

Vocal Regulation of Use of Space by Groups of Titi Monkeys *Callicebus moloch*

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Summary. The daily movements and the resulting activity and calling fields are described for three groups of titi monkeys *Callicebus moloch*. Groups move to the periphery of their home range in the early morning and then call. Playback experiments confirmed that both proximity and location of calling by neighboring animals affect the group's response. Subsequent counter-calling often regulates the approach of neighboring groups to a boundary. After encountering adjacent groups, animals return to areas near the home range center. Movements, calling behavior, and the response to neighboring groups all increase the probability of intergroup encounters in the early morning. Encounters define and reinforce the conventional location of boundaries. Boundaries decrease the probability of intergroup encounters at other times and allow exclusive use of space.

Introduction

Callicebus groups do not use all areas within their home ranges equally (Mason, 1968). This study describes variations in groups' use of their home range and the vocal regulation of spacing between groups.

Two types of models can describe the distribution of an animal's time within its home range. Based on the assumption of no behavioral or topographic limit to movement, some models of movements predict that intensity of use declines with distance from a center of activity according to a specified statistical distribution (reviewed by van Winkle, 1975). While having the advantage of mathematical simplicity, these models are not biologically realistic for primate home ranges. Many primatologists (e.g., Struhsaker, 1967, 1975; Mason, 1968; Altmann and Altmann, 1970; Fossey, 1974; Chivers, 1974; Clutton-Brock, 1975; Waser, 1976) have found it useful to superimpose a grid on the group's movements

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and calculate density of quadrat usage. The resulting probability distribution of an animal's time is termed the activity field (Wiley, 1973; Waser and Wiley, 1979). The quadrat size determines the accuracy of the estimate of total area and the resolution of differences in use with locality.

If calling affects movements of adjacent groups, interspecific variation in the temporal and spatial distribution of calling might reflect different mechanisms of intergroup spacing. I describe the spatial distribution of calling, or the calling field, and the activity field for each *Callicebus* group.

Then I consider three questions. First, what are the stimuli associated with the production of loud intergroup calls in *Callicebus*? Second, what conditions determine the response to loud calls? I examined the contributions of location and proximity of calling animals by playing back recorded vocalizations to subject groups. Third, how does this response regulate the spacing between groups, and thus generate the observed patterns of use of space and intergroup overlap?

Materials and Methods

I examined *Callicebus* populations in gallery forest at two sites, Finca la Macarena (FLM) and Finca Saravita (FS), near San Juan de Arama, Meta, Colombia. The use of space by three groups (groups T, C, and Cr) was studied continuously from 26 January to 8 April 1976 at FLM. All three groups consisted of an adult pair, a juvenile animal which appeared slightly smaller than the adults and exhibited some vocal differences (see Robinson, 1979), and an infant carried by the male until the last week in March. Supplementary observations are included from FS.

I cut trails every 80 m to form a grid in the area occupied by the three groups. Every 20 m along trails I attached numbered surveyor's tape to trees. Thus I was able to place sightings of a group on a grid of 20 × 20 m quadrats. Neville (1975) and Freese (1975) found that observers can detect groups of *Callicebus* within 20 m. I found a detection distance of 40 m applied at FLM. While remaining on the trails, I could detect all *Callicebus* monkeys in the study area.

Before 0800 each morning, I located groups by approaching calling individuals. In a regular rotation I focused on one of the three groups each morning. I recorded the quadrat in which I first found the group and each new quadrat entered.

After 0800 I systematically searched for groups by slowly walking along trails in the grid. I compensated for the time spent searching each portion of the trails by dividing the total search time by the number of 20 m segments in that portion. Assuming an audiovisual distance of 80 m (twice the detection distance, see above), I then assigned this search time to two quadrats on each side of the trail. This method might bias against quadrats farther from the trail, which were not examined as closely, yet because I could sometimes detect groups at distances over 40 m, farther quadrats were in fact searched from two trails. I did not add the time spent following groups to the overall search time for each quadrat; this bias is minor as the time spent following groups was much less than the total search time.

I computed the probability of encounter for each group for the periods before and after 0800 and described the activity fields for both time periods. I then derived the activity field for the entire day by a weighted addition of probabilities:

$$P(E_x) = \frac{[P(E_{xa}) \times 3] + [P(E_{xb}) \times 9]}{12}$$

where $P(E_x)$ is the probability of encountering a group in quadrat x at a time taken at random during the day, $P(E_{xa})$ is the probability of encounter in quadrat x at a time between 0500 and 0800, and $P(E_{xb})$ is the probability of encounter in quadrat x at a time between 0800 and 1700. The spatial distribution of these probabilities defines the overall activity field.

A number of methods have been used to measure the degree of overlap (see review in May, 1975). I have used the simple index suggested by Holmes and Pitelka (1968) which sums the probability of overlap between two groups for all quadrats:

$$O_{ij} = 1 - \frac{1}{2} \sum |P_{ia} - P_{ja}|$$

where O_{ij} is the overall overlap between the i and j groups, and P_{ia} is the probability of occupancy of quadrat a by the i group.

Hypotheses of the effects of proximity and location on the vocal and spatial response of *Callicebus* groups were tested by playing back recordings of calls to subject groups.

I compared the response of each group to four treatments: near-center, far-center, near-periphery, and far-periphery. I placed the speaker at the approximate geographic center of the home range for 'center' playbacks and at a location 20 m inside the exclusive space of the subject group for 'periphery' playbacks. I considered groups 40 m or less from the speaker as 'near' and those 80 m or more as 'far'. Each treatment to each group was replicated (3 groups \times 2 locations \times 2 distances \times replication = 24 playbacks).

For these playbacks I selected chirrup pumping (see Robinson, 1979), recorded from distant male animals which the subject group could not hear. This vocalization apparently identifies the location of the calling animal, and occurs during the first morning calling and during movements near boundaries (Robinson, 1979). Each recording for playback was composed of five one-minute recordings of chirrup-pump repetitions, delivered at a rate similar to that of rapidly calling animals. Each one-minute playback was followed by a minute of silence. Test sequences were played from a Uher 4000-L tape recorder over a Magitran speaker (33 \times 41 cm, flat response to 20,000 Hz) which was placed 3 m high in a tree and aimed at the location of the subject group. To control intensity of playbacks, I played back the test tapes at an identical setting of the Uher volume control. The intensity of playback, as judged by ear, was similar to that of a calling monkey.

