

Factors affecting group spread within wild mixed-species troops of saddleback and mustached tamarins: Species, sex, color vision, and behavior

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Abstract

We examined group spread and inter-individual spacing within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and mustached (*Saguinus mystax*) tamarins. Mustached tamarin groups were spread over larger areas than those of saddleback tamarins. Group size and behavior affected group spread and interspecific proximity; larger groups of both species were dispersed over greater areas, and the larger troop had the lowest degree of interspecific proximity. Behavior also affected group spread and interspecific proximity; when traveling individuals were spread over a larger area, and the distance between heterospecifics was greater than when stationary. Spatial proximity was examined using data on the distance from nearest neighbor. Overall, distance to nearest neighbor was not affected by group size. When specific behaviors were examined, foraging saddleback tamarins were found significantly nearer conspecifics than mustached tamarins. Tamarins have polymorphic color vision, and trichromats (having three types of visual pigment, in contrast to dichromatic individuals with two types of pigment) may be better at perceiving yellow or russet colored predators and conspecifics than their dichromatic counterparts. Color vision status affected spatial positioning, with vigilant trichromats being further from their neighbors than their dichromatic conspecifics. These findings are discussed with respect to the ecology of the species. Specifically, interspecific differences in group spread and spatial proximity are related to differences in the supports used, and the effect of troop size on interspecific proximity is related to increased resource competition. The finding that trichromats are further from their neighbors represents the first example of a behavioral correlate of color vision ability in a wild species with polymorphic color vision, and is explained through the perception of predation risk.

Key words: polyspecific association; sex differences; polymorphic color vision, trichromacy

1 **Introduction**

2

3 Spatial ecology is an important aspect of an animal's biology, not just in terms of where it is in its
4 environment but also its proximity to other individuals and species. Feeding opportunities,
5 encounters with competitors and predators, and social interactions including reproductive
6 opportunities will all be influenced by an animal's spatial ecology. Conversely, spatial ecology
7 will reflect the particular needs of a species, such as foods eaten, as well as potential predators
8 and the social system of the species in combination with environmental factors. For group-living
9 species the position of an individual with respect to other group members can have profound
10 implications for its ecology and behavior. This has been most frequently examined in terms of
11 predation risk (Bekoff, 1995; Catterall *et al.*, 1992; Elgar, 1989; Lima, 1995; Pöysä, 1987;
12 1994; Roberts, 1996; Steenbeek *et al.*, 1999), since a principal benefit of group living may be
13 antipredation (Bertram, 1980; Powell, 1974). For example, Hamilton (1971) showed that
14 theoretically the risk of predation was lower for individuals with nearer neighbors. Anti-
15 predation benefits have been suggested as a main reason for the formation of mixed-species
16 groups, both within primates (e.g. Buchanan-Smith, 1990; Gautier-Hion *et al.*, 1983; Heymann,
17 1990; Peres, 1993; Pook and Pook, 1982; Terborgh, 1983) and other taxa (e.g. birds, Munn,
18 1986; antelope, Fitzgibbon, 1990). Mixed-species groups are of particular interest since the
19 species concerned must manage their specific requirements in such a way that allows them to
20 maintain their spatial association.

21

22 The associations formed between tamarin species (*Saguinus* spp.) are some of the most stable
23 within primates, with the most stable being formed between mustached (*S. mystax*) and
24 saddleback tamarins (*S. fuscicollis*) (Heymann and Buchanan-Smith, 2000). Each mixed-species
25 troop is made up of a reproductive group of each species (Garber, 1988; Heymann, 1990;
26 Norconk, 1986; Peres, 1992; Ramirez, 1989) (troop is used when referring to a mixed-species
27 troop, and group when referring to a single-species group). The two species synchronize their

1 daily activities and may spend 50-98% of their waking periods in proximity (Garber, 1988;
2 Heymann, 1990; Peres, 1993). The degree of association has been shown to vary both with
3 respect to time of day (Garber, 1988; Heymann, 1990; Peres, 1991) and season (Smith, 1997).
4 Changes in the needs of the two species may increase the cost of association such that the costs
5 exceed the benefits gained through association. When this occurs the species may separate for
6 varying durations of time.

7
8 Whether or not the two species are in association may influence group spread. It would be
9 expected that in terms of antipredation spacing it would not matter if an individual's nearest
10 neighbor was a con- or heterospecific for these species, since they probably share the same
11 predators and are known to react to the alarm calls of the other species (Peres, 1993). Thus
12 conspecifics could spread over a larger area whilst maintaining the same functional neighbor
13 distance if they were interspersed with individuals of the other species. Further, Buchanan-
14 Smith and Hardie (1997) and Hardie and Buchanan-Smith (1997) have shown that captive
15 tamarins alter their behavior, particularly vigilance, in response to the presence of
16 heterospecifics. This is assumed to reflect a perceived reduction in predation risk as a result of
17 complimentary predator detection strategies (Buchanan-Smith and Hardie, 1997).

