coefficients), but was not maintained during other activities. Of the clear calls, only HLM coos were correlated positively with party spread during feeding, as were the harsh alarm and the kra-(a) calls. No call categories were correlated with party spread during travel. The correlation between calling rate and party spread was significant during foraging for only common kra vocalizations (“kra-(c)” calls). This particular multiple regression is unique in that it yielded a significant overall F test, but the individual $\beta$ weights did not meet the 0.05 significance criterion. This rare anomaly arises when collectively... there is sufficient evidence that there is something there, but individually, not enough evidence to identify what it is” (Cohen and Cohen, 1983, p. 175). Cohen and Cohen (1983, p. 175) suggest that a reasonable “resolution of this dilemma is to tentatively interpret as significant any [independent variable] whose $t$ is almost large enough to meet the significance criterion; whatever is lost by the inflation of the Type I error is likely to be compensated by the reduction of Type II error and the resolution of the apparent inconsistency.” The $t$ values for the standardized regression coefficients of party size and party spread are 0.849 and 1.579, respectively. Given that for $\alpha = 0.05$, $t = 1.645$ (one-tailed) and $t = 1.960$ (two-tailed) in this case, the negative correlation...
between calling rate of the kra-(c) and party size will be rejected and the negative correlation with party spread will be accepted tentatively.

The amount of variance explained by the two independent variables is greater when the four activities are analyzed separately. $R^2$ in these cases ranges from low ($R^2 = 0.09$ for HLM coos during feeding) to quite high ($R^2 = 0.40$ for LLM coos during resting), suggesting that other causative factors are involved besides party size and spread. No suppressor variables were found.

Patterns of correlations between the call categories and party spread may reflect the potential of a call class to function at least in part in systems regulating within-group spacing if the following assumptions apply.

(1) Interindividual distance is positively correlated with the maximum dispersion of individuals composing the party (i.e., the measure “party spread”). The symmetrical covariation in the two spread measures, whose product yields the index “party spread,” provides some indirect justification for this assumption.

(2) Macaques are more likely to perform a call the more their spatial relations deviate from the equilibrium state that it is useful in bringing about.

Given these premises, a statistically significant correlation between a call and party spread is not an explicit demonstration that individual vocal behavior varies in a linear way with distance from other animals. That inference is suggested by the finding that the emission rate of a given call varies significantly with party spread. Thus, for example, a call whose rate of performance increases with increasing party spread may function in part to maintain a spatial relation between two or more individuals or to maintain auditory contact as distance between individuals increases. This interpretation must be weighed against the evidence provided by other data concerning caller demeanor, context, and call emission pattern.

Occurrence rates of three call types, whimpers, “wraaghs,” and LLM coos, were correlated with party spread during resting (Table II). Since whimpers are performed by immature individuals (Palombit, 1992), any potential utility of whimpers to mediate spacing may be limited to spatial relations involving that age class. The suggestion of ad libitum evidence (Palombit, 1992) that the wraagh call was used by isolated macaques to regain proximity to others is supported by its unique status as the only call that was more frequently heard in parties of size 1 (i.e., solitary individuals) than in parties of size two or more in terms of both average absolute rate of occurrence (Mann-Whitney U Test, $U = 1077.5$, $n_1 = 16$, $n_2 = 179$, $P < 0.01$) and average proportion of calls emitted ($U = 574.5$, $n_1 = 12$, $n_2 = 148$, $P < 0.001$), analyzing only those sample periods in which at least one call of any kind occurred; Fig. 2). Thus, the positive correlation between wraagh rate of emission and party spread (during rest) may simply reflect a correspondingly higher number of animals that are alone as party spread increases (which lends some support to assumption 1 above). The individual correlations of wraaghs and whimpers with party spread during the same general activity may be due to the fact that they tend to cooccur (Palombit, 1992).

The aroused demeanor of individuals producing wraaghs and whimpers (Palombit, 1992) is also somewhat inconsistent with a function related to maintaining existing sociospatial relationships during group rest periods, which should be distinguished from the reestablishment of spatial relationships that have been terminated earlier. Thus, of these three call classes, the LLM coos are the most plausible components of a vocal system mediating intragroup spacing among adults during rest and overall. Green (1975) found that two of the three calls that he placed on the “isolation” end of an “isolation-affiliation” continuum for Japanese macaque clear calls were also relatively long, low-frequency, frequency-modulated coos similar to LLM coos.

