

Mechanisms Promoting Stability in Mixed *Saguinus mystax* and *S. fuscicollis* Troops

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Mixed-species troops composed of two species of tamarin monkeys, and rarely other ceboids, occur throughout much of western Amazonia and are notable for their long-term stability. This study identified several variables that appeared to promote mixed-species troop cohesion and yet maintained spatial segregation between species. Three variables enhanced interspecific spatial segregation: differences in support use, vertical stratification, and interindividual spacing. In contrast, early morning vocalizations and well-coordinated movement patterns contribute to cohesion within a mixed-species troop. The combination of these variables may help explain how two congeneric species accommodate one another with little apparent interspecific aggression.

The exact nature of benefits and costs to each individual in a mixed troop is still elusive; however, a comparison of population densities of sympatric and allopatric tamarins suggests that population growth of one partner (*Saguinus fuscicollis*) is enhanced in the presence of a congeneric species.

Key words: Callitrichidae, sympatric species, vertical stratification, locomotion, activity patterns, interspecific competition

INTRODUCTION

Interspecific interactions among primates range in duration from very brief encounters in feeding trees (measured in minutes) to relatively permanent formations (measured in years) [Waser, 1986]. Along this continuum of mixed-species troop stability, the sympatric tamarins of lowland Amazonia are among the most permanent.

Four tamarin species are sympatric with *Saguinus fuscicollis* (*Saguinus mystax*, *S. imperator*, *S. labiatus*, and *S. nigricollis*), but are mostly or wholly allopatric to one another [Hershkovitz, 1978, 1982]. Like cercopithecine monkeys that are habitually found in mixed-species troops [Gautier-Hion, 1988a,b], interspecific similarities in behavior and ecology seem to contribute positively to the permanence of mixed tamarin troops. Home ranges of sympatric tamarins overlap extensively [Norconk, 1986; Ramirez, 1989; Terborgh, 1983]; there is high overlap in the percentage of plant species used [Garber, 1988; Ramirez, 1989; Terborgh,

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1983]; both species are aggressive to conspecifics in neighboring troops [Norconk, 1986], but interspecific territoriality has never been described; and both species use vocal communication to maintain intratroup cohesion [Castro & Soini, 1978; Norconk, 1986; Pook & Pook, 1982]. Indeed, the stability of mixed troops probably exceeds the duration of most long-term studies [but see Terborgh, 1983; and Garber, 1988, for exceptions]. The purpose of this study was to examine mechanisms which contribute to intratroup coordination within a mixed troop and to suggest conditions under which mixed troops become unstable and eventually fission.

Anecdotal information on the relationship between successful territorial defense and reproductive activity suggests that under conditions of sympatry, mixed troops may enjoy longer tenure in the same territories [Garber, 1988; Norconk, 1986; Ramirez, 1989; Soini & Soini, 1983; Terborgh, 1983]. This may, in turn, result in higher reproductive rates for individuals participating in mixed-species troops than individuals in single-species troops. Still, there are differences in the degree to which individual troops are mixed within study populations; estimates range from about 50% to 100% for long-term studies [Heymann, this issue; Garber, 1988; Pook & Pook, 1982; Ramirez, 1989; Norconk, 1986]. What contributes to this variability?

While researchers concur that the stability of mixed troops is dependent on active participation on the part of both species [e.g., *Saguinus labiatus*/*S. fuscicollis*: Pook & Pook, 1982; Yoneda, 1984; *S. imperator*/*S. fuscicollis*: Terborgh, 1983; *S. mystax*/*S. fuscicollis*: Garber, 1988; Norconk, 1986; Ramirez, 1989; Soini & Soini, 1983], there do seem to be conditions under which mixed troops become unstable. Increasing troop size alone could result in interspecific competition over food resources and fission of a mixed troop. However, evidence from Garber [1988] suggests that troop fission may be more likely to occur intraspecifically. Members of the original mixed troop remained in the same home range and defended the same territorial boundaries. These findings add support to the data reported here and to the emerging picture of mixed-species troops as a well-adapted strategy for sympatric tamarins.