18
19 For group-living species, an individual's spatial position with respect to its neighbors will
20 influence its inclusive fitness through predation risk, feeding and social opportunities,
21 including potential mating opportunities. Group size may influence social cohesion or
22 intragroup spacing of individuals, but its effect has been shown to differ between primate
23 species (Treves, 1998). Behavior and an individual's proximity to its neighbor are also linked.
24 For example, individuals further away from their nearest neighbor are more vigilant (Cords,
25 1990; Cowlshaw 1998; 1999; Hirsch, 2002; Robinson, 1981; Rolando *et al.*, 2001; Rose and
26 Fedigan, 1995; van Schaik and van Noordwijk, 1989; Steenbeek *et al.*, 1999; Treves, 1998;
27 1999; 2000; Treves *et al.*, 2001). This has been related to increased predation risk for more

1 isolated individuals in a group (Hamilton, 1971). Spatial positioning may also be directly
2 influenced by constraints stemming from a given behavior. For example, the distribution of
3 resources affects the distribution of individuals. This is illustrated by the ideal free distribution,
4 where the numbers of individuals at each resource patch mirrors the profitability of that patch
5 (Fretwell, 1972; Milinski, 1979). Similarly, when exploiting clumped or dispersed resources
6 the distribution of individuals will reflect the distribution of the resources.

7
8 An individual's functional morphology and hence capabilities may have a profound influence
9 on its ecology, including its spatial positioning with a group. Size is perhaps the most obvious
10 difference among individuals within a species. This may be due simply to age, or it may be
11 accounted for by sexual dimorphism. Larger individuals may be better equipped to defend
12 themselves against predators, and this can influence aspects of their spatial ecology. For
13 example, during group progression in sexually dimorphic baboons the larger males may
14 occupy lead and rear positions, and this has been linked to their greater capabilities for defense
15 (Rhine, 1975; Rhine and Westlund, 1981). Not all morphological differences are as obvious as
16 size. For example, the majority of New World primates (Jacobs, 1984; Mollon *et al.*, 1984) and
17 at least some lemur species (Tan and Li, 1999) exhibit an X-linked polymorphism of their
18 color vision system. In these species all males and homozygous females are dichromatic and
19 only heterozygous females are trichromatic, the uniform condition for all Old World
20 anthropoids including humans. Consequently, individuals within these species will differ in
21 their perceptual capabilities. What one individual within a group may be able to perceive,
22 another may not. The majority of work on primate color vision has focused on the potential
23 benefits of trichromacy for feeding (e.g. Caine and Mundy, 2000; Dominy and Lucas, 2001;
24 Osorio and Vorobyev, 1996; Regan *et al.*, 2001; Smith *et al.*, 2003a; Sumner and Mollon,
25 2000a;b). However, recently the role of color vision in terms of predator and prey detection
26 (Caine, 2002; Coss and Ramakrishnan, 2000; Sumner and Mollon, 2003), vigilance (Smith *et*
27 *al.*, in press) and leadership of group progression (Smith *et al.*, 2003b) has been considered. If,

1 as it should be, vision is treated in a similar way to other aspects of functional morphology and
2 hence capabilities, differences in color vision may be expected to result in differences in
3 ecology including spatial positioning.

4
5 The link between perception and behavior can be illustrated using predation risk and vigilance.
6 Treves (2002) showed that individual monkeys are more vigilant when the density of obscuring
7 foliage is high, since predators are more likely to take prey that are unaware. This suggests that
8 individuals alter their vigilance in response to the ease with which they can perceive predators
9 within their surroundings. Similarly, Metcalfe (1984) showed that the visibility of other group
10 members influenced vigilance. If so, individuals that differ physiologically in their perceptual
11 capabilities may be expected to differ in their spatial ecology, since they will differ in their
12 perception of predators, conspecifics, and other objects within their environment.

13
14 Time of day has been shown to influence behavior (Smith, 1997), including the consumption
15 of different foods (Heymann and Smith, 1999), which in turn may effect spatial ecology. For
16 example, saddleback and mustached tamarins travel further in the morning (Smith, 1997)
17 which would result in greater group spread at this time if individuals are more spread out
18 during travel. The association between the same two species has been shown to break down
19 during periods of resource scarcity (Smith, 1997). During such times the interspecific distance
20 between heterospecifics may be predicted to increase before a total separation occurs.