Although HLM coos, alarm, and kra-(a) calls were correlated with party spread during feeding, HLM coos appear more likely than these other calls to contribute in part to routine maintenance of spatial relationships among adults. The stimuli eliciting alarm calls were usually some sudden, apparent environmental change, e.g., the presence of a feral dog (Palombit,
The kra-(a) call was also commonly performed during alarm situations (Palombit, 1992) and it may serve as an "alert" call (sensu Gautier and Gautier, 1977). Given the pronounced degree of arousal associated with their occurrence, if alarm and kra-(a) calls regulate intragroup spacing, they do so differently than low-arousal HLM coos.

The kra-(c) was the only category of calls whose occurrence was correlated with party spread during foraging. This correlation was negative, suggesting that the kra-(c) may space out individuals. *Ad libitum* observations do not oppose this interpretation (Palombit, 1992).

In summary, LLM coos (during resting), HLM coos (during feeding), and kra-(c) calls (during foraging) have substantial potential to function in part in vocal systems of intragroup spacing among adults in nonalarm situations. The wraagh call also appears to help reestablish previously breached spatial relationships.

**DISCUSSION**

**Party Size and Calling Rate**

Most of the significant correlations between calling rate and party size were negative: the number of calls/animal/5 min decreased as party size increased for HLM, LLM, HIS, LLM, and whimper coos as well as for "kra-(c)" and "wraagh" calls. This might arise from a greater reliance on visual communication in larger parties. Given that party size was positively correlated with party spread, this explanation would then imply that individual macaques communicate over shorter distances as party size increases. Alternatively, the relatively greater silence of individuals in larger, more conspicuously gregarious groups may be an antipredator strategy (Moynihan, 1976).

Like me, van Schaik et al. (1983a) measured the number of screams and "grunts" emanating from long-tailed macaque groups of different sizes. They found that the rates of such calls increased with increasing group size and interpreted this result to indicate higher levels of agonistic interactions resulting from feeding competition in larger groups. In my study, only HEM coos and "kra-(a)" calls were individually positively correlated with party size, and only during travel. HEM coos and kra-(a) calls are correlated with one another in terms of occurrence and are generally associated with slightly or moderately aroused or agitated callers, suggesting low levels of aggression, if aggression is implicated at all (Palombit, 1992). Vocal indicators of relatively severe agonistic interactions, i.e., the scream, "khreeet screech," bark, "bark-kra," "harr," and the composite "agonistic harsh calls," were not correlated with party size.

These results may be interpreted in several ways. They may suggest that rates of vocally mediated aggression do not necessarily always increase with group size in long-tailed macaques. Alternatively, the van Schaik et al. (1983a) analysis differs from my study by comparing a number of independent groups instead of parties from one group. Accordingly, the results may suggest that the processes that promote increased feeding competition with increased group size may not act on foraging subgroups whose size and composition may be dictated proximally and hence more finely tuned to resources being exploited at the time. Finally, the drought and fires may have influenced the outcome of this particular regression analysis. Macaques of the study group fed primarily on relatively evenly distributed herbaceous items or on locally abundant insect larvae during the period data were collected. These resources are less likely to promote feeding competition than are patches of fruit, which are exploited by macaques to a greater degree than my subjects did.

**Acoustic Structure and Intragroup Spacing**

Sound waves change in predictable ways as they travel through the medium and encounter heterogeneities in the environment (Wiley and Richards, 1978). The processes promoting these changes, e.g., attenuation and degradation, ultimately facilitate the localization of sounds, but they also disrupt sound transmission. Their effects on sound transmission vary with the acoustic properties of the sounds on which they act, thereby establishing selecting pressures that act on the evolution of vocal mechanisms of intragroup spacing.

What are the relative advantages and disadvantages, with respect to sound transmission, perception, and localization, of the acoustic features of the various long-tailed macaque calls whose occurrence was correlated with party spread? The following discussion explores this question by reviewing acoustic features of sound transmission and spacing with respect to LLM coos initially and then later considering other calls. The general acoustic characteristics of LLM calls distinguishing them from others are (1) low frequency, (2) long duration, (3) frequency modulation, and (4) narrow energy spectrum.

