

Vocal Regulation of Inter- and Intragroup Spacing During Boundary Encounters in the Titi Monkey, *Callicebus moloch*

JOHN G. ROBINSON

University of North Carolina at Chapel Hill

ABSTRACT. Monogamous primates maintain exclusive use of their ranges by regularly defining and reinforcing the conventional location of boundaries. *Callicebus moloch* males often call alone during the first morning bout, when groups are near boundaries but usually separated by more than 100 m. Depending on the location and proximity of neighboring animals, groups might begin duetting and approaching one another. Duetting requires close vocal and spatial coordination of the mated pair, and stimulates the approach of neighboring pairs. At the boundary, vocalizations which keep the pair together and those associated with withdrawal from the boundary increase in proportion. To determine the effect of different calls, I played back recordings of six different vocalizations during two playback experiments, holding location and proximity constant. The responses supported hypotheses generated in the normalistic study, and suggested that at the boundary aggression is primarily intrasexual. Vocalizations and their effects in specified contexts constitute the mechanisms regulating spacing. The resulting spacing patterns maintain resource availability and exclusive access to a mate.

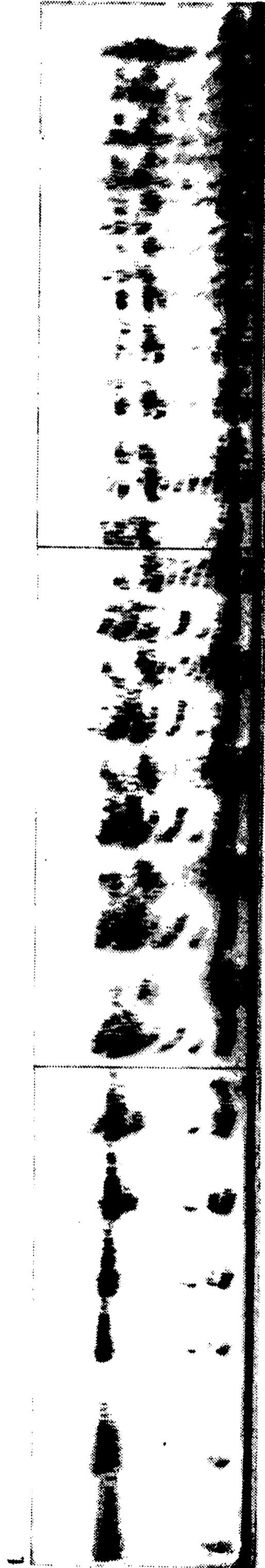
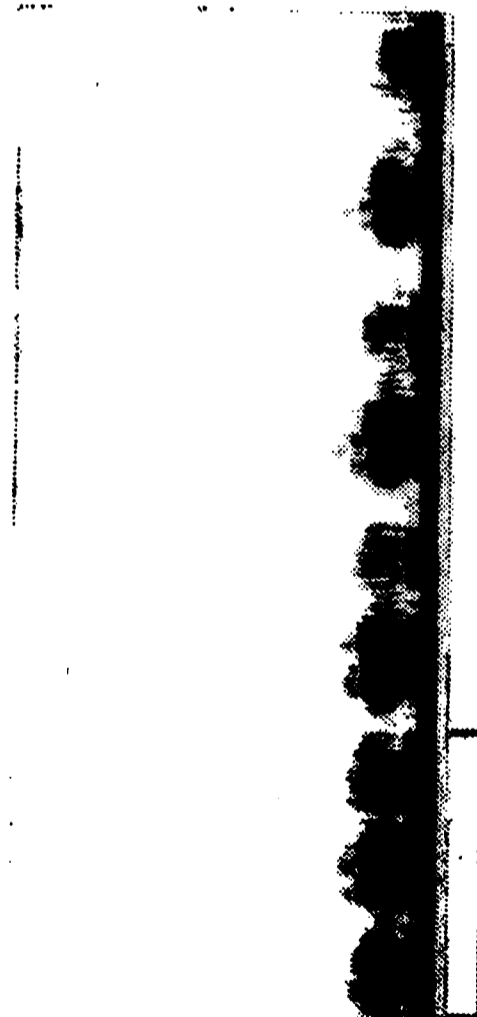
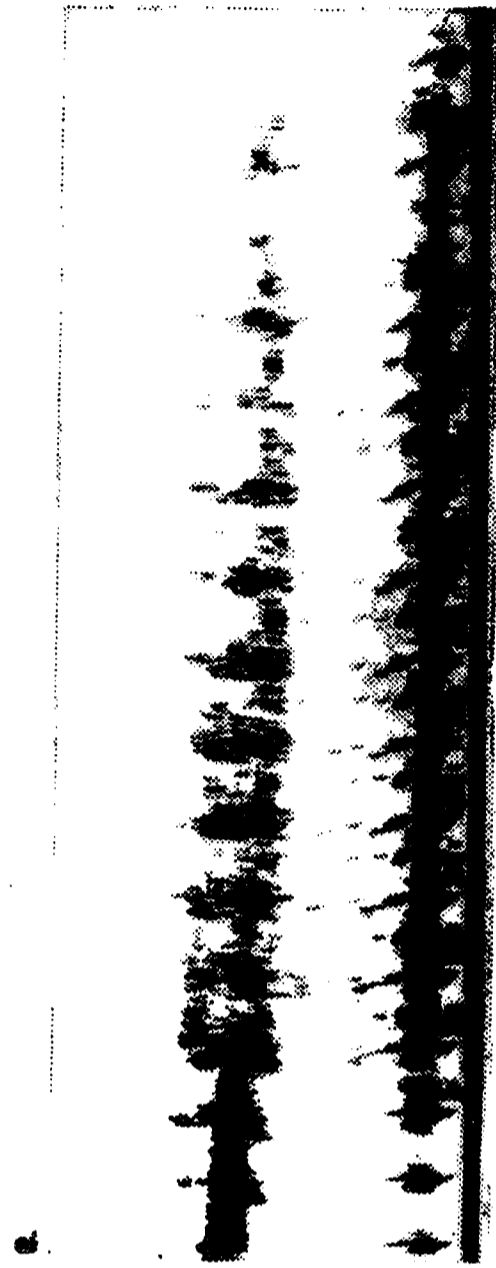
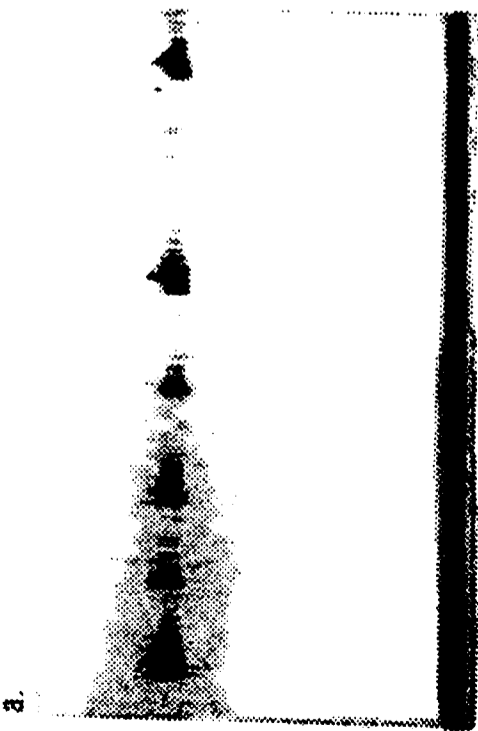
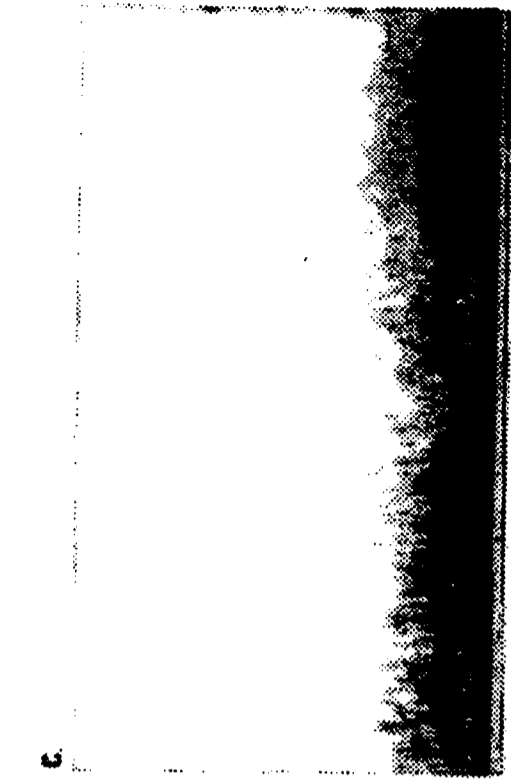
INTRODUCTION

Monogamous primates are characterized by frequent intergroup interactions and exclusive use of space (white-handed gibbons: CARPENTER, 1964; ELLEFSON, 1974; Kloss' gibbons: TENAZA, 1975; siamangs: CHIVERS, 1974; titi monkeys: MASON, 1966, 1968; ROBINSON, 1979a; Simakobu monkeys: TILSON, 1977). Complex vocal duets characterize these interactions in the white-handed gibbon (MARSHALL & MARSHALL, 1976; TEMBROCK, 1974), siamang (LAMPRECHT, 1970) and titi monkey (MOYNIHAN, 1966). In this study of the titi monkey *Callicebus moloch* I examined the vocal mechanisms with which groups (1) coordinate their approach to a boundary; and (2) define and reinforce the conventional location of that boundary.

