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USE OF TRILL VOCALIZATIONS TO COORDINATE TROOP MOVEMENT AMONG WHITE-FACED CAPUCHINS: A SECOND FIELD TEST

by

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(With 2 Figures)

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Summary

The white-faced capuchin, *Cebus capucinus*, employed a specialized vocalization, the trill, to coordinate troop movement at La Selva, an Atlantic wet-forest study site in Costa Rica. We analyse the contexts in which this intra-group vocalization was emitted, including responses elicited from other group members. A cumulative 26.6 hours of continuous samples and 3,314 spectrograms (including 1,295 trills) were analysed from a study troop with 16 focal subjects. These results generally corroborate the conclusions of a comparable field study of white-faced capuchins at Santa Rosa, a Pacific coast dry-forest site in Costa Rica (BOINSKI, 1993, Amer. J. Primatol. 30, p. 85-100). At both sites, (1) trills were closely associated with the initiation of movement by a stationary troop in a specific direction. (2) Trills were emitted at a much higher rate in the leading edge of a travelling troop than in following positions. (3) Individuals often reinforced the efforts of other troop members to coordinate troop movement. (4) Lack of consensus among troop members over the travel route was evident. (5) In rare instances trills were employed in tactical maneuvers suggestive of intentionality and the ability to anticipate behavioural effects.

Differences in the usage of trills at these two sites were also detected. (1) At La Selva all troop members, with the exception of infants, used trills in the coordination of troop movement, whereas at Santa Rosa marked age, sex and rank distinctions in the extent of participation were apparent. (2) Capuchins at Santa Rosa altered the trajectory of travell-

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ing troops with trills, even reversing directions, but not at La Selva. These disparities may follow from differences between the sites in the extent of visual and auditory contact typical among troop members, social structure, susceptibility to predation, and possible genetic variation.

Introduction

Despite the ubiquitous evidence that flocks, herds, and troops of social birds and mammals do make group decisions as to travel route, the mechanisms underlying these group decisions remain largely obscure (Norton, 1986). Nevertheless, the outcomes of these group decisions have pervasive direct effects on the individual fitness of the members of these social aggregations. In many instances the travel route taken is unlikely to be equally advantageous to all group members because of within-group differences such as foraging strategies, nutritional needs, susceptibilities to predation, and locomotor abilities. The information processing required to optimize both group decisions as to travel route and individual foraging paths within the swath of group movement could also make selection for enhanced cognitive capacities advantageous (Henzi *et al.*, 1992). For example, errors in the mental maps of the resources and other features of the ranging area (Gallistel, 1989; Menzel, 1991) would be costly. Individuals may also need to employ knowledge of the preferences and alliances of other group members, along with other social skills, to obtain a consensus and efficiently direct cohesive travel in a group (Dunbar, 1993).

The sparse data on the coordination of group movement suggests that the relative weight given social dominance and visual *versus* vocal signals varies by taxon. Sable antelope (*Hippotragus niger*) have a highly structured social organization, and the herd appears to monitor the activities of and to follow the oldest and most dominant individuals (Stine *et al.*, 1982; K. Thomas, unpubl. data). Visual coordination of group movement by dominant individuals is plausibly the usual mechanism among other herd ungulates. The nuclear species of Neotropical mixed-species bird flocks use vocalizations and, to a lesser extent, visual signals to rally and to direct flock movement (Munn & Terborgh, 1979; Powell, 1979; Gradwohl & Greenberg, 1980). Flocks of whooper and Bewick's swans (*Cygmus cygmus* and *C. columbianus*) rely on a special vocalization in combination with striking visual displays to coordinate departures from resting and foraging areas (Black, 1988).

Most of the available data on travel coordination comes from primates. Terrestrial primates appear to emphasize visual signals in coordination of movement by a troop. Field anecdotes describing intention movements by an individual or subset of group members as initiating and leading troop movement are common for baboons, as are suggestions that social dominants have the ultimate decision (*Papio anubis*: Hall & DeVore; 1965; Rowell, 1972; *P. hamadryas*: Kummer, 1968). Among distantly separated subgroups of a baboon troop, however, vocalizations function to coordinate movement, especially reunion of subgroups (*Papio papio*: Byrne, 1982). Such descriptions are less common in forest primates, but there is some evidence in species such as the pygmy marmoset (*Cebuella pygmaea*: Soini, 1981), the mandrill (*Mandrillus sphinx* and *M. leucophaeus*: Kudo, 1987), and the mantled howler monkey (*Alouatta palliata*: Milton, 1980) that intragroup vocal signals are used to initiate troop movement. The family groups of titi monkeys (*Callicebus moloch*) studied by Menzel (1993) in large outdoor enclosures generally coordinate group movement by closely following one another and restricting travel to customary routes.

Although many quantitative field studies address the sequence of individuals within troop progressions (*cf.* Altmann, 1979; Rhine & Westlund, 1981), a recent series of field studies of arboreal New World monkeys provides the first quantitative data on the initiation and subsequent leading of troop movement in primates (*Saimiri oerstedi*: Boinski, 1991; *Cebus capucinus*: Boinski, 1993; *Saimiri sciureus*: Boinski & Mitchell, 1992; *Leontopithecus rosalia*: Boinski *et al.*, *1994*). With the exception of *Saimiri sciureus*, which follows the movements of sympatric capuchin troops (Terborgh, 1983; Boinski & Mitchell, 1992), each of these species has a vocalization that is associated with the initiation and leading of troop movement in a specific direction. Although intention movements occasionally accompany travel coordination calls, the vocal signals alone probably contain sufficient information; in most situations, many troop members are unlikely to be in visual contact with the signaller due to dense foliage.

The use of these specialized calls in *S. oerstedi*, *C. capucinus*, and *L. rosalia* appears to have a significant cognitive basis (Boinski, 1991, 1993; Boinski *et al.*, 1994). First, there is evidence that vocalizers and recipients base decisions upon detailed mental maps of ranging areas (Garber & Dolins, in press). Second, the expression of this vocal behaviour has an ontogenetic component which suggests that the social context in which it is uttered is learned (Seyfarth & Cheney, 1986; Gouzoules & Gouzoules, 1989). Third, lack of consensus among troop members as to travel route is commonly detected, implying individual choice. Attempts to initiate travel may fail, and on occasion multiple individuals simultaneously attempt to initiate travel in different directions. Fourth, long-term reciprocative relationships among troop members might influence the decision-making process underlying group movement patterns (Boinski, in press). Pairs of *C. capucinus* forming cooperative alliances in food competition also reinforce each other's vocal attempts to lead group movement. Small subsets of *S. oerstedi* adult females also reinforce each other's efforts to lead group movement. Finally, *C. capucinus*, but none of the other species studied, at least rarely employs its troop coordination call in tactical maneuvers suggestive of intentionality.

