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## **An Analysis of the Organization of Vocal Communication in the Titi Monkey *Callicebus moloch***

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*With 6 figures*

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### **Abstract**

Vocalizations of titi monkeys were recorded from 6 groups at two sites in the llanos of Colombia during 8 months of study. Frequency and temporal measurements from spectrograms of recordings, and differences in their patterns of use, were used to characterize call types. Animals repeat calls to form phrases, and combine phrases to form sequences. The six sequence types, defined by different transition probabilities between phrases, varied in proportion in different contexts. To examine the effect of order of phrases on response, I played back artificially constructed sequences to subject groups. I discuss hierarchical and sequential mechanisms as generators of vocal sequences, and draw comparisons with models of human language.

### **Introduction**

*Callicebus* monkeys have a large repertoire of vocalizations, some of which are combined to form long sequences composed of a number of different classes of vocalizations (MOYNIHAN 1966). The complex organization of these sequences prompted MOYNIHAN to suggest that *Callicebus* vocalizations might represent "the maximum elaboration and complexity which can be attained by a species-specific . . . language". To form these vocal sequences, *Callicebus* monkeys repeat individual vocalizations, or *calls*, to form *phrases* of similar calls, and combine these phrases to form *sequences*.

The organization of behavioral sequences provides evidence on two questions. First, the structure of the sequences might reflect the underlying neurological organization of the animal, and second, the pattern itself, rather than a sum of the individual components, might affect the response of conspecifics (see NELSON 1973; THORPE and HALL-CRAGGS 1976).

In this paper I describe the vocal repertoire and analyze the vocal sequences of *Callicebus* monkeys with both sequential and hierarchical techniques. The merits of these different techniques are discussed by NELSON (1973) and DAWKINS (1976). These descriptions reveal that vocal sequences are order-

ed, with different transition probabilities between phrases in different contexts. This result suggests that order of phrases in a sequence has communicatory significance. To examine the effect of phrase order on response of other animals, I compared the response of subject groups to playback of recordings of artificially constructed vocal sequences.

## Methods

I examined populations in gallery forest at two sites, Finca Saravita (FS) and Finca la Macarena (FLM), near San Juan de Arama, Meta, Colombia, during the wet season (June to August, 1974; June—July, 1975) and the dry season (January—April, 1976). MASON (1968) gives a good description of a similar area. After an initial survey of *Callicebus*, I concentrated on three groups at each locality. I recorded vocalizations from undisturbed monkeys with a Uher 4000-L (in 1974) or a Nagra IV tape recorder (in 1975, 1976) and a Sennheiser MKH 815 directional microphone. I noted the stimulus conditions with which each vocalization occurred and any behavioral response, especially changes in spatial relationships.

Using criteria of pitch, temporal patterning, and differences in patterns of use, I recognized categories of calls in the field. The discreteness of these categories was confirmed by examination of sound spectrograms produced with a Kay Sona-Graph 7029A.

In the field I only rarely heard the quiet, high-pitched intragroup calls described by MOYNIHAN (1966). As my sample of these calls is small, I simply present spectrograms of these calls and note the contexts associated with their production and the responses of nearby animals. These vocalizations do not occur in the complex structured sequences.

The structural variations in the louder vocalizations are documented in more detail. These vocalizations often occur in sequences. For spectrographic analysis, I chose vocalizations randomly from my clearest recordings of calling by ♂♂. Parameters of female calls were measured from the small sample of recordings in which the ♀ called in the absence of the ♂. Temporal characteristics of each call were measured from wide bandwidth spectrograms, and frequency characteristics from narrow-band displays (effective resolution 45 and 300 Hz respectively for the analysis range 80—8000 Hz). Narrow bandwidth spectrograms are not useful when analyzing wide-spectrum vocal output such as that produced by humans and some primates (LIEBERMAN 1969), but *Callicebus* vocalizations are largely tonal so narrow-band analysis is appropriate.

From all complete calls on each spectrogram, I measured for each syllable (uninterrupted spectrographic tracings and associated frequency bands, EISENBERG 1976): (a) the duration, (b) the dominant frequency half way between the start and end of the largest, blackest part of the spectrogram (termed the dominant band, MARLER 1973), (c) the number of clear bands or harmonics at the mid-point, (d) the lowest frequency and (e) the highest frequency of the dominant band, (f) the lowest frequency and (g) the highest frequency of significant spectral energy (clear bands discernible on the spectrogram) at the mid-point. Using an acetate overlay, I measured intervals on spectrograms to the nearest 0.5 mm, so temporal measurements are accurate to approximately 5 ms and frequency to approximately 40 Hz. This resolution is approximately the same as that of the spectrograph for analysis range to 8 kHz (CHERRY 1966). I calculated the mean and coefficient of variation (C.V. = standard deviation  $\times$  100/mean) of each measurement. To compare the mean frequency and temporal measurements of call types, I used the *t*'-test (SOKAL and ROHLF 1969), which allows unequal variance of the two samples.

To examine the individual variability of chirrup vocalizations, I made spectrograms at regular intervals from randomly chosen vocal sequences given by recognized individuals in three groups (T, C, and Cr) at FLM. For each individual I measured the four clearest chirrups from each spectrogram on at least three different spectrograms from recordings on different occasions. Differences in the mean values of each parameter between individuals were tested for significance with the *t*'-test.

Vocal sequences were analyzed with a Spectral Dynamics 301D real time spectrum analyzer (similar to the system described by HOPKINS et al. 1974), which overcame the limitations imposed by the short analysis time of the sonagraph. Spectral density was displayed on the z-axis (beam intensity) of a Tectronix 5013N/D10 oscilloscope and frequency on the x-axis, so that predominant frequencies in every sweep appeared as spots of high intensity. A Grass Kymograph camera produced a continuous spectrogram from the oscilloscope display. The analysis range of the real time spectrum analyzer was set at 20 kHz, but analysis was limited to 50% (10 kHz) of this range. Effective bandwidth at this setting was 40 Hz, with statistically independent analysis of the 10 kHz spectrum every 25 ms. With film speed set

at 10 mm/s, there were four sweeps per mm. Measurement to within 0.5 mm (.05 s) thus is well within the resolution of the system.

The resulting film allowed accurate measurement of phrase length and sequencing of the vocal phrases. The observed transition frequencies between phrases were described with two models which generate sequences of behavior: a sequential and a hierarchical model. First, I calculated the transition probabilities from the marginal totals of the transition frequencies and presented the results as a matrix. These data would specify a first-order Markov process. Second, I calculated an index of similarity between phrase types based on the transition frequency matrix by taking the average of the Spearman rank correlation values for rows and columns for each pair of phrase types. In calculating the correlations, I excluded transitions between the pair in question (see DAWKINS 1976). I used these values to generate a hierarchical structure of phrase types by means of SLCA cluster analysis (MORGAN et al. 1975).

From this analysis I distinguished types of sequences by (1) the different underlying structures as revealed by transition probabilities or cluster analysis, (2) their occurrence in different situations, and (3) the sex of the vocalizer.

The playback test sequences were constructed by splicing recordings of different phrases together. The "normal" sequence, similar to "male calling" (see below), had an introduction of the phrase group "chirrup-pants-pumps" followed by repeated cycles of the phrase group "honks-bellows-pumps" (see below). The "abnormal" sequence had a similar introduction followed by a cycling of the phrase group "honks-pumps-bellows". The transition pumps-bellows occurs rarely, and the transition honks-pumps was recorded only once. Test tapes consisted of five 1-min recordings of the appropriate sequence with a min of silence following each one.

I presented both "normal" and "abnormal" test tapes twice to three groups (F, H, and Co) at FLM (3 groups  $\times$  2 treatments  $\times$  replication = 12 playbacks). Order of presentation of the two sequences to each group was randomized. 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 at the same location for all presentations to a group, midway between the boundary and the geographic center of the group's range, and aimed at the subject group. Tests began between 06.20 and 07.00 h, after at least 15 min of silence from the subjects, when they were approximately 60 m from the speaker. To avoid habituation, tests to any one group were separated by at least two days.

I recorded all vocal responses during both the 10-min playback period and the 10 following min with a Nagra-IV tape recorder, and noted all behavior. For further details of playback procedure see ROBINSON (1977).

Differences in vocal response to the two kinds of test sequences were tested with Wilcoxon's matched-pairs signed-ranks test (HOLLANDER and WOLFE 1973). Each matched pair was an abnormal and a normal sequence, presented to the same group, either in the initial experiments or in the replication.

## Results

### Description of the vocal repertoire

Two classes of *Callicebus* vocalizations emerge from an analysis of frequency and amplitude characteristics: loud, generally low-pitched calls, and high-pitched, quiet calls.

The former, which have the potential for long-range communication, are used both in intra- and inter-group signaling. I distinguished 7 classes of loud calls. All are variations on a common pattern of inhalation-exhalation to produce three syllables and a pause. (a) The "pre-introduction" is a high-pitched, quiet, short syllable, followed immediately by (b) a loud, low-pitched "introduction". These two syllables are produced by inhalation. After (c) a "pause", (d) the "climax" is then produced by exhalation (see Fig. 2 B). Not all vocal classes include all four components. All of these vocal classes usually are repeated a number of times to form phrases.

Most of the spectrograms of the quiet, high-pitched vocalizations were produced from recordings from a captive adult  $\sigma$  at FS. I have relied largely on MOYNIHAN's (1966) classification of these signals. These vocalizations,

with the exception of the grunts and sneezes (see below), appear to be elaborations of the pre-introduction component of the louder vocalizations.

I could identify most of the vocal categories described by MOYNIHAN (1966) on the basis of his descriptions and spectrograms. I include his terminology in parentheses where it differs from mine.