I began playback when the experimental group had not vocalized for at least 10 min and had moved to the appropriate distance from the speaker. All experiments were started between 0600 and 0800. I played back recordings to one group each day. Using a Nagra IV tape recorder and an MKH 815 Sennheiser directional microphone, I recorded all vocalizations and behavior during the playback period and for the following 15 min, or until the subject group began interacting with an adjacent group.

By completely crossing groups and treatments and replicating to allow the calculation of an error sum of squares, I could analyze the effect of group differences and treatments on vocal response by using a two-way analysis of variance (Hays, 1973).

Results

1. Description of Activities

Callicebus groups spend the night in a tight huddle with tails entwined. About 0515 the animals urinate, defecate, and leave the usually dense-foliaged sleeping tree. The first movement is slow, and the animals leave and return to the sleeping tree for a few minutes. Occasionally animals moan (see Robinson, 1979) quietly. This period is followed by a rapid movement by all animals toward a boundary, during which animals rarely stop to feed. This movement occurs before neighboring groups begin calling. Movement toward boundaries is thus not a direct response to the calling of neighboring groups. On arriving in a boundary area, the adult pair and sometimes the offspring huddle together high in a tree. Sometimes there is sporadic feeding. The particular boundary chosen is determined by the experiences of the preceding days. Calling by neighboring groups at a boundary, or an intergroup interaction, predisposes the

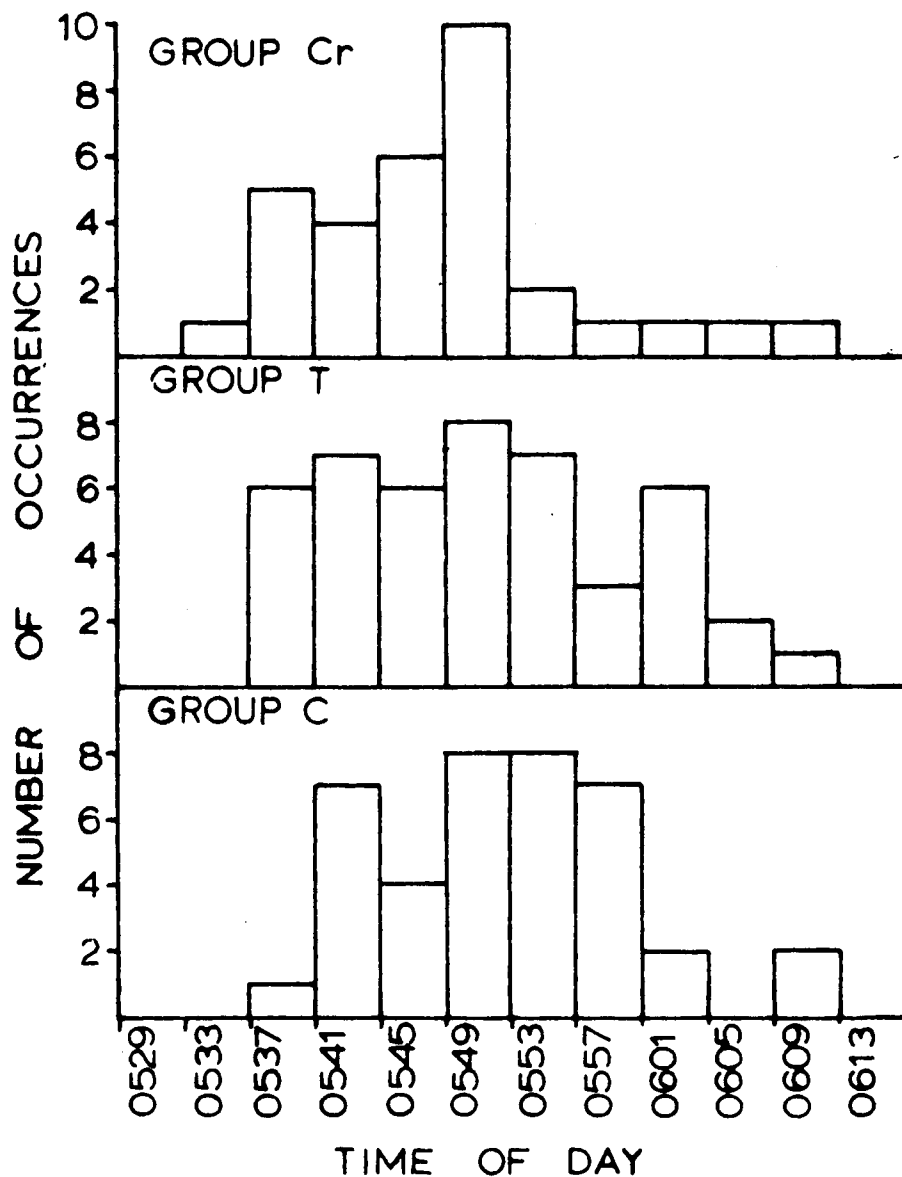


Fig. 1. Temporal distribution of the first calling bout given by groups T, C, and Cr

group to return to that boundary on succeeding days. Calling by each group begins at a similar time each day (Fig. 1) and is either spontaneous or triggered by nearby calling.

Subsequent behavior depends on the location and proximity of neighboring groups. If groups are close together or within the zone of overlap, they begin alternating calling bouts and approach one another. The juvenile and infant (if off the male's back) usually take no part in this final movement, never call, and usually forage or play until the boundary interaction is over. The adult pair call during the pauses between the neighboring group's bouts and move toward the boundary when neighboring animals are calling. At any time during this progression toward the boundaries, animals can cease calling and move away to forage. Frequently, however, this response to calling brings pairs and occasionally offspring together at a boundary.

If no neighboring groups are close to a boundary or in close proximity following the first morning bout, groups forage in the boundary zones, vocalizing sporadically, until about 0800. Then they move back into areas near the home range center.