Studies of the vocal regulation of social interactions require three approaches: (1) description of the variation and classes in the acoustic structure of vocalizations; (2) studies of conditions associated with the production of different vocalizations; and (3) studies of responses evoked by different vocalizations in specified contexts (MARLER, 1961; SMITH, 1977; CHERRY, 1966; ALTMANN, 1967; EPPLE, 1968; GAUTIER, 1974). ROBINSON (1979b) provides a physical description and sequential analysis of the vocalizations of *C. moloch*. Here I report how these vocalizations vary with context during boundary encounters. From the associations between vocalizations and contexts I inferred the possible effects that each vocalization has on spacing, both within and between groups, during the encounter. Some of these hypotheses were then tested by playing back recordings of calls to subject groups.

METHODS

I examined populations of *C. moloch* at two sites, Finca Saravita (FS) and Finca la Maca-



ia (FLM), in the *llanos* of Colombia. At FS I recorded 31 intergroup interactions during days of the wet season in 1974 and 1975. At FLM. I recorded 90 interactions during 70 days the dry season in 1976. I assigned each interaction (or part of it) to one of five contexts, defined by the distance between groups, probability of visual contact between groups, and whether one or both groups were calling (Table 1).

I calculated the proportion of time animals produced each of eight classes of vocalizations in every context. *Callicebus* vocalizations are illustrated in Figure 1. These monkeys repeat individual *calls* to form *phrases*, and order phrases to form *sequences*. Moan and chirp phrases can be given separately, but pant, bellow, pump and honk phrases always are combined in sequences. Based on phrase order I distinguished three short sequences (CPs and CRPs are illustrated, CR sequences begin with chirrups and end with pants) and three long sequences. Duets, the most complex of the long sequences, involve a close vocal and spatial synchronization of the mated pair. Both sexes usually initiate the sequence with moans, then lead into an alternation of phrases of pants and bellows (similar structurally to pants but louder and longer) which can last 5 min. Pump and honk phrases are inserted in predictable positions. Male calling, a sequence given by the male alone, begins with one of the short sequences, then passes into a regular cycling of the group of phrases honks—bellows—pumps. Female calling is given only by females. The structure of this rare sequence is identical to the female contribution during duetting. ROBINSON (1979b) provides a full description of the vocal categories.

The predictable association between vocalizations, distances between neighboring groups and spatial responses to neighboring groups (see below) suggested that vocalizations regulate the spatial and vocal responses of neighbors. To test the hypotheses suggested by these associations, I played back recordings of calls to subject groups. The first experiment compared the responses to playback of CP, CRP and chirrup vocalizations. The second compared those of duetting, male calling and female calling sequences.

Test tapes were presented over a Magitran speaker with a Uher 4000-L tape recorder. The first tape in the first experiment consisted of three 2-min repetitions of the appropriate vocalization with a 2-min pause between each, and in the second of five repetitions of a 1-min recording, each followed by a minute of silence. This presentation design mimicked the calling fre-

Table 1. Contexts of the intergroup interaction.

Context	Characteristics
A	Boundary encounters. Groups under 30 m apart, probably in visual contact, both groups calling.
B	Groups 30–80 m apart, possibly in visual contact, both groups calling.
C	Groups over 80 m apart, probably not in visual contact, both groups calling.
D	Groups over 80 m apart, probably not in visual contact, only a single group calling in response to calling from a group which is now silent.
E	First calling in the early morning. Animals usually in boundary areas but separated from neighboring groups by at least 100 m. Calling may be spontaneous or triggered by calling within hearing.

Fig. 1. Spectrograms of *Callicebus* vocalizations analyzed with a broad-band filter. a. chirps, one of the quiet high pitched calls, from a single animal; b. chirrups from two animals; c. moaning; d. honking; e. chirrup—pumps (CPs); f. chirrup—pant—pumps (CRPs). Frequency scale indicates kHz; time scale is 0.5 sec.

quency of naturally calling animals. The playback period thus lasted 10 min. Vocal responses were recorded with a Nagra IV tape recorder and a Sennheiser MKH 815 directional microphone during both the playback period and for the following 10 min. During the experiment I noted distance between the speaker and the subject group every 30 sec.