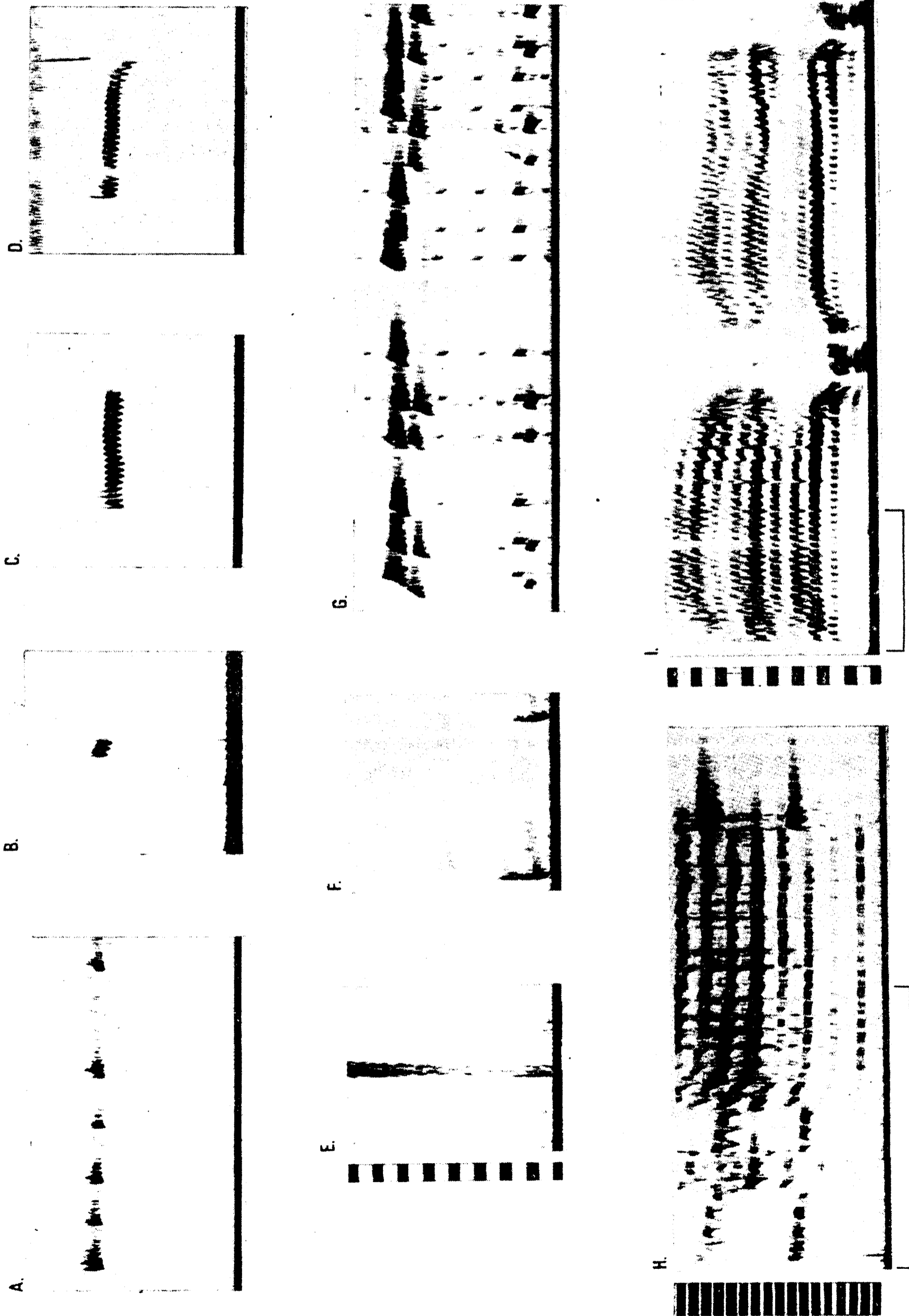


Fig. 1: Spectrograms of *Callicebus moloch* vocalizations analyzed with the broad-band filter (effective resolution, 300 Hz). A, Chirps B, Intermediate between chirp and modulated whistle. C, Whistle exhibiting frequency modulation. D, Whistle passing into trill (note separation between syllables of the trill). E, Sneeze. F, Grunts. G, Chirrups from two members of the same group with individual differences in mean frequency of the introductory syllable. H, Infant distress call and associated trills. I, Scream. Frequency scale indicates kHz; time scale is 0.5 s

The quiet, high-pitched vocalizations, excepting grunts and sneezes, apparently intergrade completely. Intermediates between all the low-pitched calls also occur during transitions between different types during sequences, but these transitions, with the exception of the pants-honks transition, are rapid, so that I could easily discriminate "modal" structural categories (see, for example, transitions between pants and bellows. Fig. 3).

*a) Quiet, high-pitched sounds*

(i) Squeaks, whistles, and trills. This intergrading series (Figs. 1 C and D) consists of pure tones, modulated in the case of some whistles and trills, usually with an average frequency of about 6 kHz. Durations vary from 0.04 to 1.0 s.

In the field, *Callicebus* produce these very soft sounds when other groups are calling, especially during movement towards the sound source. They were also given when I seriously disturbed animals. In one instance I stepped between the ♂ and infant when both were feeding only a few feet above the ground, three days after I first saw the infant off the ♂'s back. This movement elicited a distress call (see below) from the infant, who was immediately picked up by the ♂, and the animals quickly ascended into a tree. All members of the group then gave high-pitched calls for 20 min. I have recorded these calls from an isolated captive individual when he was slightly disturbed by my presence.

(ii) Chirps. The chirp, a quiet, pure tone with a frequency around 6 kHz and a duration of 0.005 to 0.04 s (Fig. 1 A) intergrades with squeaks, whistles, and trills (Fig. 1 B). It is commonly produced when habituated animals forage in my presence. Animals usually orient towards the observer before calling. No response is apparent from other animals. Chirps appear to be low intensity chirrup (see below).

(iii) Grunts. These are noisy, short (approx. 0.03 s) bursts of sound with energy up to about 3 kHz but with some tonal structure between 300 and 1000 Hz (Fig. 1 F). They are occasionally produced before and after "duetting" sequences during intergroup interactions and sometimes in response to my presence.

(iv) Sneezes. This short (approx. 0.03 s), noisy burst of sound produced by exhalation through the nasal passages, with frequencies as high as 10 kHz, is given by disturbed animals (Fig. 1 E). I have recorded sneezes following chases between monkeys of different groups and during rapid avoidance of an observer.

(v) Infant distress call. Largely tonal, this call shows many frequency bands up to at least 16 kHz (Fig. 1 H), with most of the spectral energy above 8 kHz. The mean duration of five clear recordings was 0.517 s (C.V. = 70.46). To the human listener, this call is a very faint buzz. Infants produce this call frequently in the first week off the ♂'s back, especially if disturbed by the observer's presence or if they are unable to negotiate a difficult crossing. The ♂ often approaches and allows the infant to mount. I never observed a response from the ♀ or juvenile even when they were closer than the ♂ to the infant.

*b) Loud, low-pitched vocalizations*

(i) Chirrup (chirrup and chuck notes). Composed of pre-introduction and introduction syllables only, this vocalization is apparently produced entirely by inhalation (Fig. 1 G). The pitch of the pre-introduction gradually drops prior to the transition to other low-pitched calls during sequences. This

characteristic might allow other animals to synchronize their contribution during simultaneous CP, CR, and CRP sequences (see below).

Table 1: Duration and frequency characteristics of chirrup

		Pre-Introduction Syllable		Introduction Syllable		
		Duration (s)	Dominant Frequency at Mid-Duration (kHz)	Duration (s)	Dominant Frequency at Mid-Duration (kHz)	
Group Cr	♂ (n = 16)	Mean	0.018	5.445	0.027	0.974
		C. V.	21.00	5.23	26.17	5.55
♀ (n = 16)	Mean	0.018	5.749	0.021	1.428	
	C. V.	47.69	9.91	18.68	5.95	
Juv. ♂ (n = 14)	Mean	0.014	5.280	0.021	1.110	
	C. V.	62.49	13.24	31.38	3.70	
Group C	♂ (n = 16)	Mean	0.023	5.839	0.032	1.029
		C. V.	26.23	9.48	18.68	2.73
♀ (n = 16)	Mean	0.035	5.543	0.015	1.407	
	C. V.	28.04	8.56	39.04	4.65	
Juv. ♀ (n = 16)	Mean	0.032	5.564	0.014	1.558	
	C. V.	27.04	5.81	37.28	2.98	
Group T	♂ (n = 16)	Mean	0.025	6.151	0.014	1.083
		C. V.	36.70	5.18	26.22	3.55
♀ (n = 16)	Mean	0.020	5.234	0.020	1.354	
	C. V.	57.96	4.93	28.89	1.23	
Juv. ♀ (n = 16)	Mean	0.025	5.246	0.017	1.449	
	C. V.	41.72	3.11	26.16	2.92	
Infant (n = 11)	Mean	0.012	6.675	0.013	1.728	
	C. V.	47.27	2.06	30.85	2.25	

Table 2: Comparisons of dominant frequency of introductory syllable of chirrup among recognized individuals

Individuals	Significance levels at which $H_0$ = no difference between dominant frequency of introductory syllable, can be rejected using pairwise t-tests									
	♂Cr	J♂Cr	♀Cr	♂C	♀C	J♀C	♂T	♀T	J♀T	IT
♂ group Cr	-	0.001	0.001	0.01	0.001	0.001	0.001	0.001	0.001	0.001
Juv. ♂ gp Cr		-	0.001	0.001	0.001	0.001	n. s.	0.001	0.001	0.001
♀ gp Cr			-	0.001	n. s.	0.001	0.001	0.01	n. s.	0.001
♂ gp C				-	0.001	0.001	0.001	0.001	0.001	0.001
♀ gp C					-	0.001	0.001	0.01	0.05	0.001
Juv. ♀ gp C						-	0.001	0.001	0.001	0.001
♂ gp T							-	0.001	0.001	0.001
♀ gp T								-	0.001	0.001
Juv. ♀ gp T									-	0.001
Infant gp T										-

The pitch of the introductory syllable is remarkably constant within an individual, but differs with age and sex (Table 1). It appears to drop with age, but remains higher in ♀♀ than ♂♂. The frequency at mid-duration of the introductory syllable for identified animals of groups T, C, and Cr was

remarkably constant within individuals but varied between individuals (Table 2). There were always significant differences between members of the same group (juveniles at this time were probably 14—17 months old) but not between all animals of the same age-sex class in different groups (e.g., ♀♀ of groups C and Cr do not differ). There was even overlap between different age-sex classes in different groups: group T's juvenile ♀'s syllable does not differ significantly from that of the ♀ of group Cr. MOYNIHAN (1966) suggested that chirrup might be individually distinctive. My results suggest that distinction of age-sex classes on the basis of the pitch of the introductory syllable is possible. I found that I could use these differences to distinguish the age and sex of animals in the field.