I have defined boundary encounters as any interaction in which groups were within 30 m of each other and probably in visual contact. During the final approach to neighboring groups, animals perform jump displays, long stiff-legged jumps downward into foliage. The shaking of branches and leaves makes an impressive noise. Encounters are usually limited to calling and associated arch postures, piloerection and tail lashing (Moynihan, 1966; Mason, 1966, 1968). Chases were infrequent, but when did occur they usually involved animals of the same sex. Both sexes were actively involved in boundary encoun-

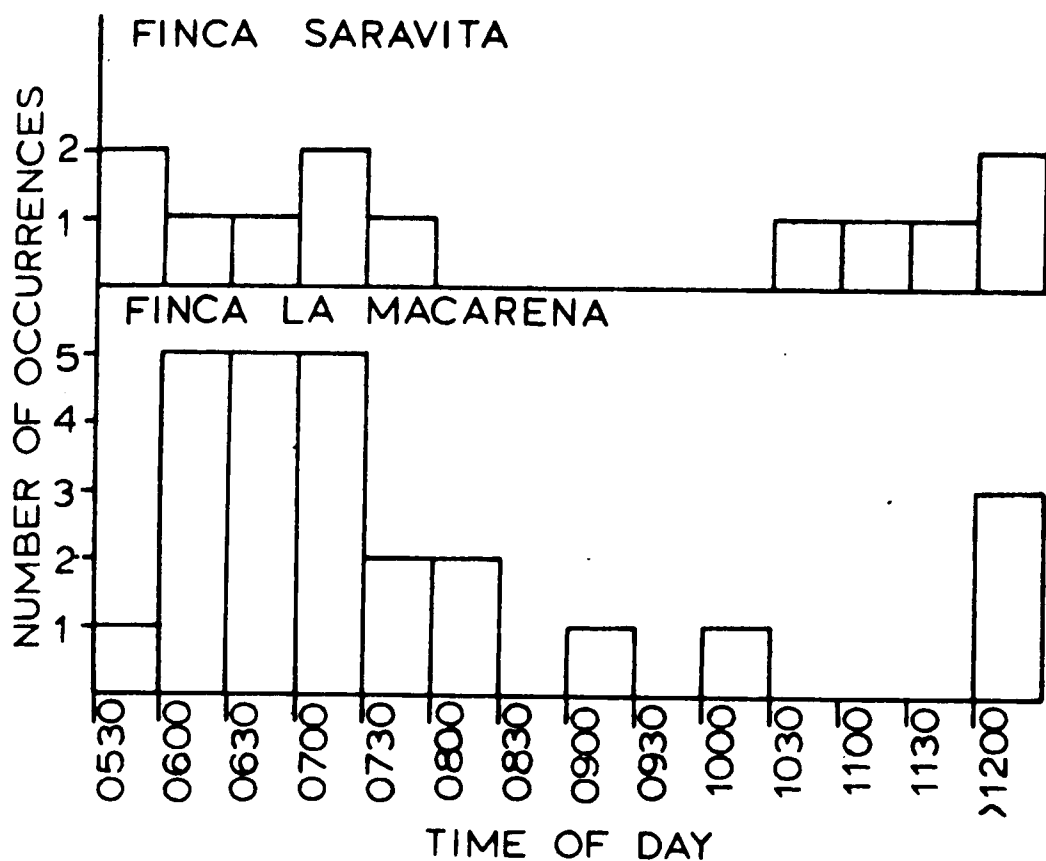


Fig. 2. Temporal distribution of the beginning of boundary encounters at Finca Saravita (FS) and Finca la Macarena (FLM)

ters. Approximately 65% ($n=35$) of all boundary encounters began before 0730 (Fig. 2). Encounter duration was longer at the FLM site ($\bar{x}=41$ min, $SD=21$ min, $n=23$) than at the FS site ($\bar{x}=29$ min, $SD=23$ min, $n=12$).

Encounters terminated when one or both groups calling and moved quietly away. Animals occasionally began foraging at the encounter site but commonly moved in the direction of the territory center before feeding. Groups spent the rest of the day principally in quadrats near the home range center.

2. Activity and Calling Fields

Figure 3 shows the probability distribution of encountering each group during the periods before and after 0800. Comparison of these two activity fields for each group reveals an overall shift in quadrat usage toward boundaries before 0800. Many quadrats at the periphery of the ranges are only occupied at this time. The division at 0800 was arbitrary but allowed the clearest distinction between early morning movement to boundaries and the subsequent utilization of quadrats near the home range center.

Figure 3 also presents the overall activity field for each group. If the home range is stable, an observer will less frequently encounter groups in new quadrats with time. This relationship describes a curve whose asymptote is the area of the home range. The cumulative number of 20×20 m quadrats entered over the course of the study does not reach a clear asymptote for any of the three groups (Fig. 4). However, use of quadrats near boundaries was detected early in the study because of the ease of locating calling animals. I observed animals entering most other quadrats within these boundaries by the study's end, so the sum of quadrats used is actually a good estimate of the home range size. Nevertheless, it is useful to have an estimate of the quadrats missed. Waser and Wiley (1979) suggest using Preston's lognormal distribution (Preston, 1948,