21 Similarly, inter-individual spacing between conspecifics may be greater as individuals forage
22 further apart. Sex may also influence spatial ecology. Several studies have found male
23 callitrichids to be more vigilant (Buchanan-Smith, 1999; Goldizen, 1989; Koenig, 1998; Price
24 *et al.*, 1991; Savage *et al.*, 1996), and vigilant primates have been shown to be further from
25 conspecifics (Cords, 1990; Cowlshaw, 1998; 1999; Hirsch, 2002; Robinson, 1981; Rolando *et*
26 *al.*, 2001; Rose and Fedigan, 1995; van Schaik and van Noordwijk, 1989; Steenbeek *et al.*,

1999; Treves, 1998; 1999b; 2000; Treves *et al.*, 2001). Consequently males would be predicted to be further from their neighbors than females.

The present study examines group spread and spatial proximity of con- and heterospecific pairs of monkeys with respect to time of day, season, behavior and the sex and visual status of individuals. Data on how the spatial proximity of the component groups within a mixed-species troop varies, not just with respect to time of day and season, but also with respect to the activity of the troop, will enable the spatial ecology of mixed-species troops to be examined in detail. Given the potential for complimentary predator detection strategies (Buchanan-Smith and Hardie, 1997) groups in association would be expected to show greater inter-individual spacing, since individual spacing is inversely related to perceived predation risk (Treves, 2002). Following the theory of the ideal free distribution (Fretwell, 1972; Milinski, 1979) tamarin groups may be expected to be more spread out when foraging for dispersed prey than when feeding on relatively clumped fruit. Further, given that perceived predation risk can alter behavior (Treves, 2002), if dichromatic individuals cannot perceive the yellow, orange, or red pelage of predators and conspecifics as well as their trichromatic counterparts, they may be expected to position themselves closer to another individual (Sumner and Mollon, 2003).

Methods

Two mixed-species troops of saddleback and mustached tamarins were observed (by ACS) for 164 full days (1612 hours) from January 2000 until December 2000 at the Estación Biológica Quebrada Blanco (EBQB) (4°21'S, 73°09'W). The site is located approximately 1 km north west from the right bank of the Quebrada Blanco in north-eastern Peru (for details see Heymann and Hartmann, 1991).

1 The composition of the troops at the beginning of the study is given in Table I. Within Troop 1,
2 neither of the female saddleback tamarins was observed to be pregnant during the study,
3 whereas both of the female mustached tamarins gave birth in February. Female 1 was seen with
4 a single infant that died on the same day it was born. Female 2 gave birth to twin males the
5 following day that were raised by both their mother and female 1 (see Smith *et al.*, 2002 for
6 details). Within Troop 2 none of the mustached tamarins were observed to be pregnant during
7 the study, whereas female saddleback 1 gave birth to male and female twins in January. Both
8 troops were habituated to the presence of human observers for at least 5 months prior to the
9 reported observations being made.

10
11 TABLE I ABOUT HERE

12
13 Each tamarin's visual status was determined (by AKS) using DNA extracted from fecal
14 samples collected opportunistically over the course of the study. These were stored in 100%
15 ethanol at ambient temperature until extraction. At least two separate DNA extractions were
16 performed for each individual. For each extraction three independent polymerase chain
17 reactions (PCRs) were performed to obtain each of three exons (3, 4, and 5) of the X-linked
18 visual pigment gene, effectively giving six replicates to confirm genotype (for further details
19 see Surridge *et al.*, 2002). In Troop 1 both saddleback females were dichromats, and both
20 mustached females were trichromats. In Troop 2, the three older saddleback females were
21 trichromats. Visual status was not determined for the infant female saddleback or for the
22 juvenile and two adult female mustached tamarins. All males were dichromats.

23
24 The tamarins were observed for approximately 14 days each month, with each species being
25 the focus of observations for seven days. Troop 1 was followed exclusively from January until
26 June 2000. From July until December 2000 observations were divided between Troops 1 and 2.
27 Each species was the focus of observations for half the time. The tamarins were followed from

1 when they left their sleep tree in the morning until they entered their next sleep tree in the
2 afternoon. Two methods were used to calculate the mean percentage of time spent by the
3 tamarins in association during their active period. The first used the actual time spent in
4 association and the length of the active period, and the second the number of half-hourly scans.
5 The two tamarin species were considered to be in association if they were within 50 m of each
6 other. The times at which the two species formed and broke the association were noted. If the
7 tamarins moved apart, and then moved back into association within ten minutes they were not
8 recorded as having broken the association.