Animals chirrup in contexts in which locating and recognizing group members foster group cohesion. The rapid transition between the pre-introduction and introduction syllables and the sharp onset and termination of both syllables allow easy localization (MARLER 1955). Chirruping is common during boundary encounters, during disturbances resulting from the observer's presence, during the confusion associated with the presence of groups of squirrel, howler, and capuchin monkeys, and when cattle moved through the area.

Chirruping animals often have an agitated demeanor and often flee from the disturbing stimulus. Other *Callicebus* orient towards the chirruping animals and chirrup themselves, but do not approach.

(ii) Moans. Moans consist of a long, low-pitched introduction, with considerable variation in the form of frequency modulation, a pause, and a long, low-pitched climax (Appendix and Fig. 2 C). Female moans are easily distinguished by a different tonal quality (differences between sexes in number of spectral bands in the climax syllable,  $p < 0.001$ ,  $t'$ -test), a shorter duration of the climax syllable ( $p < 0.001$ ,  $t'$ -test), and a higher dominant frequency at the mid-duration of the climax ( $p < 0.001$ ,  $t'$ -test). I did not record moans from juveniles.

Following moans from adult ♂♂ or ♀♀, the mate immediately approaches the vocalizing animal. Moaning is common during disturbances when groups of squirrel, howler, or capuchin monkeys pass through the area. *Callicebus* often moan after leaving the sleeping tree in the early morning before moving towards the boundaries and following rest periods. During boundary interactions, moans usually introduce "duetting sequences" (see below). The long moaning phrases before the start of duets ensure that mates are in close proximity, a condition necessary for successful coordination of the sexes' contributions.

(iii) Pants (resonating notes) (Appendix and Figs. 2 A and 3). These calls occur in phrases as part of longer sequences. The loud pants of the ♂, which can be heard 500 m away, are easily distinguishable from the much softer, fuzzier female pants, which cannot be heard over 50 m away. In ♀♀ the dominant frequency of the climax is significantly lower ( $p < 0.001$ ,  $t'$ -test) and the duration of the syllable is shorter ( $p < 0.001$ ,  $t'$ -test).

Pre-introductory syllables are absent in 77% of the pants in my sample, usually from pants which occur at the beginning of a phrase. The introductory syllable is a loud single band on a spectrogram, occasionally with softer under- and overtones, whose frequency descends sharply. The pause is followed by the loud, many-banded climax.

(iv) Honks (resonating notes) (Appendix and Fig. 2 D). I have no clear recordings of female honks, but they are similar to those of the ♂. Male honks

have no pre-introductory syllable. The introductory syllable is also absent in 26 % of my sample, consists only of slight atonal noise in an additional 10 %, and consists of two to four tonal, low-intensity bands in the rest. The climax syllable is similar to, but softer than that of pants.

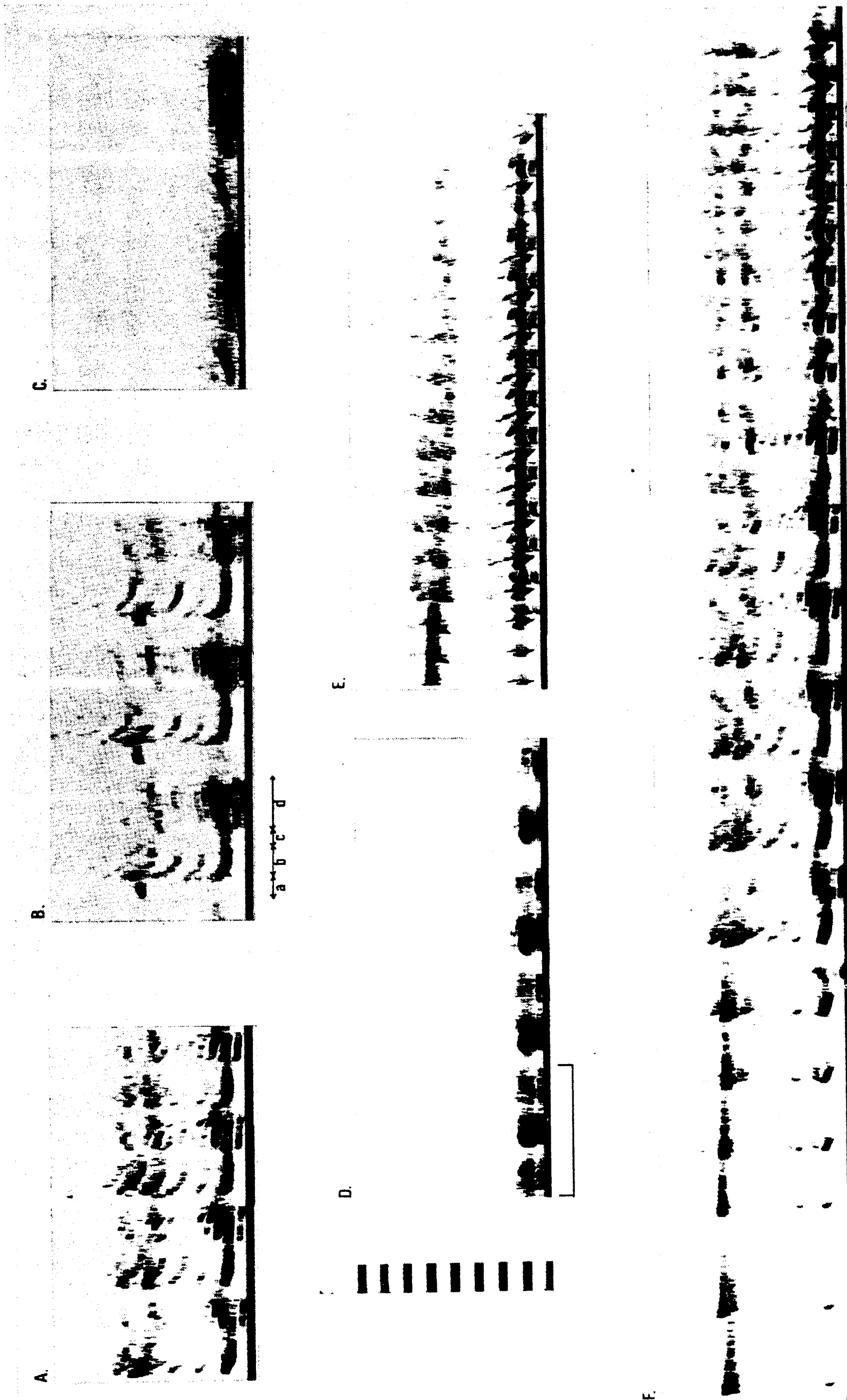


Fig. 2: Spectrograms of *Callicebus moloch* vocalizations analyzed with the broad-band filter (effective resolution, 300 Hz). A, Pants. B, Bellows (a, pre-introduction; b, introduction; c, pause; d, climax). C, Moans. D, Honks. E, Chirrup-pumping (CP) sequence. F, Chirrup-pumping (CRP) sequence. Frequency scale indicates kHz; time scale is 0.5 s



Honks intergrade completely with pants. As well as occurring following pumping (see below), honks are given between phrases of pants during duetting. I have placed them in a different category because (a) they are distinguishable by ear from pants, and (b) the transition probabilities between pants