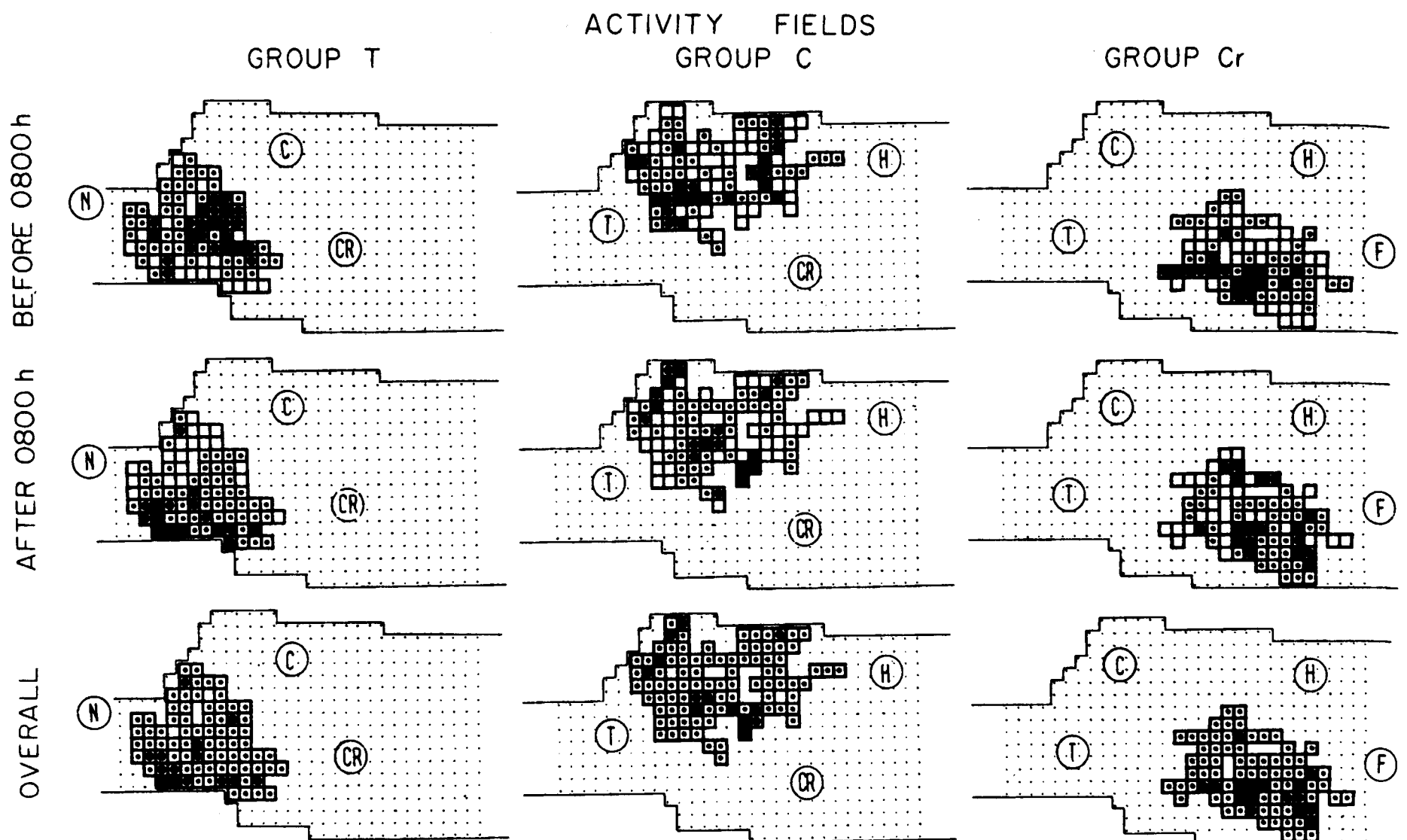


Fig. 3. Activity fields for groups T, C, and Cr before 0800, after 0800, and overall for the entire day. *Dots* define the total grid of 20×20 m quadrats. *Outlined quadrats* are those of groups T, C, and Cr, respectively. Percentage of use of each quadrat: *blank*, 0%; *small black circles*, 0–2%; *large black circles*, 2–3%; *black squares*, >3%. *Circled letters* identify neighboring groups

1962) to estimate the total number of quadrats in a home range by extrapolating the quadrat utilization curve below the class of minimum use or 'veil line' and adding the expected frequencies.

I used the lognormal distribution to estimate the number of undiscovered quadrats for each group and thus the home range area. As pointed out by Bliss (1965), equal grouping of intervals is not required to fit a normal distribution, and coarse grouping reduces the sensitivity of the estimate. I therefore divided frequency of usage into groups every 1%, starting at 0.5%. Cohen (1959, 1961) gives tables of auxiliary functions to estimate the mean and variance of a truncated normal distribution. I used the method outlined by Bliss (1965) to fit the lognormal distribution to my data on frequency of quadrat utilization (the fitting of truncated lognormal distributions to data is also discussed in Slocumb et al., 1977). The goodness of fit of my data to the lognormal distribution was tested with the χ^2 statistic (Hays, 1973). The distribution of quadrat usage did not significantly differ from log normal for all three groups ($P > 0.05$). I converted the point of truncation to a standardized z score and estimated the proportion of undiscovered quadrats from tables of the normal distribution. Table 1 presents the actual number of quadrats used by each group during this study, estimates of missed quadrats from the lognormal distribution of quadrat usage, and the calculated home range sizes. Home range sizes were considerably larger than those reported by Mason (1968), whose groups, in a very similar area, ranged over about half a hectare.

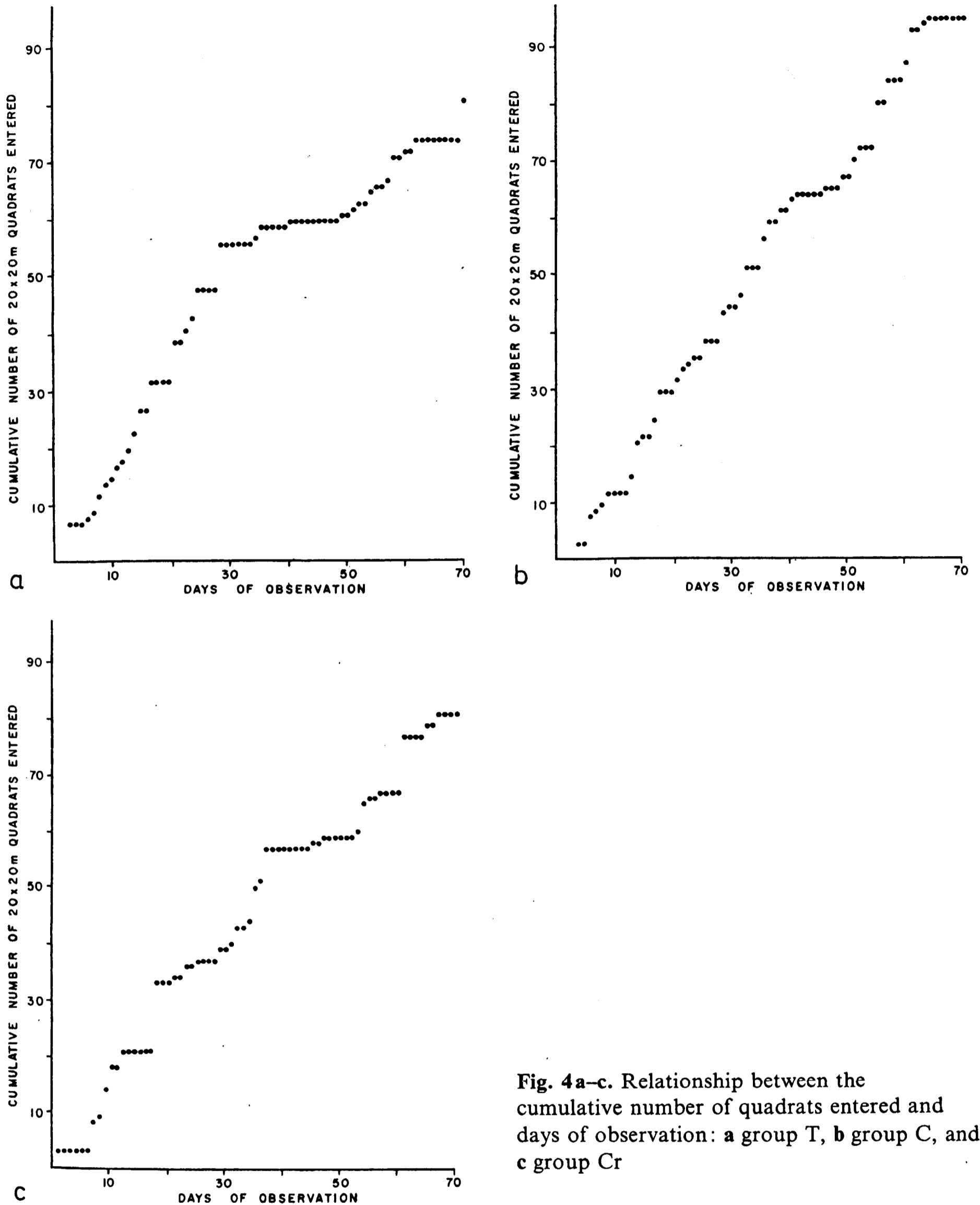


Fig. 4a-c. Relationship between the cumulative number of quadrats entered and days of observation: a group T, b group C, and c group Cr