**Low Frequency.** Compared to higher-frequency sounds, low-frequency sounds generally travel longer distances without serious loss of energy and information, are detected by macaques at lower energy levels, and are more easily localized by macaques (Table IV). Since the fundamental frequencies
### Table IV. Acoustic Properties of Vocalization Attributes

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Sound transmission</th>
<th>Sound localization</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low frequency</td>
<td>Less diffraction&lt;br&gt;Less refraction&lt;br&gt;Less amplitude fluctuation&lt;br&gt;Less atmospheric absorption&lt;br&gt;Less ground attenuation at heights above 2m&lt;br&gt;Less scattering of sound beam&lt;br&gt;Less reverberation</td>
<td>Localized more easily horizontally; maximum sensitivity to changes in horizontal position of pure tones = 1 kHz</td>
</tr>
<tr>
<td>Frequency modulation</td>
<td>Degraded less by reverberations and amplitude fluctuations in forests than amplitude modulation</td>
<td>Improves horizontal localization in anechoic chambers</td>
</tr>
<tr>
<td>Wide spectrum</td>
<td>Dissipate less energy per unit distance&lt;br&gt;Rapidly degraded by reverberations and amplitude fluctuations in forests&lt;br&gt;Less variable attenuation rates</td>
<td>Localized better in anechoic chambers with no noise</td>
</tr>
<tr>
<td>Narrow spectrum</td>
<td>Greater power per Hz&lt;br&gt;Greater signal-to-noise ratio: extends range of effective broadcast&lt;br&gt;Less, but more variable attenuation</td>
<td>Localized better in anechoic chambers with ambient noise</td>
</tr>
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</table>

Greater "scattering" in forests (which, however, may be partially compensated for by lowering and modulating the frequency of the call)

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Sound perception &amp; production by macaques</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low frequency</td>
<td>Harder to modulate frequency, but only at very low frequencies&lt;br&gt;Greater perceptual efficiency and precision, a. Maximum auditory acuity at 1 kHz (and, to a slightly lesser degree, 8 kHz; see text) b. Slight frequency differences more easily detection</td>
<td>Brown et al., 1978b; Konishi, 1973; Marten et al., 1977; Marten &amp; Marler, 1977; Michelson, 1978; Morse &amp; Ingard, 1968; Morton, 1975; Stebbins et al., 1966; Stebbins, 1971; Stebbins, 1973; Waser &amp; Waser, 1977; Wiley &amp; Richards, 1978</td>
</tr>
<tr>
<td>Frequency modulation</td>
<td>Vocal organs can produce extensive frequency modulation&lt;br&gt;Auditory organs can perceive small frequency differences (as small as 0.6% in a 2-kHz pure tone at 40 db)</td>
<td>Brown et al., 1978a, 1979; Fobes &amp; King, 1982; Kelemen, 1963; Wiley &amp; Richards, 1978</td>
</tr>
<tr>
<td>Wide spectrum</td>
<td>Frequency modulation difficult; acoustic information as amplitude modulation</td>
<td>Brown et al., 1979; Waser &amp; Brown, 1986; Wiley &amp; Richards, 1978</td>
</tr>
<tr>
<td>Narrow spectrum</td>
<td>Extensive frequency modulation possible (see benefits of frequency modulation above)</td>
<td>Brown, 1982; Wiley &amp; Richards, 1978</td>
</tr>
</tbody>
</table>
of all clear calls measured in this study fell in the 350- to 1350-Hz range (Palombit, 1992), the differences in the auditory sensitivity of long-tailed macaques to the fundamentals of HLM and LLM coo calls, in which median maximum frequencies are 5.0 and 1.8 kHz, respectively, reflecting greater energy levels among high overtones in HLM coos (Palombit, 1992). That overtones may be important features of coos is suggested by the fact that they sometimes possess as much energy as, if not more than, fundamental frequencies and that their experimental removal may disrupt recognition and discrimination of coos (May et al., 1988).

Frequency Modulation and Long Duration. Frequency modulation is superior to amplitude modulation in effectiveness of long-range transmission of information in forests if rapid, repetitive modulation is avoided (Wiley and Richards, 1978), which may account, in part, for the smooth and simple frequency modulation of LLM coos. Moreover, even subtle frequency modulation improves localization by macaques dramatically (Brown et al., 1978a, 1979) (Table IV). Indeed, frequency modulation may be of such importance that it may define natural coo categories in Japanese macaques (Zoloth et al., 1979; Moody et al., 1986; May et al., 1988).

Longer duration should offer greater opportunity for frequency modulation, which does, in fact, characterize “long” and “short” coos of long-tailed macaques (Palombit, 1992). For this reason shorter clear calls (HS and IS calls) may be less suitable for localization, and hence mediation, of spacing over extended distances. Also, increasing call duration can improve transmission success via reduced attenuation (Waser and Waser, 1977).