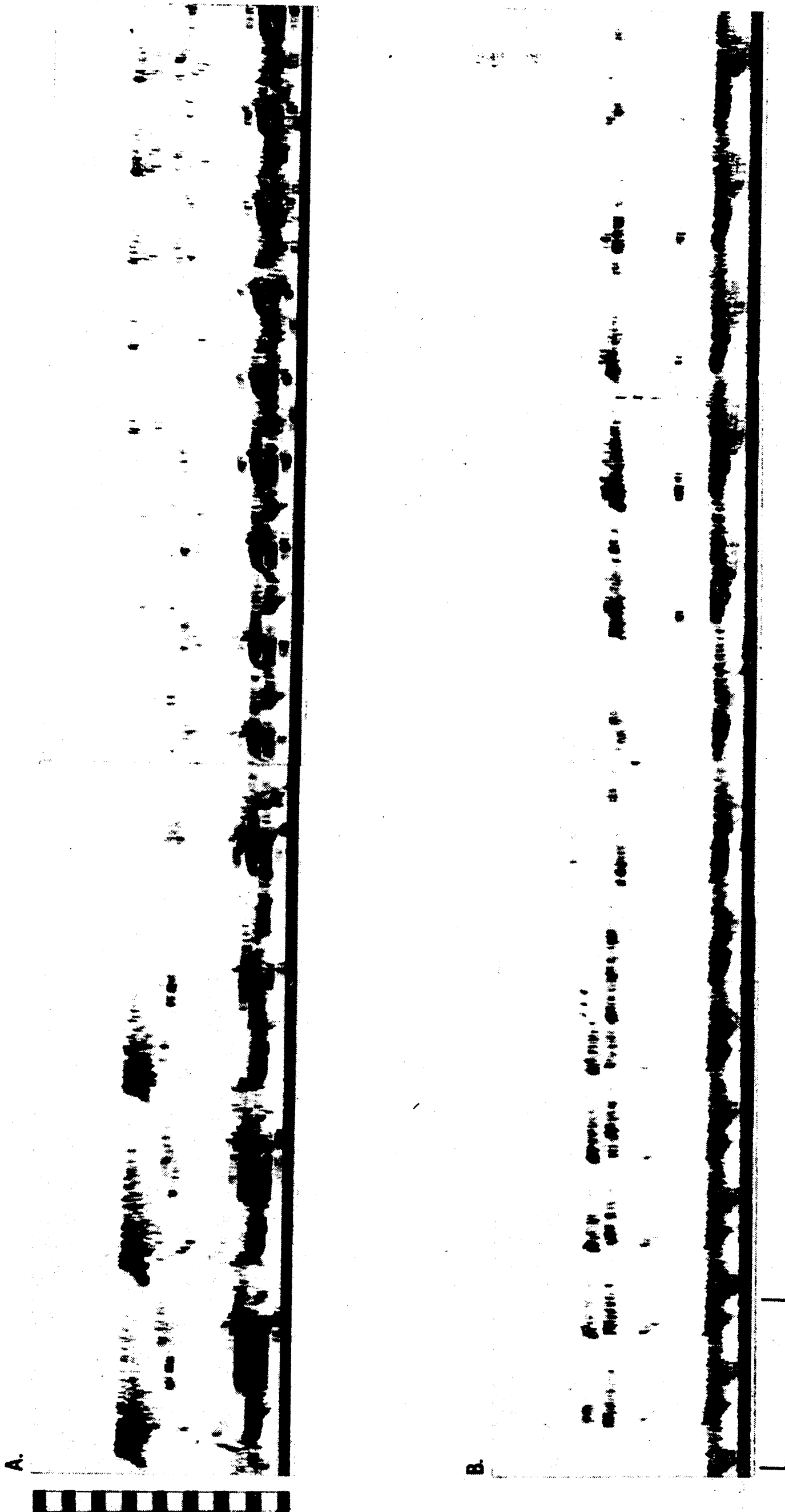


Fig. 3: Spectrograms of *Callicebus moloch* vocalizations analyzed with the broad-band filter (effective resolution, 300 Hz). A, Male contribution during duetting, showing rapid transitions from bellows to pants. B, Female contribution during duetting, showing rapid transition from pants to bellows. Frequency scale indicates kHz; time scale is 0.5 s

and other phrases are quite different from the probabilities between honks and other phrases. For example, the probability of transition from pants to pumps is high whereas honks-pumps transitions almost never occur.

(v) Bellows (resonating notes) (Appendix and Figs. 2B and 3). These sounds are the loudest in the repertoire. Bellow phrases occur in "male calling" and "female calling" and in "duetting" sequences. The softer female bellows have a distinguishable difference in tonal quality, a significantly lower dominant frequency at mid-duration ( $p < 0.001$ ,  $t'$ -test), and are shorter ( $p < 0.05$ ,  $t'$ -test).

Pre-introduction syllables occur in 67% of my sample of male bellows. They have a higher intensity than the corresponding syllable in pants, and the frequency at mid-duration is lower ( $p < 0.001$ ,  $t'$ -test). Both the introduction and climax syllables are similar to those of pants, but they have longer durations ( $p < 0.001$ ,  $t'$ -test).

(vi) Pumps (pumping notes) (Appendix and Fig. 2E). These calls occur in all sequences with the exception of the short CR sequence. Female pumps have a higher dominant frequency at the mid-point of the climax than those of  $\delta\delta$  ( $p < 0.001$ ,  $t'$ -test).

Pumps have no pre-introductory syllable. They comprise a short introduction with a rapidly descending pitch and a short climax. The rapid cadence is the most characteristic feature of pumping phrases.

I compared moans, pants, bellows, pumps, and honks for duration, frequency at mid-duration of dominant band, and highest frequency of significant spectral energy in the climax syllable. These parameters are distinguishable by ear and reflect the basic differences between these sound categories. All comparisons were significant at least at the 0.01 level ( $t'$ -test) with the following exceptions: the dominant frequency at mid-duration between pants and bellows, and the highest level of significant energy between moans and honks and between pants and bellows.

(vii) Screams. These loud, startling vocalizations are composed of two syllables (Fig. 1 I). The first is long (up to one s), with many frequency bands, and highly frequency modulated. The second is shorter and similar in structure to the climax syllables of the other low-pitched vocalizations. Spectrographically, screams bear a striking resemblance to the juvenile distress call, but the spectral energy of the latter is in a higher frequency range.

I have heard these vocalizations twice from wild animals. The first followed fighting between two young non-resident  $\delta\delta$  in the presence of a non-resident  $\text{♀}$ . Chasing, grappling, and biting continued for 30 s, followed by screaming and flight by one  $\delta$ . The second  $\delta$  remained with the non-resident  $\text{♀}$  in the same area for the next four days, whereupon both disappeared. The second screaming bout occurred during rapid approach to playback by the  $\text{♀}$  of group C. This animal appeared to encounter something in the tree, leapt back, and broke into screams. The  $\delta$  approached rapidly and both animals gave CRs (see below) simultaneously. The captive animal at FS also screamed whenever he was picked up and held.

#### Sequences of vocalizations

*Callicebus* monkeys combine phrases to form sequences. Short sequences, consisting of two to four different phrases, with a duration of no more than 3 to 5 s, occur alone or as the initial group of phrases in a long sequence. Long sequences are composed of a group of phrases which cycle regularly to produce a continuous sequence up to 5 min long.

*a) Short sequences*

(i) Chirrup-pumping (chuck-pumping gobbling, MOYNIHAN 1966; gobbling, MASON 1966) (hereafter CP sequences). During this loud sequence, the rate of chirruping increases, the pitch of the pre-introduction syllable lowers, and the animal passes suddenly into pumping (Fig. 2E). Occasionally, honking or a long sequence will follow CP sequences.

This sequence usually is produced by the ♂ alone, but sometimes the ♀ chirrup-pumps simultaneously. I have also recorded the ♀ chirrup-pumping without the ♂ in response to playback of "female calling". CP sequences are produced during the first bout of morning calls, especially at FS, during the approach to neighboring groups, and occasionally following boundary interactions. The contagious quality of this sequence is distinctive; chirrup-pumping from one group frequently elicits synchronous chirrup-pumping from up to 5 or 6 nearby groups.

The rate and pitch changes of the chirrup phrase apparently allow neighboring groups to synchronize the onsets of their pumping phrases. But synchrony is never perfect and breaks down with distance. MOYNIHAN (1966) suggested that the extent of overlap of pumping phrases during synchronous CPs might allow animals to estimate intergroup separations. CPs are more common during the first morning calling bout, and the probability of groups approaching one another following this calling bout depends on the distance between groups (ROBINSON, in press). These observations suggest that groups might indeed be using the degree of synchrony to calculate the distance to neighboring groups.

(ii) Chirrup-panting (hereafter CR sequences). In this sequence chirruping leads directly to panting. CR sequences usually occur during long chirrup phrases in situations in which animals are highly aroused and have a tendency to withdraw. I have recorded CRs from unhabituated animals responding to my presence, after other significant disturbances, and during close-range interactions with other groups. All members of a group may chirrup-pant simultaneously, especially if they are close together.

(iii) Chirrup-panting-pumping (hereafter CRP sequences). CRPs (Fig. 2F), sometimes followed by honking, are given by the ♂ or occasionally simultaneously by both the ♂ and ♀. I have recorded them in two situations. A non-resident ♂ gave CRP sequences while being chased from the range of a resident group. CRPs also are common during close-range intergroup encounters at a boundary.

*b) Long sequences*

(iv) Female calling. Delivered by the ♀ alone, this sequence is identical to the ♀'s contribution during duetting. I have recorded this sequence three times, all in response to playback. The first was in response to presentation of CP sequences at the periphery of the home range when the ♀ was only 20 m from the speaker, and the pair was separated by at least 40 m. Other instances were in response to playback of this recording of female calling.

(v) Male calling. This sequence, given by the ♂ alone, is introduced with CP, CR, or CRP short sequences. This introduction is generally followed by a regular cycling of the group of phrases "honks-bellows-pumps". Honks usually end the sequence. The slow rate of honking and bellowing gives this sequence its characteristic slow cadence. Table 3 presents the matrix of transition frequencies between phrases and transition probabilities from clear recordings of

male calling. Indices of similarity derived from this matrix are summarized in Fig. 4 in the form of a cluster diagram.