Callicebus groups occupy almost exclusive territories. During this study, the home ranges of groups T and C overlapped extensively along one boundary, and interactions between these two groups were common. Overlap was 16.6% during the period before 0800 but only 1.7% after 0800. Group Cr overlapped only slightly with C (0.9% before and 1.4% after 0800) and not at all with group T. There was no overlap between groups T and N, and only slight overlap between groups C and H and between groups Cr and F.

Table 1. Home Range Size: The number of quadrats occupied is the number of quadrats in which I found each group. The percentage of the total home range that this represents was calculated using the lognormal distribution (see text), and thus the home range was calculated

Group	Number of 20 × 20 m quadrats occupied	Percentage of range observed	Estimated home range size (hectares)
T	80	97.2	3.29
C	95	91.0	4.18
Cr	81	92.5	3.50

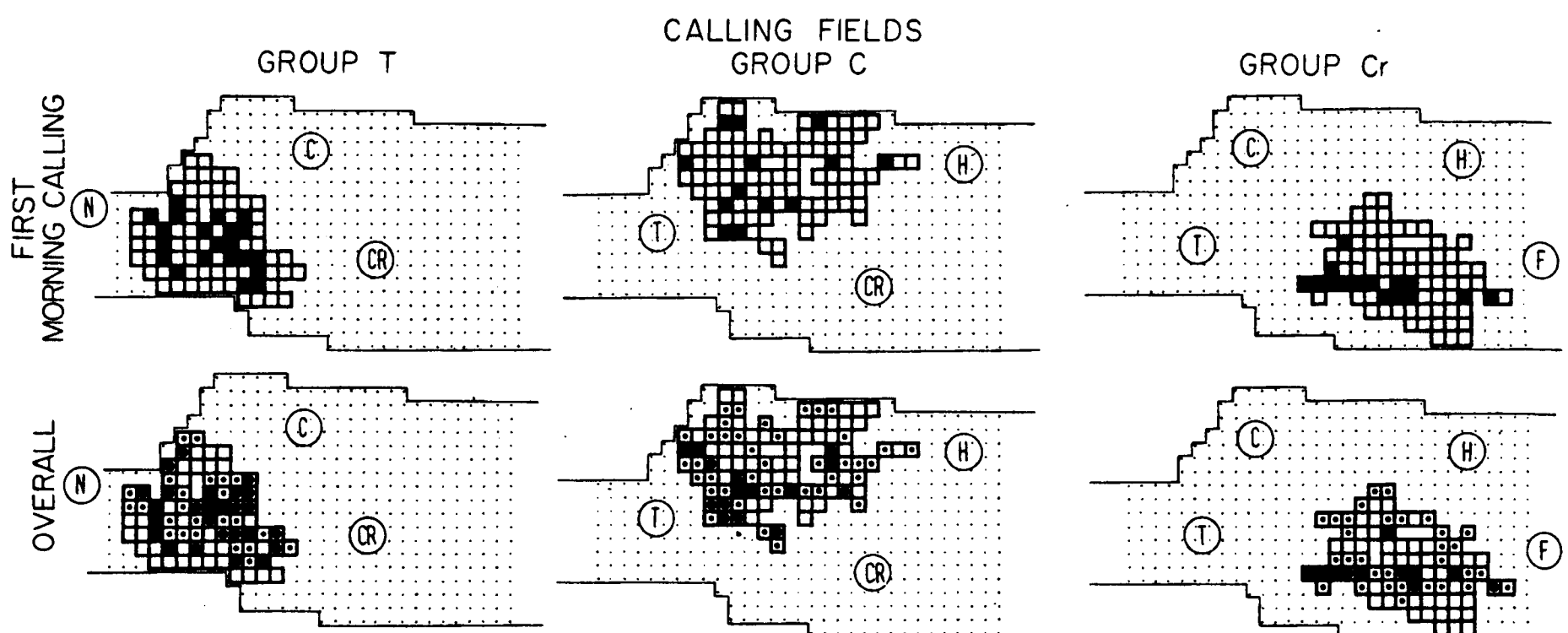


Fig. 5. Calling fields for groups T, C, and Cr for the first morning calling bout and for the entire day. Other details identical to Fig. 4

The spatial distribution of first calling bouts illustrates the tendency of groups to move to boundaries before calling (Fig. 5). The same pattern is evident on examination of the overall calling field; animals tend to call near boundaries. This distribution results partly from the increased level of calling before 0800, a time when groups are near boundaries, and partly from the higher probability of calling when in peripheral areas at other times of the day.

3. Playback Results

Table 2 presents the vocal responses of each subject group to four treatments during the first 20 min of each experiment. Only variations in duetting, moaning, and chirruping were analyzed, as other vocalizations were not consistently evoked by any treatment. Duetting, a long, complex sequence of different calls involving close vocal and spatial coordination between a mated male and female, is associated with approach to neighboring pairs at a boundary. Moaning, a call that has the effect of bringing the pair together, is often a prelude to duetting sequences. Chirruping is a call often associated with flight from a disturbance. These vocalizations are described in Robinson (1979).

Table 2. Vocal Response to Playback at Two Locations and Two Distances: The playback speaker was located at one of two locations, at the center or at the periphery of the territory, and playback began when the subject group was either close to the speaker (less than 40 m away) or far (more than 80 m away).