Narrow-Energy Spectrum. Are “clear” calls better suited than “harsh calls” for mediating within-group spacing? Wide-spectrum signals with sharp changes in intensity are easily localized (Marler, 1955; Gulick, 1971; Konishi, 1973). However, introduction of ambient noise in an otherwise controlled laboratory setting, impaired localization by macaques of playbacks of harsh calls considerably more than of playbacks of clear calls (Brown, 1982), suggesting that these narrow-band signals may convey more information about location in tropical rain forests, which are particularly noisy habitats at some frequency values (Waser and Brown, 1986). Furthermore, several features related to sound transmission (Table IV) suggest that concentration energy in a narrow frequency band is generally preferred over “spreading the same energy through a broader range of frequencies” for communication over long distances (Marten et al., 1977, p. 299).

On the other hand, the directionality of a narrow-spectrum signal reduces its usefulness if the approximate locations of potential receivers are unknown or if communication needs to be more omnidirectional (Wiley and Richards, 1978). Also, attenuation of narrow-band signals is more variable than that of harsh calls, especially at frequencies above 500 Hz, resulting in greater uncertainty in effective broadcast range under certain conditions (Table IV). Accordingly, use of wide-band calls may sometimes be a “safer” strategy (Morton, 1975; Waser and Waser, 1977).

Both of these considerations seem especially pertinent for individuals separated from others for some time, and this may partly explain the apparent use of predominantly harsh “wraagh” calls by solitary long-tailed macaques. The combination of narrow- and wide-spectrum elements in the wraagh call (Palombit, 1992) may be a strategically conservative “hedging of bets.” Transmission efficiency of a wide-band call is enhanced substantially by (1) sharp amplitude modulation, (2) low rate of amplitude modulation, and (3) pronounced repetitiveness (Wiley and Richards, 1978). The single amplitude surge occurring at the onset of the wraagh and a suggested pronounced repetition rate (Palombit, 1992) appear to conform with these features. The significantly greater amplitude of wraagh calls relative to the coo calls may further contribute to the former’s relative utility in reestablishing a spatial relationship, although this must be explored in greater empirical detail since sound-pressure level may often be less important that acoustic structure in determining call attenuation (Waser and Waser, 1977).

The distinction suggested here is that over moderately long distances those narrow-spectrum signals used to regulate intragroup spacing may function to maintain existing spatial relations, while wide-spectrum calls, used in spacing may function to reestablish previously interrupted sociospatial relationships. We might envision a scenario in which a macaque performs directional LLM coos to mediate varying spatial relations with conspecifics which are not close but whose general whereabouts are more or less known. Should the distance between two animals become so great that the relationship is essentially “disengaged,” then an individual might initially use coos in an attempt to stimulate a response from the intended recipient(s) and thereby reestablish the relationship. If this effort is unsuccessful, it might then additionally perform omnidirectional wraagh calls (which, because they are longer and much louder calls, may be more energetically expensive). This pattern might be displayed most clearly by solitary individuals that have been separated from the entire group or party, but it should also apply to individuals in proximity with others [e.g., baboons that perform “lost calls” in the presence of conspecifics (Rowell,
Wedge-capped capuchin monkeys, *Cebus nigrivitatus*, appear to employ a similar system, in which isolated individuals perform a wide-spectrum version of a more tonal call used over moderate distances (Robinson, 1982).

**Other Considerations.** The previous discussion has emphasized the benefits of communicating locational information to conspecifics. However, there may be serious ecological or reproductive costs associated with communicating position to competitors within the foraging party given that many primate calls, including coos, permit individual recognition (Dittus, 1988) and probably disclose caller location to some degree (Brown, 1982). Although use of call variants may be affected by many factors, including environmental pressures on transmission (Wiener and Keast, 1959; Marten and Marler, 1977; Marten et al., 1977; Wiley and Richards, 1978) and ecological pressures [e.g., predator avoidance (Marler, 1959)], the importance of competition for food and mates in the lives of long-tailed macaques (van Noordwijk, 1985; van Schaik and van Noordwijk, 1986; van Noordwijk and van Schaik, 1987; van Schaik, 1988) suggests repercussions extending to vocally mediated social behavior.