METHODS

Subjects and Study Site

The study animals were free-ranging moustached tamarins (*Saguinus mystax mystax*) and saddle-back tamarins (*S. fuscicollis nigrifrons*) inhabiting evergreen tropical forest in northeastern Peru (4°15' S, 73°4' W). The study site was located approximately 110 km south of Iquitos, Peru, on a narrow whitewater stream (Quebrada Blanco) draining into a blackwater river (Rio Tahuayo) and subsequently into the Amazon River. Two other long-term tamarin studies were conducted at this field site, prior to [Ramirez, 1989] and following [Garber, 1986, 1988; Garber and Teaford, 1986] the study reported here.

Dawn to dusk observations, totaling 627 hours, were made on two mixed troops of tamarins during 13 months in 1982–1983. At the onset of the study, G troop consisted of seven *Saguinus mystax* (four adults, two females and two males; a subadult female; two infants) and four *S. fuscicollis* (three adults and one juvenile). At the end of the study, G troop increased to a total of 15 individuals, nine *S. mystax* and six *S. fuscicollis*. All infants were born as twins and raised successfully to the juvenile stage. Accurate troop counts were more difficult for R troop, because they were never fully habituated to the presence of observers. At the onset of the study, there were five adult-sized individuals and two infant *S. mystax* and seven self-locomoting *S. fuscicollis*. At the end of the study, *S. mystax* subtroop had increased to nine individuals, two of which were juveniles, and *S. fuscicollis* sub-

troop had increased to 11 individuals. Individual recognition was possible for *S. mystax* members of G troop only.

The study area consisted of approximately 260 ha of predominantly undisturbed, high (well-drained), slightly undulating forest with pockets of low, perpetually inundated areas dominated by *Mauritia flexuosa* palms. Five types of forest were identified based on predominant tree height, presence of emergents, and characteristics of the understory within the home ranges of two troops (G and R) [Norconk, 1986]. Data on tree density, tree height, and canopy breadth were collected on trees exceeding 5 cm dbh in randomly selected 0.25 ha plots (G troop = 19 quadrats or 14% of home range; R troop = 13 quadrats or 9% of home range) [Norconk, 1986]. Tree height ranged from 10 to 14 m in "high forest" plots, with emergents to a maximum of 30 m. There were fewer emergents in "low forest," and the tallest trees were approximately 26 m in height. "Bajial" referred to low shrub-like vegetation along the edges of streams and clearings resulting from treefalls. Shrub height was rarely over 2.5 m in these edge habitats. Locomotor data were sampled primarily in these three habitat types, since the tamarins generally skirted palm swamps and open fields ("chacras").

Data Collection

For the purpose of this study, the term "troop" refers to a tamarin mixed-species troop. *S. fuscicollis* and *S. mystax* components of a mixed troop were designated as "subtroops." Instantaneous scans [Altmann, 1974] of individuals in G troop were collected at a minimum interval of 10 minutes and for a duration of 3 seconds. Intervals between scans varied because the scans required good visibility of all or most of the troop members. Samples were biased toward activities that involved movement (i.e., travel, search, forage, feed) and against stationary activities (i.e., rest and vigilance). For each instantaneous sample, I scored time of day (divided into six categories for analysis: 0500–0700; 0701–0900; 0901–1100; 1101–1300; 1301–1500; 1501–1700 hours) and designated broad age categories (infant, juvenile, sub-adult, adult: grouped for analyses presented below). Locomotor behavior, vertical height, orientation and size of support, general activity, and interindividual distances were also scored during each sample.

I designated five locomotor categories: quadrupedal walk, quadrupedal run, climb (ascend or descend), vertical cling and leap, and leap between discontinuous support (e.g., terminal branches). Height was estimated to the nearest 0.5 m at 2 m intervals from the ground to 20 m (0–2 m; 2.5–4 m; 4.5–6 m; 6.5–8 m; 8.5–10 m; 10.5–12 m; 12.5–14 m; 14.5–16 m; 16.5–20 m; 20.5–24 m). Midpoints of the ten height categories were used as "medians" for comparisons between species. Support structure size was scored as "narrow (< 10 cm diameter) single" and "narrow/multiple" supports; "medium" (11–30 cm); "large" (31–50 cm); and "trunk" or bole (> 50 cm).