10 Group spread was determined as the maximum horizontal and vertical distance between
11 conspecifics following Waser (1974) and Olupot *et al.* (1997). Interspecific proximity was
12 determined as the minimum horizontal and vertical distance between a saddleback and a
13 mustached tamarin. These values were noted, to the nearest meter, every 30 minutes, at 15 and
14 45 minutes past the hour. Whether or not the troop was moving in a definable direction was
15 noted. When a group, of either species, was foraging in a dispersed manner with no obvious
16 overall direction, it was deemed stationary even if the component individuals were moving.

18 The behavior of all visible tamarins of the focal species was recorded every 30 minutes, at zero
19 and 30 minutes past the hour. The behaviors analyzed were foraging, locomotion, and
20 vigilance. A foraging tamarin was actively manipulating or paying visual attention to a
21 substrate, including slowly moving through foliage scanning and manually inspecting leaves. A
22 locomoting tamarin was traveling with no other immediate purpose such as foraging. A
23 vigilant animal was stationary and actively attending to the surrounding environment.

25 **Data analysis**

26 Data from infants or those that were infants at the beginning of the study were excluded in
27 analyses. Where appropriate mean daily values were calculated and these used for analysis (i.e.

time spent in association and group spread). When individual characteristics were examined data were restricted to those of identified individuals and mean values were calculated for each tamarin and analyses performed on these (i.e. distance to nearest neighbor).

A t-test was used to examine differences between troops in the amount of time spent in association. Regression analysis was used to investigate the relationship between horizontal and vertical spread. Group spread in and out of association was compared using paired t-tests. Since the majority of non-associated records were either from soon after exiting from or entering a sleeping tree, mean half hourly values were calculated for the whole study to avoid a potential time of day effect. Time of day was then used to pair the mean values in the t-test. Two repeated measures ANOVAs were used to examine factors effecting intraspecific group spread and minimum distance between heterospecific pairs in moving and stationary groups. A univariate ANOVA was used to examine factors effecting distance to nearest conspecific neighbor. Factors included troop (1 or 2), species (saddleback or mustached tamarin), traveling (moving in a discernible direction or stationary) and visual status (trichromat or dichromat). For analysis of distance to nearest conspecific neighbor mean values were calculated for each tamarin. Since group size was shown to affect group spread, and group spread may be related to inter-individual spacing the effects of troop and species were examined first. Data were pooled between troops for subsequent analyses following the result that troop had no significant effect. Mean values are reported \pm standard deviation.

Results

Over the whole year Troop 1 spent a mean of $91.8 \pm 16.5\%$ (n=118 days, a total of 1141 hrs 16 min) of their daily active period in association, based on the amount of time expressed as a percentage of the total waking period of the focal species. Troop 2 spent $89.0 \pm 9.8\%$ (n=36 days, a total of 360 hrs 3 min) of their daily active period in association between July and December. During the same period Troop 1 spent 93.2% of their waking period in association

(n=44 days, a total of 423 hrs 16 min), slightly more than for the year as a whole and significantly more than Troop 2 ($t=2.15$, 78df, $p<0.05$). The other simpler method of data collection, scan sampling, was shown to provide an accurate estimate of the time spent in association (Troop 1, whole year 93.0%; July-December 94.21%; Troop 2 July-December 90.8% in 2268, 846 and 714 scans respectively).

There was no real pattern of seasonal variation in the amount of time that the two species spent in association, although it is interesting to note the particularly high variation around the early to mid dry season, from July till September (Figure 1). In January Troop 1 spent 3 complete days apart, contributing to the lower mean time spent in association, and high variation, for that month.

FIGURE 1 ABOUT HERE

The species spent less time in association towards the start and end of their daily active period. The degree of interspecific association increased as groups of both species left their sleeping sites and located and joined one another. It reached a plateau at 0800h, and remained stable until 1500h, when it declined as the tamarins moved apart to different sleeping sites. Figure 2 shows the latency to join heterospecifics after exiting a sleeping site and the length of time prior to entering a sleeping site that the tamarins were separated. Troop 1 regrouped significantly more quickly than Troop 2 ($t=-2.78$, 77df, $p<0.01$). There was also a tendency for Troop 1 to remain in association for longer, but this difference was not significant ($t=-1.86$, 77df, $p>0.05$). No evidence was found for an effect of time of day or month on group spread.