At each of the three neotropical study sites where a travel coordination call has been identified, the usage of this vocalization was indistinguishable among all conspecific troops examined (*L. rosalia*, 5 troops: Boinski *et al.*, 1994; *C. capucinus*, 3 troops: Boinski, 1993; *S. oerstedi*, 5 troops: Boinski, unpublished data). To date, however, no study has investigated differences among sites in the usage of travel coordination calls of any one species. Locale-specific differences might be expected because of the number of potentially differing genetic, social and environmental contributions to this complex vocal behaviour (Galef, 1990). In fact, little data exists addressing geographic (Byrne, 1982; Whitehead, 1995) or taxonomic variation (Hohmann, 1991; Owren *et al.*, 1993; Boinski & Mitchell, 1995) in the usage of specific vocalizations among primates, although variation in the acoustic structure of homologous vocalizations are relatively well documented (Macedonia & Taylor, 1985; Boinski & Newman, 1988; Gautier, 1988).

Here we report a field study that permits a between-site comparison of the use of travel coordination calls in a primate species. Specifically, we studied the coordination of group movement in a troop of *C. capucinus* at the La Selva Biological Station in northeastern Costa Rica, 120 km inland from the Atlantic coast. Parque Nacional Santa Rosa, where the coordination of troop movement in *C. capucinus* was previously studied (Boinski, 1993), borders the Pacific Coast of northwestern Costa Rica.

The sites are separated by a mountain range and approximately 360 km. This comparison is unlikely to be highly confounded by genetic variation. Insufficient morphological or behavioural variation has been detected in *Cebus capucinus* to warrant division into multiple subspecies (Groves, 1987; Mittermier *et al.*, 1981; P. Hershkovitz, pers. comm.). Another factor facilitating comparison is that the acoustic structure of the trill vocalization of *C. capucinus* is indistinguishable between La Selva and Santa Rosa in all quantitative measures examined, including duration, frequency range, peak frequency, and number of pulses (Fig. 1; Boinski, in prep.). No association of specific contexts with variation in the acoustic structure of the trills has been identified at either site (Boinski, 1993, in prep).

Methods

Site and study animals.

This study was conducted at the La Selva Biological Station (10°26′ N, 83°59′ W) located in the Atlantic lowlands of northeastern Costa Rica (see McDade & Hartshorn, 1994 for a detailed description of this reserve). La Selva is located in the tropical wet forest life zone (Hartshorn & Peralta, 1988). The climate has been described as "ever wet [and] ever warm" (Clark, 1990: 9), with a mean annual rainfall of 3,796 mm. The field work took place in January 1992.

For the 14 months previous to our field project the behaviour and ecology of the capuchin troop together with a spider monkey (*Ateles geoffroyi*) troop were studied by AFC (Campbell & Sussman, 1994). Group members were individually recognized and were well-habituated to the presence of human observers. During our study period the capuchin troop was comprised of 19 animals: two adult males, five adult females each with small infants, four immature males, and three immature females. The five infants ranged in age from 6.5 months to less than 1 month of age at the start of data collection. The two oldest infants were often locomoting independently of their mother and were included among the focal subjects. The youngest three infants were seldom observed off their mothers' backs and they did not serve as focal subjects. Adult males were generally dominant over adult females.

Detailed data on dominance hierarchies in the capuchin troop are not available as AFC's long-term study focussed on foraging behaviour and habitat use. Adult males were generally dominant over adult females. Relative dominance ranks among females were not rigid; dominance interactions were observed over access to feeding sites, but outcomes were not always predictable [AFC, unpubl. data].

The foraging behaviour of white-faced capuchins at La Selva was similar to capuchins at other Costa Rican sites. Fruits were the major components of the diet, followed by arthropods, and small amounts of pith and foliage was ingested (Boinski, 1989; Chapman & Fedigan, 1990; Campbell, unpubl. data). Manipulative foraging techniques were used to harvest arthropods from woody materials, and much time was allocated to visually scrutinizing surfaces in search of potential foraging sites (Janson & Boinski, 1992). Favored fruit sources during January 1992 included *Dipteryx panamensis* (Papilionoideae), *Welfia georgii* and *Socratea exorrhiza* (Arecaceae), *Hampea appendiculata* (Malvaceae), and several *Inga* spp. (Leguminosae) (Campbell, unpubl. data).

Data collection.

Recording conditions were good. All of the vocal recordings were taken within 10 m and at least 75% within 5 m of the focal animal. A continuous sample of the vocalizations of the focal animal, termed a bout, was recorded onto one channel of a Marantz PMD 430 field recorder fitted with a Sennheiser ME88 directional microphone with a windscreen, and using Maxell XLII 90 min cassette tape. SB, and AFC, or SB and a long-term field assistant of AFC, simultaneously dictated observations of all occurrences of individual and group behaviours. AFC and the assistant also alternated in closely monitoring spatial dispersion of the troop and positions of individuals within the troop dispersion.

The non-vocal behavioural data obtained for each subject included descriptions of social behaviour (*i.e.* grooming, play, and nursing), foraging and locomotor activity, identity to the greatest specificity possible of the nearest neighbor, distance to the nearest neighbor (in 1 m units) and estimates of spatial position within stationary and travelling groups. Minimum durations of continuous periods in which the study troop was engaged in stationary or travel activities were also determined for most of the observation time. Members of a stationary troop had one of two positions: 1) *edge*, a 10 m wide periperal zone with the outside edge defined by the perimeter of troop dispersion; or 2) *core*, the area interior to the edge. Four positions were defined for a travelling troop: 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 the back; and 4) *center*, the interior of the troop dispersion enclosed by the vanguard, sides, and back.

During preliminary observations at La Selva the depth of the vanguard and edge positions was defined based our estimation of the positions most critical in coordinating troop movement. These designations of vanguard and edge positions at La Selva were identical with the vanguard and edge spatial positions shown to be important in the vocal coordination of troop movement at Santa Rosa (Boinski, 1993). To further the consistency in the data collection methods between the two capuchin field studies, at La Selva we also employed the same definitions for the center, side and back spatial positions in the travelling troop that were used in the Santa Rosa study. Preliminary observations at La Selva, however, did not suggest that these positions played an important role in coordination of troop movement.

Focal animal data (N = 16) were collected from each adult and immature capuchin, and the two independently mobile infants in the study troop. It was not feasible to locate individual group members on a random schedule. Thus a pseudo-random technique for selecting focal animals was employed (Fragaszy *et al.*, 1992). From the animals observable at a given moment, the individual judged to be most 'undersampled' was selected. Recording bouts were terminated when the focal animal moved out of recording range, and when calls could not be identified. Data were rarely collected from focal animals in large and dense fruit patches (*i.e.* all *Dipteryx panamensis* and some *Inga* spp. fruiting crowns) because the rate of food-associated vocalizations was so great as to preclude accurate identification of the source of individual calls. Possible bias caused by this nonrandom protocol is reduced because many of the data are analysed as vocal rates within contexts. Analyses do not depend on estimates of allocation of time across contexts by focal subject.

