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## RESEARCH ARTICLES

# Vocal Coordination of Troop Movement Among White-Faced Capuchin Monkeys, *Cebus capucinus*

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Coordinated travel by social groups is well documented, often with evidence that cognitive spatial maps are employed. Yet the mechanisms by which movement decisions are made and implemented within social groups are poorly known. In a field study of white-faced capuchin monkeys in Costa Rica it was demonstrated that a specific call, the "trill," is used by adults in the initiation and directing of troop movement. The trills of subadults were restricted to vocal exchanges with other subadults. Continuous vocal recordings were collected of the vocalizations of the 14 members of the study troop. A cumulative 33.7 h of continuous samples and 1,892 sonagrams were analyzed. In addition to vocalizations clearly associated with alarm, distress, or agonistic contexts, two distinct call types were identified, trills and huhs. Age-sex classes differed in the rate at which both types of calls were produced in different spatial positions within the troop. Adult females and males produced higher rates of trills when in the leading edge compared to all other spatial positions in a traveling troop. Trills at the edge of a stationary troop represented 36 "successful" and 3 "unsuccessful" start attempts; the troop usually moved in the trajectory predicted by a trilling adult's location on the troop periphery within 10 min of the initiation of trilling. Adults also altered the trajectory of traveling troops by trilling at the side and back of the troop (10 "successful" and 4 "unsuccessful" attempts). Huh vocalizations were most predictably produced when a capuchin is in a dense fruit patch. These results emphasize the role vocalizations serve in the coordination and trajectory of group movement in nonhuman primates, especially those populations that are arboreal or in which visual contact is otherwise impeded. © 1993 Wiley-Liss, Inc.*

**Key words: vocal communication, capuchin monkey, social manipulation, food-associated call**

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## INTRODUCTION

Among many animals, detailed knowledge of the spatial distribution of food sources and other environmental features appears to underlie the selection of travel routes [Gallistel, 1989; Garber, 1988; Gill & Wolf, 1975]. Yet among social birds and mammals the mechanisms for the coordination of group travel remain obscure [Norton, 1986]. In many instances the travel route taken is unlikely to be equally advantageous to all group members because of factors including within-group differences in foraging strategies, nutritional needs, susceptibilities to predation, and abilities to traverse challenging terrains or substrates. Moreover, group members should be able to communicate trajectory or intention and resolve differences in individual preferences if a group split is to be avoided.

Most of the current information on mechanisms of travel coordination in social groups comes from primates. The likely existence of mental maps within at least a subset of troop members has been shown in numerous field studies [Sigg & Stolba, 1981; Boesch & Boesch, 1984; Robinson, 1986; Menzel, 1991]. Field anecdotes describing intention movements by an individual or subset of group members as initiating and leading group movement are common for the terrestrial baboon [*Papio anubis,* Rowell, 1972; Hall & Devore, 1965; *P. hamadryas,* Kummer, 1968]. Such descriptions are more fragmentary in forest primates, but there is some evidence in species such as the pygmy marmoset [*Cebuella pygmaea,* Soini, 1988], the mandrill [*Mandrillus sphinx* and *M. leucophaeus;* Kudo, 1987], and the mantled howler monkey [*Alouatta palliata,* Milton, 1980] that vocal signals are used to initiate troop movement. Although many quantitative field studies address the sequence of individuals within troop progressions [cf. Altmann, 1979; Rhine & Westlund, 1981], the only quantitative studies addressing the initiation and subsequent directing of troop movement in primates are based on the Costa Rican squirrel monkey, *Saimiri oerstedi* [Boinski, 1991] and *S. sciureus* in Amazonian Peru [Boinski & Mitchell, 1992]. Adult female *S. oerstedi* produced a frequency modulated call, the twitter, in two restricted contexts: 1) when in the leading edge of a travelling troop, and 2) when at the periphery of a stationary troop, usually prior to the troop traveling in a trajectory predicted by the twittering female's location. In contrast, no call analogous in structure or function to the twitter was identified in the vocal repertoire of adult female *S. sciureus.* Unlike *S. oerstedi,* South American squirrel monkey troops usually follows capuchin monkey (*Cebus* spp.) troops and are responsible for the formation of mixed-species troops [Terborgh, 1983; Boinski, 1989]. Instead of directing troop movement with their own vocalizations, members of *S. sciureus* troops in Peru probably loosely monitor the location of capuchin monkeys both visually and by attending to capuchin calls [Terborgh, 1983; Mitchell & Boinski, pers. obs].

Here I report the results of a field study on mechanisms underlying the coordination of troop movement in another arboreal primate, the white-faced capuchin monkey, *Cebus capucinus,* in Parque Nacional Santa Rosa, Costa Rica. *Cebus* is a good candidate for such a study for two reasons. First, based on the literature and my personal experience, arboreal primates tend to use vocal signals in the coordination of troop movement, presumably because intervening foliage impedes visual contact. In this context vocal signals are less ambiguous for the observer to quantify than intention movements. Second, Chapman [1988] described capuchin troops at P. N. Santa Rosa as frequently moving between preferred foraging sites rather than lingering in one location for extended periods. Thus, numerous opportunities to document travel coordination were expected. The specific objectives of this study were to use focal observations of individual behavior in association with troop movement patterns to identify 1) the vocal signal(s), if any, used to coordinate travel; 2) how such vocal signals are used; 3) which troop members were active in movement decisions; and 4) if within-group conflict over travel route is detected, how concensus for the selected route is achieved.