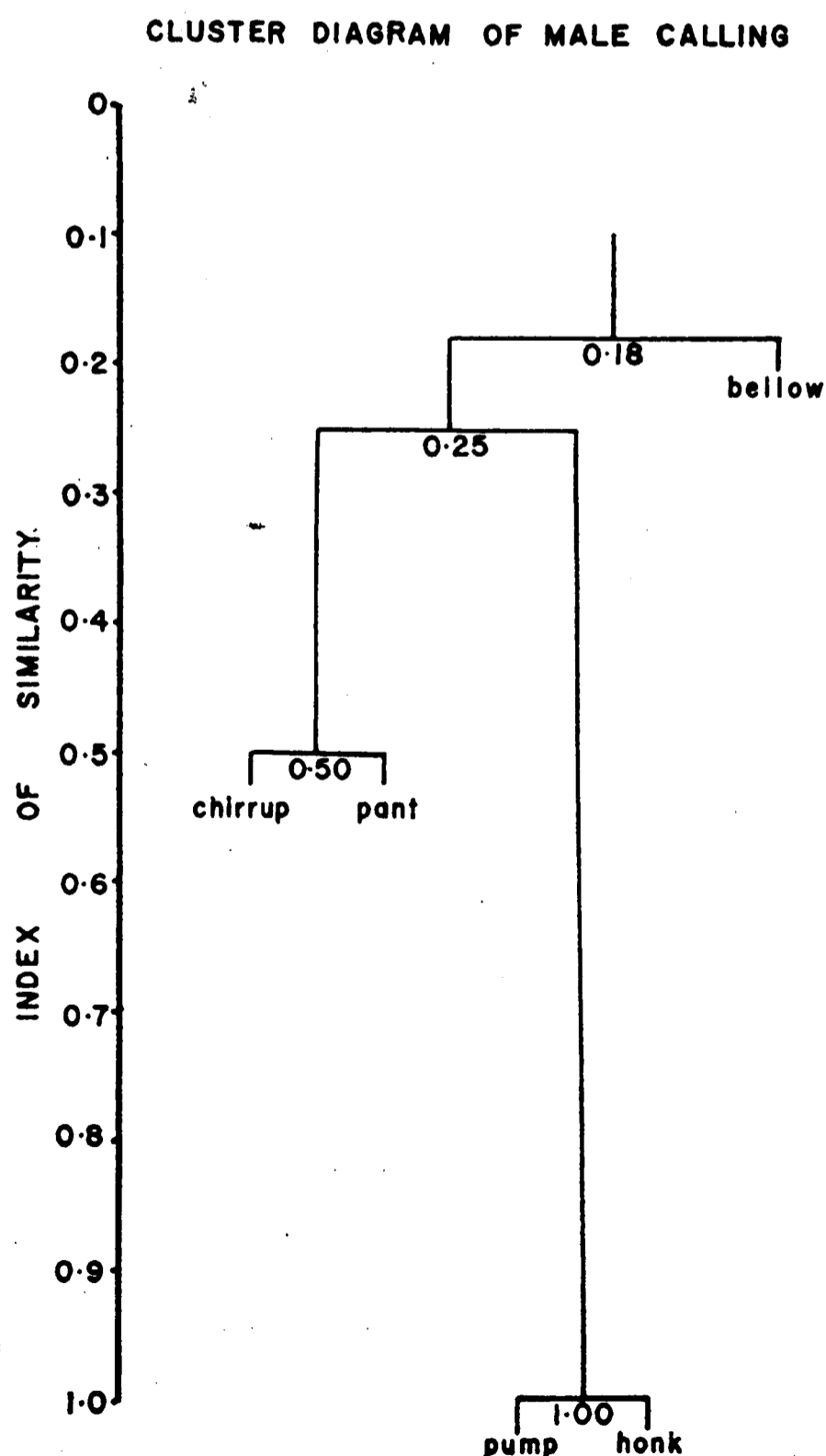
Table 3: Contingency tables based on phrase sequences during male calling

A: Transition matrix of phrases during male calling

Preceding phrases	Following phrases						Marginal Totals
	Chirrup	Pant	Bellow	Pump	Honk	End	
Begin	35	0	7	0	1	0	43
Chirrup		22	6	8	0	0	36
Pant	0		11	22	9	1	43
Bellow	0	0		87	14	10	111
Pump	0	12	15		78	13	118
Honk	1	9	65	0		30	105
Marginal Totals	36	43	104	117	102	54	456

B: Transition probability matrix for the data above

Preceding phrases	Following phrases					
	Chirrup	Pant	Bellow	Pump	Honk	End
Begin	0.814	0	0.163	0	0.023	0
Chirrup		0.611	0.167	0.222	0	0
Pant	0		0.256	0.512	0.209	0.023
Bellow	0	0		0.784	0.126	0.090
Pump	0	0.102	0.127		0.661	0.110
Honk	0.009	0.086	0.619	0		0.286



$\sigma\sigma$  call alone whenever they are not closely associated with a  $\text{♀}$ . For instance, non-resident, non-paired  $\sigma\sigma$  give male calls. In one instance, repeated calling for two h from a small  $\sigma$  in an unoccupied area elicited approach from a non-paired  $\text{♀}$ . The juvenile  $\sigma$  of group Cr occasionally engaged in male calling. Paired  $\sigma\sigma$  produced this sequence during the first calling bout in the morning and during boundary encounters, especially at FS, if separated from the  $\text{♀}$  by 20 m or more.  $\sigma\sigma$  calling alone during the first morning bout were on occasion 40 m from the rest of the group. KINZEY et al. (1977) reported that "dawn calls" in *Callicebus torquatus* were also given

Fig. 4: Cluster diagram of phrases in male calling. The index of similarity is based on mutual replaceability in sequences and clustered using SLCA criteria (see text)

by the ♂ alone, while "he ran and leaped through the trees" followed closely by the ♀, a behavior I have not seen in *C. moloch*.

(vi) Duetting. During this coordinated vocalization between a mated ♂ and ♀, individuals produce the identical sequence. The ♀'s calls are much softer and have different tonal quality, a difference apparent from examination of spectrograms (Fig. 3). Especially if the pair are initially separated, duetting sequences are usually initiated with moaning, a vocalization which elicits mutual approach. During duetting the mated pair are within 0.5 m of one another and usually touching. Partners more widely separated are unable to coordinate their vocal output and attempts to duet end quickly.

An alternation of pant and bellow phrases follows the introductory moaning phrase. As the sequence continues the animals begin to add pumps, either after pants or bellows, and insert honks between pant phrases and after pumps. Honking usually ends the sequence. I present the transition matrix between phrases for the ♂'s contribution (Table 4). The structure of the female contribution appears to be identical, but the louder ♂'s vocalizations overlapping the ♀'s makes sequential analysis more difficult. The relationships among male phrases are presented in a cluster diagram (Fig. 5) derived from the transition matrix.

Table 5 presents an analysis of association between male and female vocalizations. A test of overall heterogeneity using the G statistic (SOKAL and ROHLF 1969) demonstrates that certain male calls are associated with certain female calls. The association results primarily from an alternation of pant and bellow phrases by the two individuals; during 67% of the samples in which the ♂ was panting, the ♀ was bellowing; and during 73% of male bellowing, the ♀ was panting. The ♂ and ♀ switch phrases almost simultaneously, but it is my impression that the ♀ begins the transition slightly before the ♂.

Knowledge of male vocal type reduces the probability of error in predicting the female vocal type by 0.49. (Goodman and Kruskal index, HAYS

Table 4: Contingency tables based on phrase sequences during duetting

A: Transition matrix of phrases during duetting

Preceding phrases	Following phrases							Marginal Totals
	Chirrup	Moan	Pant	Bellow	Pump	Honk	End	
Begin	18	134	9	8	0	0	0	169
Chirrup		3	12	1	0	0	0	16
Moan	0		53	80	0	7	2	142
Pant	0	0		371	251	198	26	846
Bellow	0	0	354		226	124	30	734
Pump	2	0	260	65		148	8	483
Honk	1	6	136	191	0		144	478
Marginal Totals	21	143	824	716	477	477	210	2,868

B: Transition probability matrix for the data above

Preceding phrases	Following phrases						
	Chirrup	Moan	Pant	Bellow	Pump	Honk	End
Begin	0.107	0.793	0.053	0.047	0	0	0
Chirrup		0.188	0.750	0.063	0	0	0
Moan	0		0.373	0.563	0	0.049	0.014
Pant	0	0		0.439	0.297	0.234	0.031
Bellow	0	0	0.482		0.308	0.169	0.041
Pump	0.004	0	0.538	0.135		0.306	0.017
Honk	0.002	0.013	0.285	0.400	0		0.301

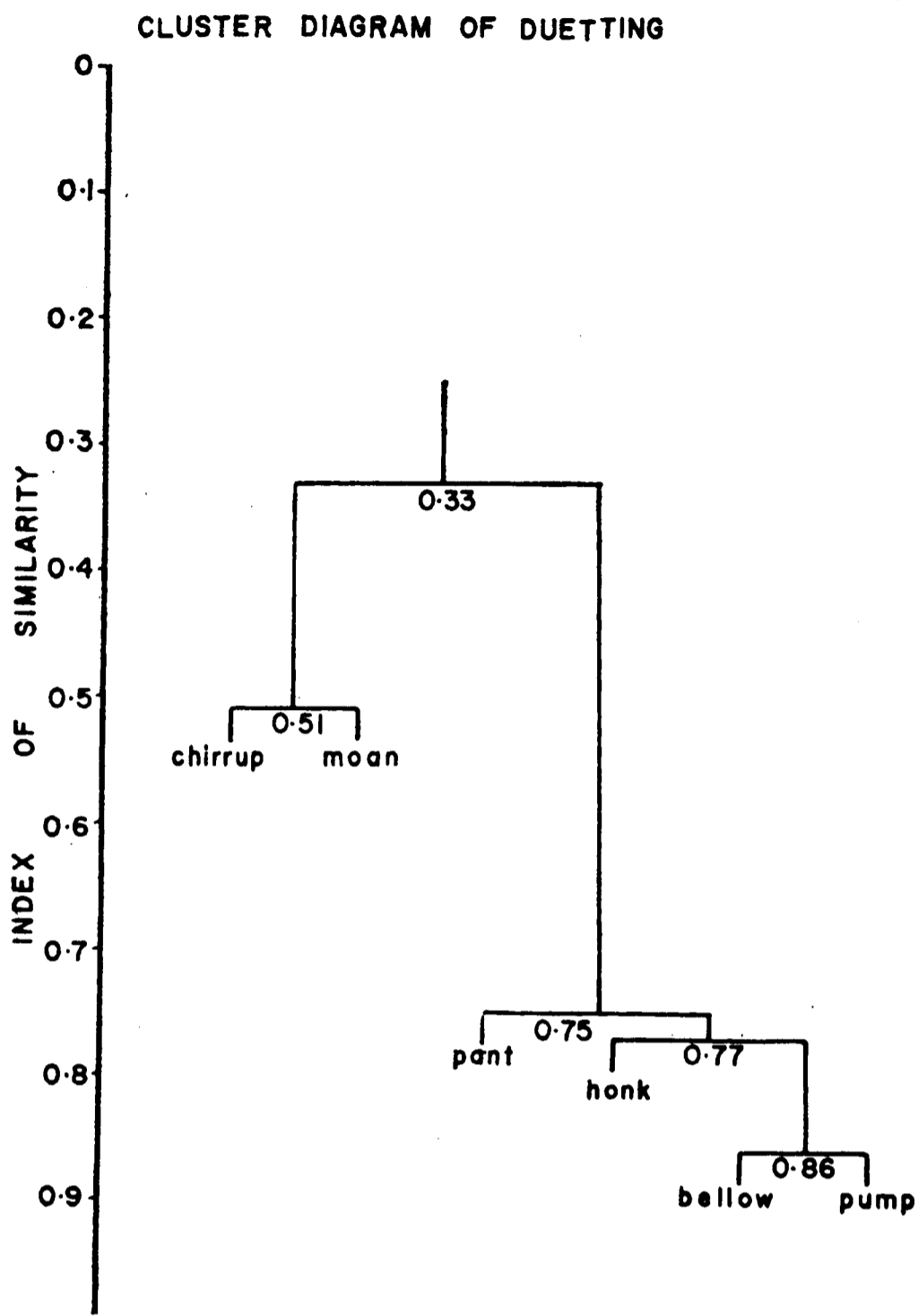


Fig. 5: Cluster diagram of phrases in duetting sequences. The index of similarity is based on mutual replaceability in sequences and clustered using SLCA criteria (see text)

1973). Knowing the female vocal type reduces the probability of error by 0.50. These values are low because of the occurrence of other vocalizations in duetting sequences in addition to pants and bellows. I examined the association between ♂ and ♀ for bellowing and panting by collapsing the matrix around the cell of interest. The very high value of G in the cell for male bellows/female pants suggests that these particular vocalizations are highly coordinated.