A previous study of this species concluded that the trill functioned in the direct coordination (leading and initiation) of group movement (Boinski, 1993). Preliminary observations suggested that the trill might also serve this function in the vocal repertoire of the capuchins at La Selva. To quantify this use of the trill vocalization a subject was described as making a 'start attempt' when it made at least one trill while the group was stationary. If the group began travelling within 10 min subsequent to the first trill, the azimuth of the group movement relative to the center of the stationary group and the subject's position were determined by estimation and use of a Suunto compass. On three occasions the outcomes of trills could not be determined as the sudden onset of heavy rains terminated observations.

Trills emitted in the vanguard of a travelling group were interpreted as 'leading' the current troop travel. Similarly, a subject was identified as apparently attempting to 'change' troop direction when it made at least one trill while in the side, back or center of a travelling group. The azimuth of the group movement relative to the azimuth predicted by the trilling capuchin's location was determined, as was the azimuth of the troop's movement 10 min later. The 10 min critierion was chosen because it represented in SB's experience (Boinski, 1991, 1993; Boinski *et al.*, 1994) a pragmatic balance between the minimum time necessary for group members to concur with or to reject the 'start attempt', but not so long that troop travel would occur independently.

We collected 26.6 h of continuous recordings containing 3,314 vocalizations. Each of the 16 subjects contributed an average (SE) of 99.5 (19.7) min, 207.1 (34.7) calls, and 22.6 (4.0) recording bouts. The temporal sequence and duration of the individual and troop behaviour and the time and context of each vocalization were coded from the tapes. Spectrograms of all 3,314 vocalizations were made with a Multigon Uniscan II (settings 5, 10, and 20 kHz; 256 FFT) and a Panasonic KY-P1180 printer.

Call classification.

Spectrograms were assigned by visual inspection into six types: trill (N = 1,295), huh (N = 1,643), heh (N = 157), arrawh (N = 173), and gyrrah (N = 29, not depicted) (Fig. 1). Context was not employed in assigning call types. Although subtle variants in the acoustic structure of the vocalizations of many primate species may convey dramatically different categories of information to conspecifics (Cheney & Seyfarth, 1982; Friedman *et al.*, 1995), our analyses were insensitive to detecting this potential source of variation in the data.

In this report, analyses and discussion are focussed on the trill vocalization. The structures of the trill, as well as the huh, heh, and awarrh were qualitatively indistinguishable from those recorded from *C. capucinus* on the Pacific coast of Costa Rica (Boinski, 1993 and see call descriptions therein; see also Freese & Oppenheimer, 1981). Gyrrahs, or alarm calls, represent a composite of highly variable, usually high frequency calls clearly associated with the presence of potential predators or threats from a dominant animal (Oppenheimer, 1968; Robinson, 1982). Given the structural diversity of gyrrahs, the sample size was too small to characterize them in greater detail. A small group of calls produced by infants and usually directed to their mothers was unassigned (N = 17, not depicted) because they did not fit into any of the above categories.

Descriptions of trills from *C. capucinus* in Panama (Oppenheimer, 1968, 1973), as well as *C. olivaceus* in Venezuela (Robinson, 1984) were more finely distinguished into subtypes than the unitary twitter category employed in this study and Boinski (1993). Moreover, neither Oppenheimer (1968, 1973) nor Robinson (1984) suggested that twitters perform a role in the coordination of group travel. Instead, both workers assigned more purely social functions, particularly affiliation and indication of status in potentially agressive interactions. Oppenheimer (1973) recognized the twitter and the purr. The purr is a pulsatile call, like the twitter, usually produced at a low volume, with a predominant frequency range 8-10 kHz. He concluded that purrs were directed specifically by infants and juveniles to other infants and juveniles during close social contact. The twitter, in contrast, was usually emitted at a louder volume than a purr, and has a narrow, but intense frequency range about 2 kHz, which may be accompanied by higher harmonics. Robinson (1984) recognized four twitter categories based on the extent and contour of the twitter's frequency modulation: descending trills, U trills, ascending trills, and FM trills.

Some of the broad range of within-individual variation typical of each age and sex class of capuchin at La Selva is evident in Fig. 1 (See also Fig. 1 in Boinski, 1993). Furthermore, no association of specific contexts with variation in the acoustic structure of the trills has been found at either site, although many analyses have sought unsuccessfully to identify such an association (Boinski, 1993, in prep.). Variation in the acoustic structure of the trills

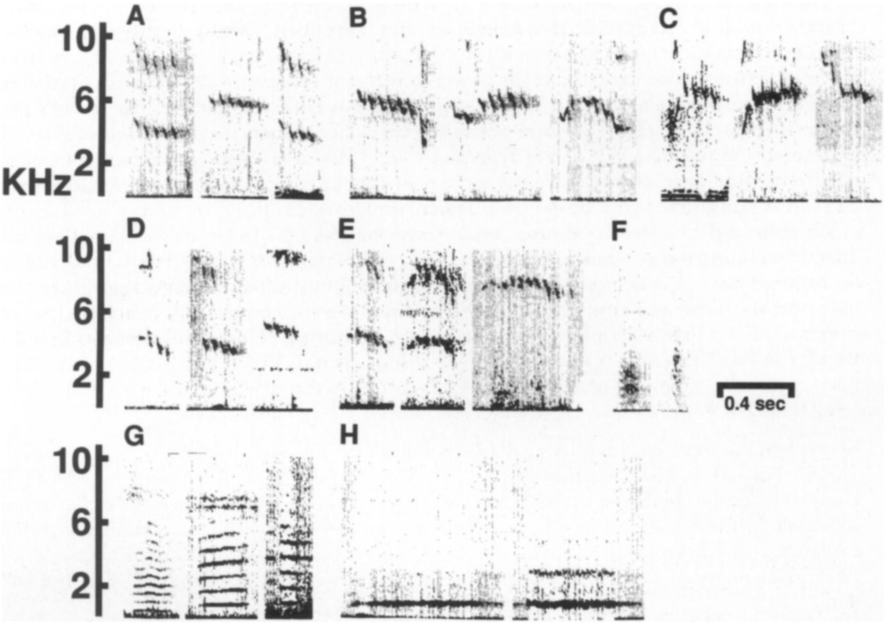

Fig. 1. Examples of the call categories used in this study and individual variation in acoustic structure of trills from members of the study troop at La Selva: a) trills from an adult female, Mom#3; b) trills from an adult male, Maton; c) trills from an immature female, Chinga; d) trills from an immature male, Renco; e) trills from an infant, Bienvenido; f) hehs; g) huhs; and h) arrawhs.

emitted by infants and adult capuchins at La Selva and Santa Rosa easily encompassed nearly all the subcategories recognized by Oppenheimer and Robinson (Boinski, 1993, unpublished data). The only exception is Oppenheimer's (1973) description (and illustration) of a trill as a loud, pulsatile call with an intense, narrow energy band at about 2 kHz. None of the trills recorded at La Selva or Santa Rosa or published in other sources ever exhibited such a striking acoustic feature (Boinski, unpublished data). SB suspects that the high intensity, low frequency band identified by Oppenheimer as characteristic of trills, and distinguishing them from purrs, may be an artifact due to equipment malfunction when the vocal signal was intense. The "higher harmonic" of a trill illustrated in Oppenheimer (1973: 264) is what other workers would consider the fundamental frequency contour of a trill.