## MATERIALS AND METHODS

### Site and Study Animals

Parque Nacional Santa Rosa is located in a tropical dry forest situated along the Pacific coast in northwestern Costa Rica and has been previously described [Chapman, 1988]. The local climate is characterized by an extreme dry season (mid-December to mid-May) and the 900–2,400 mm in annual rainfall occurs during the remainder of the year. The study took place in January and February 1991, a period when no rain occurred and many non-riparian trees had lost their leaves.

For the 8 years previous to my study Linda Fedigan and her colleagues have studied troops of capuchins in Santa Rosa in an ongoing investigation of capuchin ecology, social behavior, and demography [cf. Fedigan, in press]. Troops have been observed on a regular monthly basis throughout this time period. I selected the Cerca de Piedra troop for my focal troop because the terrain was easier to negotiate while carrying recording equipment, and the trees within this troop's approximately 1 $km^2$ range tended to be lower in height than in the ranges of other troops. Qualitative observations of the vocal behavior of two other troops of capuchins, the Los Valles and the Sendero troops, were also made to corroborate results from the focal troop. All three troops were well habituated to the presence of human observers.

The Cerca de Piedra troop comprised 14 animals: 4 adult females and 3 adult males (minimum ages 5 years), 2 female and 2 male juveniles (ages 18–60 months), and 3 infants (ages 6–18 months). Infants traveled independently of females. The size, composition, and social structure of the troop was within the range of variation of *C. capucinus* at this site [Fedigan, in press]. One adult male, Junior, was the alpha male, and males generally were dominant over the adult females. The alpha female was Limp, and the sequence of increasingly subordinate adult females was Blanche, Chops, and Patch [Rose, 1992].

*C. capucinus,* like its congeners, is insectivorous and frugivorous, and frequently employs extractive foraging techniques requiring deft manipulative abilities [Chapman & Fedigan, 1990; Janson & Boinski, 1992]. Females eat more embedded prey (requiring more foraging effort) and allocate more total time to foraging while males eat larger invertebrates, capture more vertebrate prey, and ingest more animal protein [Rose, 1992, in press; Fedigan, in press].

### Data Collection

Preliminary observations determined that the age-sex classes differed in the variability of vocal behavior across contexts, females being more variable than the other age-sex classes. Thus a stratified sampling regime was employed to achieve power more efficiently in statistical analyses [Fragaszy et al., 1992]. The objective was to sample the behavior of females (in number of bouts and in cumulative duration) four times as frequently as the other age-sex classes. As it was not feasible to locate individual troop members of this arboreal monkey according to the dictates of a randomized, pre-selected list, a pseudo-random technique was used to select focal subjects. In a sequence of behavioral samples females were sampled four times and other troop members once. Adult females could not have consecutive samples. From the animals observable at a given moment, the individual judged to be most "undersampled" was selected. Adult males, the most visible and readily identified individuals, were oversampled by about 50% in the cumulative duration of observation time. Possible bias caused by this non-random protocol is reduced because much of the data are analyzed as vocal rates within contexts.

Over 50% of the recordings were made when the subject was within 3 m of the microphone and nearly all recordings occurred within 5 m. A colleague (L.M. Rose), simultaneously engaged in a long-term foraging study of the focal troop, verified the identity of each focal subject. A continuous recording of the vocalizations of the focal animal was collected onto one channel of a Marantz PMD 430 field recorder fitted with a Sennheiser ME88 directional microphone covered with a windscreen, and using Maxell XLII 90 min cassette tape. I dictated descriptions of the simultaneous individual and troop behavior. Recording terminated when the focal animal moved out of recording range, when calls could not be accurately identified, or when the focal subject fell asleep.

The non-vocal behavioral data obtained for each subject included foraging activity, identity of the nearest neighbor, estimates of spatial position within stationary and traveling troops, and distance to the nearest neighbor (in 1 m units). The effects of spatial position on capuchin vocal behavior will be emphasized in this report. A stationary troop had two positions: 1) edge, a 10 m wide peripheral zone with the outside edge defined by the perimeter of troop dispersion; and 2) core, the area interior to the edge. Five positions were defined for a traveling troop (nearly always 3–4 times longer in dimension than wide): 1) vanguard, a 10 m deep zone starting at the leading edge; 2) back, a 10 m deep zone ending at the trailing edge; 3) side, a 10 m wide zone on the side of a troop between the vanguard and back; and 4) front and 5) center, approximately equal divisions of the length of the troop interior.

Based on preliminary observations I identified the trill call as the most likely vocalization to function in the coordination of troop movement. A subject was described as making a "start attempt" when it was in the edge of a stationary troop (most often the far periphery) and made at least one trill. The subject usually looked back into the core of the troop and in less than half the instances the subject paced at least several meters further away from the troop in what could be described as an "intention movement." It must be stressed, however, that the production of at least one trill vocalization at the edge of the troop was the sole criterion; any intention movements I perceived were described but did not contribute to the definition of the start attempt. If the troop moved within 10 min subsequent to the first trill, the azimuth of the troop movement relative to the center of the stationary troop and the subject's position (to the nearest 15°) was determined by estimation and using a Suunto compass. A 10 min criterion was selected as the maximum lag time because I judged (based on my experience with squirrel monkeys [Boinski, 1991]) that there would be adequate time for a signal to be transmitted to troop members, and yet the time elapsed would be sufficiently brief to demonstrate an association between the start attempt and any subsequent troop movement. Similarly, a subject was identified as attempting a change of direction when it made at least one trill while in the side or back of a traveling troop and usually facing back towards the troop. The azimuth of the troop movement relative to the azimuth predicted by the trilling animal's location was determined to the nearest 15°, as was the azimuth of the troop's route 10 min later.