Three groups acted as subjects in each experiment. By testing one group each day, I allowed two days between successive tests to each group, and thus reduced the possibility of habituation. For other precautions used and for experimental details, see ROBINSON (1981).

Each presentation began after morning calling when the subject group had not vocalized for 10 min, and lasted for 10 min after the playback. The speaker was placed approximately 60 m from the subject group, and inside the boundary. All presentations began between 0620 and 0915.

In each experiment, the three test vocalization types were presented to three groups and replicated for a total of 18 presentations. Groups and treatments were completely crossed and each presentation was replicated to allow calculation of an error sum of squares. Thus the effect of group differences and treatments on vocal response could be detected with a two-way analysis of variance (HAYS, 1973). However, in the first experiment, Group 2 moved out of the area after the first three test presentations, so I was unable to replicate presentations to this group. The resulting small sample size precludes the use of statistical analysis in this experiment, so I simply present the mean and standard deviation of the vocal response to each treatment.

RESULTS

ASSOCIATION OF VOCALIZATIONS WITH CONTEXTS

Figure 2 illustrates the proportion of each vocalization in the five contexts at both FS and FLM. Groups move toward a boundary in the early morning and then call (Context E). CP and male calling sequences, in which the male calls alone, occur most often at this time. I noted no response from other group members, but neighboring males often responded with similar vocalizations.

First calling often is followed by convergence of neighboring groups on a common boundary. Usually only the mated pair move, while the juvenile and infant (if off the male's back) remain at or near the site of the first calling bout. Duets predominate during Contexts B, C and D, while the frequency of male calling and CPs declines with the approach to other groups.

As a group approaches the boundary and the neighboring group (Context A), the percentage of time spent duetting drops. This decreased tendency to duet as groups come near each other is reflected in two other measures: The proportion of honks, a low intensity call which normally ends duets, is significantly higher in Contexts A, B and C compared to Contexts D

Table 2. Duration of duets (sec) in five contexts.

	Context				
	A	B	C	D	E
Mean	31.27	36.86	63.52	65.88	60.41
S.D.	21.58	33.73	48.79	49.67	29.82
N	52	108	63	31	14