Table 5: Coordination of male and female vocal phrases during duetting sequences

A: Association of phrases in 133 samples drawn at random from sequences

Male phrases	Female phrases						
	Moans	Pants	Bellows	Pumps	Honks	Chirrup	Silence
Moans	9	0	0	0	0	0	3
Pants	0	10	29	2	0	0	2
Bellows	0	30	0	4	1	3	3
Pumps	0	10	3	0	0	0	4
Honks	0	1	3	1	5	0	6
Chirrup	0	0	0	0	0	2	0
Silence	2	0	0	0	0	0	0

Overall statistical association between male and female vocal phrases,  $G = 42.43$ ,  $df = 4$ ,  $p < 0.001$

B: Goodman and Kruskal Index of Predictive Association

Information about one category reduces the probability of error in predicting the second as follows: given male vocalization  $\lambda_A = 0.487$   
 given female vocalization  $\lambda_B = 0.500$

C: Association of male and female pants and bellows. For each cell, the first value is G, and the value in parentheses is the probability at which independence between male and female vocalizations can be rejected

Male phrases	Female phrases	
	Bellows	Pants
Bellows	15.54 (0.001)	65.90 (0.001)
Pants	27.48 (0.001)	3.19 (n. s.)

This striking synchrony probably develops slowly between a pair. A newly formed pair observed for four days moaned extensively and began duetting, but never sustained the sequence. Group 1 at FS did not duet during my study periods in 1974 and 1975, but they did in response to playback in April, 1976. KINZEY (in press) reports that his study group of *Callicebus torquatus* did not duet in 1974, but duetting was frequent in all subsequent years.

Duetting is the most common vocalization of mated pairs during the approach and encounter with neighboring pairs at a boundary.

### Playback

If *Callicebus* are sensitive to variation in order, differences in vocal response to the playback of the two test sequences might be detected in one of the following ways. (1) Duetting response to an abnormal sequence might be either higher or lower than to a normal sequence. Differences require a two-tailed test. (2) Moaning response would be higher to the abnormal sequence, because *Callicebus* moan in response to disturbing circumstances. This hypothesis can be tested with a one-tailed test. (3) Chirruping would be higher. This vocalization occurs during high arousal in the presence of a disturbing stimulus. Animals chirrup in response to an observer, but my conspicuousness during playback was minimized and similar for all tests.

There were no differences in chirruping response to abnormal and normal sequences either during or following playback. The average duetting response was higher to abnormal sequences but this difference was not statistically significant either during or following playback.

Table 6: Moaning response (in s) during playback of an "abnormal" and a "normal" sequence

Groups	"Abnormal"	"Normal"
Co	31	16
F	14	2
H	1	0
Co	13	8
F	0	0
H	9	0

Moaning response was significantly higher for the abnormal sequence ( $p = 0,031$ , one-tailed Wilcoxon matched-pairs signed-ranks test,  $n = 5$ ).

Moaning responses during playback were significantly higher for the abnormal sequence (Table 6). The direction of the response is as predicted. Average moaning response was also higher in the 10 min following playback but differences between the treatments are not statistically significant. These results indicate that animals can discriminate between the playbacks on the basis of order of phrases.

## Discussion

### Individual variation in vocalizations

To allow individual recognition, some characteristics of a vocal signal must have greater variability among individuals than within any one individual. Individual recognition of acoustic signals has been suggested for the

chimpanzee (MARLER and HOBLET 1975), gorilla (FOSSEY 1972), rhesus macaque (ROWELL and HINDE 1962), pigtailed macaque (GRIMM 1967), red-tailed and blue monkeys (MARLER 1973), and night monkeys (MOYNIHAN 1964). By playing back the individually distinctive whoopgobble to mangabeys, WASER (1977) demonstrated that animals can discriminate the RA ♂ (an adult ♂ which approached whoop-gobbles of neighboring groups more frequently than any other adult ♂) in their own group from RA ♂♂ of other groups and from other ♂♂ within the group. This discrimination might involve individual recognition or habituation to the most commonly heard whoopgobble.

The frequency of the introductory syllable of the chirrup vocalization is individually distinctive. The coefficients of variation of this syllable were lower than those of the same syllable of other calls. This relative stereotypy suggests selection for individual distinctiveness allowing individual recognition.

Chirrups, however, provide only a limited form of individual recognition. I analyzed the frequency of this syllable for individuals in groups T, C, and Cr, which interact extensively with one another at boundaries. Yet the frequency of this syllable among animals in the same age-sex class but in different groups is similar, and in three cases differences were not statistically significant. Chirrups are thus not useful for individual recognition between individuals in different groups. This conclusion is supported by the observation that playback of chirrups from unfamiliar animals elicited little response from subject groups (ROBINSON 1977). Thus chirrups probably are not used for communication between groups at all.

Chirrups potentially identify the age-sex class of the vocalizer and its location. Because most groups are composed of one animal from each age-sex class, and groups can be relatively certain of their isolation within their territories, age-sex recognition and knowledge of the location of the caller usually amount to individual recognition of other group members.

I did not detect any consistent individual differences in any of the loud vocalizations which are important for intergroup spacing. However, as *C. moloch* territories are relatively exclusive, knowledge of the location of a vocal source is almost always sufficient to discriminate groups. Although single, non-resident ♂♂ do call, residents and non-resident animals can be easily distinguished because duetting is the most frequent vocalization by residents during approach to a boundary.

### The vocal sequences of *Callicebus* monkeys

Long vocal sequences have been described in four primate genera: chimpanzees (MARLER and HOBLET 1975), siamangs (LAMPRECHT 1970), gibbons (TEMBROCK 1974; TENAZA 1976; MARSHALL and MARSHALL 1976), and titi monkeys *Callicebus* (MOYNIHAN 1966; this study). MARLER and HOBLET described the pant-hoot in the chimpanzee as a brief "introduction", then a "build-up" increasing in loudness, a "climax", and a "letdown". A similar description applies to the gradual elaboration of elements in the loud calls of gibbons, siamangs, and titi monkeys. But in this last genus, instead of a short sequence repeated at intervals, animals continuously cycle the phrases to produce long sequences. Long continuously cycled phrases have also been described in whales (PAYNE and MCVAY 1971). *Callicebus*, however, appears unique in varying transitions between phrases; the order of phrases in whales' song sequences is invariably the same.



A number of techniques can (1) describe variations in the order of elements in sequences or (2) model the actual mechanism generating the sequences. These two goals are quite distinct; mathematically precise descriptions do not necessarily specify the correct generating mechanism.

The relationships between elements in a sequence are usually initially summarized in a transition matrix. Different analyses of this matrix can then describe the structure of the observed sequences.

One technique involves converting the transition matrix into a probability matrix based on the marginal totals. By scanning, the investigator can determine the basic order from high transition probabilities. A related method is to compare the observed and expected values on the assumption of independent occurrence. Differences between the observed and expected values are then tested for significance with the log likelihood G-statistic (SOKAL and ROHLF 1969). Significant transitions can be summarized in a flow diagram (e.g., FABRICIUS and JANSSON 1963). These techniques are summarized in CHATFIELD and LEMON (1970) and SLATER (1973).

Another technique involves the use of cluster analysis (MAURUS and PRUSCHA 1973; MORGAN et al. 1975; DAWKINS and DAWKINS 1976). An index of similarity is calculated between each pair of behaviors in the matrix. Behaviors are then grouped into clusters and results are presented as a cluster diagram or a dendrogram.

I have used both transition probability matrices and cluster analyses when describing *Callicebus* long sequences. The cluster analysis chosen emphasizes the mutual replaceability of different phrase types rather than their contiguity within sequences. While this analysis stresses the transition relationships of different phrases (see DAWKINS 1976), it does not imply a different causal mechanism from one stressing sequential proximity, and I use it solely as a descriptive mechanism. The cluster diagram distinguishes the introductory from the following component in both male calling and duetting sequences, and differences in structures between the two sequences are easily discernible. However, some information is lost: for example, CP sequences often introduce male calling, but this strong relationship between chirrups and pumps is masked by the high frequency of bellow-pump transitions.

These same techniques have been used to identify hypotheses about the actual mechanism generating a sequence. However, different mathematical descriptions of sequences can attain equal precision and suggest different generating mechanisms. Furthermore, there is no necessary assurance that the most elegant mathematical description (greatest precision for degrees of freedom) will suggest the most realistic mechanism.