Thus, with its choice of a call, a macaque may sometimes attempt to balance the need to communicate with allies that may intervene on its behalf during competitive interactions with the need to avoid communication of its position to adversaries likely to interfere with its activities. That is, it may use its calls to select its nearest neighbors (*sensu* Dittus, 1988). Narrow-spectrum signals, such as coos, are already well suited for this strategy of restricted communication because they "permit a signaler to limit its signals to a specific receiver" (Wiley and Richards, 1978, p. 88). By varying the acoustic structure of coos, a macaque can further regulate their transmission and hence locatability, as *Cebuella pygmaea* and *Callimico goeldii* do with their "contact trills" (Snowdon and Hodun, 1981; Masataka, 1982). Thus, the presumed reduced transmission distance of HLM coos compared to LLM coos may facilitate limited communication with conspecifics which are nearer on average. That such a situation should arise during feeding is consistent with this interpretation since agonistic interactions in macaques often relate to food resources during nonmating periods (*e.g.*, Dittus, 1977), but this hypothesis requires further testing. The "spatial sub-grouping" of intercommunicating potential allies necessary for such a system is suggested by the preferential spatial associations of individuals of similar age, rank, kinship, or sex and by patterns of agonistic behavior in a number of macaque species (Datta, 1983; van Noordwijk and van Schaik, 1987; Calcobott, 1986).

Alternatively, HLM coos might simply be viewed as high frequency versions of LLM coos produced by smaller individuals, most likely juveniles, which may experience difficulties generating lower frequency sounds (Gould, 1982). But a physically small vocal apparatus may not necessarily strictly limit output to high-frequency sounds (Mounihan, 1967), especially if there is no need for the call to be particularly loud (Waser and Waser, 1977), as seems to be the case with coos. *Ad libitum* data establish that adult female and juvenile long-tailed macaques of my study were, in fact, frequent performers of LLM and LS coos. Likewise, adults of both sexes were capable of producing sounds classified as HLM coos, but there were some indications that adult males may nevertheless perform more lower-frequency coos. Finally, it is not clear why the rate of juvenile coo calling would correlate with party spread during feeding and, conversely, why adult (or adult male) coo calling would correlate similarly with party spread during resting.

Although feeding occurs in patches of varying size, all are relatively large compared to sources exploited by macaques during foraging. Rodman (1988) argued that minimizing individual returns to "exhausted" patches is a primary concern for foraging long-tailed macaques, and van Schaik et al. (1983a, p. 179) maintain that this translates directly into avoidance of neighbors since "foraging efficiency decreases when other individuals are allowed to join at the foraging site." The negative correlation between kra-(c) calling rate and party spread during foraging suggests that this call may be part of a mechanism that spaces individuals out to enhance foraging success. Given the limitations on transmission of harsh calls in forest habitats, the short, low-amplitude kra-(c) call is presumably used to communicate with conspecifics relatively close to the forager. The acoustic structure of the "heh" call used by wedge-capped capuchin monkeys to space each other out is remarkably similar to the kra-(c) call (Robinson, 1982; Palombit, 1992).

**CONCLUSIONS**

The functions we ascribe to primate calls are a direct result of the methodology available to us. Given measurements of the occurrence of aurally discriminated calls and group attributes (party spread, size, and activity), I have focused here on only one possible function of certain long-tailed macaque calls, namely, relative differences in their potential utility in regulating intragroup spatial relations. Multivariate analyses were employed here to generate hypotheses concerning the functional relationships among these variables (*sensu* Short and Horn, 1984). Absence of a significant correlation with party spread does not necessarily imply that the call type in question is functionally unrelated to within-group spacing. A
call that is part of a mechanism regulating spacing may vary with group spread in other ways besides call rate (e.g., amplitude (Struhsaker and Leland, 1979)) and in ways other than those reflected by maximum party spread. Also, such a call type may have its function obscured by subsuming it with functionally disparate, but acoustically similar, variants within the same aural category. Finally, Gautier and Gautier (1977) have argued that a vocal system in which interindividual distance correlates with acoustic structure may be confounded by “psychological distance” resulting from variation in excitation level. A significant correlation between call occurrence rate and party spread in my study is suggestive: at least some of the calls constituting that call category are likely to play a role in mediating intragroup spacing.

Clearly, the analysis presented here is a mere beginning to the study of vocal mediation of intragroup spacing in this species. More generally, it indicates some suites of acoustic features that may be especially useful in long-tailed macaque vocal systems of within-group spacing in specific circumstances and that can be scrutinized and tested in future observational and experimental studies.

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Macaque Vocal Communication and Spacing