The data set consisted of 33.7 h of continuous recordings. Each adult female contributed an average (SE) of 288.8 (19.8) min and 331.5 (24.3) calls, adult males 117.9 (31.6) min and 35.7 (14.7) calls, juveniles 75.8 (10.2) min and 40.5 (21.1) calls, and infants 70.6 (12.2) min and 99 (16.2) calls. The temporal sequence and

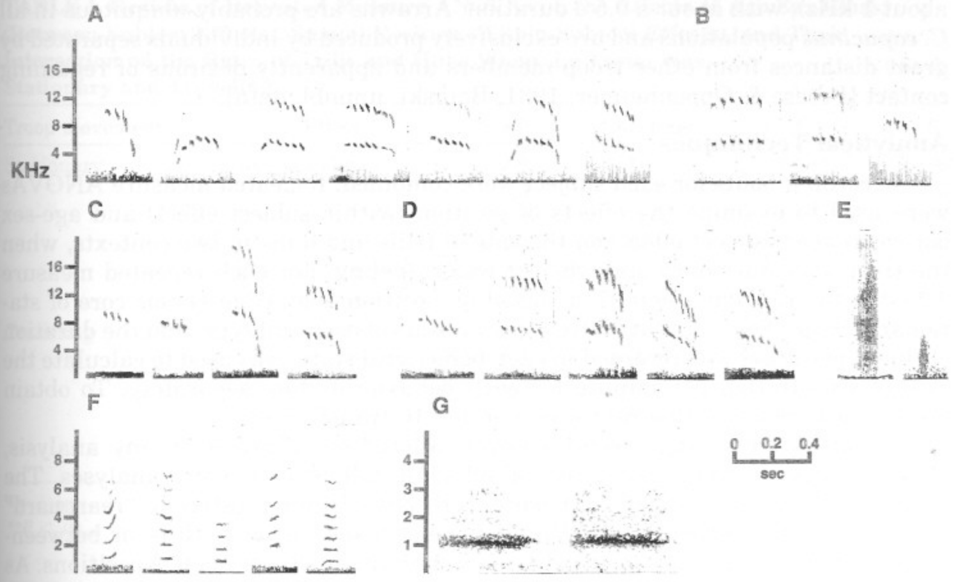

Fig. 1. The major call categories used in this study: (**A**) trill, 7 examples from the same adult female, (**B**) trill, 3 examples from 2 adult males, (**C**) trill, 4 examples from the same juvenile, (**D**) trill, 5 examples from the same infant, (**E**) heh, 2 examples from the same adult male, (**F**) huh, (from left to right) an adult female example, 2 juvenile examples, and 2 infant examples, and (**G**) arrawh call, 2 examples from the same adult male. See Materials and Methods for a description of the structural characteristics used to distinguish the call categories.

duration of the focal subject and troop behavior and the time and context of each recording were coded from the tapes. Sonagrams of 1,892 vocalizations recorded during the focal samples (none were excluded) were made with a Multigon Uniscan II (settings: 5, 10, and 20 kHz; 256 spectrals) and a Panasonic KY-P1180 printer.

## Call Classification and Measurement

The 1,892 sonagrams were assigned by visual inspection into 4 types: trill (N = 1258), huh (N = 428), heh (N = 150), and gyrrah (N = 56, not depicted) (Fig. 1). Trills [Robinson, 1984] consist of a loud, rapid series of pulses that compose an often undulating frequency contour. Within-individual variation in the shape of the frequency contour could be marked. The lowest frequency band ranged between 4 and 9 kHz, and usually the first harmonic, occasionally the second harmonic, and rarely the third harmonic were detected. The duration and number of pulses were determined for each trill. Huhs [Oppenheimer, 1968; Robinson, 1984] are soft, brief, low-frequency calls. The frequency of every huh was close to 1 kHz and harmonics were numerous. Eight-seven percent of huhs were less than 0.1 s in duration. Hehs [Robinson, 1982] are noisy, brief calls. All but two hehs were clearly associated with situations of alarm or aggressive social interaction. Alarm calls, gyrrahs [Oppenheimer, 1968; Robinson, 1982], represent a composite of highly variable, usually high-frequency calls clearly associated with the presence of potential predators or threats from a dominant animal. Given the structural diversity of gyrrahs, the sample size was too small to characterize them in greater detail. Also depicted in Figure 1 are two arrawh calls [Oppenheimer, 1968], a common call at the study site but, by chance, not included in any of the focal samples. Arrawh calls are low-frequency, noisy calls (intense energy present about 1 kHz), with about a 0.5 s duration. Arrawhs are probably ubiquitous in all *C. capucinus* populations and are exclusively produced by individuals separated by great distances from other troop members and apparently desirous of regaining contact [Freese & Oppenheimer, 1981; Boinski, unpubl. data].