Analytical techniques.

Unlike vocalizations used in overt social interactions or associated with potential predation, many other intra-troop vocalizations can be difficult to associate with specific contexts. The rate of trilling was selected as a key measure in our analyses because capuchins produced great numbers of trills concomitant with frequent changes in behavioural states. Furthermore, an individual capuchin was usually simultaneously engaged in multiple behavioural states that potentially affected vocal behaviour (*e.g.* a nearest neighbor within 2 m, foraging, and in the vanguard position of the troop). Comparisons of the rates of vocalizations between specific situations may clarify the relationship between the call and call context.

The recording bouts for each subject were combined. Repeated-measure ANOVAs were used to examine each of three factors (see Table 1). For each repeated-measure ANOVA, the raw data were first sorted by behavioural state (*e.g.* foraging *versus* non-foraging). The cumulative frequency of trills and the duration of time a subject was recorded in each behavioural state were used to calculate the rate of trilling per min for each behavioural state. This rate was then log 10 transformed to obtain normal distributions. The states center, side and back were pooled into a more inclusive 'rearguard' state for the factor called travelling troop position because repeated measure ANOVAs detected no significant within- or between-subject effects on the rates of trills across these spatial positions.

Interaction factors employed in these repeated measure analyses included 1) the between-subject effects of age, sex, and age × sex; and 2) the within-subject effects and their interaction with age, sex, and age × sex. Of these interactions, only the between-subject effect of age was significant at the $p < 0.05$ level for the rate of trills within the factor activity. These interactions will not be further detailed in this report.

The duration of the available focal samples varied across the behavioural states being compared. In particular, troop members varied in their relative allocation of time among different positions within the troop dispersion. For example, infants were seldom in the periphery, and immature males were rarely in central positions (see Janson, 1990). Therefore, for each focal animal a minimum criterion of five min per cell was established for inclusion in a repeated-measure ANOVA. The sample size of individuals included in each repeated measure analysis is given in Table 1. Each repeated measure ANOVA analysis for each factor included at least two subjects within each of the four age-sex categories with the exception of stationary troop position (no immature males included). The two infants were never included in statistical analyses as their vocal behaviour markedly differed from that of older animals. Infant data for the factor activity are, however, presented in Fig. 2a as the focal data from each infant exceeded five min per cell.

We used the V-test, a modified version of the Rayleigh test (Batschelet, 1981) to determine whether the observed azimuths of troop movement were clustered about the position of the subject apparently attempting to initiate or change the direction of movement. Instances in which the troop did not move subsequent to such an attempt, or in which the capuchin produced trills from the core of the stationary troop, were treated as if the troop had instead moved 180° from an angle predicted by a capuchin's position on the troop periphery (Boinski, 1991, 1993). The azimuths of troop movement 10 minutes after an attempt to change the trajectory were compared to the azimuths predicted by the subject's position on the side and back of a travelling troop. Instances in which a capuchin emitted a trill in the center of a moving troop were treated as if the direction indicated was

Table 1. Behavioral states contrasted within each factor in the series of repeated measure ANOVAs of the rate of trill vocalizations

Factor	Behavioral states	N Subjects
Stationary troop position	At the edge *versus* core of a stationary troop	9
Travelling troop position	At the vanguard *versus* rearguard of a travelling troop; the latter category represents a pooling of the side, center, and back positions	12
Activity	Two activity categories: foraging *versus* non-foraging (rest, locomotion, and social interaction)	11

180° from the current travel direction. The angular data were grouped into arcs of 90° prior to analysis.

We made two sets of calculations from our field observations to serve as controls in the analyses of the initiation of group movement in response to trills. Both provide an estimate of the likelihood that any vocalization, not specifically trills, could be associated with a change in group movement. First, we determined the mean (SE) durations of periods in which the troop was stationary and travelling. Second, the absolute number and proportion of each call type (trill, huh, heh, arrawh, and gyrrah) that was followed within 10 min by a change in group movement was tabulated for when the study troop was stationary. Whether group movement was inititated within 10 min subsequent to call production could be determined in most, but not all, instances (see Table 3).

The data describing the average (SE) number of calls emitted in start attempts and the duration of start attempts are based on the individual means. Rates of instances in which focal animals attempted to initiate travel in a stationary troop or produced trills when in the vanguard of a travelling troop were calculated relative to the focal sample time within those two spatial positions. Subjects which never produced trills in a spatial position during focal samples were assigned a rate of 0 trill bouts / h in that spatial position in subsequent analyses. Differences in the rates of adults versus immatures to initiate travel in a stationary troop or to lead travel in the vanguard of a travelling troop were examined using unpaired t-tests (2-tailed); four-way ANOVAs comparing age-sex class differences (adult males, adult females, immature males, immature females) and unpaired t-tests comparing the sexes were not significant and therefore are not reported.

Results

Troop movement, spatial position, and individual activity.

During periods when data were collected from the study troop, its diameter when stationary was, on average, approximately 60 m, and the dimensions of the troop when travelling averaged approximately 100 m long and 60 m wide.

When the troop was stationary there was a significant within-subject effect on the rate of trills; the mean rate of trills was five times higher on the edge of the troop compared to the core (Table 2; Fig. 2a). A highly significant within-subject effect on trill rate was found for the factor travelling troop position (Table 2; Fig. 2b). Trills were produced, on

TABLE 2. Results of within-subject repeated measure ANOVAs examining the effects of three factors on the rate of trill vocalizations

Factor	df	F	R^2
Stationary troop position	1,8	11.30 **	0.59
Travelling troop position	1,11	39.43 ****	0.78
Activity	1,10	12.71 **	0.56