FIGURE II ABOUT HERE

Horizontal spread accounted for a significant amount of the variation in vertical spread both in terms of maximum intraspecific spread (saddleback $r^2=0.177$, $F=357.6$, $p<0.001$; mustached $r^2=0.225$, $F=508.6$, $p<0.001$) and also minimum interspecific distance ($r^2=0.125$, $F=239.5$, $p<0.001$). Importantly, horizontal spread, unlike vertical spread, it is not limited by tree height. Consequently, horizontal spread was used in all subsequent analyses, as it is indicative of both measures of group spread. Vertical spread was not used in any further analyses.

Troop 1 mustached tamarins were spread over a significantly larger area when in association with saddleback tamarins (assoc. 10.7 ± 1.0 m vs. not assoc. 8.9 ± 1.4 m; $t=-4.24$; 15 df, $p<0.01$), but there was no evidence that the spread of the saddleback tamarin group was affected by association (assoc. 6.8 ± 0.4 m vs. not assoc. 5.5 ± 1.5 m; $t=-1.52$; $p>0.05$). For Troop 2 there was no evidence that association affected group spread for either mustached (assoc. 10.4 ± 1.5 m vs. not assoc. 9.9 ± 2.6 m; $t=-0.80$; $p>0.05$) or saddleback tamarins (assoc. 11.7 ± 1.6 m vs. not assoc. 12.1 ± 5.7 m; $t=0.23$; $p>0.05$).

An ANOVA was then used to examine the effects of species, group, and whether the troop was stationary or traveling in a discernible direction on intraspecific spread, with stationary or traveling as a repeated measure (Table II). Troops were spread over a significantly larger area when they were moving than when they were stationary ($F_{1,230}=251.8$, $p<0.001$). Further, mustached tamarins were spread out over a greater area than saddlebacks ($F_{1,230}=130.7$, $p<0.001$). Also, as might be expected, both groups of Troop 2 (the larger troop) were spread out over a larger area than the groups of Troop 1 ($F_{1,230}=137.0$, $p<0.001$). The interaction between species and group was significant ($F_{1,230}=24.5$, $p<0.001$). The interaction between traveling and species was not significant ($F_{1,230}=0.007$, $p>0.05$), whereas traveling and troop was significant ($F_{1,230}=4.4$, $p<0.05$).

A second ANOVA was then used to examine the effects of group and whether the troop was stationary or traveling on interspecific spread, again with stationary or traveling as a repeated measure. The minimum interspecific distance followed a similar pattern to intraspecific spread (Table II). The groups of the larger mixed species troop (Troop 2) were further apart ($F_{1,115}=69.4$, $p<0.001$). Groups that were traveling showed a significantly lower degree of interspecific proximity when compared to those that were stationary ($F_{1,115}=24.3$, $p<0.001$). The interaction between traveling and troop was also significant ($F_{1,115}=6.9$, $p<0.05$).

TABLE II ABOUT HERE

Neither troop ($F_{1,19}=1.9$, $p>0.05$) nor species ($F_{1,19}=0.59$, $p>0.05$) had a significant effect on the distance to nearest neighbor (saddleback Troop 1; $2.6\pm0.1\text{m}$, $n=4$; Troop 2; $2.8\pm0.2\text{m}$, $n=6$; mustached Troop 1; $3.3\pm0.4\text{m}$, $n=5$; Troop 2; $2.4\pm0.8\text{m}$, $n=8$). The distance to nearest neighbor for the specific behaviors of foraging, traveling and vigilance were then examined. Since troop had no significant effect on inter-individual spacing data were pooled from both troops for these analyses. For all behaviors trichromats had further nearest neighbors than dichromats, although this was only significant for vigilance. Similarly, mustached tamarins were generally further from their nearest neighbors than saddleback tamarins, although this was only significant during locomotion. None of the interactions between color vision and species were significant (Table III).

TABLE III ABOUT HERE

The effect of species and color vision status on the percentage of half hourly scans allocated to each of the three examined behaviors was investigated. The results are given in Table IV. Neither species nor visual status significantly affected the amount of time spent foraging, vigilant, or locomoting.

Table IV ABOUT HERE

Discussion

The two species spent a high proportion of time in association, which is in agreement with previous reports for saddleback and mustached tamarins at both the same (Heymann, 1990; Smith, 1997) and different sites (Garber, 1988; Peres, 1992). The high variation between days in the amount of time spent in association also agrees with that previously observed (Heymann, 1990; Peres, 1991; Smith, 1997). Smith (1997) reported a significant reduction in association for a mixed-species group at the same site from July until September 1995, coinciding with a period of apparent fruit scarcity, confirmed by subsequent phenological studies at the site (Tirado Herrera and Heymann, unpublished data). A less marked reduction in association for both groups in the present study was also found for July until September. As Smith (1997) notes, interspecific fission of mixed-species groups may be expected during periods of resource scarcity as the larger, dominant species could exclude the smaller species from the few available resources. The smaller species would then be forced to search for food away from the larger congener.