## Analytical Techniques

Recording bouts for each subject were combined. Repeated measure ANOVAs were used to examine the effects of position (within-subject effect) and age-sex class (between-subject effect) on the rate of trills and huhs in two contexts, when the troop was stationary and when it was traveling. For each repeated measure ANOVA the raw data were first sorted by position (e.g., edge versus core of stationary troop). The cumulative frequency counts of each call type, and the duration of time the subject was recorded in each behavioral state, was used to calculate the rate of vocalization per minute for each behavioral state separately. To obtain normal distributions, this rate was then log 10 transformed.

Because infants and juveniles never differed significantly in any analysis, these age groups were pooled into a subadult category in many analyses. The positions front, side, center, and back were pooled into a category "rearguard" because repeated measure ANOVAs detected no significant within- or between-subject effects on the rates of either trills or huhs across these spatial positions. As subadults were never or rarely sampled in the vanguard of a traveling troop the repeated measure analyses comparing vanguard to rearguard positions had a sample size of 7. Similarly, 2 infants and 2 juveniles never ventured into the edge of a stationary troop. Thus, the sample size in the analysis of spatial position within a stationary troop was 4 adult females, 3 adult males, and 3 subadults.

A circular statistic called the V-test, a modified version of the Rayleigh test [Batschelet, 1981], was used to determine whether the observed azimuths of troop movement were clustered about the position of the subject attempting to initiate movement in a stationary troop. Instances in which the troop did not move subsequent to such an attempt were treated as if the troop had instead moved 180° from the angle predicted by the female's position on the troop periphery. The success of a subject's attempt to change the trajectory of a traveling troop was also evaluated with the V-test. The azimuths of troop movement 10 min after an attempt to change trajectory were compared to the azimuths predicted by the subject's position. In both V-tests the angular data were grouped into arcs of 45° prior to analysis.

The statistics describing the average (SE) number of calls emitted in the start attempts, the duration of start attempts, and measures of call structure are based on the individual means.

# RESULTS

## Measures of the Frequency Structure of Trills

The average (SE) duration and number of pulses per trill did not differ among age-sex classes: 1) duration (s), adult females = 0.25 (0.01); adult males = 0.20 (0.01); juveniles = 0.23 (0.04); and infants = 0.23 (0.02) (one-way ANOVA, $N = 14$, $df = 3,9$ $F = 0.92$, $P > .23$); and 2) number pulses, adult females = 4.92 (0.23); adult males = 3.84 (0.40); juveniles = 4.22 (0.21); and infants = 4.57 (0.45) (one-way ANOVA, $N = 14$, $df = 3,9$, $F = 2.13$, $P > .17$). No significant differences were found either within or between age-sex classes by spatial position in these measures of the acoustic structure of trills (unpublished data). Similarly, no significant age-sex or contextual differences were found in a subsample of trills in which the peak and minimum frequency, mean pulse duration, and interval were

**TABLE I. Results of Repeated Measure ANOVAs on the Effects of Age-Sex Class (Between-Subject Effects), Spatial Position (Within-Subject Effects), and Their Interaction on the Rates of Trills and Huhs When the Troop Was Stationary and Traveling**

| Troop movement | Effect | df | Call type | F | R |
|---|---|---|---|---|---|
| Stationary | Age-sex class | 2,8 | Trill | 7.74* | 0.66 |
| | | 2,8 | Huh | 5.62* | 0.59 |
| | Position | 1,9 | Trill | 0.08 | 0.00 |
| | | 1,9 | Huh | 3.73 | 0.31 |
| | Position by age-sex interaction | 2,8 | Trill | 1.74 | 0.15 |
| | | 2,8 | Huh | 0.17 | 0.01 |
| Traveling | Sex class | 1,5 | Trill | 9.58* | 0.66 |
| | | 1,5 | Huh | 5.22 | 0.50 |
| | Position | 1,6 | Trill | 18.12** | 0.66 |
| | | 1,6 | Huh | 1.61 | 0.14 |
| | Position by sex interaction | 1,5 | Trill | 8.74* | 0.27 |
| | | 1,5 | Huh | 5.02 | 0.43 |

*$P < .05$.
**$P < .01$.

quantified and the shape of the frequency contour was categorized (unpublished data).

### Vocalization Rates by Spatial Position and Age-Sex Class

When a troop was stationary there were significant age-sex class (between-subject) effects on the rate of trills and huhs (Table I; Fig. 2). No positional (within-subject) or position by age-sex interaction effects were detected. Adult females emitted trills seven times more frequently on the edge than in the core. Males had very low rates of trills in both positions. Subadults (infants and juveniles pooled) trilled twice as often in the core of the troop compared to the edge. Huhs also exhibited a disparate age-sex response. In the edge the rate of huhs was 4 times greater for adult males and twice as great for females than in the core.

Significant sex (between-subject) and positional (within-subject) differences as well as an interaction effect were found on the rate of trills within a traveling troop (Table I; Fig. 3). Both males and females emitted trills at a significantly greater rate in the vanguard versus the rearguard positions, with females calling more than males in both positions. No significant effects were detected in the rates at which adult males and females produced huhs within a traveling troop.