In order to estimate interindividual distances during the scans, I counted the number of individuals within a 1 m radius of the subject and recorded the age category and the species to which the individual(s) belonged.

Activities sampled during the scans were defined as follows:

1. Feed—consuming plant exudates or fruit.
2. Forage—consuming insect prey.
3. Search—characterized by start-stop forward progression and unsynchronized as a group.
4. Travel—rapid, group-synchronized forward progression.
5. Rest—non-active periods during the day.
6. Vigilance—scanning of habitat by a stationary animal.

TABLE I. Comparison of Locomotor Differences Between *Saguinus mystax* and *S. fuscicollis* (G Troop: Blanco Stream) by Using Observed (and Expected) Chi Square Values*

	<i>Saguinus mystax</i>	<i>S. fuscicollis</i>
Quadrupedal Walk	221 (156.46)	17 (81.53)
Leap ^a	104 (99.93)	48 (52.06)
Quadrupedal run	68 (76.26)	48 (39.74)
Climb ^b	54 (78.89)	66 (41.1)
Vertical cling and leap	4 (39.45)	56 (20.55)
	N = 451	N = 235

*X² test of homogeneity = 196.7, 4 df, $P < .005$.

^aSamples of leaping between oblique or horizontal terminal and nonterminal supports were grouped.

^bAscending and descending categories were grouped.

Long-distance calls or "long calls" [Snowdon & Hodun, 1985] were audibly distinct between the two species. This permitted an assessment of interspecific calling rates, even though individuals were often obscured from view. Long calls were tallied on an hourly basis for *S. mystax* beginning with first calls in the morning in the vicinity of sleeping trees. Time of first calls (but not hourly calling rates) were recorded for *S. fuscicollis*.

Analysis

Absolute frequency data derived from the scans were tested for interspecific differences (support size and orientation; median height) by using two-way X² tests for homogeneity [Daniel, 1978]. Spearman rho rank test (two-tailed) of correlation was used to analyze the strength of association between the activity budgets of the two species.

Between-population comparisons were tested for differences from parity by using X² test for homogeneity [Daniel, 1978] and population densities of *S. fuscicollis* to a congener were compared by using Wilcoxon matched-pair tests (two-tailed) [Colquhoun, 1971]. Population densities of *S. fuscicollis* both in the presence and in the absence of a congener were collected from published studies and compared by using a Mann-Whitney U test (two-tailed). Levels of significance were set at $< .05$.

RESULTS

Factors Contributing to Interspecific Spatial Segregation: Locomotion

Instantaneous scan samples demonstrated that locomotor differences between the two species were more apparent in degree than kind (Table I). Quadrupedal walking was used more often than expected by *S. mystax*, while both climbing and vertical clinging and leaping were used less often than expected. *S. fuscicollis* exhibited the opposite pattern. Climbing and vertical clinging and leaping were common and occurred more often than expected by chance. In contrast, quadrupedal walking was rarely observed during the scans of *S. fuscicollis*. Frequencies of quadrupedal running and leaping between nonvertical supports were scored within the range of expected values for both species.

Focusing on support size, no interspecific differences were found in the size of structures used by the two tamarin species during locomotion ($X^2 = 7.32$, $df = 4$, ns) (Table II). The majority of supports used by both tamarin species were classified

TABLE II. Summary of Support Structure Size and Orientation Data Collected During Instantaneous Scan Samples of *Saguinus mystax* and *S. fuscicollis* (Troop G: Blanco Stream)

	<i>Saguinus mystax</i>		<i>S. fuscicollis</i>	
	Frequency	(%)	Frequency	(%)
Size of support structures used during locomotion: ^a				
Narrow/single (<10 cm)	321	(71.2)	161	(68.7)
Narrow/multiple (<10 cm)	58	(12.9)	26	(10.8)
Medium/single (11–30 cm)	48	(10.6)	23	(9.8)
Trunk (> 50 cm)	15	(3.4)	18	(7.8)
Large/single (31–50 cm)	9	(1.9)	7	(2.9)
Totals	451	(100.0)	235	(100.0)
Orientation of supports used during locomotion: ^b				
Vertical	55	(12.2)	124	(52.8)
Oblique	213	(47.2)	69	(29.4)
Horizontal	183	(40.6)	42	(17.8)
Totals	451	(100.0)	235	(100.0)

^aUsing a 2×5 contingency table, the X^2 test of homogeneity failed to show significant interspecific differences in support sizes used by the two species ($X^2 = 7.32$, 4df; ns).