ALTMANN (1965) suggested that Markov processes might adequately predict the next behavior of an animal. A first-order Markov process generates sequences in which each behavior depends only on the immediately preceding behavior and is equivalent to the actual transition probabilities observed. First-order Markov processes are identical to the finite state machines or regular grammars of linguists (e.g., CHOMSKY 1957, 1965). Higher-order Markov processes take into account more than one preceding event. In his analysis of the communicative interactions of rhesus monkeys, ALTMANN found that knowledge of at least four preceding behaviors increased the power of prediction of the next behavior. Markov processes of an even higher order potentially have even greater predictive power. Thus ALTMANN argues that this generative capacity of Markov processes, where behavior depends probabilistically on preceding behaviors, supports their adequacy to explain sequences of behavior. The "stochastic contingencies are, in a sense, a measure of the social memory of the animals".

Although there is no apparent mathematical advantage of models based on Markov processes as opposed to hierarchical structures derived from cluster analysis (DAWKINS and DAWKINS 1976), DAWKINS (1976) has argued that two considerations suggest that complex

sequences are hierarchically generated in the organism. First, when generating long complex sequences, hierarchical rather than sequential mechanisms seem simpler, in the sense that a large number of behaviors and possible transitions would, in a sequential mechanism, entail storage of many transition rules, much information, especially in the case of higher order Markov processes, and a cumbersome retrieval system. This argument is not compelling, particularly if we assume that transitions have an element of chance or error and thus are not completely determined by preceding events. If some error is permitted, relatively simple transition rules would generate a relatively complex sequence. In addition, even if the probability of transition is strictly determined, there is no reason to suspect that, in the animal, a sequential generating mechanism is necessarily more complex than a determinate hierarchical one.

Second, DAWKINS argued, certain structural characteristics of some sequences suggest an underlying hierarchical organization. These would include sequences in which groups of behaviors are distinguishable, with high transition probabilities between behaviors in the same group, and low transition probabilities between those in different groups. Transitions between behaviors of different groups would be similar to transitions between groups as a whole. DAWKINS also suggested that certain transitions might be constrained to a certain group, so some intergroup transitions would be impossible.

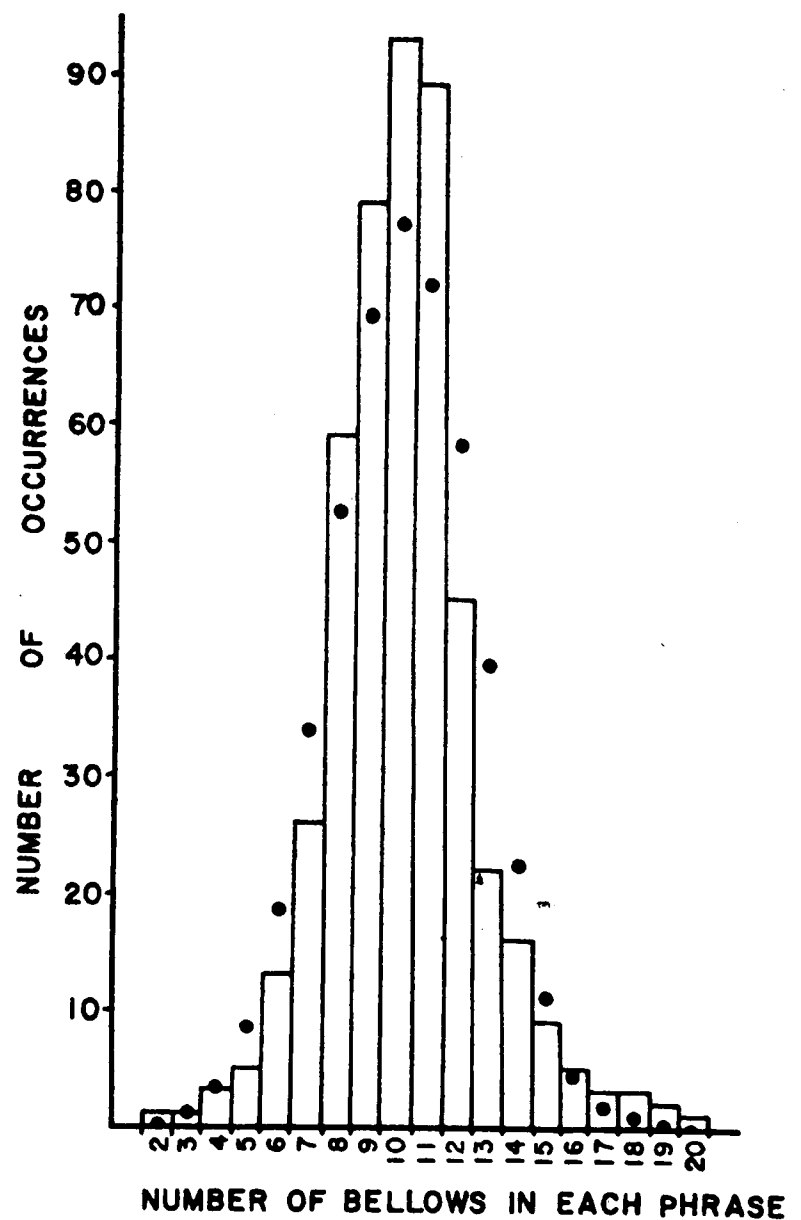
The examples examined by DAWKINS involve the relationship between different behaviors in sequences. In the vocal repertoire of *Callicebus*, it is the organization of the same phrases (or behaviors) into different sequences which indicates hierarchical structure. Sequences with different transition probabilities between the same types of phrases occur in different contexts: CPs occur during the first morning calling bouts, when groups are usually separated by over 100 m, while animals give CRs and CRPs when proximate to neighbors at boundaries. Male calling occurs predominantly when groups are widely separated, while pairs duet during the approach to a boundary. A mechanism which depends on context must specify the transition probabilities within sequences. This is identical to DAWKINS's characterization of hierarchies, with no single "global set of transition rules", but rather "nested sets of transition rules, each set of rules holding sway within a circumscribed cluster of elements".

In addition to varying with context, transition probabilities between phrases vary with their position in sequences. Long sequences are differentiated into an introductory phrase or group of phrases, and a following group of phrases which are cycled continuously. The introductory component often is repeated a number of times, with short breaks between repetitions, before passing into the following component. There is an even finer organization in the following component of duetting. At the beginning of this component pants and bellows alternate, but towards the end, pumps and honks are inserted into the bellow-pump matrix in predictable positions.

The observed transition probabilities between phrases can be described with a non-stationary Markov process specified by contextual and sequence-position rules. But any non-stationary Markov process specified by rules which have "options" or make "decisions" is indistinguishable conceptually from DAWKINS's hierarchies. Both postulate a higher-level mechanism regulating changes in the lower-level sequential mechanism.

The transition probabilities of *calls within phrases* likewise cannot be generated with a simple Markov process. If the probability of transition from one call to the next is stationary, the distribution of number of calls in each phrase should follow a geometric distribution (NELSON 1964). To test this prediction, I examined the distribution of number of bellows in a randomly drawn sample of 475 phrases taken from sequences recorded at FLM, by dividing the average duration of a bellow into the duration of the bellow phrase and rounding off to the nearest whole number. Average duration of a bellow is based on the sample of 74 bellows (Appendix). The distribution

Fig. 6: Distribution of number of bellows in each phrase, based on a random sample of 475 bellow phrases. Darkened circles indicate predicted values of a normal distribution



(Fig. 6) obviously does not follow the geometric, in which the probability of transition to the next phrase would be highest following the first bellow, and would decrease monotonically for longer phrase lengths. Phrase length is apparently determined by some counting or timing mechanism.

If this mechanism is subject to random perturbations (as in a one-dimensional random walk around the expected end time with both direction and step length variable), the distribution of end times should be normal (FEYNMAN et al. 1963). However, the distribution is significantly different from normal ( $G = 35.58$ ,  $df = 12$ ,  $p < 0.001$ ). Tests for skewness and kurtosis (SOKAL and ROHLF 1969) revealed a positive skew ( $t = 4.93$ ,  $df = \infty$ ,  $p < 0.001$ ) and a significant leptokurtosis ( $t = 7.68$ ,  $df = \infty$ ,  $p < 0.001$ ). A leptokurtic distribution would result from a centrally biased random walk, implying that the mechanism determining end times of phrases is subject to random perturbations but is capable of some homeostasis, with greater deviations from the expected end times subject to disproportionately greater resistance. The positive skew indicates the homeostasis is not symmetrical around the expected end time. Thus transition probabilities of phrases within sequences and calls within phrases are consistent with a hierarchical mechanism. Furthermore, the distribution of calls within phrases suggests that the phrase length is determined by a counting or timing mechanism subject to random perturbations but capable of some homeostasis.

Hierarchies derived by examining behavioral sequences and hierarchical phrase structure grammars of linguists (e.g., POSTAL 1967) may be more than superficially similar. Differences may reflect no more than different methods of construction. Cluster analysis, for instance, examines the relationships among vocal events and clusters them statistically according to some index of similarity. Phrase structure grammars (PSGs) are created by examining word sequences (sentences) and deriving a hierarchically arranged set of common rules. Hierarchies of PSGs and cluster analysis have been equated before. VOWLES (1970) argued that these hierarchies are the same if it is assumed "that the number of nodes of a PSG that must be traversed to pass from one word to another is reflected in the transition probabilities between words". As noted by VOWLES, an important difference between animal signals or behavior and

human language is that in the latter the same word is seldom repeated in "acceptable" or "correct" sequences.

CHOMSKY (1957, 1965) argued persuasively that PSGs are distinguished from simple sequential models by the characteristic of nested dependencies. In human sentences, words can depend on the occurrence of previous words (e.g., "if" . . . "then") and be independent of intervening words. These dependencies can be nested without theoretical limit: words with dependencies can occur before other dependencies are closed. However, CHOMSKY restricts his discussion of sequential models to first-order Markov processes. As ALTMANN (1965) points out, higher-order Markov processes can generate sequences where behavioral events depend on particular past behaviors but not on intervening, more recent behaviors. Whether the mechanisms which generate human and/or animal vocal sequences are organized hierarchically, sequentially, or with some mixture of both remains to be determined by the neurologists (see SZENTÁGOTHAÏ and ARBIB 1974). But unless it is assumed a priori that human language is qualitatively different from animal communication, ethologists can make use of some of the insights provided by the linguistic analysis of human language.