### Coordination of Troop Movement

The high rate of trills by adult females when in the edge of a stationary troop (1.3 trills/min) represents 36 instances in which a female made an apparent attempt to initiate movement in a stationary troop (Table II). Adult males also made three apparent attempts to initiate troop movement. Thirty-six of the 39 total start attempts that were documented in the focal samples were termed "successful" because within 10 min of the beginning of the start attempt the troop traveled in the direction predicted by the subjects's location relative to the center of the troop. The azimuths of troop movement subsequent to a start attempt were significantly clustered about the angle predicted by the focal's position ($u = 7.67$, $N = 39$, $P < .0001$).

In at least 19 of the start attempts documented in focal samples more than one

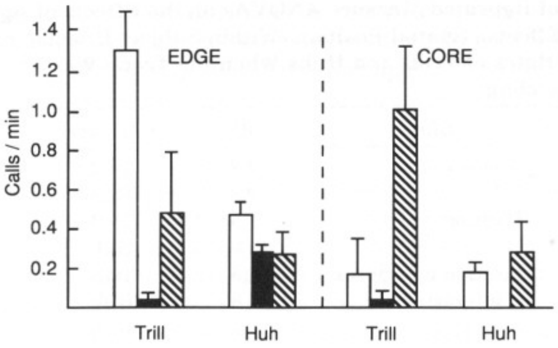

Fig. 2. The mean (SE) age-sex class rates of trill and huh production within the edge and core spatial positions of a stationary troop: □, adult females; ■, adult males; ▧, subadults (infants and juveniles pooled).

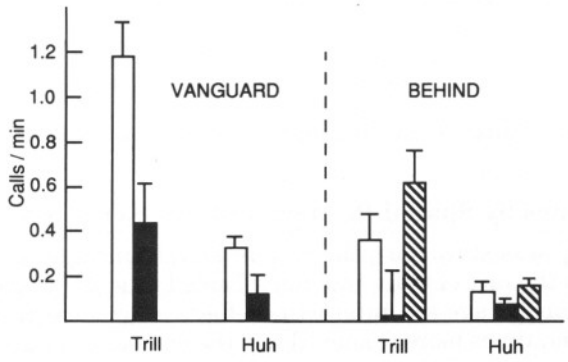

Fig. 3. The mean (SE) age-sex class rates of trill and huh production within the vanguard and rearguard spatial positions of a traveling troop: □, adult females; ■, adult males; ▧, subadults (infants and juveniles pooled). The data for subadults are given to document age-sex patterns more completely, but are not used in statistical analyses.

adult produced trills in the same start attempt. The sex, but not always the individual identity, of others active in the start attempt was determined. No mixed–sex start attempts were observed. The 4 adult females and 2 of the 3 adult males made successful start attempts. Each of the 36 successful starts comprised an average (SE) of 3.8 (7.1) trills, 1.0 (0.4) huhs, and 2.1 (0.3) min (N = 6 subjects). In two of the three "failed" start attempts, the troop did not start traveling within 10 minutes of the beginning of the start attempt. Patch, an adult female, produced 72 trills and 4 huhs in a start attempt lasting 9 min 22 s before returning towards the center of the troop. Another unsuccessful female, Chop, produced 93 trills and 7 huhs before apparently abandoning efforts to initiate troop movement. While I was recording from Patch on another occasion, the adult female Limp was simultaneously engaged in a start attempt 60° from Patch's position. Eight minutes and 51 trills and 22 huhs after Patch initiated her start attempt, the troop traveled in the trajectory predicted by Limp's location on the edge of the troop.

Based on both focal and ad libitum observations during this study, all but one of the instances in which the troop initiated travel after being stationary for a minimum of 5 min was subsequent to an adult emitting at least one trill from the

**TABLE II. Tabulation of the Number and Type of Instances in Which Adult Females and Males Attempted to Lead Troop Movement***

| Focal | Successful start of travel in stationary troop | Failed attempt to start travel in stationary troop | Successful change in traveling troop angle | Failed change in traveling troop angle | Rate of successful attempts per hour of focal observation |
|---|---|---|---|---|---|
| Adult females | | | | | |
| Limp | 10 | | 4 | | 3.41 |
| Blanche | 9 | | 3 | | 2.58 |
| Chops | 9 | 1 | | 2 | 2.04 |
| Patch | 5 | 2 | 2 | 2 | 1.50 |
| Adult males | | | | | |
| Junior | 2 | | 1 | | 1.08 |
| Winston | 1 | | | | 0.84 |
| Blackie | | | | | 0.00 |
| Total | 36 | 3 | 10 | 4 | |

*Also given is the rate of successful attempts per hour of focal observation for each individual. Within each sex individuals are ranked by relative dominance as determined by Rose [1992].

edge of the troop, and the direction was predicted by the adult's location. The one exception was when the alpha male, Junior, the focal subject, appeared to initiate and lead troop traveling on the basis of intention movements alone in an area with little foliage where he was likely visible to all troop members. Shortly after Patch and Limp had begun trilling 180° across from Junior on the edge of the stationary troop, he began walking away from the troop on a branch until he was 10 m ahead of Winston, and more than 20 m from the next closest troop member. Junior then turned around and looked back at the troop. After sitting for approximately 2 min he continued to walk outward in his previous trajectory. Within 1 more minute the rest of the troop followed, with Patch and Limp trailing at the far back of the troop.