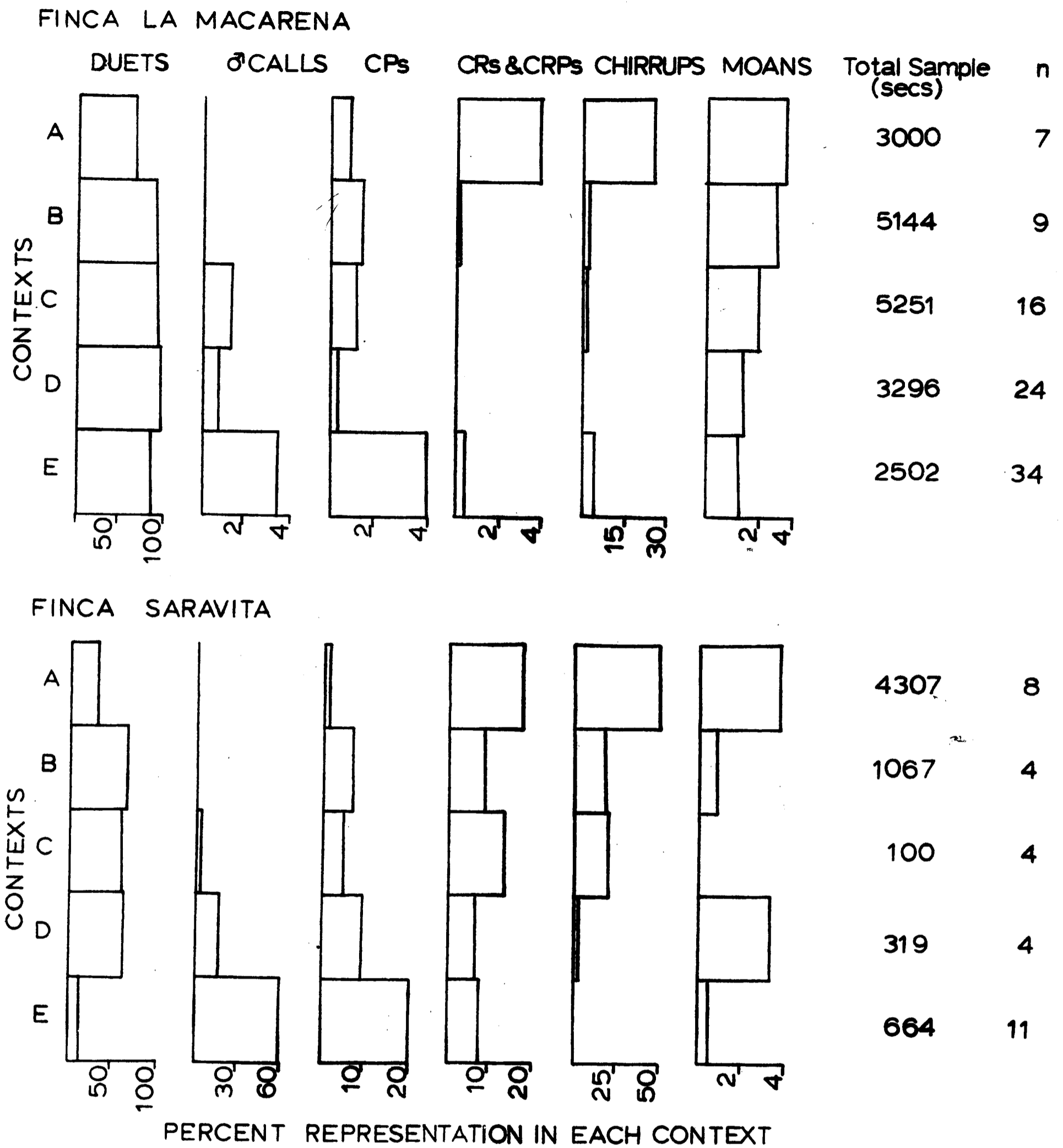


Fig. 2. Variation in the proportional use of vocalizations in the contexts at Finca la Macarena and Finca Saravita. Each row specifies one context, and columns illustrate the percent representation of each vocalization. n: number of recorded interactions or isolated calling bouts used for this sample.

and E ($p < 0.001$, Mann-Whitney U test). And the mean durations of duets in Contexts A and B (Table 2) are significantly lower than the mean duet durations in Contexts C, D and E ($p < 0.01$, for each comparison, two-tailed t test).

At the boundary animals moan more. This is primarily a within-group signal; in other circumstances this vocalization stimulates the calling animal's mate to approach (ROBINSON, 1979b).

The proportions of three other vocalizations also increase. Chirrup, which in other contexts are associated with disturbance and flight, increase. CR and CRP sequences also increase. These sequences are produced in other circumstances when an animal's tendencies to approach and withdraw are balanced (ROBINSON, 1979b). These vocalizations stimulate a response with the same vocalizations, and groups soon begin to move away from each other

and the boundary. Following encounters, groups occupy areas near the home range center for the rest of the day.

EFFECTS OF VOCALIZATIONS ON SPACING BETWEEN GROUPS

Three stages are discernible during an interaction between groups. The first, when males first call with CP and male calling sequences in the early morning, is not associated with movement towards a boundary. These vocalizations appear to identify the location and proximity of neighboring groups. Both of these variables affect the probability of subsequent approach to a boundary, as ROBINSON (1979a) demonstrated by playing back CPs from either the center or the periphery of the range, and from either near (<40 m) or far (>80 m) from the subject group.

If groups are not widely separated or if they are near a common boundary, there is an increased probability that they will begin to approach each other. During this stage the mated pairs duet. Duetting stimulates the neighboring group to approach, for groups move towards calling neighbors when the latter are duetting.

The final stage, at the boundary, is characterized by a decreased tendency of animals to duet, and thus approach one another, and an increased tendency to give chirrups, CRs and CRPs, and thus withdraw from the proximity of the neighboring group and the boundary.

EFFECTS OF VOCALIZATIONS ON SPACING OF THE MATED PAIR

During CPs and male calling the pair can be separated by up to 20 m, but during duetting, in addition to the close synchronization of each mate's vocal contribution (ROBINSON, 1979b) the pair are spatially coordinated, normally within 1 m of each other and usually touching. If separated further, mates are probably unable to hear each other well enough to sustain the duet. Thus during the approach stage of boundary interactions, members of the pair are close to one another. At the boundary, duetting declines in frequency, but this is not accompanied by a breakdown in the pair's spatial coordination, for moaning increases. Moaning keeps the pair in close proximity to one another by constantly stimulating the approach of the calling animal's mate. Thus during both the approach and the withdrawal stages, vocalizations, first duetting and then moaning, keep the members of the pair close to one another.

PLAYBACK RESULTS

Some of these inferences of the effect of vocalizations on the spacing between groups were tested by playing back recordings and noting the vocal and spatial responses of the subject group.

Responses to Playback of CPs, CRPs and Chirrups

This experimental series compared responses to three vocalizations which are associated with the different stages of the interaction: identification of location, approach and withdrawal stages. CPs occur in the first calling bouts, CRPs express a strong tendency to approach as well as to withdraw and animals give chirrups when they are withdrawing. In addition, the vocalizations are structurally similar. Chirrups are an important constituent of the other two. In CPs, chirrups lead into pumps, while in CRPs they lead into pants, then pumps.