** $p < 0.01$; **** $p < 0.0001$.

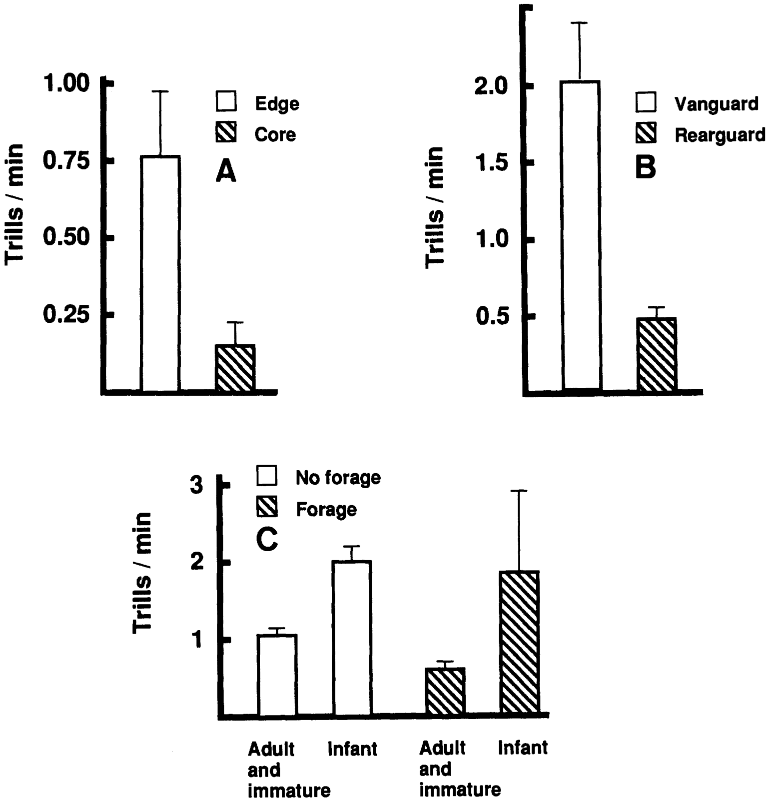

Fig. 2. The mean (+SE) individual rate of producing trills (pooled across four age-sex classes) across three factors: a) stationary troop position; b) travelling troop position; and c) activity. The data for infants are also presented for the factor activity, but these data were not included in statistical analyses.

average, four times more frequently in the vanguard compared to the rearguard position.

Foraging was negatively associated with the rate of emitting trills. Trills were produced by adults at twice the mean rate in non-foraging compared to foraging contexts (Table 2; Fig. 2c). In contrast, infants trilled at a high mean rate (2 trills / min) regardless of activity.

Coordination of troop movement.

The higher rate of trills by capuchins when in the edge of a stationary troop (Fig. 2a) represents instances in which troop members made an apparent attempt to initiate movement in a stationary troop (Tables 3, 4). Eighteen of the 23 start attempts in stationary troops were termed 'successful' because the troop travelled in the direction predicted by the subject's location relative to the center of the troop within 10 min of the beginning of the start attempt. On average (SE), these 18 successful starts were initiated 5.3 (0.8) minutes after the first trill and after a total of 9.5 (2.7) trills (N = 10 subjects). The azimuths of troop movement subsequent to a start attempt were significantly clustered about the angle predicted by the subject's position ($u = 4.59$, $N = 23$, $p < 0.0001$).

Considering failed start attempts, two were in 'contested' situations in which the alpha male was trilling concurrently with another capuchin at a different position on the edge of the troop. In both of these cases the troop travelled in the direction predicted by the second caller. Mom#1 also failed several times to initiate troop movement. In two instances the troop did not move within 10 minutes subsequent to her initial trill. A third instance of trilling by Mom#1 was also categorized as a failed attempt. She trilled from the core of the troop while moving toward the edge where Mom#4 and Matón were also trilling. Shortly thereafter the troop travelled in the direction indicated by the latter capuchins. The average (SE) of the time and number of trills expended by Mom#1 and Maton in these failed attempts were a miniumum of 8.5 (0.5) min and 7.0 (2.0) trills (N = 2 subjects).

Of the 667 calls produced by focal subjects when the study troop was stationary, trills were the only vocalization associated with the initiation of travel within 10 min or less (Table 3). Moreover, the association between trill production and subsequent initiation of travel in a stationary troop cannot be explained as an artifact because of frequent transitions between stationary and travelling states in the study troop. The mean (SE) duration of time intervals at which the troop when stationary initiated travel, 48 (5) min (N = 37 intervals), and a travelling troop either changed the trajectory of travel or ceased travel and became stationary, 43 (6) min (N = 35 intervals), greatly exceeded the 10 min criterion.

The numerous trills by capuchins in sectors within the rearguard of a travelling troop (sides, center, and back) did not significantly predict changes in direction of troop travel ($u = -1.337$, $N = 131$, $p > 0.70$; Table 4). The only changes noted in troop movement after a trill was produced within the rearguard were two instances in which a travelling troop

TABLE 3. Tabulation of changes in group movement within 10 min following the production of a vocalization by a focal capuchin in a stationary troop

Call type	N	Travel	Remain stationary	Undetermined
Trill	218	83.8%	14.6%	2.3%
Huh	364	16.2%	70.6%	13.2%
Arrawh	6	0%	100%	0%
Heh	40	15.0%	80.0%	5.0%
Gyrrah	39	5.1%	89.7%	5.1%

TABLE 4. Tabulation of the type, number, and rate per h of focal sample time in each context (in parentheses) of instances in which troop members attempted to initiate travel in a stationary troop and emitted trills in the four spatial positions within a travelling troop

Focal	Successful start of travel in stationary troop	Failed start of travel in stationary troop	Instances of trills within a travelling troop			
			Vanguard	Rearguard		
				Center	Side	Back
Adult males						
Matón	4 (3.4)	2 (1.7)	6 (13.4)	6 (4.1)	1 (2.2)	1 (2.6)
Ñajo	1 (1.8)		2 (12.5)	2 (4.0)		
Immature males						
Renco			2 (6.6)	1 (4.1)		
Nariz			1 (6.6)	1 (3.4)		
Orejón	1 (3.9)		3 (12.5)	1(13.1)		
Herido			1 (4.6)	1 (4.4)		
Adult females						
Mom#1	1 (0.5)	3 (1.6)	5 (14.0)	7 (5.4)	1 (4.3)	3 (4.2)
Mom#2	1 (2.5)		8 (14.2)	7 (7.2)	2 (5.2)	
Mom#3	2 (5.5)		11 (17.4)	11 (7.7)	3 (16.3)	
Mom#4	5 (5.5)		9 (16.9)	8 (13.4)	2 (6.4)	
Mom#5	1 (4.2)		7 (11.1)	2 (5.4)		3 (6.4)
Immature females						
Chinga	1 (2.5)		2 (10.4)	1 (5.4)		
Labia Negra	1 (2.5)		1 (5.8)		1 (3.1)	2 (12.7)
Cara Sucia			1 (6.5)	2 (3.5)	1 (5.0)	2 (6.4)
Sum of trill bouts	18	5	59	49	11	12
Mean (SE) number of trills per bout per individual	9.5 (2.7) N = 10	7.0 (2.0) N = 2	8.0 (1.2) N = 14	3.9 (1.0) N = 12	2.9 (0.3) N = 6	4.5 (0.4) N = 6

abruptly stopped after a capuchin trilled in the back sector. Trills produced in the rearguard differed from those produced in the edge of a stationary troop and the vanguard of a travelling troop in number of trills per bout. Capuchins produced about twice the number of trills within the edge and vanguard compared to the rearguard, 7-10 *versus* 3-4.5 trills per bout (Table 4).