^bThere were significant differences between species comparing orientation of supports ($X^2 = 134$, 2df; $P < .005$).

as “narrow” supports (< 10 cm diameter) and were either single supports or multiple (e.g., terminal branches). Both species were scored relatively infrequently on supports > 10 cm, although *S. fuscicollis* used trunks more often than *S. mystax*.

In contrast to the negligible differences between species in the size of support structures used during locomotion, they showed marked divergence in the orientation of supports. I observed *S. fuscicollis* on vertical supports during more than 50% of the scans, while *S. mystax* rarely used vertical supports. Instead, *S. mystax* was seen most often on oblique and horizontal supports.

In order to compare the locomotor repertoires of the two species, they were ranked separately for the five most frequently occurring locomotor “combinations.” Combinations included locomotion, support characteristics, and “median” heights (midpoints of the median height categories) (Table III). *S. mystax* habitually used quadrupedal walking on a slightly varied assortment of supports within a height range of 4.5 m to 12 m. In contrast, *S. fuscicollis* combined climbing, leaping between nonvertical supports, and vertical clinging and leaping on narrow/vertical or narrow/oblique supports at lower heights (from the ground to 6 m).

Vertical Stratification

The ten height categories were collapsed to five due to lower sample sizes at the upper and lower ends of the sample. Visual inspection of Figure 1 shows very low frequencies of samples for *S. mystax* at 4 m or below and *S. fuscicollis* at 17 m or higher. In general, *S. mystax* used higher levels of the forest than *S. fuscicollis* (2×5 contingency tables; $X^2 = 119.6$, df = 4, $P < .005$; $N = 451$ for *S. mystax* and $N = 235$ for *S. fuscicollis*). During 65% of scan samples recording vertical height, *S. fuscicollis* was seen in the understory and lower canopy levels of the forest at heights of 8 m or less (Fig. 1). In contrast, *S. mystax* was observed at heights above 8 m in middle canopy levels during 75% of the scans.

If height in the forest is re-examined in conjunction with the activity data (using midpoints of the ten height categories as “medians”), then vertical stratification is evident for all activities (Table IV). Although some activity/height com-

TABLE III. Comparison of Top Five Ranked Locomotor Combinations for *Saguinus mystax* and *S. fuscicollis* (G troop)*

Rank	Locomotor category	Support size/orientation	Median height (m)
<i>S. mystax</i>			
1.	Quadrupedal walk	Narrow/oblique	7.25
2.	Quadrupedal walk	Narrow/oblique	11.25
3.	Quadrupedal walk	Narrow/horizontal	7.25
4.	Quadrupedal walk	Narrow/horizontal	11.25
5.	Quadrupedal walk	Narrow/oblique	5.25
<i>S. fuscicollis</i>			
1.	Climb (up and down)	Narrow/vertical	5.25
2.	Vertical cling/leap	Narrow/vertical	3.25
3.	Leap between non-vertical supports	Narrow/oblique	1.00
4.	Vertical cling/leap	Narrow/vertical	1.00
5.	Climb (up and down)	Narrow/vertical	1.00

*Combinations include Locomotor Category, Support Characteristics, and Median Heights. "Median" heights are midpoints of the median height categories. See Methods.