It is of interest that group size affects the degree of association. Not only did the larger troop (2) spend less time in association, but heterospecific pairs of individuals were also further apart than those from the smaller troop. This may be linked to increased competition for resources. Mixed-species troops may accrue the benefits of increased group size without the reproductive costs incurred by an intraspecific increase in group size (Buchanan-Smith, 1989; Peres, 1992), since tamarin groups typically contain a single breeding female (Terborgh and Goldizen, 1985; Garber *et al.*, 1984) (but see Smith *et al.*, 2002). However, as the constituent groups of each species increase in size intraspecific reproductive competition and direct exploitation competition of resources increase until the benefits of association are outweighed. However,

1 before the association is endangered a gradual increase in resource competition would force a
2 greater partitioning of resources between the species (Nilsson, 1969; Reynoldson and Davies,
3 1970) until the association is endangered. The greater partitioning of resources would be
4 reflected in a greater distance between the two species and a lower degree of association, as
5 observed for Troop 2.

6
7 The findings of this study are in accord with those for grey-cheeked mangabeys (*Cercocebus*
8 *albigena*) which showed group spread to be relatively constant throughout the year (Olupot *et*
9 *al.*, 1997), despite theoretical grounds based on parasite re-infection for it being greater during
10 the dry season (Freeland, 1980). That larger groups were spread over a larger area is expected,
11 since they contain more individuals. This is supported by the fact that inter-individual spacing
12 was independent of group size. Although individuals within a larger group may benefit from
13 both greater increased predator detection (Pulliam, 1973; Lima, 1995) and collective vigilance
14 (Powell, 1974; Lazarus, 1979; Boland, 2003), distance from neighbors (Hamilton, 1971) may
15 still exert a strong influence on predation risk.

16
17 The finding that groups were more spread out when traveling than when stationary is expected,
18 since stationary activities such as fruit feeding or grooming typically result in a clumping of
19 individuals. The greater spread of mustached tamarin groups in comparison with those of
20 saddleback tamarins may be related to differences in their locomotion and use of support by the
21 two species. Saddleback tamarins which practice cling and leap locomotion through the under-
22 story, typically use vertical trunks, whereas mustached tamarins locomote quadrupedally
23 through the canopy on more horizontal branches (Castro and Soini, 1978; Garber, 1991; Garber
24 and Leigh, 2001). The contiguous nature of the canopy would allow mustached tamarins to
25 spread over a large area. In contrast, saddleback tamarins are presented with fewer potential
26 routes and resting places by the isolated trunks that they leap between resulting in a greater
27 spatial convergence.

1
2 The lack of interspecific differences in the amount of time allocated to foraging, locomotion
3 and vigilance may be explained by the fact that the two species generally co-ordinate their
4 activities, thus allowing them to maintain the observed close association as they move through
5 the forest. That color vision phenotype did not affect the time budgets is contrary to expected
6 given the advantages of trichromacy in the detection and selection of ripe fruits (e.g. Osorio
7 and Vorobyev, 1996; Smith *et al.*, 2003a) and yellow or russet colored predators (Coss and
8 Ramakrishnan, 2000). However, it may simply reflect the complimentary capabilities of the
9 various phenotypes which have been proposed as a mechanism maintaining the color vision
10 polymorphism (Caine, 2002). Specifically, as Caine (2002) notes, in contrast to the advantages
11 of trichromacy, dichromacy may be beneficial in certain circumstances, in particular the
12 detection of camouflaged prey or predators where form is masked by color (Morgan *et al.*,
13 1992). Differences in the time budgets of the phenotypes may be revealed through examination
14 of behaviors at finer resolution than was possible in the present study. For example,
15 trichromats may spend less time foraging for ripe fruit, and dichromats may spend less time
16 foraging for camouflaged insects.

17
18 An important and original finding is that species and color vision status influenced inter-
19 individual spacing during particular behaviors. With respect to species, foraging mustached
20 tamarins were found further from their neighbors than saddleback tamarins. This difference
21 may again be linked to differences in the use of supports by the two species, which are
22 particularly pronounced during foraging (e.g. Garber, 1992; 1993; Peres, 1993). Mustached
23 tamarins visually scan and manipulate terminal foliage, whereas the saddleback tamarins probe
24 blind knot-holes, leaf curls and epiphytes associated with trunks. As before, the discrete nature
25 of the trunks presents the saddlebacks with fewer foraging sites and fewer travel routes
26 resulting in a greater spatial convergence.