Each row is the vocal response during the first 20 min of one experiment. Duetting, moaning, and chirruping are discussed in the text. ♂ calling and ♀ calling are long vocal sequences given by the male or the female, respectively. CPs, CRs, and CRPs are short vocal sequences. For discussions of context and effect on other animals of each vocalization, see Robinson (1979)

Groups	Vocal response (s)						
	Duet	♂ Call	♀ Call	Moan	Chirrup	CP	CRP and CR
1. Near-periphery playbacks							
T	582	0	0	25	11	0	0
C	424	0	0	15	0	0	0
Cr	178	0	0	14	41	0	2
T	347	0	0	12	63	0	0
C	447	0	51	41	4	4 ^a	0
Cr	0	0	0	8	0	0	0
2. Far-periphery							
T	0	0	0	10	0	0	0
C	195	0	0	0	0	28	0
Cr	116	0	0	0	91	4	9
T	57	0	0	5	0	0	0
C	0	0	0	2	3	0	0
Cr	156	0	0	0	0	24	0
3. Near-center							
T	175	0	0	21	27	0	0
C	248	0	0	46	0	0	0
Cr	77	12	0	36	430	6	60
T	0	0	0	7	0	0	0
C	31	0	0	18	643	0	10
Cr	0	0	0	0	7	0	0
4. Far-center							
T	0	0	0	43	0	0	0
C	37	0	0	5	0	0	0
Cr	0	0	0	0	0	2	0
T	39	0	0	9	0	0	0
C	0	0	0	0	13	0	0
Cr	0	0	0	0	0	0	0

^a Given by the female

A two-way analysis of variance of duetting response indicates that there is a significant difference between treatments ($P < 0.01$), but no difference in response between groups ($P > 0.05$) and no interaction between groups and treatments ($P > 0.05$). Treatments affected response, but groups responded in similar ways to treatments.

This result justifies lumping the results obtained from all three groups for an analysis of the effects of location and proximity on duetting response. The

calculation of the error sum of squares is now based on six values in each cell, and location and proximity effects are still completely crossed and balanced.

There was a significant effect of location ($P < 0.01$) and proximity to the speaker ($P < 0.01$), but no interaction between location and proximity ($P > 0.05$). *Callicebus* pairs duet more in response to calling from nearby and from the territorial boundary. These two effects are independent; the effect of proximity does not change with location nor vice versa.

The results of a two-way analysis of variance of chirruping responses show no significant effects, as a result of the high variability in chirruping responses, even though in certain experiments animals chirruped strongly during near-center playbacks. Moaning responses were significantly higher to nearby playbacks ($P < 0.025$), but there was no effect of location. This result accords with observations that moaning is more frequent during close-range encounters (Robinson, 1977).

Discussion

Because of their loud volume and low rate of attenuation over distance (Waser and Waser, 1977), the loud calls of many primates have the potential for communication between groups, and thus might be important as regulators of intergroup spacing (Marler, 1968, 1972; Bates, 1970). They could also serve to increase group cohesion; this is indicated by the correlation of loud calls with the start of disruptive behaviors such as group movement. This has been reported in many species, including rain forest cercopithecines (Struhsaker, 1969, 1970; Gautier and Gautier-Hion, 1969), howler monkeys (Carpenter, 1964), and langurs (Jay, 1965).

Indeed, Kinzey et al. (1977) feel that morning calls in *Callicebus torquatus* principally influence the spacing within groups. However, in their population, distances between groups were large, and the lack of response from adjacent groups might explain this conclusion. My observations confirm that in *C. moloch*, calling affects intragroup spacing; duetting, the most common vocalization during morning calls, only occurs when adult pairs are within 0.5 m of each other (Robinson, 1979). However, unlike Kinzey et al., I noted an association between calling and intergroup spacing.

The loud calls of *C. moloch* exhibit all the characteristics with which Marler (1968, 1972) defined calls used to maintain distance between groups: (a) they are given spontaneously in the absence of external triggering stimuli, (b) once given they stimulate calling in other groups, and (c) they occur at particular times of the day. In addition, examination of the calling fields of the three study groups reveals that animals tend to call near boundaries. This association can be explained by three hypotheses, all related directly or indirectly to the presence of neighboring groups. First, probability of calling may vary directly with location. This hypothesis is supported by the observation that animals sometimes call in peripheral areas during the day irrespective of the proximity of neighboring groups, but very rarely do so from positions near the home range center. Animals will also often call from areas which on previous days

have been associated with intergroup interactions. Chivers (1974) found a similar response in siamangs. He played back a recording of a siamang group's calls, and the group returned to that location to call for the next three days. Second, proximity of neighboring groups at boundaries might stimulate calling. Finally, animals might tend to call in the early morning, a time of day when environmental conditions in a tropical forest are optimal for long-range vocal signaling (Waser and Waser, 1977). *C. moloch* groups move to the boundaries at this time. Gibbons, whose social organization closely parallels that of *Callicebus*, also move to the periphery of their range following the first feeding bout (Ellefson, 1974). A similar movement is described in some territorial birds (e.g., Marler, 1956; Weeden, 1965) and certain prosimians which defend exclusive areas (Charles-Dominique, 1974, 1977). This regular movement to boundaries has been interpreted as patrolling in chaffinches (Marler, 1956) and siamangs (Chivers, 1974).

C. moloch groups also respond, both spatially and vocally, to calling by other animals. Detection of neighboring groups can result in one of three reactions: groups can avoid, approach, or maintain their separation (Marler, 1968). Chivers (1969) and Baldwin and Baldwin (1976) note that howler monkeys avoid roaring animals in most contexts. Langur groups in north India avoid contact, presumably locating whooping animals (Jay, 1965). In contrast *C. moloch* groups approach calling animals. The gibbon group also "sometimes moves a hundred yards or more to make contact with another group that is giving morning calls" (Ellefson, 1968). Female Kloss' gibbons approach other calling females (Tenaza, 1976). Ripley (1967) reports that gray langurs "seek other groups and engage them in aggressive encounters". These interactions are "not the result of accidental meeting". Approach to neighboring groups is also reported in nilgiri langurs (Poirier, 1968, 1974) and purple-faced langurs (Rudran, 1973).

To provide a null hypothesis of intergroup interactions, Waser (1976) has developed an 'ideal gas' model of intergroup interactions based on group speed, spread of group, detection distance of neighboring groups, and the density of groups in the area. Waser and Wiley (1979) used this model to predict frequency of interactions in a number of species. The ratios of the expected/observed frequencies are calculated; values higher than unity suggest groups are avoiding one another, while values lower suggest groups are approaching. Waser's model is useful in establishing the nonrandom nature of intergroup interactions, but not the behavioral mechanism underlying them. Based on Mason's (1968) data, Waser and Wiley suggest that *Callicebus* groups generally avoid one another, as the observed rate of interaction is lower than the expected. *C. moloch* in reality respond to calling animals with countercalling and approach to a boundary. The low overall frequency of interaction results from preferential use of areas at the center of the home range following boundary encounters.