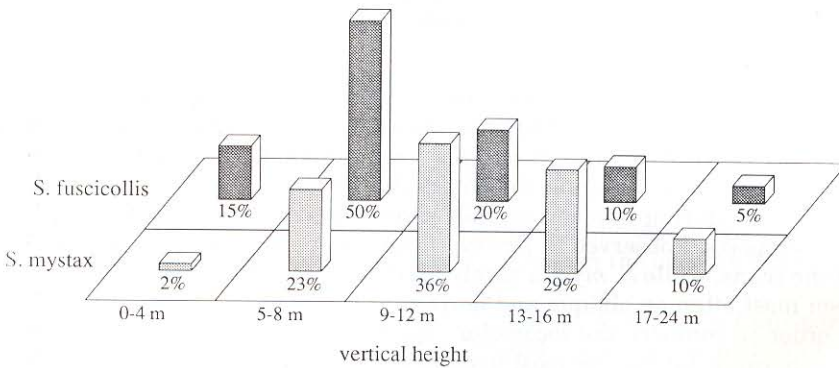


Fig. 1. Comparison of vertical height ranges used during locomotion (all activities combined) for *Saguinus mystax* (N = 451) and *S. fuscicollis* (N = 235) members of G troop. The ten height categories used during data collection were collapsed to five for the illustration.

binations used by the two species are more strikingly dissimilar than others, the range of heights used by each species broadly overlapped.

Median heights when feeding on fruit were similar for the two species, reflecting a tendency for both species to feed in the same tree [Norconk, 1986]. *S. fuscicollis* also fed in small trees and shrubs not used by *S. mystax*, thus expanding the range of feeding heights at the lower end of the scale. Median heights used during diurnal resting periods showed the most marked difference between species; *S. mystax* tended to rest at higher levels of the forest, separated from *S. fuscicollis*. Vigilant individuals were seen either when the remainder of the troop was resting or as the troop moved slowly during search activities. Median heights of individuals when vigilant shared characteristics with both individuals at rest and individuals during search activities.

As might be expected from the locomotor data discussed above, the two species exhibited pronounced vertical separation both during rapid directed travel and during meandering search activities. The range of heights used by *S. mystax* while

TABLE IV. Height Differences at Which Activities Were Seen Are Compared Between Species*

Activity	<i>Saguinus mystax</i>		<i>S. fuscicollis</i>	
	Median height ^a	(Range)	Median height	(Range)
Feed on fruit	13.25	(2.5 to > 20)	11.25	(<2 to > 20)
Rest	11.25	(2.5 to 20)	5.25	(2.5 to 12)
Travel	9.25	(2.5 to 20)	5.25	(<2 to 16)
Scent mark	9.25	(2.5 to 20)	5.25	(< 2 to 20)
Vigilance	9.25	(2.5 to 20)	5.25	(2.5 to 14)
Search	9.25	(< 2 to 14)	3.25	(< 2 to 16)
Feed on insects	5.25	(< 2 to 14)	3.25	(< 2 to 16)

*Paired height samples demonstrate non-overlap of median heights, although overlap is apparent in the height ranges used by both species.

^aMedians determined as in Table III.

searching was more restricted with a higher median value than that of *S. fuscicollis*. The tamarins were seen capturing and eating insects at relatively low heights, particularly for *S. mystax*. Intuitively, median heights for search and insect capture should be the same, and they were similar for *S. fuscicollis*. Although the range of heights is the same for *S. mystax* during search and capture activities, median heights for these two activities were different.

Interindividual Spacing

I rarely scored any individual within a meter of the subject of an instantaneous scan, whether it was a member of the same species or a congener. Individuals were within 1 m in only 27.1% of the *S. fuscicollis* scans (N = 303) and 26.4% of the *S. mystax* scans (N = 625). Of the samples of individuals within a meter, 14.6% were infants in the *S. fuscicollis* samples and 24.8% were infants in the *S. mystax* samples.

Only a few of the samples documented *S. mystax* within 1 m of *S. fuscicollis*. During scans of *S. fuscicollis*, *S. mystax* was seen within a meter on nine (3%) occasions. During scans of *S. mystax*, *S. fuscicollis* was seen within a meter on 10 (1.6%) occasions. It might be expected that vertical stratification could result in interspecific segregation of individuals of the two species. Spatial separation of at least 1 m between conspecific troop members may be common as well, particularly during non-social activities such as those described in this study.