1 Color vision status was important in determining the spacing of vigilant individuals; vigilant
2 dichromats were closer to a neighbor than trichromats. Although some potential predators of
3 tamarins, such as boa constrictors (*Boa constrictor*) (Shahuano, 2002) exhibit pattern-based
4 camouflage, many, such as the majority of felids that may take tamarins are yellow or russet
5 colored. Trichromats should be more adept at spotting both these predators (Coss and
6 Ramakrishnan, 2000) and in the case of the saddleback tamarins, similarly colored conspecifics
7 (Sumner and Mollon, 2003). Consequently, Sumner and Mollon (2003) predicted that
8 dichromats would adjust their spatial positioning to account for a greater perceived predation
9 risk as a result of their visual perception. This study provides the first quantitative evidence,
10 albeit from a relatively small sample size, of an effect of color vision status on spatial
11 positioning. It is predicted that color vision status will be shown to influence other aspects of
12 an individual's spatial ecology and behavior.

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1 **Table I.** Composition and visual status of study animals at the beginning of the study.

	Tamarin species	ID	Age class	Visual status
Troop 1	Saddleback	Female 1	Adult	Dichromat
		Female 2	Subadult	Dichromat
		Male 1	Adult	Dichromat
		Male 2	Adult	Dichromat
	Mustached (F2 emigrated 15/10/2000) (born 2/2000) (born 2/2000)	Female 1	Adult	Trichromat
		Female 2	Adult	Trichromat
		Male 1	Adult	Dichromat
		Male 2	Adult	Dichromat
		Male 3	Subadult	Dichromat
		Male 4	Infant	Dichromat
		Male 5	Infant	Dichromat
Troop 2	Saddleback (born 1/2000) (born 1/2000)	Female 1	Adult	Trichromat
		Female 2	Adult	Trichromat
		Female 3	Juvenile	Trichromat
		Female 4	Infant	Unknown
		Male 1	Adult	Dichromat
		Male 2	Adult	Dichromat
		Male 3	Juvenile	Dichromat
		Male 4	Infant	Dichromat
	Mustached	Female 1	Adult	Unknown
		Female 2	Adult	Dichromat
		Female 3	Adult	Unknown
		Female 4	Juvenile	Unknown
		Male 1	Adult	Dichromat
		Male 2	Adult	Dichromat
		Male 3	Adult	Dichromat
		Male 4	Juvenile	Dichromat

2

1 **Table II.** Comparison of intraspecific group spread and interspecific proximity when moving
2 and when stationary in mixed-species troops of saddleback and mustached tamarins.

	Mean max. intraspecific dist. \pm SD (n days)		Mean min. interspecific dist. \pm SD (n days)
	Saddleback	Mustached	
Group 1			
Stationary	5.6 ± 2.0 (83)	8.6 ± 2.0 (83)	6.4 ± 2.0 (84)
Moving	7.7 ± 1.5 (82)	11.5 ± 2.0 (80)	7.1 ± 1.8 (82)
<i>Total</i>	6.6 ± 2.0 (165)	10.1 ± 2.4 (163)	6.8 ± 1.9 (166)
Group 2			
Stationary	8.3 ± 2.1 (36)	10.0 ± 2.3 (36)	8.5 ± 3.6 (35)
Moving	11.9 ± 1.9 (36)	12.9 ± 1.9 (36)	10.9 ± 2.6 (35)
<i>Total</i>	10.1 ± 2.7 (72)	11.5 ± 2.6 (72)	9.7 ± 3.4 (70)

3

1 **Table III.** Effect of species and color vision status on distance to nearest neighbor (m) during
2 foraging, vigilance and locomotion.

		Behavior		
		Forage \pm SD	Vigilance \pm SD	Locomotion \pm SD
Saddleback	Dichromat (n=7)	3.7 \pm 0.6	3.2 \pm 0.4	3.1 \pm 0.4
	Trichromat (n=3)	4.0 \pm 0.8	4.2 \pm 0.5	3.0 \pm 0.7
	Mean	3.7 \pm 0.6	3.5 \pm 0.6	3.0 \pm 0.5
Mustached	Dichromat (n=9)	5.2 \pm 1.5	3.7 \pm 1.7	3.2 \pm 0.2
	Trichromat (n=2)	6.2 \pm 2.0	5.4 \pm 0.5	3.7 \pm 0.1
	Mean	5.4 \pm 1.5	3.9 \pm 1.6	3.3 \pm 0.3
Effect	Species	F _{1,17} =5.7, p<0.05	F _{1,17} =1.6, p>0.05	F _{1,17} =2.7, p>0.05
	Vision	F _{1,17} =2.0, p>0.05	F _{1,17} =15.0, p<0.05	F _{1,17} =0.9, p>0.05
	Species x Vision	F _{1,17} =0.6, p>0.05	F _{1,17} =2.6, p>0.05	F _{1,17} =0.6, p>0.05