Changes in direction during troop travel were also associated with trills produced by an adult at the sides or back of a traveling troop (Table II). Ten successful and 4 unsuccessful changes in troop trajectory were documented. The azimuths of troop movement 10 min subsequent to these attempts were significantly clustered about the position predicted by the calling animal's position ($u = 3.114$, $N = 14$, $P < .001$). For the 3 females and 1 male who successfully changed the azimuth of the troop trajectory the change attempt represented an average (SE) of 11.6 (2.3) trills, 5.8 (1.9) huhs, and 4.3 (1.5) min ($N = 4$). Two adult females each made two unsuccessful attempts with an average (SE) of 13.3 trills, 0 huhs (0.0), and 3.2 (2.0) min per attempt ($N = 2$).

Regardless of position, activity, or whether the troop was stationary or moving, trills were nearly exclusively produced by adults in contexts associated with the coordination of troop movement. During focal recordings all but seven trills emitted by adults in the central and front positions of a traveling troop and in the core of a stationary troop occurred when the individual was en route to the troop periphery where it continued emitting trills. The exceptions comprise two trills produced by females in exchange with a subadult and four other instances when a female looked into the distance, uttered a single trill (possibly in response to a trill I did not hear), and resumed her former activity. An adult male made one trill in an interaction in the core of a stationary troop after a female jumped on a branch adjacent to the male and the branch broke. The female who fell responded as if the male had attacked her. After two nearby females then ran to the male in a highly aggressive manner, the male emitted a trill while leaping away.

Two instances of change of troop direction were noteworthy for their indications of strategic maneuvers. Blanche was in the vanguard leading the troop on a trajectory that intersected with a favored fruit-foraging area and emitting occasional trills. Junior and Winston, the alpha and beta male, rapidly ran forward from the troop center to a position directly facing Blanche in the vanguard. Several seconds later when Blanche emitted another trill, both Junior and Winston uttered loud hehs and gave threat faces to Blanche. Junior lunged at Blanche with bared canines. Blanche ran back into the front position and produced no additional trills. Junior and Winston, now alone in the vanguard, immediately turned 120°, trilled, and led the troop directly to a water hole. In another example, both Chop and Limp initiated simultaneous start attempts at different positions on the troop periphery and the troop began traveling in the trajectory indicated by the latter female's position. Chop traveled in the center of the troop for 2 min then directly ran in a purposeful manner to the vanguard of the troop while trilling very loudly and frequently, such that she "overwhelmed" Limp's trills. Once Chop surpassed Limp in the vanguard she angled back while continuing the intense signaling, thus altering the travel path back to the route she had originally indicated.

Within each sex there was a perfect concordance between an individual's dominance rank and the number of successful attempts to lead troop movement (Table II); the greater the dominance rank, the greater the total number of successful initiations and changes of troop movement. This relation also holds true when the number of successful attempts is converted to the rate of successful attempts per hour of focal observation. Only the two lowest ranking females had failed attempts.

## Other Vocal Behavior

Subadult trills were never associated with the coordination of troop movement. Instead, over 90% of the trills produced by subadults were in vocal exchanges with other subadults or during social interactions, usually play, with subadults. Nine percent of trills had no overt social connotations. On three occasions within all focal and ad libitum observations a female responded to the trill of a subadult with a trill. Adult males never exchanged a trill with a subadult.

Huhs tended to increase in rate among the adults in spatial positions associated with the initiation of troop movement, but not significantly so (Figs. 2, 3) Yet huhs were extremely predictable and produced at high rates in one context by all age-sex classes, when foraging in fruit trees with dense patches of apparently preferred fruits (unpublished data; L. Fedigan & L.M. Rose, pers. obs.). Data on rate of huhs presented here does not reflect this restricted context because the individual rate and absolute number of huhs were so great that the identity of which animal produced which huh was difficult to accurately monitor in most instances. When the troop was foraging within the two fruit trees in the study site with abundant and dense crops of ripe fruit during the study period, a *Ficus* spp. (Moraceae) and a *Sloanea terniflora* (Elaeocarpaceae), the minimum mean individual rate of huhing exceeded 3 huhs/min, based on the total number of huhs detected per time period divided by the number of animals within the fruit tree. When troop members foraged on the fruits of the common *Luehea* spp. (Tiliaceae) and *Manilkara zapota* (Sapotaceae) trees, but which were presented in smaller, relatively sparse patches, the rate of huhs was not significantly different from that of non-foraging contexts (unpublished data).

## DISCUSSION

Adult white-faced capuchins rely on a specific call, the trill, to initiate, lead, and change the trajectory of troop movement. The utterance of even one trill by an adult in the edge of a stationary troop was highly predictive of the troop initiating travel within the next 10 min. Moreover, the azimuth of the travel path was also closely predicted by the position of the trilling animal on the periphery relative to the troop center. Adult females and males when in the vanguard of a traveling troop emitted a higher rate of trills than when in spatial positions behind this leading front. Presumably the trills from the vanguard functioned as auditory beacons indicating the trajectory of troop travel for those following. When an adult emitted trills from the side or back of a traveling troop, the troop's trajectory 10 min later was usually indistinguishable from the trajectory indicated by the position of the trilling adult relative to the center of the traveling troop. Of the relatively low numbers of trills produced by adults in the core of a stationary troop or the center or front positions in a traveling troop all but seven trills were emitted by adults that were in the process of moving from a central to a peripheral position. Qualitative observations of two troops with ranges contiguous to the study troop demonstrated that trills were used in the same manner to coordinate troop movement (pers. obs.). I suggest that reevaluations of the vocal behavior of other wild populations of arboreal primates, particularly in the Old World, may identify further examples of vocalizations with this function.