Factors Contributing to Mixed-species Troop Cohesion: Vocalizations

Subtroops often (83%, N = 42 nights) slept in different trees, but the sleeping trees were rarely separated by more than 50 m. Calling began between 0536 and 0646 hours and was initiated by *S. mystax* on all but one morning (18 of 19 mornings when the observer reached the sleeping tree before any movement). Organized movements of the troop normally followed the initiation of long calls by one or the other species.

The temporal duration between the first call by *S. mystax* and the first call by *S. fuscicollis* was highly variable (\bar{x} = 17.2, \pm 22.3 minutes, range = < 1 minute to 88 minutes, N = 18). Thus only in some cases could the call of *S. fuscicollis* be interpreted as a response to the call of *S. mystax*. Nevertheless, it was assumed that calls were audible to *S. fuscicollis*, even when a verbal response was not forthcoming. Calls were audible to human observers over a distance of about 150 to 200 m and individuals in a mixed troop were rarely separated by greater distances.

TABLE V. A Comparison of Activities by Time of Day for the Two Tamarin Species of G Troop Using Spearman Rank Coefficients*

Activity	r_s	Statistical significance of correlation
Vigilance	.99	<.005
Search	.94	<.005
Feed on insects	.86	<.025
Travel	.81	<.05
Feed on fruit	.64	ns
Rest	.46	ns

*See Methods section for definitions of activities. "Time" was divided into categories for analysis. See Methods.

Scheduling of Daily Activities

The two species of G troop demonstrated strong temporal coordination during vigilance, search activities, insect feeding, and directed travel (Table V). Resting for both species showed a mid-day peak, but *S. mystax* was seen resting earlier in the day. The two species also exhibited less coordination when feeding on fruit. *S. fuscicollis* fed earlier in the morning than *S. mystax*, but feeding rates for both species declined after noon. It was previously mentioned that, unlike *S. mystax*, *S. fuscicollis* fed opportunistically from small feeding sources and these data on temporal asynchrony of feeding also reflect such a pattern. Furthermore, the only data collected on interspecific aggression occurred in a feeding tree. On four occasions, *S. mystax* displaced *S. fuscicollis* from its feeding perch.

DISCUSSION

Habitat Segregation and Mixed-species Troop Coordination

Spatial segregation, particularly vertical stratification, was the most prominent characteristic of the mixed *S. mystax* and *S. fuscicollis* troops of this study. First noted by Castro & Soini [1978] for these two species, vertical stratification is not simply characterized by separation in height, but also entails species-specific differences in locomotor patterns and support use. Vertical stratification during travel was also evident in studies of *S. fuscicollis* and *S. labiatus* mixed troops [Pook & Pook, 1982; Yoneda, 1984], although among the three well-studied tamarin pairs, differences exist in species-specific height preferences while foraging for insects [Pook & Pook, 1982; Terborgh, 1983; this study]. Variation in forest composition among the sites may contribute to species differences in absolute foraging height, but there appears to be little difference in the search strategy employed by the congeners. The members of the moustached tamarin group [Hershkovitz, 1978] (*S. imperator*, *S. mystax*, and *S. labiatus*) all use a visual search method, while *S. fuscicollis* ssp. are more investigatory [Ramirez, 1989; Terborgh, 1983; Yoneda, 1984].

Troop coordination is enhanced by vocal communication and coordination of activity patterns. Long-distance calls given by both species may provide the major means of interindividual communication during active periods of the day since nearest-neighbor distances were rarely less than 1 m. Antiphonal calling was described by Pook & Pook [1982] for *S. labiatus* and *S. fuscicollis* in Bolivia, although I failed to demonstrate rapid sequences of calls exchanged between species during my early morning vocal sample.