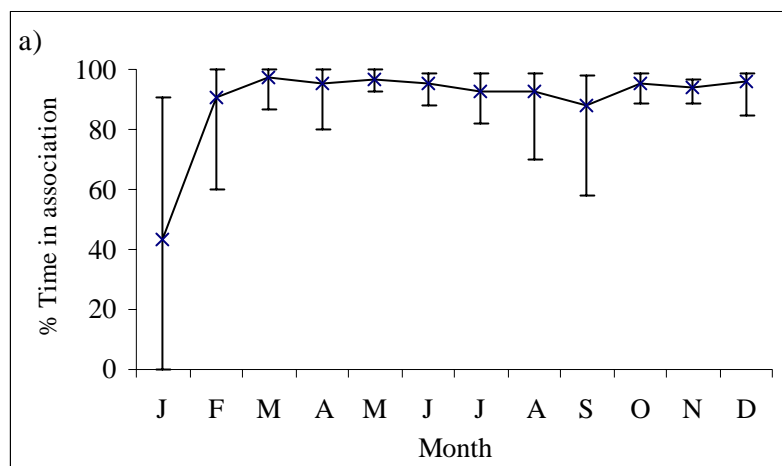
1 **Table IV.** Effect of species and color vision status on percentage of scans allocated to
2 foraging, vigilance, and locomotion.

		Behavior		
		Forage \pm SD	Vigilance \pm SD	Locomotion \pm SD
Saddleback	Dichromat (n=7)	4.6 \pm 1.3	7.5 \pm 4.3	15.5 \pm 5.5
	Trichromat (n=3)	3.2 \pm 2.9	3.8 \pm 3.0	7.8 \pm 3.0
	Mean	4.2 \pm 1.9	6.4 \pm 4.2	13.2 \pm 6.0
Mustached	Dichromat (n=9)	4.1 \pm 7.3	6.4 \pm 9.9	9.4 \pm 4.1
	Trichromat (n=2)	2.1 \pm 0.5	6.6 \pm 0.6	16.2 \pm 0.2
	Mean	3.7 \pm 6.5	6.5 \pm 8.7	10.8 \pm 4.6
Effect	Species	F _{1,17} =0.1, p>0.05	F _{1,17} =0.5, p>0.05	F _{1,17} =0.2, p>0.05
	Vision	F _{1,17} =0.4, p>0.05	F _{1,17} =0.2, p>0.05	F _{1,17} =0.04, p>0.05
	Species x Vision	F _{1,17} =0.1, p>0.05	F _{1,17} =0.3, p>0.05	F _{1,17} =9.4, p<0.05

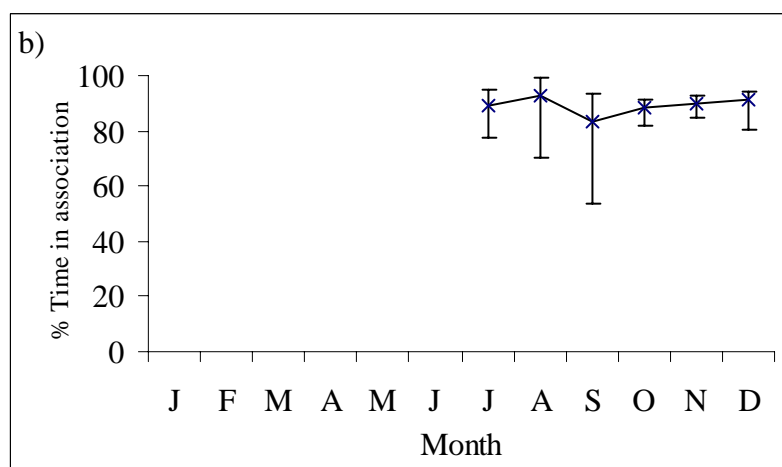
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- 1 **Figure 1.** Seasonal variation in the average proportion of the daily activity period spent in
2 association a) Troop 1, b) Troop 2 (bars indicate minimum and maximum values).

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- 1 **Figure 2.** Latency to join heterospecifics after exiting sleeping tree and length of time
- 2 separated before entering sleeping tree (bars indicate SD).

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