Thus one would predict that playback of CPs would elicit CPs and male calling from the subject group, but there would be no tendency to approach. CRPs should elicit approach and the vocalizations associated with approach—duets and CRPs; and chirrups should elicit chirrups and the subject group should move away.

The playbacks did not produce any detectable difference in spatial response; groups always approached the speaker rapidly. Two factors might explain these results. To avoid interference from neighbors, the speaker was placed just inside the boundary of the subject group. It is unusual for another group to call from this location. In addition, the high within-treatment variance in approach tendencies, probably influenced by the original position of the subject group and their subsequent approach route, would mask between-treatment effects.

However, vocal differences were detected (Fig. 3), and were in accord with expectations. CP sequences elicited frequent CP responses in all presentations, and male calling in three of the five presentations. Only CRP sequences stimulated duetting from subject groups, and chir-

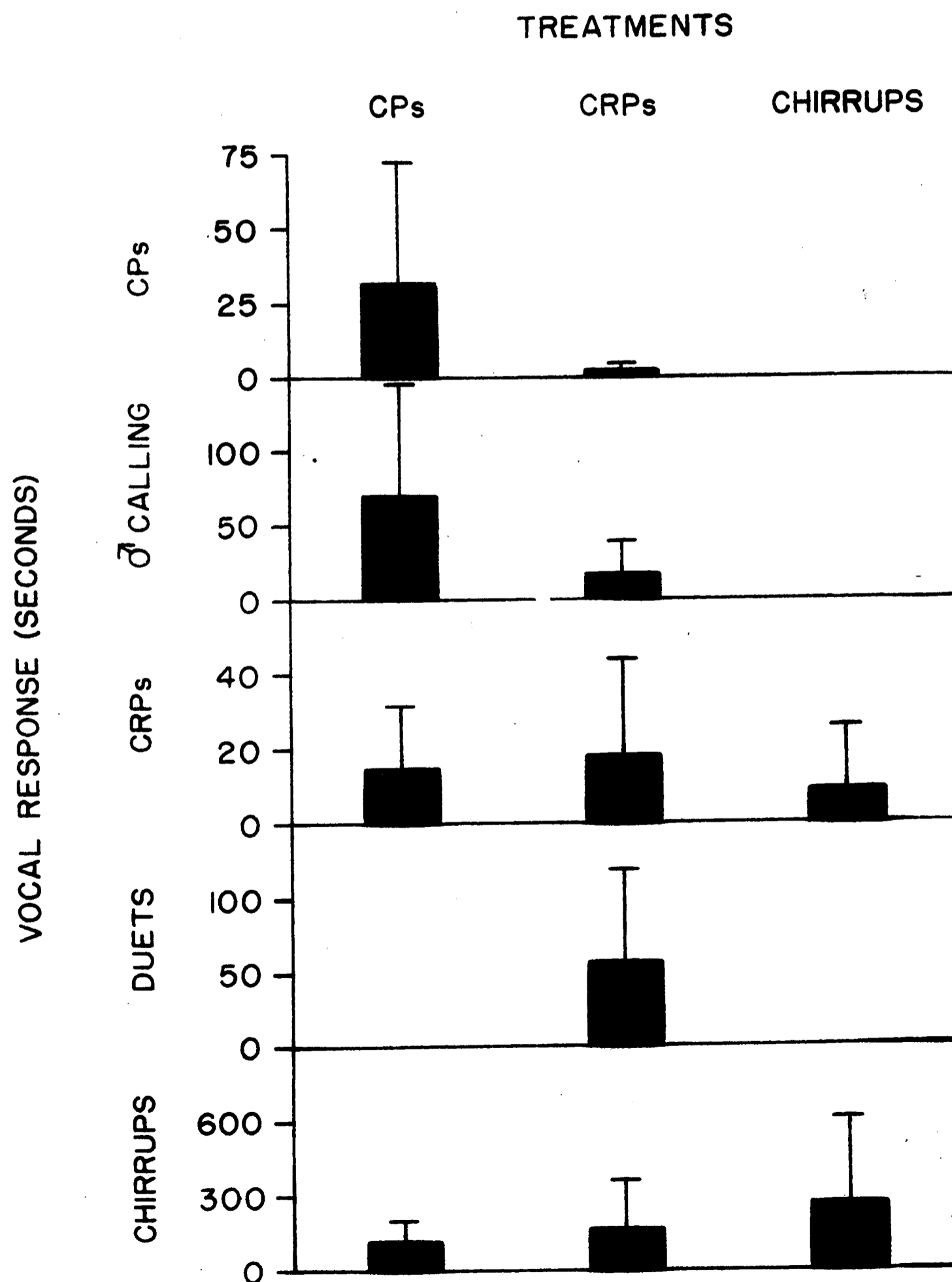


Fig. 3. Vocal responses in seconds to experimental playback of CPs, CRPs or chirrups. For each of five vocal classes the mean and standard deviation of the response to each treatment is illustrated.

ruping elicited a very weak vocal response. In three of the five chirrup tests groups approached but did not vocalize. In the other tests they only chirruped.