A breakdown of the specific contexts in which trills were emitted indicates marked differences between the rearguard (N = 72) and the edge and vanguard positions (N = 82) (Table 4). 1) Intention movements, such as pacing and staring fixedly in an outward direction (ROWELL, 1972; BOINSKI, 1991) were noted in only two instances within the rearguard (see more detailed descriptions below). In contrast, intention movements were associated with approximately 50% of attempts to initiate travel in a stationary group. (Intention movements were not, however, used to define start attempts). 2) Trills were exchanged between the two independently locomoting infants and adults and immatures (N = 21 instances) only within the rearguard positions, and were never documented within the edge of a stationary troop or the vanguard of a travelling troop. 3) Most instances (a minimum of 43 or 60%) of trill production by adults and immatures in the rearguard of the troop did not suggest that the caller was attempting to alter group movement. These situations included particularly heavy forest (with little visual contact among troop members); low density of group members within at least a subsection of group dispersion; a sudden increase in the speed of troop travel; and exchanges of trills with distant (usually far ahead or following) troop members.

Social aspects of troop coordination.

Representatives of each of the four age and sex classes successfully initiated troop movement, but age was an important factor (Table 4). All seven adults, but only three of the seven immatures, initiated troop movement at least once. The difference in the rate per h at which adult compared to immature troop members attempted to initate travel closely approached significance (unpaired t-test, df = 1,12, N = 14, $t = 2.168$, $p < 0.051$, mean (SE) = 3.5 (0.7) adults; 1.3 (0.6) immatures). Similar to the distribution of efforts to initiate travel, all adults and immatures produced trills within both the vanguard and rearguard of a travelling troop. Adults had significantly higher rates of bouts of trilling in the vanguard of a travelling troop compared to immatures (unpaired t-test, df = 1,12, N = 14, t = 4.88, p < 0.0004, mean (SE) = 14.2 (0.9) adults; 7.6 (1.1) immatures). Aside from this predominance of adults in attempts to initiate and lead travel, there was only weak evidence that social dominance of specific individuals or a single age-sex class, such as adult females or adult males, was important in coordination. The alpha male, for example, failed to initiate movement in two of his six attempts.

In at least 13 instances in which trills were produced at the edge of a stationary troop or in the vanguard of a travelling troop, pairs of troop members appeared to reinforce each other's efforts to lead troop movement (Table 5). The pairs were either closer than about 7 m to each other, or if separated at greater distance, positioned at approximately the same azimuth relative to the center of the troop or direction of travel. In each instance, a primary and a secondary triller were readily distinguished; secondary trillers started trilling subsequent to the primary triller, produced trills at a lower rate, and these trills were often less intense in volume to our ears than those of the primary triller. There was no tendency in our limited sample for an age or sex class to predominate in

TABLE 5. Tabulation of pairs of troop members that acted jointly to coordinate troop movement using trills vocalizations

Primary triller and age-sex class*	Secondary triller and age-sex class	Context
Mom#3 (AF)	Mom#5 (AF)	successful initiation of troop movement
Mom#4 (AF)	Orejon (SM)	,,
Matón (AM)	Mom#4 (AF)	,,
Unidentified adult	Matón (AM)	,,
Unidentified adult	Matón (AM)	,,
Ñajo (SM)	Labia Negra (SF)	,,
Mom#4 (AF)	Matón (AM)	,,
Chinga (SF)	Matón (AM)	successful initiation of troop movement then led travelling troop in vanguard
Adult female	Mom#2 (AF)	,,
Mom#1 (AF)	Mom#2 (AF)	failed attempt to initiate troopmovement
Renco (SM)	Herido (SM)	led travelling troop in vanguard
Mom#2 (AF)	Adult female	,,
Mom#5 (AF)	Chinga (SF)	,,

* Abbreviations for age-sex classes: AF, adult female; AM, adult male; SF, immature female; and SM, immature male.

being the primary or secondary triller. A female and male cooperated to lead group movement in five (38%) of the instances. Age classes were similarly mixed in two (23%) instances of apparent reinforcement, and in one instance (8%) two immature capuchins led a travelling troop together.

Aside from the 21 bouts of trills exchanged by adults and immatures with infants, there was no indication that trills were used by adults and immatures for social communication functions such as contact calls, or indicators of reconciliation or relative status. Social interactions of any sort occurred at extremely low rates (< 0.5 social interactions / h) in the 5 min preceding or following trill production by adult and immature troop members. Two notable exceptions, however, suggest trills might be used infrequently in tactical maneuvers for access to desirable fruit patches.

In the first instance, Mom#3 and Chinga were foraging in a *Welfia georgii* palm with a dense crop of ripe fruits. Mom#2 was pacing several meters outside the tree and staring at the clumps of ripe fruit, and appeared eager, but extremely hesitant to enter the palm crown. After several minutes, Mom#2 started trilling and giving intention movements from a position 3 m outside the palm; she acted as if she were trying to start a stationary group, but her attention and efforts remained focussed on the fruiting palm and its two occupants. After 24 trills over a 6 min 50 sec period, Mom#2 abandoned this activity and moved rapidly forward in a direction more than 90° away from the direction indicated by her position and intention movements while trilling.

A second anecdote of trills possibly being employed in manipulation of a troop member was also given by an adult female. Mom#3 was the only capuchin in a fruit-laden *Hampea appendiculata* tree. She suddenly looked up into the distance, and moved out of the *Hampea*. About 30 secs later Mom#4 walked into the vicinity from the direction Mom#3 had looked, and remained at least 10 m from the *Hampea*. Mom#4 appeared to be scanning desultorily for foraging opportunities, and was not focussed on the nearby fruiting tree. Mom#3, while looking directly at Mom#4, made intention movements and two trills away from the direction of the *Hampea*. Mom#4 approached and displaced Mom#3 from the general area. Only after more than two minutes of visual foraging did Mom#4 appear to discover the *Hampea* fruit patch.

Infant use of trills.

The two independently mobile infants were similar in their use of trills as well as other aspects of behaviour. Foraging had no effect on the rate of infant trills (Fig. 2c). Furthermore, there was no evidence that infant trills were associated with troop movement. Infants spent little time (< 5% sample time each) in the periphery of the troop. Both infants spent more than 50% of focal sample time within 5 m of their mothers, and 100% within 10 m of their mothers. The majority of the vocalizations recorded from infants were trills (Bienvenido, 66 of 111 total calls or 59% trills; and Paciencia, 40 of 66 total calls, or 61% trills).