Coordination of daily activities, particularly those involving movement from one place to another, added a second measure of intratroup cohesion, *S. mystax* and *S. fuscicollis* were well coordinated throughout the day during search activities, showed early morning differences in traveling and while feeding on insects, and were most divergent in the time and proportion of samples devoted to feeding on fruit and resting. I attempted to segregate resting from vigilance (two stationary activities) and to distinguish searching for insect prey from insect consumption; thus activity budgets from other studies were not directly comparable. However, inspection of Terborgh's activity budgets for *S. imperator* and *S. fuscicollis* troops [1983: Figure 4.2] show poor interspecific coordination of resting activities (which included vigilance), strong coordination of directed travel, particularly toward the end of the day, and intermediate coordination for fruit/exudate feeding.

In summary, species-specific patterns of locomotion and habitat use are apparent in all tamarin species pairs, contributing to a reduction in spatial intermingling between species. Coordination of activity patterns provides preliminary evidence for interspecific cohesion, particularly during periods of movement. However, reports that troops are variably mixed within local populations [Garber, 1988; Heymann, this issue; Pook & Pook, 1982; Ramirez, 1989] suggest that costs and benefits to troop members may not be equal in all mixed troops. Increasing troop size, for example, might lead to either interspecific or intraspecific competition. Direct evidence from Garber [1988] on one case of troop fission suggests that the latter might be more influential in limiting overall troop size. Furthermore, the characteristics of mixed troops outlined above and documented during other studies suggest that mechanisms are in place to offset potential costs of interspecific competition, while benefits accrued interspecifically depend on the integrity of the mixed troop.

Does One Species Benefit More Than the Other?

Interspecific agonistic behavior has been described in mixed-species tamarin troops, seems to occur most often in feeding trees, and is always directed toward *S. fuscicollis* by a congener [Heymann, this issue; Norconk, 1986; Ramirez, 1989; Terborgh, 1983]. In contrast to what might be expected if interspecific competition [sensu Pianka, 1981] was severe between *S. fuscicollis* and a congener, data on population densities collected during 13 field studies or censuses show population densities of *S. fuscicollis* to be significantly higher than those of a congener at the same site (Wilcoxon matched pairs, $T = 14.5$; $P < .025$). In all but three cases (sequential years at the same field site), the density of *S. fuscicollis* exceeded the density of the congener (average density ratio = 1.43; range = 0.82 to 3.5) (Table VI). The three lowest density estimates were not significantly different from parity (X^2 test of homogeneity = 2.25; 1.96; 3.24; ns), but they do stand out as the only reported cases in which a congener reached a higher population density than *S. fuscicollis*. These lower ratios, all at the Blanco Stream field site, resemble the postcropping depression of *S. fuscicollis* following trapping and removal of "many more *S. mystax* than *S. fuscicollis*" [Glander et al., 1984:95] (ratio of *S. fuscicollis* to *S. mystax* = 1.3 precropping; ratio = 0.82 five years postcropping at Los Angeles). A few *S. mystax* (one or two) were trapped at the Blanco by R. Castro and P. Soini in 1975 (M. Ramirez, personal communication); however, it is unlikely that population densities would have been decreased for 10 years subsequent to trapping.

Of the five tamarin species inhabiting lowland Amazonia, only *S. fuscicollis* is found in populations without a congener. (Studies of *S. nigricollis* have been conducted in the apparent absence of *S. fuscicollis* [Izawa, 1978]; thus there appear to

TABLE VI. Population Density of *Saguinus* Tamarins and Ratio of *S. fuscicollis* to a Congener

<i>Saguinus</i> species				Ratio ^a	Source
<i>fuscicollis</i>	<i>mystax</i>	<i>labiatus</i>	<i>imperator</i>		
33 ^{b/c}	32.1			1.02	Ramirez, 1984 ^d
28.3 ^b	33.2			0.85	Garber, 1988 ^e
28.0	23.0			1.20	Soini and Soini, 1983
28.0	21.5			1.30	Glander et al., 1984
26.0 ^b	30.0			0.86	Norconk, 1986 ^e
18.0	22.0			0.82	Ramirez, 1989 ^e
10.5	8.0			1.30	Glander et al., 1984
33.0		22.0		1.50	Pook and Pook, 1982
25.2 ^c		16.8		1.50	Cameron et al., 1987
20.8 ^b		14.7		1.40	Yoneda, 1981
13.5		3.8		3.50	Encarnacion and Castro, 1978
16.0			123.0	1.33	Terborgh, 1983
10.8			5.4	1.94	Freese et al., 1982
Average ratio:				1.43	

^aRatio of the population density of *S. fuscicollis* to a congener.