Response to calling by neighboring groups might be site- or distance-dependent. Without the use of playback which can control each variable independently, it is difficult to separate the relative contribution of each in different species. In *C. moloch*, response to calling conspecifics depends on intergroup separation; calling animals which are far apart do not approach. Vocal response

to playback was much stronger if the initial distance separating the speaker and the subject group was small. Gibbons have a higher probability of approaching each other if they begin calling in close proximity (Ellefson, 1974). Chivers (1969) found that howler groups less than 150 yards apart approach one another, while beyond that range they move away. Waser (1975) observed that mangabeys withdraw from whoopgobbles closer than 600 m away and there was possibly a tendency to approach distant whoopgobbles. Playback supported these observations although the tendency to approach distant calls was not statistically significant.

In *C. moloch*, response to calling conspecifics is also site-dependent; calling animals are only approached if they are near the boundary or within the home range of the group. Chivers (1974) noted in siamang, also, that "groups only approach each other if their territory is threatened". Response to other groups depends on location in gorillas; movement patterns differ if other groups are encountered at the center of the home range rather than the periphery (Fossey, 1974). Waser (1977), on the other hand, found response of mangabeys to playback was independent of the location of the speaker.

Interactions between groups in species that approach one another can take one of two forms. Approach is sometimes followed by distance-increasing signals (Marler, 1968), and these interactions have been interpreted as active competition for space. In species that defend an exclusive area, there is a different pattern of intergroup interaction. In *C. moloch*, the strong response near boundaries, which depends on both location and intergroup separation, together with the tendency of groups to move to boundaries on leaving the sleeping tree and the high probability of calling when in peripheral areas, all increase the probability of boundary encounters in the early morning. Pairs duet during the approach to the boundary, but close analysis of these sequences (Robinson, 1977) reveals that as pairs move into close proximity (< 30 m), the tendency to approach neighbors and the animals' level of arousal decrease. Termination of the encounter does not involve a 'retreat,' but rather one or both groups move quietly away and begin feeding. Gibbons have similar behavior. Gibbon "males appear to become bored with the proceedings and gradually drift off to eat or groom with the rest of their group, which has usually tired of the conflict proceedings first and moved off" (Ellefson, 1974).

Groups of these monogamous, territorial species appear to be defining and reinforcing the conventional location of a boundary. Establishment of boundaries in turn allows exclusive use of space. The lower rate of intergroup interaction than expected from Waser and Wiley's calculations results from groups recognizing territorial boundaries and utilizing more central areas during most of the day. Paradoxically, low rates of intergroup interaction result from the tendency of neighboring groups to approach one another and reinforce the location of the boundary.

These differences in the responses of groups following approach might be related to differences in the spatial distribution of aggressive tendencies, or aggression field (Wiley, 1973). *C. moloch* groups called less in response to playback at the center than at the periphery of their territories. This result is in contrast to the stronger response to playback at the center in bird studies

(Ickes and Ficken, 1970; Krebs, 1971; Goldman, 1973; Brooks and Falls, 1975). Waser (1977) also reported greater responses to playback at the center in initial experiments to primate groups at Kibale: black-and-white colobus groups responded more to playback at the center than at the periphery; blue monkey males approached more rapidly to playback at the home range center. Thus the aggressive field in *C. moloch*, rather than decreasing as one moves out from the home range center as in many species, is highest near the boundaries. This difference reflects a fundamentally different mechanism of regulating spacing between groups. Variation in spacing behaviors was also noted by Owen-Smith (1977) in a review of ungulate territoriality, and he distinguishes 'centripetally focussed' from 'boundary orientated' territories. Presumably in the former, aggressive tendencies diminish with distance from the home range center. Boundaries are potentially unstable and ranges of groups overlap. In the latter, the aggressive field is highest near the boundaries, which are stable and constantly reinforced, and there is little between-group overlap of ranges.

Ultimately, what determines species' tendencies to approach or avoid neighboring groups? Groups gain from agonistic interactions only if they increase their use of some resource. Animals should approach only if the overall gain from an interaction exceeds the total energy expended in movement toward the neighboring group and in boundary displays. Thus one would predict that groups would approach each other only if their initial separation fell within a certain maximum distance. Frequent boundary encounters will tend to occur in species, such as *Callicebus*, where the daily path length is considerably greater than the diameter of the home range, so the cost of movement to the boundary is not too high. Frequent encounters will allow the establishment of a well-defined boundary and an exclusive use of space. Exclusive use of space is only possible when a group's share of the habitat will reliably contain enough to eat (see Waser and Wiley, 1979). In species with very large home ranges in relation to daily progressions, costs of boundary encounters are high, and one would predict that groups would not establish well-marked boundaries.

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References

- Altmann, S.A., Altmann, J.: Baboon ecology. Chicago: University of Chicago 1970
Baldwin, J.D., Baldwin, J.I.: Vocalizations of howler monkeys (*Alouatta palliata*) in southwestern Panama. *Folia Primatol.* **26**, 81-108 (1976)
Bates, B.C.: Territorial behavior in primates: A review of recent field studies. *Primates* **11**, 271-284 (1970)