Responses to Duets, Male Calling and Female Calling

This experimental series compared responses to male calling and duets, the two complex, long sequences, the former apparently identifying the location of the calling group and the latter stimulating the approach of a neighboring group. The series also examined responses to female calling. Whereas duetting and male calling are common in natural circumstances, female calling was recorded only three times, twice in response to playback.

From the association of vocalizations with contexts one would expect subject groups to respond to playback with similar vocalizations. Playback of duets should elicit approach to the speaker, while playback of male calling should not. However, using an analysis of variance, I detected no significant differences in use of any vocal class among treatments although the average duetting response following playback of duetting ($\bar{X} = 172 \pm 96$ sec) was longer than that following male calling ($\bar{X} = 82 \pm 55$ sec). Neither did I detect any difference in the measures of spatial response: latency of approach, speed of approach and time spent within given distances of the speaker.

The absence of a significant difference between responses to male calling and duetting probably resulted from the location of the speaker 40 m inside the boundary and 60 m from the subject group. Neither duetting nor male calling occurs naturally at this location, and male calling normally occurs when groups are separated by more than 100 m. Perhaps effects of location and proximity override effects of different vocalization types.

While the mean total response with each class of vocalization did not differ among the three treatments, presentation of female calling elicited a strong response from the female of the subject group. During the first presentation to Group C, the female and the juvenile female reached the speaker when the male was still 20 m away and began female calling synchronously. In response to four of the six presentations of female calling, the female arrived at the speaker location at least 10 m ahead of the male. During the second presentation to Group CR, the female CPed alone. During another test, the Group T female, giving high pitched vocalizations, descended from a tree and closely examined the speaker.

As duetting can be initiated by moaning from either sex, one difference in the sexes' responses to the three treatments might be their relative contribution in initiating duets. Although animals start moaning almost simultaneously, the slight differences are probably a good indicator of which animal is responding more strongly. Table 3 presents the sex differ-

Table 3. Differences between sexes in the initiation of duetting sequences in response to three treatments.

Initiator	Treatments		
	Duetting	Male calling	Female calling
Male	21	30	2
Female	2	0	29
Unknown	14	4	12

Entries are the number of times each sex initiated a duetting sequence in response to playback of duetting, male calling and female calling. Overall statistical association between treatments and initiator, excluding unknowns, $G = 82.2$, $df = 2$, $p < 0.001$. Goodman and Kruskal index of predictive association, information about one category reduces the probability of error in the second: given the sex, $\lambda_A = 0.87$; given the treatment, $\lambda_B = 0.53$.

ences in initiation of duetting sequences during experiments. Unknown initiations occurred when animals were too distant or too closely synchronized for me to distinguish the initiator. Males generally initiated duetting during presentation of male calling and duetting, while females initiated duetting in response to female calling ($p < 0.001$, G log-likelihood test).

DISCUSSION

The first calling bout in the morning identifies the location and proximity of neighboring groups. At this time males, whose loud calls transmit up to 500 m, often call alone, especially at FS when intergroup separations are generally greater than at FLM. If groups begin the approach, the mated pair begin the vocally synchronized duet. The quieter female calls cannot be heard 50 m away, but her contribution alters the transition probabilities between phrases in the male's vocal sequences (ROBINSON, 1979b). As a result neighboring groups can discriminate between mated pairs and solitary males as soon as male calling and duetting become distinguishable. To a human listener on the ground, the critical distance for this discrimination is about 250 m from the vocalizing pair. Thus when an intergroup separation during the first calling bout is over 250 m, as it usually is at FS, there is no advantage in female participation. This discrimination between pairs and solitaries ensures that animals only approach neighboring groups. Animals do not respond strongly to male calling by non-resident males that are outside the group's range.