The trill is an efficient signal for the coordination of troop movement within an arboreal habitat where members of the capuchin troop were usually separated by more than 5 m and the adults were often more than 10 m from their nearest neighbor (unpublished data). Intention movements or other visual displays are unlikely to be reliable cues in this situation to coordinate troop movement. Trills are probably readily locatable by even distant receivers because the loud pulses that comprise a trill provide repetitive intensity and time of arrival cues for binaural comparisons evaluating the angle at which the sound source deviates from the midline [Thurlow, 1971; pers. obs.]. The successful attempts to initiate (N = 36) and change (N = 10) the trajectory of troop movement each required on average only 5.5 trills and 2.6 min.

Adult females appear to be more active than adult males in the coordination of troop movement, even when the adult male samples are weighted to approximate the size of the adult female samples. The rate of trills produced by adult males was much lower than that of adult females in all spatial positions and was negligible when the troop was stationary. Males and females were never observed to reinforce vocally attempts by the other sex to start or change the trajectory of troop movement. These sex differences are consistent with three other observations. 1) Same-sex social interactions are most common at Santa Rosa, and adult females are more socially interactive than males overall [Fedigan, in press]. 2) Adult females forage more, although less efficiently, than adult males [Rose, 1992] and would be predicted to be more motivated in directing movement to new, potentially more productive foraging sites. 3) It is possible that adult females, which are consistently philopatric in this population [Fedigan, in press], best know the range and its resources. Recently immigrated adult males from neighboring troops often attempt to lead the troop to their former range, and those males immigrated from distant troops have a tendency to become lost when not in the immediate proximity of the troop (L. Fedigan, pers. comm.).

Conflicts over a selected travel path commonly occurred, but were usually subtle. Individuals made a start attempt simultaneously from more than one position on the periphery of a stationary troop (N = 3) or trilled from the side or back of a traveling troop being led by others (N = 14). Twice the troop was "hijacked" by individuals seemingly commandeering the vanguard position. Two instances of conflicts could only be inferred from the fact that the troop did not initiate travel despite a protracted start attempt. Future studies should investigate the association found in this study between rank and the number and rate of successful instances of initiating and changing the direction of troop movement within each sex. In both males and females the higher the rank of the individual, the more frequently they led troop movement. Furthermore, only the two lowest ranking females had failed attempts. Most other troop members were concordant in their support of each initiative, either moving in the indicated direction within a brief time period or continuing as they were. Those individuals whose movement attempts were not supported always rejoined the troop; thus majority (and possibly dominant) decisions had precedence.

Two other factors related to dominance may have affected the outcome of decision-making in regard to troop movement. First, cooperative alliances in food competition could possibly be extended to cooperation in the manipulation of troop movement. The two highest ranking females, Blanche and Limp, who cooperated in aggressive defense and acquisition of foraging sites, also tended to reinforce each other's attempt to direct troop movement (pers. obs.). Second, Kummer [1968] and Rowell [1969] distinguished between "initiative" and "decision" roles in the determination of the movement of baboon troops. Troop members attempting to lead the troop would be successful only if individuals controlling the decision (adult males in Kummer's and adult females in Rowell's study) followed the nominal leaders. Although the data from this study are insufficient to directly address the existence of a lead versus control decision process in *C. capucinus,* it is interesting to note that the alpha male, Junior, was able to initiate and lead the troop in a direction opposite that indicated by two calling females without himself calling. On two occasions L.H. Rose (pers. comm.) also observed Limp and Blanche in an attempt to initiate troop movement apparently directing their bleets specifically to the alpha male, as if "appealing" for his concurrence. This suggests the possibility that the alpha male may play a "decision" role in group movements at least sporadically among *C. capucinus*. In the congeneric tufted capuchin monkey (*C. apella*), the alpha male appears to consistently determine the direction of troop movement by his acquiescence or declination to movements led by adult females and other troop members (C.H. Janson, pers. obs.; S. Boinski & C.H. Janson, unpubl. data).

No age-sex or contextual distinction in the acoustic structure of trills was identified within the limits of the techniques and measures used. Yet adults employed trills as vocal signals to coordinate travel, and the trills of subadults (juveniles and infants pooled) occurred in vocal exchanges nearly exclusively with other subadults and had no detectable association with troop movement. The hypothesis that subadults use trills in an effort to coordinate travel, but have little social power, and thus are ignored, is unlikely because subadults so seldom produced trills at the periphery at the troop and never in the vanguard. Given the available data the function of subadult trills is probably best described as a contact call to maintain spatial cohesion [Byrne, 1982; Caine & Stevens, 1990; Boinski, 1991] and possibly as an auditory signal to notify adults of their location to facilitate anti-predator vigilance and deterrence [Biben & Symmes, 1986]. Although in a broad sense the adult trill can also be interpreted as a contact call, this cross-sectional study has identified a change in trill usage from a general to a specific context. The restricted adult usage might have evolved or have been adapted from subadult usage. This finding is also interesting in regard to ontogentic studies on call development in primates that describe how appropriate call usage "improves" as individuals age [Seyfarth & Cheney, 1980; Gouzoules & Gouzoules, 1989; Elowson et al., 1992]. Subadult capuchins are unlikely to be using trills inappropriately, just differently.