- Bliss, C.I.: An analysis of some insect trap records. In: Classical and contagious discrete distributions. Patil, G.P. (ed), pp. 385–397. Calcutta: Statistical Publishing Society 1965
- Brooks, R.J., Falls, J.B.: Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. *Can. J. Zool.* **53**, 879–888 (1975)
- Carpenter, C.R.: Naturalistic behavior of non-human primates. University Park: Pennsylvania State University 1964
- Charles-Dominique, P.: Aggression and territoriality in nocturnal prosimians. In: Primate aggression, territoriality and xenophobia. Holloway, R.L. (ed.), pp. 31–48. London, New York: Academic Press 1974
- Charles-Dominique, P.: Urine marking and territoriality in *Galago alleni* (Waterhouse, 1837 – Lorisoidea, Primates) – A field study by radio telemetry. *Z. Tierpsychol.* **43**, 113–138 (1977)
- Chivers, D.J.: On the daily behaviour and spacing of howling monkey groups. *Folia Primatol.* **10**, 48–102 (1969)
- Chivers, D.J.: The siamang in Malaya: A field study of a primate in tropical rain forest. *Contrib. Primatol.* **4**, 1–335 (1974)
- Clutton-Brock, T.H.: Ranging behaviour of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Anim. Behav.* **23**, 706–722 (1975)
- Cohen, A.C.: Simplified estimators for the normal distribution when samples are singly censored or truncated. *Technometrics* **1**, 217–237 (1959)
- Cohen, A.C.: Tables for maximum likelihood estimates: Singly truncated and singly censored samples. *Technometrics* **3**, 535–541 (1961)
- DeVore, I., Hall, K.R.L.: Baboon ecology. In: Primate behavior. DeVore, I. (ed.), pp. 20–52. New York: Holt, Rinehart and Winston 1965
- Ellefson, J.O.: Territorial behavior in the common white-handed gibbon, *Hylobates lar* Linn. In: Primates. Jay, P. (ed.), pp. 180–199. New York: Holt, Rinehart and Winston 1968
- Ellefson, J.O.: A natural history of white-handed gibbons in the Malayan peninsula. *Gibbon and Siamang* **3**, 1–136 (1974)
- Fossey, D.: Observations on home range of one group of mountain gorillas (*Gorilla gorilla beringei*). *Anim. Behav.* **22**, 568–581 (1974)
- Freese, C.: A census of non-human primates. In: Primate censusing studies in Peru and Colombia, pp. 17–41. Washington, DC: PAHO, WHO 1975
- Gautier, J.P., Gautier-Hion, A.: Les association polyspecifics chez les Cercopithecidae du Gabon. *La Terre et la Vie* **116**, 164–201 (1969)
- Goldman, P.: Song recognition by field sparrows. *Auk* **90**, 106–113 (1973)
- Hays, W.L.: Statistics for the social sciences, 2nd ed. New York: Holt, Rinehart and Winston 1973
- Holmes, R.T., Pitelka, F.A.: Food overlap among co-existing sandpipers on northern Alaskan tundra. *Syst. Zool.* **17**, 305–318 (1968)
- Ickes, R.A., Ficken, M.S.: An investigation of territorial behavior in the American redstart utilizing recorded songs. *Wilson Bull.* **82**, 167–176 (1970)
- Jay, P.: The common langur of north India. In: Primate behavior. DeVore, I. (ed.), pp. 197–249. New York: Holt, Rinehart and Winston 1965
- Kinzey, W.G., Rosenberger, A.L., Heisler, P.S., Prowse, D.L., Trilling, J.S.: A preliminary field investigation of the yellow-handed titi monkey, *C. torquatus torquatus*, in northern Peru. *Primates* **18**, 159–181 (1977)
- Krebs, J.: Territory and breeding density in the great tit, *Parus major* L. *Ecology* **52**, 2–22 (1971)
- Marler, P.: Territory and individual distance in the chaffinch *Fringilla coelebs*. *Ibis* **98**, 496–501 (1956)
- Marler, P.: Aggregation and dispersal: Two functions in primate communication. In: Primates. Jay, P. (ed.), pp. 420–438. New York: Holt, Rinehart and Winston 1968
- Marler, P.: Vocalizations of East African monkeys. II. Black and white colobus. *Behaviour* **42**, 175–197 (1972)
- Mason, W.A.: Social organization of the South American monkey, *Callicebus moloch*: A preliminary report. *Tulane Stud. Zool.* **13**, 23–28 (1966)
- Mason, W.A.: Use of space by *Callicebus* groups. In: Primates. Jay, P. (ed.), pp. 200–216. New York: Holt, Rinehart and Winston 1968
- May, R.M.: Some notes on estimating the competition matrix α . *Ecology* **56**, 737–741 (1975)

- Moynihan, M.: Communication in the titi monkey *Callicebus*. *J. Zool. Lond.* **150**, 77–127 (1966)
- Neville, M.: 'Census of primates' in Peru. In: Primate censusing studies in Peru and Colombia, pp. 3–15. Washington, DC: PAHO, WHO 1975
- Owen-Smith, N.: On territoriality in ungulates and an evolutionary model. *Q. Rev. Biol.* **52**, 1–38 (1977)
- Poirier, F.E.: Nilgiri langur (*Presbytis johnii*) territorial behavior. *Primates* **9**, 351–364 (1968)
- Poirier, F.E.: Colobine aggression: A review. In: Primate aggression, territoriality and xenophobia. Holloway, R.L. (ed.). London, New York: Academic Press 1974
- Preston, F.W.: The commonness and rarity of species. *Ecology* **29**, 254–283 (1948)
- Preston, F.W.: The canonical distribution of commonness and rarity. *Ecology* **43**, 185–215, 410–432 (1962)
- Ripley, S.: Intertroop encounters among Ceylon gray langurs (*Presbytis entellus*). In: Social communication among primates. Altmann, S.A. (ed.), pp. 237–253. Chicago: University of Chicago 1967
- Robinson, J.G.: Vocal regulation of spacing in the titi monkey *Callicebus moloch*. Unpublished Ph. D. Dissertation. Chapel Hill: University of North Carolina 1977
- Robinson, J.G.: An analysis of the organization of vocal communication in the titi monkey *Callicebus moloch*. *Z. Tierpsychol.* (in press) (1979)
- Rudran, R.: Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia Primatol.* **19**, 166–192 (1973)
- Slocomb, J., Stauffer, B., Dickson, K.L.: On fitting the truncated lognormal distribution to species abundance data using maximum likelihood estimation. *Ecology* **58**, 693–696 (1977)
- Struhsaker, T.T.: Behavior of vervet monkeys (*Cercopithecus aethiops*). *Univ. Calif. Publ. Zool.* **82**, 1–64 (1967)
- Struhsaker, T.T.: Correlates of ecology and social organization among African cercopithecines. *Folia Primatol.* **11**, 80–118 (1969)
- Struhsaker, T.T.: The red colobus monkey. Chicago: University of Chicago 1975
- Tenaza, R.R.: Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Z. Tierpsychol.* **40**, 37–52 (1976)
- Waser, P.M.: Experimental playbacks show vocal mediation of intergroup avoidance in a forest monkey. *Nature* **255**, 56–58 (1975)
- Waser, P.M.: *Cercocebus albigena*: Site attachment, avoidance, and intergroup spacing. *Am. Nat.* **110**, 911–935 (1976)
- Waser, P.M.: Individual recognition, intragroup cohesion and intergroup spacing: Evidence from sound playback to forest monkeys. *Behaviour* **60**, 28–74 (1977)
- Waser, P.M., Waser, M.S.: Experimental studies of primate vocalization: Specializations for long-distance propagation. *Z. Tierpsychol.* **43**, 239–263 (1977)
- Waser, P.M., Wiley, R.H.: Mechanisms and evolution of spacing behavior. In: Handbook of behavioral neurobiology: Social behavior and communication. Marler, P., Vandenberg, J.G. (eds.). New York: Plenum (in press) 1979
- Weeden, J.S.: Territorial behavior of the tree sparrow. *Condor* **67**, 193–209 (1965)
- Wiley, R.H.: Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. *Anim. Behav. Monogr.* **6**, 87–169 (1973)
- Winkle, W. van: Comparison of several probabilistic home range models. *J. Wldl. Manag.* **39**, 118–123 (1975)