Vocal synchronization of members of the mated pairs ensures that they are spatially coordinated. At the boundary this has two consequences. First, the two animals side by side probably present a more imposing stimulus to neighboring animals. Pairs of many duetting species which encounter neighbors at boundaries are spatially coordinated (*Laniarius* shrikes: THORPE, 1972; orange-chinned parakeets: POWER, 1966; stripe-backed wrens: WILEY & WILEY, 1977). Second, close proximity to the mate enables each animal to prevent neighboring animals from obtaining sexual access to its mate. This is a potential problem, for MASON (1966) reports between-group copulations during boundary encounters in *C. moloch*.

This second interpretation is supported by the observation that in monogamous primates, animals are more aggressive towards like-sex conspecifics. In gibbons, CARPENTER (1964) reports an interaction in which a young male repeatedly approached the resident female, only to be chased away by her mate. The female ignored the intruder. In Kloss' gibbons, TENAZA (1976) gives an account of a female chasing intruding females from the territory while the male ignored the trespassers. Male calls in these gibbons stimulate similar vocalizations from males of adjacent groups, while females reply to female calling. BROCKLEMAN, ROSS and PANTUWATANA (1974) present evidence that before territories are established, male gibbons chase away other males, and females expel other females. Captive marmosets are more aggressive towards conspecifics of the same sex (EPPLÉ, 1975).

Gibbon and siamang pairs avoid this problem because only one sex approaches the boundary. Male siamangs and white-handed gibbons display at the boundary and chase one another while the females and offspring remain at a distance (CHIVERS, 1974; ELLEFSON, 1974). In Kloss' gibbons, it is the females that approach and call at the boundary (TENAZA, 1976).

Although in *C. moloch* both sexes approach the boundary, the sexes differ in behavior. As distance between neighboring groups decreases, the probability of female participation in the long vocal sequences increases (i.e., the proportion of male calling declines as duetting increases). During close intergroup interactions the female is vocalizing so strongly that spec-

trographic analysis of the overlapping contribution of males and females is difficult. In this context, the female moans to initiate duets more than the male and maintains duets by continued vocalization during the increasingly frequent pauses in the male's contribution. Yet, in spite of this increased female duetting, the proportion of duetting in the total vocal output falls due to the male's decreased tendency to duet as groups come closer together.

Thus there is sexual differentiation, not only in the amplitude characteristics of duetting vocalizations, but also in the circumstances of their use. The male's contribution is loud enough to communicate between groups, identifies the group's location, and regulates the approach to a boundary. The female's contribution affects the male's sequences, and its prominence during close-range interactions constrains the spacing of the pair. MASON and his associates (e.g., MASON, 1971, 1975; MASON & EPPLE, 1969) found that in captive *C. moloch*, males are less xenophobic than females, a characteristic which is consistent with a role in coordinating the movement of neighboring groups to a boundary. Females showed a greater preference than males for their mates when in the presence of strangers, which is consistent with a role in maintaining the close proximity of the pair during interactions with neighboring pairs.

At the boundary, vocalizations associated with approach are replaced by vocalizations which occur when tendencies to approach and withdraw are balanced or when animals are withdrawing. Termination of the encounter does not involve a "retreat"; instead, one or both groups move quietly away and begin feeding. Intergroup interactions are not efforts in "territorial expansion." They involve regular definition and reinforcement of the conventional location of boundaries (ROBINSON, 1979a). Establishment of boundaries in turn allows the exclusive use of space.

Exclusive use of space allows exclusive access to resources, and it can only evolve if the home range reliably contains enough to eat. It also excludes sexual competitors from the home range. The consistent association in primates between monogamy and exclusive use of space suggests that the exclusion of sexual competitors has been important in the evolution of territorial behavior in monogamous primates. Members of the *C. moloch* pair are never close to extragroup animals except at the boundary, where mates are close to one another. Within their boundaries mates frequently forage 50 m from one another, but as they rarely encounter other animals, they can be relatively certain of their offspring's parentage, a necessary condition for the evolution of dual parental care.

Monogamy in primates is associated with small group size, dual parental care, exclusive use of space and vocal and spatial coordination between the male and female. These characteristics form an adaptive complex. Defense of boundaries is only possible when the diameter of the home range is small in relation to the daily path length. Small home ranges are only possible in species which live in small groups and exploit relatively dense resources which are predictable in time and space. Vocal and spatial coordination during boundary encounters enables the pair to define and reinforce the location of the boundary, while preventing sexual access to the mate from neighboring animals. Boundaries enforce exclusive use of space, which in turn ensures that sexual competitors will not usually be encountered on the home range. Exclusive access to a reproductive partner allows dual parental care and cooperation in boundary defense.

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Author's Name and Present Address: JOHN G. ROBINSON, *Florida State Museum and Department of Zoology, University of Florida, Gainesville, Florida 32611, U.S.A.*