Indeed, PSGs have been used by ethologists to describe the rules generating sequences of behavior (MARSHALL unpubl., in HUTT and HUTT 1970 and VOWLES 1970; KALMUS 1969; FENTRESS and STILWELL 1973). PRIBRAM (1973) speculates on the symbolic capabilities of non-human primates and draws interesting comparisons with human grammar. If similarities between human and animal communication signals are more than superficial, it suggests that some animals respond to the specific order of events in a sequence, just as the meaning of a human sentence depends on word order.

REYNOLDS (1968) reviews abilities of primates to discriminate different sequential relations. ALTMANN's (1965) work with rhesus monkeys suggests that behavior depends on the order of past behaviors. But few studies have shown that effect of order in vocal sequences can be discriminated by animals. By playing back recordings of rearranged sequences FICKEN and FICKEN (1973) demonstrated that golden-winged warblers discriminate order variations. BREMOND (1968) reported similar experiments with the European robin. By comparing responses to sequences composed of rare transitions with more commonly occurring sequences, I have shown that *Callicebus* discriminate variations in order. No study, however, has shown conclusively that different variations in order evoke qualitatively different responses in natural situations. Chimpanzees can be taught to use order differences for communication (e.g., PREMACK 1971; GARDNER and GARDNER 1969), but there is as yet no evidence that they do so in the wild. ITANI (1963) suggested that different orders of vocalizations in the Japanese macaque affect responses differently, but he gives no examples. The difference in order between *C. moloch* male calling and duetting, and between CRs, CRPs, and CPs, and the association of these vocal sequences with contexts, strongly suggest that order differences do in fact affect response, but I have not demonstrated that they do so. Different responses to these sequences could be attributed to different proportions, rather than the order, of phrases.

However, the vocal repertoire of *Callicebus* is composed of modal categories: transitions between phrases during sequences are rapid, and phrase types are clearly distinguishable. This would allow a receiver to detect differences between phrases. GREEN (1975) in a study of the Japanese macaque concluded that structural differences in vocalizations were associated with variations in the physiological state of the animal. If different phrase types

express different physiological states, sequences of phrases would express cyclic fluctuations in states; but there appears to be no utility in signaling such fluctuation, even if the animal's state changes in such a manner, which seems unlikely. Rather the differentiation might serve to distinguish variations in order. This is a further suggestion that variation in the order of phrases in *Callicebus* vocal sequences has communicatory significance.

### Summary

1. I describe the large repertoire of vocalizations of titi monkeys *Callicebus moloch*, the circumstances commonly associated with each call, and the response of conspecifics.

2. The frequency characteristics of chirrups, calls which locate group members, identify age-sex classes.

3. A number of different calls are often combined to form long vocal sequences. I distinguish three short and three long sequences by differences in the order of call types. These differences were revealed by both sequential and hierarchical analyses of the observed transition frequencies between calls. The evidence suggests that the mechanisms generating these sequences are hierarchically structured.

4. Different sequence types occur in different contexts. The results of a playback experiment indicate that *Callicebus* monkeys can discriminate different sequences on the basis of order of calls in the sequence.

5. Duetting, one of the long sequences, is a highly synchronized vocalization between the ♂ and the ♀ of a mated pair, in which the sexes produce the same vocal sequence simultaneously, but alternate the different types of calls.

### Zusammenfassung

1. Beschrieben sind die Vielfalt der Lautäußerungen von *Callicebus moloch* (Cebidae), die Situationen, in denen jeder Ruf auftritt, und die Antwort der Artgenossen.

2. Die Frequenzverteilung in Chirrupen, Rufen, die den Ort von Gruppenmitgliedern angeben, kennzeichnen Alter und Geschlecht.

3. Verschiedene Rufe bilden oft eine lange Lautsequenz. Nach der Reihung der Rufotypen unterscheidet ich drei kurze und drei lange Sequenzen, und zwar sowohl nach sequentieller als nach hierarchischer Analyse der Ruffolgen. Die Ergebnisse lassen vermuten, daß die Mechanismen, die diese Sequenzen erzeugen, hierarchisch strukturiert sind.

4. Verschiedene Sequenztypen treten in unterschiedlichem Zusammenhang auf. Ein Tonbandexperiment macht wahrscheinlich, daß *Callicebus* verschiedene Sequenzen an der Anordnung der Rufe unterscheiden können.

5. Duette, eine Form der langen Lautmuster, sind sehr genau aufeinander abgestimmte Lautäußerungen zwischen ♂ und ♀ eines Paares; dabei erzeugen die Partner dieselben Lautmuster, verwenden aber die verschiedenen Typen der Rufe abwechselnd.

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*Appendix: Duration and frequency characteristics of calls*

	Duration (s)	Dominant Frequency at Mid - Duration (kHz)	Number of Bands at Mid - Duration	Lowest Frequency of Dominant Frequency (kHz)	Highest Frequency of Dominant Frequency (kHz)	Lowest Significant Spectral Energy (kHz)	Highest Significant Spectral Energy (kHz)
<b>1. Moans</b>							
♂ (n = 32)							
Introduction							
Mean	0.144	0.553	1.38	0.511	0.617	0.468	0.768
C. V.	23.68	25.90	47.99	27.90	25.14	27.84	48.37
Pause							
Mean	0.072						
C. V.	69.15						
Climax							
Mean	0.269	0.719	4.00	0.626	0.787	0.275	1.162
C. V.	22.59	30.79	37.03	35.02	28.42	28.20	29.92
♀ (n = 14)							
Introduction							
Mean	0.112	0.737	1.14	0.675	0.837	0.662	0.878
C. V.	25.14	36.75	31.77	36.10	31.86	22.91	32.78
Pause							
Mean	0.056						
C. V.	62.10						
Climax							
Mean	0.184	0.913	8.21	0.851	0.934	0.200	1.447
C. V.	24.75	26.09	27.50	26.91	25.96	33.16	25.44
<b>2. Pants</b>							
♂ (n = 75)							
Pre - Introduction (n = 17)							
Mean	0.016	4.926	1	4.887	4.935	-	-
C. V.	94.40	4.65	0	4.67	4.47		
Introduction							
Mean	0.080	0.872	2.43	0.716	1.004	0.509	1.600
C. V.	32.41	19.54	63.97	28.84	19.89	46.78	73.06
Pause							
Mean	0.070						
C. V.	47.37						
Climax							
Mean	0.114	0.144	3.80	1.043	1.151	0.457	1.454
C. V.	24.82	15.70	26.67	17.89	18.70	71.80	21.06
♀ (n = 31)							
Pre - Introduction (n = 20)							
Mean	0.016	5.020	1	4.990	5.041	-	-
C. V.	34.20	3.36	0	4.44	3.28		
Introduction							
Mean	0.074	1.032	1	0.864	1.233	-	-
C. V.	36.40	5.50	0	4.08	6.60		
Pause							
Mean	0.072						
C. V.	20.29						
Climax							
Mean	0.094	1.066	4.13	1.012	1.077	0.256	1.205
C. V.	26.10	6.65	12.10	7.72	6.59	8.76	9.84



Appendix (continued)

	Duration (s)	Dominant Frequency at Mid-Duration (kHz)	Number of Bands at Mid-Duration	Lowest Frequency of Dominant Frequency (kHz)	Highest Frequency of Dominant Frequency (kHz)	Lowest Significant Spectral Energy (kHz)	Highest Significant Spectral Energy (kHz)
<b>3. Honks</b>							
♂ (n = 20)							
Introduction							
Mean	0.102	0.553	2.56	0.495	0.559	0.369	1.019
C. V.	21.35	44.98	37.01	46.23	44.62	46.14	31.50
Pause							
Mean	0.062						
C. V.	54.57						
Climax							
Mean	0.150	0.860	3.50	0.766	0.872	0.375	1.253
C. V.	30.92	17.62	21.01	19.54	18.18	41.61	12.46
<b>4. Bellows</b>							
♂ (n = 74)							
Pre-Introduction (n = 57)							
Mean	0.028	4.620	1.04	4.588	4.643	4.588	4.647
C. V.	63.08	7.64	17.93	7.94	7.46	7.94	7.47
Introduction							
Mean	0.128	0.889	4.23	0.813	1.040	0.418	2.757
C. V.	24.49	9.73	46.89	10.16	11.01	65.03	50.28
Pause							
Mean	0.046						
C. V.	35.32						
Climax							
Mean	0.210	1.164	4.24	1.103	1.188	0.377	1.528
C. V.	20.52	14.41	22.34	16.35	13.06	41.76	28.84
♀ (n = 19)							
Pre-Introduction (n = 15)							
Mean	0.028	4.422	1.13	4.364	4.455	4.312	4.496
C. V.	52.47	5.69	31.05	5.50	5.53	4.86	6.42
Introduction							
Mean	0.144	1.038	1	0.945	1.200	-	-
C. V.	15.82	6.11	0	7.55	5.60		
Pause							
Mean	0.024						
C. V.	41.64						
Climax							
Mean	0.190	1.059	4.21	1.010	1.107	0.280	1.205
C. V.	17.07	10.39	14.98	11.75	10.99	23.33	9.65
<b>5. Pumps</b>							
♂ (n = 75)							
Introduction							
Mean	0.048	0.686	1.08	0.596	0.789	0.593	0.807
C. V.	28.26	8.19	36.53	12.27	36.76	14.22	30.86
Pause							
Mean	0.028						
C. V.	35.74						
Climax							
Mean	0.078	0.834	2.27	0.705	0.837	0.387	0.918
C. V.	15.76	10.80	20.94	10.84	10.65	14.11	18.23
♀ (n = 20)							
Introduction							
Mean	0.062	0.992	1	0.844	1.124	-	-
C. V.	37.03	6.67	0	7.69	5.57		
Pause							
Mean	0.032						
C. V.	61.51						
Climax							
Mean	0.074	0.984	3.40	0.910	1.013	0.299	1.040
C. V.	20.75	9.74	14.78	10.56	10.45	28.26	10.51