In two previous descriptions of *C. capucinus* vocal behavior [Oppenheimer, 1968; Freese & Oppenheimer, 1981] no call was characterized as a signal employed in the control of troop movement. The trill, huh, and gyrrah are among the numerous call types defined by these workers. The discrepancy in the number of call types is partially accounted for because my study was shorter, I did not distinguish among diverse alarm calls, and infant-mother vocal interactions (a major source of vocalizations for Freese and Oppenheimer) were exceedingly rare in my study troop. In the only description pertinent to travel coordination in this species, Freese [1978] described an adult male bias among capuchins in the first quartile of progressions to water holes at Santa Rosa, and his impression was that females and juveniles typically led troop travel in other contexts.

Robinson's [1982] study of the congeneric wedge-capped capuchin, *C. olivaceus,* in Venezuela addressed how regulation of the spacing of animals within a troop was accomplished with heh, huh, and arrawh acting as contact calls. He suggested that heh calls served to increase spacing between crowded animals and arrawh calls brought separated animals closer; huh calls were produced at intermediary distances and discouraged other individuals from approaching. Food competition was identified as an important factor encouraging spacing between animals.

One of the original objectives of my field work with was to document the comparable vocal mechanism regulating spacing in *C. capucinus*. Despite the fact that detailed data on nearest neighbor identity and distance and foraging activity were collected with the concurrent vocalizations, no significant pattern suggesting a relationship between within-troop spacing and the heh and huh calls was detected. My study was much briefer than Robinson's, but the data were not consistent; heh calls were a rarity in all contexts among all troop members and huh calls were common only in the close proximity to dense, high quality fruit patches, and at lower rates during initiation and leading of troop movement. Arrawh calls were never even recorded during focal samples. Moreover, even very low rates of huh calls by the standard of Robinson's *C. olivaceus* study, 1–3 huhs per minute, were attained only during the extreme situations among the *C. capucinus*. If the heh-huh-arrawh system of within-troop spatial regulation described by Robinson is common to the genus *Cebus,* I suspect that disparities in food distribution might be the proximate factor accounting for disparities in vocal usage between the Costa Rican and Venezuelan sites. The large nearest neighbor distances between *C. capucinus* suggest that food availability was low and indirect food competition high. Vocal regulation of spacing might be unnecessary in this situation.

Capuchins (*Cebus* spp.) display remarkable levels of manipulative intelligence and problem-solving abilities that appear to derive from their foraging specializations: extraction of food items encased within substrates, a precision grip, and the ability to integrate time and space in complex routes between foraging patches [Parker & Gibson, 1977; Westergaard & Fragaszy, 1987; Boinski, 1988; Janson & Boinski, 1992]. The capuchins in this study also evinced unexpected ingenuity in two aspects of vocal behavior. First, capuchins were able to change the trajectory of an often rapidly traveling troop as much as 180° using trills. Squirrel monkeys in Costa Rica did not display this flexibility, but traveled in a more or less straight line between points and changed direction after the troop was stationary [Boinski, 1991]. To the best of my knowledge no report in any other primate suggests that vocalizations alone are sufficient to establish a new trajectory in a traveling troop. Second, the relation between another troop member trilling in the vanguard of a troop and the troop following is apparently recognized. The troop was successfully "hijacked" by individuals usurping the vanguard position, once by aggression and in another instance by outdistancing the nominal leader and overwhelming her trills. These maneuvers suggest intentionality and the ability to anticipate behavioral effects and are reminiscent of instances of social manipulation documented in chimpanzees and other primates [de Waal, 1991]. The wedge-capped capuchin (*C. olivaceus*), provides another possible example of exceptional intelligence being expressed in vocal behavior. In this species compound calls were produced in contexts intermediate between the usage of the two calls produced separately [Robinson, 1984].

Huhs, which were most predictably produced when capuchins were in dense fruit patches, also tended to increase, but not significantly so, among adults in spatial positions associated with the initiation and leading of travel. Several workers suggest that the "food calls" reported in some other primate species are better described as communicating excitement about a positive feature in their environment [de Waal, 1991; Elowson et al., 1991]. That capuchin huhs are produced both when foraging on preferred foods and when individuals are presumably anticipating travel to a new foraging area is consistent with this interpretation. A contradictory interpretation that cannot be excluded is that if huh calls were subdivided more finely into structurally distinct subtypes that were not recognized in this study one structural variant could be associated with troop movement and another with food.

## CONCLUSIONS

1. Adult capuchins in Santa Rosa actively coordinate (initiate and lead) troop travel and use trills as a vocal signal to indicate the direction of travel.
2. Within-group differences in preferred travel routes were detected and consensus achieved through majority decisions, possibly influenced by dominance rank and social coalitions, and occasionally facilitated with maneuvers that suggest intentionality and social manipulation.
3. Infants and juveniles do not participate in coordinating troop movement and appear to use trill vocalizations as a general contact call.
4. Huh vocalizations are most predictably emitted in the vicinity of dense fruit patches.

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