More than 70% of the trills produced by both infants were in vocal exhanges with their mothers when separated by more than 3 m. Trills were also exchanged by both infants with other mothers in the troop and the alpha male when these adults were less than 10 m from an infant. Approximately 10% of the trills emitted by separated infants appeared neither to provoke nor be a response to another troop member's trill. In *ad lib* observations of the rare instances in which two younger infants left the immediate proximity of their mothers, these infants also exchanged trills with their mothers. None of the five infants in the study troop trilled when they were being carried by their mother.

Discussion

La Selva capuchins.

Trill calls produced by the non-infant members of a troop of white-faced capuchins, *Cebus capucinus*, at the La Selva Biological Station in Costa Rica were strongly associated with the initiation and leading of troop movement. Trills emitted by a capuchin in the periphery of a stationary troop significantly predicted not only that the troop would commence travel within a 10-min period, but the trajectory of travel relative to the approximate center of the stationary troop. Trills were the *only* vocalization in the repertoire of the study troop associated with initiation of group movement. Furthermore, the average length of time that the study troop remained stationary during our study, 48 minutes, greatly exceeded the 10 min time lag we employed to define a causal link between trill production and subsequent troop movement. These long intervals between instances of travel initiation relative to the short 10 min criterion minimize the likelihood that the association between trill production and travel initiation was an artifact.

Trills emitted within the vanguard, or leading edge of a travelling troop, appeared to function as an auditory beacon indicating the trajectory of troop travel for those following, often at distances exceeding 80 m. The mean individual rate of trills was four times greater in the vanguard than in the rearguard (the center, side and back) of a travelling troop. Capuchins also produced trills at significantly lower rates when foraging than when engaged in non-foraging activities. All else being equal, a foraging capuchin would be predicted to be less motivated to lead the troop away from its foraging site to a new area than a capuchin that was not foraging.

Why did capuchins at La Selva also produce trills in the rearguard of a travelling troop? Most of these trills emitted by capuchins in the rearguard (60% of trill bouts) possibly functioned to *relay* or *boost* the trill signal produced by capuchins leading the troop in the vanguard. These rearguard trills were associated with particularly heavy forest and extreme troop dispersion, which reduced the audibility in the rearguard (to human observers at least) of trills emitted in the vanguard. Most of the remaining trills in the rearguard (29% of trill bouts) were used in brief exchanges with infants. Two anecdotes of trilling in the rearguard leave open the possibility that in rare instances trills were used to gain or retain access to fruit patches by leading the recipients away from the fruit patch. Contrary to the results of other studies of trill use in capuchins (*C. capucinus*: OPPENHEIMER, 1968, 1973; FREESE & OPPENHEIMER, 1981; *C. olivaceus*: ROBINSON, 1984), our study in La Selva and that of BOINSKI (1993) in Santa Rosa found no evidence that social communication such as expressions of affiliation or dominance between adults was an important function of trills.

The available data suggest that the use of trills by infants in the study troop was limited to exchanges of trills with their mothers, and to a lesser extent with other adults, when the infants were separated from their mothers by more than about 3 m. The rate of trills by infants was unaffected by their foraging activity. Moreover, infants not being carried by their mothers were rarely observed to venture into the periphery of the troop. This lack of activity at the edge of a stationary troop or vanguard of a travelling troop would appear sufficient to limit stringently opportunities to coordinate movement. These infant trills are probably best described as contact calls to maintain spatial cohesion (Caine & Stevens, 1990; Boinski, 1991).

All adults, and three of the seven immatures successfully initiated troop movement in focal samples, and all adult and immature troop members produced trills in the vanguard and rearguard of a travelling troop. Adults were more active than immatures in both initiating and leading travel. The age difference was significant for the rate of bouts of trilling in the vanguard, and nearly so for the rate of attempts at initiation of travel in a stationary troop. Yet no individual troop member or specific age-sex class appeared preeminent in coordinating or determining travel in the study troop; within age groups both the absolute number and the rate of trill bouts varied widely. Moreover, of the five failed attempts to initiate troop movement, the alpha male failed twice in six attempts and an adult female failed three times in four attempts.

Thirteen pairs of troop members cooperated, or at least indicated concordant preferences, in leading troop movement. These pairs represented every possible combination of the four age and sex classes with the exception of adult and immature male pairs. Each pair had an identifiable primary triller that inititated and seemed to lead the trilling and a secondary triller that produced trills at a lower rate and volume. In at least one instance the primary triller was an immature female and the secondary triller was the alpha male.

Comparison with Santa Rosa capuchins.

Similarities.

Comparable data from capuchins at Santa Rosa and La Selva provide strong evidence for voluntary expression of this complex vocal behaviour. Conflict and lack of consensus was frequently evident when simultaneous efforts to initiate travel in divergent trajectories occurred, and when the troop failed to follow troop members attempting to initate travel in a stationary troop. Qualitative observations suggest that individuals often attempted to lead their troop to preferred foraging patches or caused them to be resistent to leave preferred foraging patches (Boinski, 1993; SB & AFC, pers. obs.). Detailed knowledge of the distribution of resources and features within the home range appears to be a necessary precondition for this level of divergent individual preferences to be expressed (Boinski, in press).

On the other hand, the common observation of individuals at both sites reinforcing the efforts of other troop members to coordinate troop movement provide a second source of evidence for the importance of cognition, in this instance social cognition (Harcourt, 1988). At Santa Rosa, specific dyads of adult females predictably reinforced each other's efforts to coordinate troop movement (Boinski, 1993). In many respects the process of initiation of travel can be regarded as a social behaviour on a very grand scale, particularly with a large social group. When an individual transmits a signal, a positive response may hinge on negotiation, concurrence, reciprocation, and acquiescence with a large proportion of group members.

Trills should probably be considered a representational vocal signal. This classification is consistent with two criteria set forth by Macedonia & Evans (1992): (1) that the signal be closely associated with specific contexts, and (2) be sufficient in itself to provoke the appropriate response. Trills emitted by older troop members at La Selva and Santa Rosa sites were nearly exclusively associated with coordination of travel. The second criterion was met because troop members were able to respond appropriately to trills within brief time periods, even though the typical dispersion of a capuchin troop in an arboreal habitat provided only limited opportunities for visual contact with the signaller. At both sites it was common to observe individuals that appeared to be totally isolated visually from other troop members orientating and moving in the appropriate direction after hearing trills (but not other capuchin vocalizations) in the distance. Orientation and travel responses of visually isolated troop members would be amenable to playback experiments to further examine our proposition that trills are representational vocalizations. We predict differences in responses to playbacks dependent on call type (*i.e.* trill *versus* arrawh *versus* huh), indicated trajectory, and identity of the vocalizer and recipient.