^bIncludes infants carried by adults. For all other studies, method not stated.

^cDensities prior to trapping.

^dYarapa River, Peru.

^eQuebrada Blanco, Peru.

be regions where *S. nigricollis* is allopatric to *S. fuscicollis* [Hershkovitz, 1982].) Nine censuses of *S. fuscicollis*, conducted in areas beyond the geographic range of a congener, reported lower average and lower minimum population densities for *S. fuscicollis* compared with *S. fuscicollis* in sympatric populations (Table VII) (Mann-Whitney U test, $Z = 24.5$, $P < .025$). (Population density of *S. nigricollis* was estimated at 10–13/km² [Izawa, 1978] and falls within the range of densities reported for *S. fuscicollis* in the absence of a congener.) While there is a general trend for population densities of *S. fuscicollis* to be higher close to the equator ($r = -0.54$, $N = 9$), at latitudes where the effects of seasonality are minimized, latitude alone accounted for less than one-third of the variance ($r^2 = 0.29$). Without excluding the possibilities that local differences in habitat quality, habitat disturbance, and the presence or absence of primate or nonprimate competitors could limit population growth of *S. fuscicollis* in the absence of a congener, the presence of a congener appears to have a positive effect on population densities of *S. fuscicollis*. Lastly, it should be noted that population density estimates were collected by using a variety of methods and by different investigators.

While a complementary comparison for the congeners (*S. imperator*, *S. mystax*, and *S. labiatus*) is not possible due to distribution patterns, the reduction of congener population size has been simulated by trapping more *S. mystax* than *S. fuscicollis* from three sites in northeastern Peru. While recovery of population size was substantial for *S. mystax* within 3 years [Yarapa: Ramirez, 1984] or complete within 2 years [Santa Cecilia: Glander et al., 1984], the population size of *S. fuscicollis* declined. The positive effects of *S. fuscicollis* population densities in the absence of a congener, and the negative effect on population growth when a congener is absent, suggest that *S. fuscicollis* may benefit more than *S. mystax* from mixed-troop associations. However, on a daily basis, observers have not been able to segregate individual costs and benefits for each species.

TABLE VII. Population Densities of *Saguinus fuscicollis* With and Without a Congener

	Densities of <i>Saguinus fuscicollis</i>			N ^a
	Average	Minimum	Maximum	
With a congener:				
<i>S. mystax</i>	24.5	10.5	33.0	6 ^b
<i>S. labiatus</i>	24.0	13.5	33.0	5 ^c
<i>S. imperator</i>	14.8	10.8	20.0	3 ^d
Without a congener:				
	12.6	2.4	29.4	9 ^e

^aN = number of localities censused or sampled during long-term studies.

^bCastro & Soini [1978]; Garber [1988]; Glander et al. [1984]; Norconk [1986]; Ramirez [1984]; Soini & Soini [1983].

^cCameron et al. [1987]; Encarnacion & Castro [1978]; Freese et al. [1982]; Pook & Pook [1982]; Yoneda [1981].

^dEncarnacion & Castro [1978]; Freese et al. [1982]; Terborgh [1983].

^eFreese et al. [1982]; Soini [1987].

CONCLUSIONS

1. Mixed tamarin troops were characterized by a combination of mechanisms that assured spatial segregation, yet provided temporal coordination of daily activities. Interspecific spatial segregation was evident both in vertical stratification and in interindividual spacing. The two species were well coordinated during movement—both rapid, directed travel and meandering search activities.

2. Mixed tamarin troops required daily reorganization since subtroops often slept in different sleeping trees. Long calls probably facilitated regrouping prior to directed movement in the morning.

3. Interspecific aggression has been noted while feeding on fruit and characteristically involves aggression toward *S. fuscicollis* by a congener. Very general data provided by population densities of *S. fuscicollis* in the absence and in the presence of a congener suggest that interspecific competition is not high in contemporary populations.

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