A few instances at both sites in which capuchins employed trills in strategic maneuvers, in addition to frequent usage in initiating and leading travel, suggest a recognition of the effect of trills on recipients, what Dennett (1983) and Cheney & Seyfarth (1990) describe as first-order intentionality. La Selva capuchins twice employed trills in efforts of possible deception to gain access to desirable fruit patches. Santa Rosa capuchins twice 'hijacked' a travelling troop and then altered its trajectory by repressing the trills of the troop members originally trilling in the vanguard. In one instance trills were repressed by direct threats and in the other instance by trilling much louder and at a higher rate (BOINSKI, 1993).

One way to assess whether full first-order intentionality can be invoked is to determine if the caller subsequently monitors the behaviour of its audience. Monitoring would be expected if an individual gives a signal with the intent to inform and affect. Monitoring of the effect of trill calls on the other troop members was, in fact, ubiquitous, among capuchins at La Selva and Santa Rosa (SB, pers. obs.). A capuchin emitting trills to initiate travel in a stationary trooop repeatedly looked backwards and scanned for evidence that the troop had begun travel, if it was not already facing the troop. No capuchin gave trills in the periphery of a stationary troop and then travelled onward more than a short distance by itself. In like fashion, capuchins leading the troop with trills in the vanguard commonly stopped and looked backward, especially if troop members in the rearguard had slowed or altered trajectory.

Differences due to forest structure.

A marked difference between the two sites exists in the apparent function of trills produced in the rearguard of a travelling troop. Capuchins at Santa Rosa altered the trajectory of travelling troops with trills produced in the rearguard, even reversing directions, but not at La Selva. We suspect that the disparate forest types at the two sites ultimately account for this difference; vocalizations of a given structure propagating through a refective medium, like a forest, will exhibit a degraded structure (WASER & BROWN, 1986). This is because reverberation, often in the form of echoes, will manifest itself in the received signal in the same band as the original signal. As a result, reverberation obscures the structure of the original broadcast signal to a greater extent in dense forest compared to one with sparse foliage and branches.

Most trills produced by capuchins at the tropical dry forest site of Santa Rosa (at the peak of dry season when most deciduous trees had lost their leaves) appeared clearly audible to all other troop members (SB pers. obs.). In our study, the low rate of trilling by capuchins in the rearguard of the La Selva troop, at a densely foliated, tropical wet forest site, had no detected effects on changing direction of troop travel. Instead, these vocalizations seemed necessary and effective in relaying the trill signals produced in the vanguard to distant troop members that were unlikely to be in acoustic contact with the vanguard. Another line of evidence supporting this qualitative evaluation is that the spectrograms of trills recorded at La Selva generally evidence marked reverberation of the acoustic signal compared to trills recorded at Santa Rosa at equivalent distances (SB, pers. obs., also compare Fig. 1 in Boinski, 1993 and Fig. 1 in this study). In other words, the lower propagation distance in La Selva compared to Santa Rosa probably limited the flexibity of the trill signal, and thus troop movement patterns, at La Selva.

There are alternative approaches for testing the hypothesis that the use of trills to change trajectory in a travelling troop is a facultative response to forest type. Trill usage at Santa Rosa could be studied during the wet season when foliage density peaks (Hartshorn, 1983) and compared to vocal behaviour during the extreme dry season reported in Boinski (1993) and that reported here. We would not expect to find detectable seasonal effects on vocal behaviour from the relatively aseasonal forest at La Selva (McDade & Hartshorn, 1994). Capuchin vocal behaviour could also be studied at additional sites. Preliminary observations of capuchins at a third site in Costa Rica with forest density intermediate between La Selva and Santa Rosa, La Suerte Biological Station, also indicate that trills are employed to coordinate troop movement (P. Garber, pers. comm).

Differences in participation in travel coordination.

In Santa Rosa only full adults, primarily adult females, used trills in coordination of troop movement. Moreover, within each sex, there was a perfect concordance of relative rank and the number and rate of successful attempts to direct troop movement. Juveniles, and infants limited trills to use as contact calls exchanged with peers. When pairs of individuals jointly acted to coordinate travel, the pairs were either two adult females or two adult males. In contrast, at La Selva immatures successfully led troop movement using trills; the only troop members using trills exclusively as contact calls were infants 6 months of age and younger. Adults, however, were more active than immatures in vocally coordinating troop movement. La Selva capuchins also differed because pairs of individuals from every possible age-sex class combination except adult and immature males were observed to cooperate in initiating or leading travel. Rank relationships were poorly documented in the La Selva compared to the Santa Rosa study troop. Yet we predict relative rank will be less important in determining which troop members select travel routes in La Selva than in Santa Rosa. This is because variation among troop members in the absolute number and rate of successful efforts to coordinate travel appears much more moderate at La Selva than Santa Rosa.

Several hypotheses could account for these site differences in the subset of troop members vocally participating in coordination of group travel. First, the distribution of resources such as food, locomotor substrates, or areas of reduced exposure to predators could be relatively homogeneous at La Selva compared to Santa Rosa, a regenerating, patchy habitat. For example, the primary and a preferred fruit source for capuchins at La Selva, *Welfia georgii* (CAMPBELL, unpubl. data), is the second most common tree at La Selva (VANDERMEER, 1983; HARTSHORN & HAMMEL, 1984), and this contributes to distribution of high quality fruit being much less patchy at La Selva than at Santa Rosa (FRANKIE *et al.*, 1974). As a result, at La Selva dominants would be more likely to acquiesce to travel initiatives by subordinants or other troop members with different foraging strategies. A second, related hypothesis is that the numerous, large, dense fruit patches available to the La Selva capuchins during our study, especially from the synchronously fruiting *Dipteryx panamensis* trees, made individual travel route preferences concordant. Third, one week before the start of the La Selva study the alpha male was usurped and seriously wounded. He later died. This may have resulted in marked social instability in the study troop. In this circumstance, the failure of start attempts by the new alpha male, and efforts to lead troop travel by immatures and subordinates would not be surprising. Fourth, several studies indicate that a peripheral position in a capuchin troop, an apparent prerequisite to leading travel, is more susceptible to predation (VAN SCHAIK & VAN NOORDWIJK, 1989; JANSON, 1990). Perhaps immature Santa Rosa capuchins incurred an enhanced exposure to predation when in the periphery of a troop compared to immatures in Santa Rosa. This may have reduced benefits Santa Rosa immatures received from participation in the coordination of troop movement.

Implications.

This study of the capuchins at La Selva, together with the previous study at Santa Rosa, provides additional evidence that geographic variation in the usage of a vocalization in a social species can be identified with variation in specific ecological and social factors (East & Hofer, 1991; Clark, 1993). Similarly, the presence or absence of a call type in the vocal repertoire of closely related species may also be most easily understood in light of detailed knowledge of ecological and social factors that might distinguish the species (Boinski & Mitchell 1992, 1995). More emphasis on quantitative studies of the patterns of vocal behaviour among social groups whose social structure and ecology are well known will allow fresh insights into the functions of intra-group vocal communication.

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